Growth parameter estimates and the effect of fishing on size-composition and growth of snappers and emperors: implications for management

Final Technical Report

MRAG

October 1999

Final Report - Administrative Details

DATE COMPLETED: Day\Month\Year: 29/10/1999

TITLE OF PROJECT	R6465: Growth parameter estimates and the effect of fishing on size-composition and growth of snappers and emperors: Implications for management	
PROGRAMME MANAGER / INSTITUTION	Professor John Beddington MRAG Ltd 47 Princes Gate London SW7 2QA	
	FROM	TO
REPORTING PERIOD	01/04/96	30/09/99
AUTHORS OF THIS REPORT	Dr G.M. Pilling; Dr C.C. Mees; Ms C. Barry; Dr G Kirkwood; Mr S. Nicholson, Mr T. Branch	

Acknowledgments

The project was funded through the UK Department for International Development (DFID) Fisheries Management Science Programme (FMSP), which is managed by MRAG Ltd. Throughout the project, MRAG enjoyed excellent collaboration with the directors and staff of the collaborating institutions, who collected and made available data for the analyses:

- Seychelles Fishing Authority
- Albion Fisheries Research Centre, Mauritius

The Commissioner and Director of Fisheries of the British Indian Ocean Territories Administration of the Foreign and Commonwealth Office (UK) also made available data for the Chagos Archipelago.

Contents

List of tables

List of figures

Final Technical Report

1 Executive Summary

The purpose of this project was to address constraints to management and development arising from the use of uncertain estimates of growth parameters in analytical fishery models such as yield per recruit. Through case studies of Indian Ocean fisheries for snappers and emperors, the project addressed the questions: how important is accurate estimation of growth rate and the changes associated with fishing?; how inaccurate are length based methods, and is there a need to allocate scarce resources to more costly methods?; what degree of uncertainty in management advice can we expect? This purpose is directly relevant to the RNRRS goal of improved management of aquatic resources.

Fisheries targeting the Lutjanidae (snappers) and Lethrinidae (emperors) are important in tropical countries as sources of both employment and protein. However, the long-lived, slow growing nature of these species renders them vulnerable to over-fishing; sustainable exploitation requires accurate management. In the absence of age-validation studies, growth estimation is limited to length-based methods. However, the characteristics of these species suggest such estimates may be inaccurate. Furthermore, the direct and indirect impacts of fishing (removal of individuals and density dependent growth) also affect growth estimates. Stock assessments derived using these growth parameters are therefore uncertain.

Through both simulations and field studies, this project investigated the effects of fishing on growth, and the resulting impacts on assessments of snapper and emperor fisheries in the central Indian Ocean.

Validation of annual increments in otoliths of *Lethrinus mahsena*, *Aprion virescens*, and *Pristipomoides filamentosus* was attempted, so that age-based assessments could be performed. Validation was successful for the emperor *L. mahsena* and snapper *A. virescens*. Validation was unsuccessful for *P. filamentosus*.

Using back-calculated length-at-age data derived using otoliths, individual growth variability in *L. mahsena* was quantified. This used an original method employing a nonlinear random effects model. This model avoided the additional negative bias that arose in the growth parameter estimates from the direct use of the von Bertalanffy growth model.

A simple model of density dependent growth was developed, and used in simulations examining the effects of fishing on catch length structure. Comparative studies of catch length, age and growth rate in the study fisheries were performed to examine whether such effects can be identified in practice.

Using Monte-Carlo simulations, the accuracy and precision of length- and age-based growth parameter estimation methods was examined. The effects of fishing, including density dependent growth, on the growth parameter estimates was examined. In turn, outputs of these growth assessments were used to assess further biological and fishery parameters, with the goal of identifying the knock-on effects of the use of uncertain growth parameter estimates in further analyses.

A technique known as management strategy simulation was employed to simulate the whole management process. Conclusions were derived on the effect on management performance of uncertainty in growth parameter inputs to the management process and the effects of fishing. Age- based and length-based methods of assessment were compared. Neither age- nor length-based methods performed well, though age-based methods were better. Uncertainty arising from the use of length-based assessment methods with both length- and age-based inputs led to poor management performance, exacerbated by the indirect effects of fishing investigated through density dependant growth of fish. Management guidelines were derived, but it was concluded that it would be appropriate to investigate the management performance of a full age-based assessment of fish stocks.

In the light of the results of the simulations, stock assessments of the study fisheries were performed using both length- and age-based methods. This examined whether trends found in the simulations could be identified in actual fisheries data. In addition, the first age-based estimates of growth and mortality were derived for the study species. The feasibility of the use of otolith weight to assess age and mortality were also assessed.

Finally, a cost-benefit analysis was performed to identify whether advantages resulting from age-based methods were outweighed by the costs involved. It was concluded that, where feasible, age-based growth estimation methods are the most accurate and cost-effective for snappers and emperors.

Data collection and management guidelines were developed as an output of this project and presented to target institutions during national workshops. The adoption of these guidelines will contribute directly to the project goal: 'Optimum sustainable yield from capture fisheries achieved by improved resource management', and the super goal (ie RNRRS goal) of improved management of aquatic resources.

2 Background

A previous FMSP project, R5484, 'Management of tropical multi-species fisheries', developed guidelines for management based on analytical yield-per-recruit models of demersal fisheries for snappers, groupers and emperors. It was apparent that uncertainties in key input parameters to these models, such as estimates of growth rates and other biological reference points derived from them, could lead to uncertainties in management performance. In particular, the commonly used length-based methods of assessment that are applied in tropical developing countries to fisheries assessments were considered to lead to growth parameter estimates of uncertain accuracy and precision. That project recommended that this constraint to management be further investigated.

Species of the Lutjanidae (snappers) and Lethrinidae (emperors) are widespread throughout warm waters of the world. They are highly valued food fish in many tropical countries; for example, Seychelles (Mees, 1989), Mauritius (Ardil, 1986), Australia (Kailola *et al.*, 1993), the Caribbean (Thompson and Munro, 1974), Hawaii (Okamoto, 1982; Parrish *et al.*, 1997) and the Pacific (Dalzell and Preston, 1992)). They represent both a cheap source of protein, and, where they form the basis of an export trade, an important component of the national economy of many developing countries. Fisheries based on these species are therefore important to the livelihoods of both artisanal and semi-industrial fishermen. In 1995, over 150,000t of Lutjanidae and Lethrinidae were caught from reef fisheries, with approximately 40% of this total taken from the Indian Ocean region (FAO, 1997).

Lutjanids and lethrinids can be characterised as bottom dwelling carnivores. Their slow growth, low reproductive capacity and low rates of natural mortality makes them vulnerable to overfishing (Russ, 1991; Haight *et al.*, 1993a). Since these species are favoured for consumption or sale, they are commonly targeted by fishermen (Munro, 1983b; Koslow *et al.*, 1988), while their aggressive nature and relatively large size also make them particularly vulnerable to fishing gears (Munro and Williams, 1985). Sound management advice is therefore important for the long term sustainability of fisheries targeting these species.

Studies of the age structure and growth rates of a fish population are an essential component in the assessment of exploited population dynamics (Rowling and Reid, 1992). Von Bertalanffy growth parameters (L_∞, K, t_0) are inputs into many assessment methods which estimate further biological and fishery parameters (*e.g.* mortality, yield-per-recruit). Hence, they are important in the derivation of reference points for fisheries management (*e.g.* $F_{0.1}$; Gulland, 1973). Clearly, growth parameters have the potential to influence the outcome of particular stock assessments strongly.

The assessment tools described above are principally designed for single species. However, modifications exist to apply them in the multispecies case. Fish Management Science Programme project R4823 developed a fully age-structured simulation model, which follows the mathematical structure of the dynamics of exploited fish populations described by Beverton and Holt (1957), and incorporates density dependence in the form of a stock recruitment relationship. This was called the ‘Age-Structured Population Dynamics model’, ASPD (Kirkwood *et al.*, 1994).

Project R5484 investigated management strategies for multispecies demersal grouper and snapper fisheries, and developed ASPD into the Multispecies Interactive Dynamic Age-structured Simulation model (MIDAS) for this purpose. Using this age-structured model, the project developed simple guidelines for management based on data typically available in developing country situations, such as catch, effort and length frequency data. In age-structured models such as ASPD and MIDAS, estimates of growth parameters are a key component. These models allow such variables to be changed with time, in order to simulate changes resulting from fishing, for example.

Fishing can directly affect the accuracy of growth estimates derived from either length or age data. Due to gear selectivity, fishing commonly targets larger, older individuals (Bohnsack, 1982; Polovina, 1986; Russ and Alcala, 1989). Fishing is therefore expected to affect both the length and age structure of an exploited fish population (Craik, 1981; Russ, 1991; Rowling and Reid, 1992). Therefore, catch samples are unrepresentative of the underlying population structure. In turn, over periods of sustained fishing, gear selectivity may remove larger size classes from the population. This will truncate the size and age range, and hence reduce the information on which growth parameter estimates are based.

Fishing can also indirectly affect growth, and hence the parameters used to describe it. Two mechanisms have been suggested through which fishing can affect growth. The first hypothesis suggests that, over time, fishing has an effect on the genetic structure of an exploited population (*e.g.* Parma and Deriso, 1990). Through simulation, however, Martinez-Garmendia (1998) found that evolutionary changes in growth may be modest, and are likely to be overshadowed by other density dependent responses. This forms the second hypothesis on the method through which fishing may affect growth; ‘density dependent growth’ (Beverton and Holt, 1957). Where individual growth is limited by population density (*e.g.* through competition for food resources), decreases in density due to fishing may allow growth rates to increase (Gulland, 1983). Several authors have shown that the state of development of the fishery (either on a virgin resource or an established resource at equilibrium) can significantly affect the overall growth of fish (*e.g.* Filipsson, 1989; Ross and Nelson, 1992). Commonly, these have been temperate freshwater species in enclosed experimental systems (*e.g.* Barlow, 1992), or fish culture ponds and lakes (*e.g.* Lorenzen, 1996). However, density dependent growth has also been identified in larger marine systems. For example, it has been identified in plaice (*Pleuronectes platessa*) and haddock (*Melanogrammus aeglefinus*) in the North Sea (Beverton and Holt, 1957). In turn, it has been identified in a limited number of tropical species (*e.g.* Doherty, 1982; Jones, 1987a, 1987c). Fishing has been shown to reduce the biomass of lutjanids and lethrinids (Russ, 1985; Jennings *et al.*, 1996). The assumption of static life history parameters in fish stock assessment models for the study species may therefore be inappropriate.

Growth can be estimated through a number of methods. In temperate fish species, growth is frequently determined using age data derived from counts of annual growth rings in hard tissues such as otoliths. Until relatively recently, however, they had not been employed on a large scale for tropical species. This was related to two factors. Fisheries in tropical regions are frequently less developed when compared to their temperate counterparts, attracting a lower research effort. Perhaps more importantly, there has been a historical perception that the tropical marine environment was relatively constant. Fish were assumed to respond to this by growing and spawning continuously throughout the year. Hence, they lacked 'growth checks' from which an incremental otolith structure would arise (Fowler, 1995). Increased confidence in the use of tropical fish otoliths for ageing purposes led to a number of studies assessing annual rings, including those in a number of snappers and emperors (*e.g.* Loubens, 1980; Mason and Manooch, 1982; see also Manooch, 1987 and Fowler 1995, for reviews). However, due to the financial constraints operating in the majority of developing country fisheries research centres, cheaper length-based methods of growth assessment are more commonly used (*e.g.* Posada and Appledorn, 1996). Unfortunately, these methods are not particularly well suited to long-lived, slow-growing species, such as lutjanids and lethrinids. These methods commonly utilise modes in length frequency data (assumed to represent individual cohorts) to estimate growth parameters. Such modes are favoured where growth is rapid (generally correlating with a short lifespan) and spawning season restricted (MacDonald, 1987). In slow growing species, modes representing fish cohorts frequently overlap, offering limited information on growth. Under such circumstances, the accuracy of growth parameters derived through length-based methods is uncertain.

Uncertainty in growth parameter estimates may be transferred into further parameter estimates, and hence stock assessments based on those parameters. Critically, uncertain growth parameters may lead to the over-exploitation of the resource. Alternatively, they may result in under-exploitation, which may have undesirable socio-economic impacts (*e.g.* loss of jobs or reduction in food supply). As a result of slow growth and overlapping modes in length frequency data from many tropical species, length-based growth parameter estimates contribute toward this uncertainty; age-based methods of growth estimation may reduce uncertainty, improving management assessments, and hence resource use.

3 Project Purpose

Snappers and emperors form the basis of valuable fisheries important to the livelihoods of many small scale fishers in developing countries. As these fish are high level predators with slow growth and low reproductive capacity, they are easily overfished. A widespread demand for management exists in order to sustainably manage and develop these fisheries.

Analytical fisheries models used to provide management advice may be based on the length or age of fish. A key component for such models is the von Bertalanffy growth parameters, L_∞ and K. Age-based models have generally been considered to be the most appropriate, and in developed countries age and growth for temperate water fish species are most frequently determined by examining annual growth rings on hard parts such as otoliths. In tropical waters, however, it was believed that annual banding did not occur due to less pronounced climatic seasonality. As a result, and also due to financial constraints, significantly cheaper length-based methods of age and growth assessment have most frequently been employed. These methods, however, are not well suited to long-lived, slow growing species such as snappers and emperors. The accuracy of growth estimates derived by these methods is questionable, and as a result they are unlikely to be able to identify changes in population growth due to fishing pressure (density dependent growth). Consequently, management advice derived from age-based models using such length-based growth parameter estimates is also subject to uncertainty. Recent studies, however, have identified and validated seasonal growth marks in otoliths of long-lived, slow growing tropical fish species, suggesting that improved management may be feasible.

The purpose of this project was to address these constraints to management and development by questioning: how important is accurate estimation of growth rate and the changes associated with fishing?; how inaccurate are length based methods and is there a need to allocate scarce resources to more costly methods?; what degree of uncertainty in management advice can we expect? This purpose is directly relevant to the RNRRS goal of improved management of aquatic resources[1].

4 Research Activities

This was a process project involving a two-stage practical study, and desk-based assessments and fisheries simulations. As there was some uncertainty over the use of hard parts such as otoliths for ageing tropical fish species (see above). Stage 1 practical studies were aimed at validating this technique for study species. The details of the project were such that Stage 2 practical studies utilising these techniques to perform stock assessments could only be undertaken if Stage 1 was successful.

At the inception of the project, the collaborating fisheries institutions monitoring the study locations were limited to length-based methods of stock assessment. Before age-based methods could be employed, increments identified in the otoliths of selected species had to be validated as annual (Stage 1). These studies were undertaken in two phases. In the first phase, otolithometry experts at CEFAS, Lowestoft (formerly MAFF), examined sectioned otoliths from a number of lutjanid and lethrinid species from Seychelles and Mauritius: the lutjanids *Pristipomoides filamentosus*, *Aprion virescens*, *Aphareus rutilans* and *Lutjanus bohar*, and the lethrinids *Lethrinus variegatus*, *Lethrinus croccineus*, and *Lethrinus mahsena*. Otoliths were examined to assess the clarity of the increment structure, and consistency of 'age' assessments, the latter through between-reader count comparisons. Additionally, this study determined the most suitable technique for reading identifiable increments. A range of techniques were tested, including the examination of whole otoliths, breaking and burning, and viewing thin sections. Based on the results of phase 1, and the species' commercial importance, three species (*P. filamentosus*, *A. virescens* and *L. mahsena*) were selected for further study.

In phase 2 of the study, otoliths from the three study species were collected through port sampling by the collaborating institutions in Seychelles (Seychelles Fishing Authority, SFA) and Mauritius (Albion Fisheries Research Centre, AFRC), and through observer programmes in the Chagos Archipelago (BIOT). Using these samples, validation of the

---

[1] It should be noted that this purpose and the outcomes of the project are also relevant to the RNRKS goals of poverty elimination through the mechanism of sustainable development, and to the FMSP goal of improving livelihoods through sustainable enhanced production with benefits delivered by application of the knowledge generated from this project to develop improved management guidelines.

increments seen in thin sections of the otoliths of these species was attempted. To achieve validation, three criteria had to be fulfilled (Fowler and Doherty, 1992):

- the otolith must grow throughout the life of the individual;
- the otolith must show an internal structure of increments; and
- this structure must correspond to a regular time scale.

Validation was attempted using three techniques: back-calculation (*e.g.* van Leeuwen and Rijnsdorp, 1986), and a combination of marginal increment analysis and edge analysis (*e.g.* Mason and Manooch, 1985; Manooch and Drennon, 1987). Back-calculation was used to test the validity of the first two criteria for ageing. Marginal increment analysis and edge analysis were then used to validate mark periodicity, fulfilling the third criterion.

Simulations of the length and age structure of exploited populations were performed, using individual-based models. To make these simulations as realistic as possible, a measure of individual variability in growth was required. Despite the recognised importance of individual variability in growth when performing fish stock assessments (*e.g.* Sainsbury, 1980), it has seldom been quantified. Estimates of this variability were obtained using back-calculated length-at-age data from validated *L. mahsena* otoliths. Two methods were used: that described in Isaac (1990), and an original method involving a non-linear random effects model (Walker, 1996). The random-effects model explicitly characterised individual growth variability in the true population growth parameters. Unlike the method of Isaac, therefore, estimates of individual growth variability were not supplemented by the negative correlation between individual L_∞ and K estimates derived using the von Bertalanffy growth equation. A covariance matrix describing the relationship between the three growth parameters was output directly from the random-effects model. A covariance matrix was also calculated from the individual growth parameter estimates derived through Isaac's method. Using these matrices, the correlation between the growth parameters L_∞ and K was estimated.

Through density dependent growth, a change in growth rate can result as an indirect effect of fishing. Three simple models for density dependent growth were developed, based on the biology and ecology of the study species. These models allowed the effects of competition between different sections of the population to be modelled (*e.g.* spatial separation of juveniles and adults). Models were incorporated into MIDAS. Density dependent growth was modelled through changes in the von Bertalanffy growth parameters L_∞ or K. Density dependence is generally modelled as changes in the value of L_∞ (*e.g.* Lorenzen, 1996), due to the formulation of the von Bertalanffy growth equation. However, in shoaling species, (such as the study species), metabolic activity (K) may also be influenced by density. Population density and the selected growth parameter were related through a declining straight line. The effects of different levels (gradients) of density dependent growth in each model were assessed based on the yield-effort curve of the study species. From these assessments, one model was selected. This model was used in simulations examining both the direct (removal of individuals) and indirect (density dependent growth) effects of fishing on catch length structure.

Using length data and age data derived from otoliths collected by the collaborating institutions, comparative studies examined the effects of fishing on the length and age structure, and growth rate of the study species populations (Stage 2). This was performed both within and between locations. The study aimed to identify whether the expected effects of fishing (declines in mean length or age, increased length-at-age) could be identified in the study populations. Catch mean length and age were related to the level of cumulative effort exerted in each study location, while growth (using mean length-at-age as a proxy) was related both to the level of cumulative effort, and to the level of demersal CPUE. The latter was assumed to provide a more accurate measure of stock density.

Simulations were performed to examine the effects of identified fishing-induced changes in catch structure and growth on the estimates of growth parameters derived using length- and age-based methods. Length frequency distributions were simulated using MIDAS, and growth parameters estimated using the algorithms available in LFDA (length-based growth estimates). Age-based growth assessments were derived from length-at-age data simulated within an EXCEL^{TM} spreadsheet. The effects of different levels of fishing pressure on growth assessments were examined in both a fishery at exploited equilibrium, and a ‘developing’ fishery, in the initial stages of exploitation. Simulations were performed with and without density dependent growth (using the model selected from the study described above). The knock-on effects of the use of these growth parameters in further assessments of biological and fishery parameters (mortality, yield-per-recruit) were simulated.

Next, a technique known as management strategy simulation was employed to examine the whole management process. Whilst the simulations described above relate to improved assessments of the fisheries, management strategy simulation is technique which aims to analyse the behaviour of complex systems, and of all the processes in fisheries management, using a simpler model of the system. An operating model of the fish stock and the effect of fishing on it was developed by modifying MIDAS, which was incorporated into the wider management model. The effect on management performance of uncertainty in growth parameter inputs to the management process and the indirect effects of fishing through density dependant growth were investigated for an $F_{0.1}$ management strategy ($F_{0.1}$ is a biological reference point on which management targets are sometimes based, and is explained fully in the following technical report). Age-based and length-based methods of assessment were compared. Management performance was assessed against conservation measures and fleet performance.

In the light of these studies, length- and age-based assessments were performed for the study fisheries to derive estimates of growth, and further biological and fishery parameters (Stage 2). This aimed to identify whether the results of the simulation studies held when examining actual fisheries data. The study also derived the first age-based assessments of growth for the study species. In addition, age-based estimates of total mortality were also derived. Based on the most accurate estimates identified, the status of the study stocks was assessed.

One of the main drawbacks of the use of otoliths for the assessment of growth is the expense of such methods (*e.g.* Mathews, 1987). This potentially renders them prohibitive for developing countries. However, assessments of costs alone do not take into account benefits arising from age-based assessments, when compared to the use of length-based methods. A cost-benefit analysis was therefore performed to examine this further. Costs were calculated based on the actual costs incurred during the study. Benefits were assessed through the simulation of yield, and hence fishery revenue, from fisheries managed using the two growth parameter estimation methods. These were compared using the net-benefit investment ratio, and the most financially acceptable method identified.

5 Outputs

Through the combination of theoretical and two-stage practical studies described in the previous section, the project aimed to answer a number of questions. By answering these questions, the project provided guidelines for data collection, assessment and management both of the study fisheries, and of related fisheries targeting long-lived, slow-growing species.

All the anticipated outputs from the project were achieved. In the following section, the results which specifically answered the questions posed at the start of the project are described. The guidelines resulting from the project are then detailed.

- **How accurate, and how precise, are length-based methods of estimating growth parameters when applied to lutjanids and lethrinids?**

Simulations examining length frequency distributions output from MIDAS were analysed using the algorithms available in LFDA (Holden *et al.*, 1995). Only the performance of ELEFAN was examined in detail. Both SLCA and PROJMAT resulted in implausible growth parameter estimates. SLCA tended to produce unfeasibly high L_∞ and K estimates, while PROJMAT estimates tended toward high values of L_∞, and low values of K. The outputs of these algorithms were therefore highly inaccurate for the long-lived, slow growing species examined.

Simulations using ELEFAN indicated that while growth parameter estimates from this method were more plausible than those from SLCA or PROJMAT, they too showed considerable bias. This was a result of the slow growth rate and level of individual growth variability of *L. mahsena*. As a result of growth variability, individuals were present in the length distributions at sizes considerably greater than the mean population L_∞ value. Since the ELEFAN L_∞ estimate was influenced by the largest individual present in the length frequency distribution, L_∞ was overestimated (*e.g.* at low fishing mortality levels, bias in L_∞ was 50%). K was also overestimated (bias in K was 36%). Both estimates were also imprecise (CV for L_∞ = 15%, K=42%).

The results for K were in contrast to those of previous studies (*e.g.* Rosenberg and Beddington, 1987; Isaac, 1990), where K was found to be underestimated. Unlike the current study, however, these studies simulated relatively fast growing species. As a result of slower growth, modes in the data of the species studied in this thesis were comprised of a number of age classes. A growth curve fitted through such modes therefore overestimated the growth rate. In faster growing species, the more widely spaced modes that resulted may have been interspersed with modes unrelated to the age structure. Growth curves fitted through such additional modes would result in the underestimation of the growth rate.

The underlying accuracy and precision of the growth parameter estimates was affected by the direct effects of fishing (removal of individuals). Simulations of the direct effects of fishing on the length structure identified a decrease in the catch mean length with increasing fishing pressure. This was a result of gears selecting for larger sizes in the population. Similar changes were noted when catch mean length both between and within locations was significantly related to cumulative fishing effort. In the actual fisheries, however, trends were frequently obscured by environmental differences between locations, and a high level of inter-annual variability in the length structure. The latter was attributed to both sampling variations and localised population structure.

As noted, length-based estimates of L_∞ were influenced by the size of the largest individuals in the catch. Under equilibrium conditions ('existing fishery'), the removal of such individuals with increasing fishing pressure improved both the accuracy and precision of the L_∞ estimate. However, the resulting decreases in the L_∞ estimate with increasing fishing mortality corresponded with an increasing overestimation of K.

In a 'developing fishery' (a transient simulation of the application of fishing mortality to a previously unexploited population), the level of fishing mortality did not affect the growth parameter estimates, which remained highly overestimated. Since estimates of L_∞ were influenced by the largest individuals in the catch, these corresponded to the length frequency in the first year of the simulation, the year after exploitation had begun. As a result, K was also consistently overestimated.

Overall, therefore, length-based estimates of growth for long-lived, slow growing species were generally neither accurate, nor precise. Although increasing fishing mortality improved both the accuracy and precision of L_∞ estimates in the equilibrium simulation, estimates of K became increasingly biased. Such improvements in the L_∞ estimate were not found in the developing fishery simulation, due to the minimal impact of fishing on the length structure.

- **Can age-based methods be used to estimate growth parameters for these families? If so, are these more expensive methods of growth assessment more accurate than length-based methods?**

Through the combined studies by CEFAS and MRAG, validation of annual increments in the otoliths was successful for *L. mahsena* and *A. virescens*. It should be noted that this has been achieved for individuals at very low latitudes, which has rarely been attempted in previous otolithometry studies. Validation was unsuccessful for *P. filamentosus* due to the presence of 'indeterminate increments', unrelated to the annual time scale. When considered with other successful validation studies on tropical species, the successful validation of otoliths from two of the study species helps dispel the view that otoliths cannot be used to age tropical fish species. It also enabled the first age-based assessments of growth and mortality to be performed for the study species, and allowed the identification of the effects of fishing on age structure. Such studies are rare in tropical species. Local staff in Mauritius and Seychelles participated in the collection of otoliths, and became skilled in the art of rapid otolith extraction.

From the simulations of growth parameter estimation, age-based estimates of growth were both more accurate and precise than those from length-based methods (for comparison, at low fishing mortality levels, bias in age-based estimates of L_∞ and K was 4%, while the CVs of the estimates were 5% and 10% respectively).

However, age-based growth parameter estimates were influenced by the structure of the samples analysed. From the practical stock assessments, age-based growth assessments were strongly affected by the absence of young individuals from the sample, due to gear selectivity. As a result, K was underestimated, while L_∞ was overestimated.

Age-based estimates were also affected by the direct effects of fishing. From the equilibrium simulations, as fishing mortality increased, the information available from length-at-age samples on the value of L_∞ was reduced (higher fishing mortalities reduced the number of older, slower growing individuals present at larger lengths). In turn, this affected estimates of K; while L_∞ tended to increase with increasing fishing mortality, estimates of K decreased, becoming negatively biased. However, K estimates, and to a lesser extent L_∞ estimates, were consistently more accurate and precise than those resulting from length-based methods.

In contrast to length-based estimates, age-based estimates of growth were highly accurate and precise when assessed using data from the simulated developing fishery. Due to the transient nature of the simulation, the effects of fishing on the length and age structure was minimal. Hence there was more information on the values of both L_∞ and K in the length-at-age data, improving the accuracy and precision of the estimates.

In summary, age-based growth estimation methods can now be used for two of the three study species. Despite being affected by fishing, this method generally resulted in more accurate and precise growth parameter estimates than those from length-based methods.

- **What effects does density dependent growth have on the ability to estimate growth parameters accurately and precisely?**

From the equilibrium simulations of growth parameter estimation, density dependent growth tended to increase the estimate of L_∞ from length-based methods, increasing the bias in this parameter. Correspondingly, estimates of K were decreased, slightly improving these estimates.

In contrast, density dependent growth tended to increase the estimate of K derived through age-based methods, notably increasing the overestimation of this parameter at high fishing mortality levels. Correspondingly, estimates of L_∞ were slightly improved, being less positively biased.

The effect of density dependent growth on the growth parameters estimated by both methods was dependent on the level of fishing mortality. The effect of density dependent growth on the length structure, and hence length-based growth parameter estimates, was minimal at low fishing mortality levels. The same pattern was found for age-based growth parameter estimates.

In the developing fishery simulation, the effects of density dependent growth on growth parameters could only be examined for length-based methods. This was a result of the limitations of the age-based simulation model (performed in an EXCEL^{TM} spreadsheet). In this situation, density dependent growth did not affect the length-based growth parameter estimates, regardless of the level of fishing mortality. As seen in the situation where density dependent growth was not operating, the influence of the large individuals present in the early years of the fishery strongly influenced the L_∞ estimate. While density dependent growth affected the length structure in later years, as seen in the simulations of length frequency distributions, these effects were insufficient to counteract the reduction in mean length due to the removal of individuals through fishing. The effects on age-based methods could not be simulated. However, since the effects of density dependent growth only became apparent in the later years of the simulation, the effects on the age-based growth parameters would depend on when length-at-age samples were taken after the initiation of fishing.

The two growth estimation methods assigned the effects of density dependent growth to a different growth parameter, regardless of the parameter actually affected in the underlying simulation model. The accuracy of estimates resulting from each method therefore depended on the parameter affected by density dependent growth. For example, if density dependent growth was operating in K, age-based methods resulted in the most accurate estimates, since this method assigned the effects to that parameter. In turn, length-based methods were the most accurate when density dependent growth was operating in L_∞.

In actual populations, the action of density dependent growth may not be attributable to changes in a single growth parameter. This would be particularly true where the level of fishing mortality varied during the life of an individual. Hence, a judgement on the most appropriate growth assessment method to use under density dependent growth cannot be made. However, as shown, density dependent growth did result in less accurate estimates from both growth assessment methods.

- **Are either length-based or age-based methods sufficiently precise to detect density dependent growth?**

From the simulations of length frequencies, density dependent growth tended to increase the proportion of larger individuals in the length frequencies. It also increased length-at-age, as identified both in the assessments of fish length-at-age in the study fisheries, and through simulation.

The equilibrium simulations of growth assessment indicated that, in theory, both methods could identify the presence of density dependent growth under equilibrium conditions. Length-based methods interpreted increases in the number of large individuals in the catch as an increase in the estimate of L_∞. In contrast, increased length-at-age was interpreted by age-based methods as an increase in the estimate of K.

In a developing fishery, however, length-based methods failed to identify density dependent growth, due to the presence of large individuals in the catch from the early years of the fishery (see above).

In practice, estimates derived by both length- and age-based growth estimation methods are strongly influenced by the structure of the samples on which estimates were based. As a result, changes in growth parameters due to density dependence were likely to be obscured by between-year variations in the data. It was concluded that direct assessments of age-at-length derived using otoliths, as performed in the practical studies, had a greater potential to identify density dependent growth.

- **How important for appropriate management are the accurate and precise estimation of growth and the identification of changes in growth due to density dependence?**

As noted, both the direct and indirect effects of fishing affected the accuracy and precision of growth parameter estimates. These growth parameter estimates were used to estimate further biological and fishery parameters. These parameters were then employed in the management strategy simulation to examine the ‘knock-on’ effect of inaccuracies and imprecisions in the growth parameter estimates.

Both fishing and density dependent growth affected the outputs of length-based biological and fishery parameter estimates, both directly (*e.g.* total mortality estimates), and indirectly through the effects on growth parameter estimates (*e.g.* natural mortality estimates derived using empirical formulae, and $F_{0.1}$ derived using those estimates). These effects are described in detail in the technical report which follows.

These effects had direct impacts on the results of the management strategy simulations, which were used to investigate the effect of uncertainty in growth parameter estimation and effects of fishing on management performance. Length and age based methods of assessment were also compared. To achieve this, management actions were simulated over a 20 year period. The conclusions relating to management performance derived from management strategy simulation were that:

- Uncertainty and variability in growth parameter estimation led to poor management performance for both length-based and age-at-length based methods of assessment;

- Where density dependent growth (DDG) occurs management performance is worse for both length based and age-at length based methods of assessment compared to the case where DDG does not occur;

- To improve management performance it was necessary to apply a correction factor to the target $F_{0.1}$ value, and a different correction factor was required for fisheries at different levels of fishing intensity: without DDG, neither age- nor length-based methods performed well, except at the F value used to determine the correction factor. At that value, age-based methods of assessment performed better than length-based methods, but neither was especially good;

- The use of length based components in stock assessment leads to inadequate management performance despite the use of accurate age-based growth parameter estimates;

- With density dependent growth operating, application of a correction factor determined through simulations where density dependent growth was not operating led to significantly worse management performance.

- **If age-based methods provide more appropriate management information for an exploited stock, are these benefits outweighed by the cost of the methodology?**

Initial (startup) costs involved in age-based methods were far greater than those of length-based methods. However, where the preparation of otoliths was sub-contracted to another organisation (and hence startup costs were lower), costs were outweighed by benefits (assessed as simulated revenue from the fishery) resulting from improved management actions based on age-based growth parameters.

Where age-based methods were performed on a per-species basis, and otoliths were prepared in-house, high startup costs were incurred. As a result, length-based methods showed a greater financial advantage. However, this conclusion ignored the additional unquantified benefits arising from age-based methods; the use of these growth parameters resulted in more precise and accurate stock assessments, and reduced the probability of overexploitation. In turn, the preparation of otoliths in-house also opened further benefit streams where a regional otolithometry centre could be established. The increased numbers of species examined by such a centre (or sets of analyses on the same species from different locations) would reduce the negative impact of the startup costs on the cost-benefit ratio. As a result, the financial advantage of length-based growth assessment methods would be reduced.

Where funds are available, age-based methods provide an appropriate and cost effective method of growth assessment both for the study species, and potentially for other long-lived, slow growing species.

A number of additional outputs were obtained during the project which did not refer directly to the questions posed at the beginning of the project. These are now described.

Training of local staff in preparation of otoliths and ageing of study species

Workshops were held at the collaborating institutions to disseminate the techniques involved in the preparation of otoliths for validation and routine ageing. The methods used to achieve validation and those involved in the routine ageing of individuals using otoliths were also presented.

Assessment of individual variability in growth

A new and more appropriate method of assessing individual growth variability was derived with the assistance of the Imperial College Mathematics Department. Using this method, the extent of individual growth variability in *L. mahsena* was estimated. Using these results, the first assessment of the correlation between L_∞ and K for individual fish was derived. While individual variability in growth has been noted as an important factor in the assessment of many biological characteristics, including growth, it has rarely been quantified.

Identification of density dependent growth in study fish populations, and localised population structures

Trends consistent with density dependent growth were identified in both *L. mahsena* and *A. virescens*. This represents the first identification of such signs in large predatory tropical fish species. Density dependent growth had a number of important impacts on the assessment of both growth parameters and further fishery and biological parameters, and hence on subsequent management advice. These were identified though simulations. Given these effects, the knowledge of the presence of density dependent growth in the study populations is important, so that they can be incorporated into the assessment of the impacts of management decisions.

Assessment of data by statistical area within Seychelles and BIOT indicated localised population structures in *L. mahsena*, and to a lesser extent in *A. virescens*. This had important implications for assessments performed in the study locations. Assessments in the study locations are generally performed at the level of the study location. This ignores the localised population structure of these species. In the case of mortality estimates, for example, assessments for a location will not detect localised stock depletion. With the exception of *A. virescens* in BIOT, where assessments at the level of the location appear warranted, assessments should be made at as high a spatial resolution as possible.

Identification of the effects of fishing on the study populations

Through the analysis of length frequency data, and the use of otoliths to derive catch age structures, the effects of fishing on the study populations was examined through comparative studies. A number of declining trends in *L. mahsena* and *A. virescens* catch mean length and age were found with increasing exploitation rate. While a number of studies have examined the effects of fishing on the length structure of tropical fish, examinations of effects on age structure are rare. In a number of cases, the expected decreases in mean length and age were not found. However, these trends were still attributable to the pattern of fishing, or fishing practices. The effects of these impacts on the estimation of growth parameters are noted in the above sections. However, the results of the study also had a number of important impacts for the assessment methods used by the fishery institutions in the study locations.

The results have particular importance for the assessment methods used in Mauritius. Currently, the impacts of annual decreases in TAC on *L. mahsena* catches from the Mauritian banks are assessed by monitoring for increases in both CPUE and mean length. This study has indicated a number of problems with this method:

- Considerable between-year variability in catch mean length has been identified. Consistent trends in mean length are unlikely to be identified over a small number of years, confounding any changes resulting from the management regime;
- CPUE assessments at the spatial level of the bank will also be affected by localised population structure. Such effects may be reduced by performing assessments at a higher spatial resolution (*e.g.* statistical grid square, as collected in the Mauritian fishing logbook);
- Density dependent growth will affect assessments. Decreases in effort through the management regime will result in increased population densities. Hence, increases in mean length through decreased fishing mortality will be reduced by decreased growth rate. CPUE may also be affected, since it is measured as catch weight-per-unit-effort. The overall effect will depend on the relationship between decreases in growth rate, and any corresponding increase in condition factor;
- Discarding of small ‘undersized’ fish, or separation from the catch before return to port may result in increases in mean length compared to previous years in which such practices were less prevalent. Such increases may be mis-interpreted as the result of annual decreases in effort.

A more appropriate measure is required to assess the effects of such reductions in TAC. Assessments of localised CPUE can now be supplemented by those of age structure. While minimising the effects of density dependent growth, such assessments would also provide additional information on growth, mortality, and localised population structure.

Derivation of the first age-based stock assessments for the study fisheries

From the results of the simulations, age-based methods were the most appropriate for long-lived, slow-growing species. Since increments in the otoliths of the study species have been successfully validated as annual in nature, as noted above, age-based methods could be used to perform stock assessments for the study fisheries.

Patterns in the length- and age-based growth parameter estimates followed those identified in the simulations. While age-based estimates of growth parameters for *L. mahsena* were comparable to those employed historically in the study locations, estimates for *A. virescens* indicated that this species grew at a notably slower rate than that indicated through length-based methods.

While the use of length-based growth parameters indicated little concern over the status of the stock, the use of age-based growth parameters, in particular with more reliable age-based methods of total mortality estimation (due to the potential for density dependent growth in the study populations; see above), indicated serious concern for the status of *L. mahsena* resources on both the Mauritian banks, and at Seychelles. Stock status at BIOT indicated sustainable exploitation. Assessments for *A. virescens* indicated limited impacts due to exploitation. Indeed, estimates of total mortality (Z) were close to empirical estimates of natural mortality (M), indicating that the estimates of Z were comparable to that natural mortality rate for this species. This provided an independent estimate of this important biological parameter.

As such, age-based methods provided more accurate estimates of growth (for *A. virescens*, and confirmed the suitability of the growth parameter estimate currently employed for *L. mahsena*) and mortality for the study species in these locations. In turn, the use of these estimates resulted in more appropriate assessments of stock status.

Identification of otolith weight as a suitable method for estimating age

One of the potential limitations to the use of age-based methods of assessment is the cost of diverting routine assessments to those based on otolith readings. One method which has been put forward to reduce these costs is the use of otolith weight as a measure of age. The suitability of this relationship was examined for *L. mahsena*. Relationships were derived for each of the study locations. While otolith weight explained a relatively high degree of the variation in age, the relationship was not accurate enough to identify individual ages. In contrast, the relationship proved appropriate for the rapid assessment of catch age structures, from which assessments of total mortality could be derived. The use of such relationships in the study locations offers considerable savings in time and money, offering a cheaper method to obtain the advantages of age-based methods when performing stock assessments.

Guidelines for data collection, assessment and management of the study fisheries

Through the outputs of the study, which are described above, a number of guidelines were derived, related to improved methodologies for assessment and management.

- **use age-based methods for estimating growth parameters for long-lived, slow growing species**

  Through both simulations and practical studies, the use of age-based methods (otoliths) was shown to result in the most accurate and precise estimates of von Bertalanffy growth parameters. The cost-benefit analysis showed that this method was also the most cost effective, providing a net benefit nationally, while offering further advantages in more sustainable management, increased supplies of protein through better management, and therefore increased employment in the fishery.

- **set up a regional otolithometry centre**
  Age-based methods were particularly cost effective where a regional otolithometry centre could be set up. This reduced the impacts of the high initial expenditure required for age-based methods, while opening an additional income stream by preparing otoliths for other regional organisations.
- **to estimate growth parameters, use the sampling programme employed in the current study**
  The sampling programme used in the current study, where both random and targeted sampling was undertaken, was recommended. This allowed both the estimation of total mortality, using only the randomly sampled individuals, while the combination of such data with that from the targeted sampling improved the growth parameter estimates.
  Where validation was required, the sampling programme could be modified so that samples were taken in each month of the year. In this way, samples would be available for marginal increment and edge analysis.
- **ensure young individuals are present in samples**
  To achieve accurate growth parameter estimates, it was recommended to ensure that small (young) individuals were present in the sample. Such individuals were highly influential on the age-based growth parameter estimates. It was recommended that research cruises, and/or alternative gears were employed for this purpose.
- **obtain otoliths/growth parameter estimates early in the life of the fishery**
  Due to the effects of fishing on the growth parameter estimates, it was recommended to sample early in the life of the fishery, where the lightly exploited population would provide more information on the growth parameters. However, such recommendations only held where density dependent growth was not operating.
- **use length-at-age data to identify the presence of density dependent growth**
  As shown through the simulations, the identification of density dependent growth in tropical fisheries is important. However, the identification of the presence of density dependent growth through the comparison of growth parameters is inappropriate. Changes due to density dependent growth are likely to be overshadowed by the strong influence that the sampled size distribution has on the resulting length- or age-based growth parameter estimates. Therefore, the use of (mean) length-at-age data to assess for the presence of density dependent growth was recommended, as performed in the current study.
- **if density dependent growth is operating, avoid large changes in fishing effort where possible**
  Where density dependent growth was identified, large changes in effort were not advised, unless necessary to conserve the stocks. If such changes were made, the growth parameters previously estimated would become void, since the biomass of the population would increase.
- **estimate total mortality through age frequency distributions**
  Length-based methods of total mortality estimation were shown to have a number of drawbacks, including the need for growth parameter estimates in the computation, the effects of density dependent growth on the length frequency distribution, and the variability seen in the annual length frequencies from the study fisheries. Therefore, age-based methods were recommended. The use of age frequency distributions avoided the requirement for growth parameter estimates, and minimised the impacts of density dependent growth on the estimates. The sample size required would depend on the growth rate of the species, and therefore the number of age classes present. For *L. mahsena*, age frequencies can now be estimated using the age-otolith weight relationship derived during the current study.
- **assessments should be made at as a fine spatial accuracy as possible**
  The practical studies of the length and age structure of the stocks indicated localised ‘meta-populations’ at the study locations. Such populations, where exposed to different levels of fishing mortality, have the potential to mask differences in length, age or

growth rate assessed at the gross scale of the bank. In turn, identification of localised stocks more resilient to fishing mortality (*e.g.* faster growth rate due to higher localised productivity) could allow improved resource use. In turn, the current statistical sectors, which were derived purely for statistical convenience, could be improved by basing them on the underlying population structure.

  Such improved spatial assessments will require liaison with the fishing companies and fishermen, to obtain their cooperation during data collection. In turn, such data could be collected easily by the initiation of observer programmes.

- **stock assessments should be tuned to the current level of exploitation in a particular fishery**

  The management strategy simulations indicated that the use of the management reference effort level $F_{0.1}$ was inappropriate at certain fishing mortality levels. This measure needed adjustment (tuning) so that the aim of reaching $F_{0.1}$ over a set period was achieved. This tuning was affected by the presence or absence of density dependent growth.

  For lightly exploited fisheries, the appropriately tuned correction factor should be applied. Whether or not density dependent growth was present did not have an effect on this tuning.

  For heavily exploited fisheries, the precautionary approach was to assume density dependent growth was operating. In this case, a reduction in the target F was required, *i.e.*, tuning with density dependent growth would lead to a correction factor of less than 1.
- **accurately assess the current fishing mortality level for the fishery**

  Due to the need to tune the stock assessments appropriately, an accurate assessment of the level of fishing mortality in the fishery is required. For this, an estimate of natural mortality is needed (F=Z-M). This value is generally estimated through empirical formulae. As such, this remains a source of uncertainty into the stock assessments.

  Assessments of fishing mortality at the level of the bank are further complicated by the localised structure of the populations. Again, such assessments should be made at as high a spatial resolution as possible.
- **examine the performance of a full age-based stock assessment**

  It was noted that the increased accuracy and precision resulting from the use of age-based growth parameter estimates was diluted by the use of length-based methods at any stage of the stock assessment. As such, the use of a full age-based stock assessment may retain the accuracy obtained by the use of age-based methods of growth assessment for long-lived, slow growing species.

For management strategies based on analytical models of the fishery, such as yield per recruit assessments, the outputs of this project indicate that improved management performance can be achieved by using age-based rather than length-based stock assessment methods. However, this will require investment in capital equipment, in human resources and training, and will result in budgetary changes. It is thus recommended that during the process of changing to age-based methods of assessment, fisheries institutions should maintain any current length-based data collection and assessment practices.

6 Contribution of Outputs

6.1 Towards DFIDs developmental goals

This project began in 1996 and relates to DFID goals defined in the original RNRRS and FMSP logframes. However, the outputs of the project are also directly relevant to the revised strategy: the RNRKS and the recently modified FMSP logframe.

The DFID RNRRS goal to which the project relates was “to enhance the productivity and productive potential of the land water interface through improved management of aquatic resources” as defined in the FMSP logframe, with the purpose of achieving optimum sustainable yield in capture fisheries through improved resource management. The project directly addressed the FMSP indicative output “ New and improved biomathematical and bioeconomic methods and models for stock assessment and aquatic resource management and appropriate data management systems developed and promoted”. The outcomes of this project are also related to the RNRKS goals of “poverty elimination through sustainable development”, and to the FMSP goal of “improving livelihoods through sustainable enhanced production”, with benefits delivered to the target poor by application of the knowledge generated from this project to develop improved fisheries management guidelines.

The target beneficiaries of this project were small scale artisanal and semi-industrial fishing communities, and national and regional fisheries departments. Small-scale fisheries based on demersal fish stocks represent an important source of nutrition and income for fishers and dependant communities throughout the Indian Ocean, and more widely in the Caribbean and Pacific. The potential for overfishing of demersal fish stocks of snappers and emperors requires that these important resources be managed effectively to safeguard the livelihoods of rural communities who are dependent upon them. This project presented management guidelines based on analytical stock assessment models. These guidelines for improved data collection and management of exploited snapper and emperor fisheries have been developed from the outputs of the theoretical and practical components of the project. Adoption by the target organisations will contribute directly to the project goal: ‘Optimum sustainable yield from capture fisheries achieved by improved resource management’ and the RNRRS goal of improved management of aquatic resources.

6.2 Promotion of outputs

The guidelines developed will be most directly relevant to government organisations responsible for fisheries management in Mauritius, Seychelles and to the British Indian Ocean Territories administration. However, they will also be relevant to fisheries management institutions elsewhere, and to the fisheries scientific community. Implementation of the management guidelines arising from this project is required in order to achieve DFIDs developmental goals. In order to reach both a national (in collaborating countries) and international audience of target organisations, a number of means of promoting project outputs were pursued, and will continue to be pursued beyond the life of the project. In particular, national workshops were held by the project to disseminate results and develop and promote management guidelines, while results were also disseminated at a number of other international workshops and symposia (see below). A number of technical reports and publications were also prepared during the life of the project. A number of further scientific papers are to be produced after the completion of the project.

As already indicated, implementation of the management guidelines is required for them to achieve their developmental benefit. Considerable interest in developing and applying the guidelines was expressed during the project workshops, suggesting that the potential for uptake of the outputs of this strategic research project is good. In Seychelles, staff indicated that assessments would now shift to the use of age-based methods of assessment. Due to previous historical studies of otoliths performed at this location, and the work performed for this project, the equipment and experience required for these assessments is already present at the institution. The shift in assessment methods therefore represents relatively small additional investment.

In Mauritius, staff indicated that age-based methods could be employed for a number of other species, including those caught in the local lagoon fishery. However, some investment would be required before such techniques could be employed routinely. Some justification for the funding required for age-based assessment methods was identified through the cost-benefit analysis performed in the current study. However, the potential for the use of age-based methods in this location will depend on the decision of government to fund such studies.

Staff at the University of Mauritius expressed an interest in jointly developing a future project to address some of the remaining outstanding issues arising from this study, such as the potential for improved management performance with full age-based stock assessments.

The guidelines for management developed through this study will be applied in relation to the British Indian Ocean Territory (BIOT) fishery, and there is high potential for their uptake in both Seychelles and Mauritius, where MRAG continues to work collaboratively within the target organisations through fisheries commissions related to the BIOT fisheries.

6.2.1 Publications

Mees, C. C. and J. A. Rousseau (1997) The potential yield of the lutjanid fish *Pristipomoides filamentosus* from the Mahé Plateau, Seychelles: managing with uncertainty. *Fisheries Research* 33 (1997) 73-87.

Pilling, G.M., Millner, R.S., Easey, M.W, Mees, C.C., Rathacharen, S., Azemia. R. (Accepted, subject to revision). Validation of annual growth rings in the otoliths of the lethrinid *Lethrinus mahsena* and the lutjanid *Aprion virescens* from sites in the tropical Indian Ocean, with notes on the nature of growth rings in *Pristipomoides filamentosus*. Submitted to *Fishery Bulletin*.

6.2.2 Internal reports

Preliminary report to Marine Resources Assessment Group in completion of Phase 1: The use of otoliths to determine the age of snapper and grouper from the Seychelles and Mauritius fisheries. 1996

Second report to Marine Resources Assessment Group in completion of Phase 1: The validation of otoliths of *Pristipomoides filamentosus* and *Aprion virescens*.1998

6.2.3 Other dissemination of the results

Dissemination and training workshops were undertaken at Albion Fisheries Research Centre (AFRC) in Mauritius and at the Seychelles Fishing Authority (SFA). 20 April 1998 - 2 May 1998.

Presentation of a poster entitled "Validation of annual growth rings in the otoliths of the lutjanids *Pristipomoides filamentosus* and *Aprion virescnes*, and the lethrinid *Lethrinus mahsena*, from sites in the tropical Indian Ocean" at the Second International Symposium on fish Otolith Research and Application. 20/6/98 - 26/6/98, Bergen, Norway.

Presentation of a poster entitled “The effects of density dependence on the growth and assessment of tropical snappers and emperors in the Indian Ocean” at the Annual International Symposium of Tropical Fish Biology. 13-16 July, 1998, Southampton, UK.

Dissemination of project results during workshops undertaken at Albion Fisheries Research Centre (AFRC) in Mauritius, 20-21 September 1999, and the Seychelles Fishing Authority (SFA), 15-16 September 1999.

1. Introduction

The current project resulted from the recommendations of FMSP project R5484, ‘Management of tropical multi-species fisheries’. This project developed guidelines for the management of snappers, groupers and emperors, based on analytical yield-per-recruit models. It was noted that the commonly used length-based methods of fisheries assessment, in particular when assessing growth in species of these families, resulted in uncertainty in the accuracy and precision of estimates. Therefore, where such parameter estimates were used to derive stock assessments, uncertainty would result in the management actions based on these assessments. That project recommended that this constraint to management be further investigated.

The current project again concentrated on species of the Lutjanidae (snappers) and Lethrinidae (emperors). Such species are widespread throughout warm waters of the world. They are highly valued food fish in many tropical countries; for example, Seychelles (Mees, 1989), Mauritius (Ardil, 1986), Australia (Kailola *et al.*, 1993), the Caribbean (Thompson and Munro, 1974), Hawaii (Okamoto, 1982; Parrish *et al.*, 1997) and Tonga (Langi *et al.*, 1992). Fisheries based on these species provide both a cheap source of protein, and where they form the basis of an export trade, an important component of the national economy of many developing countries. Fisheries based on these species are therefore important both to artisanal and semi-industrial fishermen. However, the slow growth, low reproductive capacity and low rates of natural mortality of lutjanid and lethrinid species makes them vulnerable to overfishing (Koslow *et al.*, 1988; Russ, 1991; Haight *et al.*, 1993a). Sound management advice is therefore important for the long term sustainability of fisheries targeting these species.

An essential component in the assessment of exploited population dynamics are studies of the age structure and growth rates of a fish population (Rowling and Reid, 1992). Von Bertalanffy growth parameters (L_∞, K, t_0) are inputs into age-based production models, analytical models such as yield-per-recruit (Beverton and Holt, 1957), and cohort/virtual population models (*e.g.* Pope, 1972). Clearly, growth parameters have the potential to influence the outcome of particular stock assessments, and hence fisheries management, strongly.

In temperate fish species, growth is frequently determined using age data derived from assessments of annual growth rings in hard tissues such as otoliths. Such annual banding is believed to form in many tropical species, although the process is said to be complicated by reduced seasonality (Manooch and Drennon, 1987). For this reason, and due to financial constraints, cheaper length-based methods of growth assessment are more commonly used. However, these methods are not particularly well suited to long-lived, slow-growing species, such as lutjanids and lethrinids. They commonly utilise modes in length frequency data (assumed to represent individual cohorts) to estimate growth parameters. In slow growing species, modes representing fish cohorts frequently overlap, offering limited information on growth. Under such circumstances, the accuracy of growth parameters derived through length-based methods is uncertain.

Due to gear selectivity, fishing commonly targets specific sizes. Therefore, catch samples are unrepresentative of the underlying population structure. In turn, over periods of sustained fishing, gear selectivity may remove larger size classes (and hence older age classes) from the population. This may truncate the size range, reducing the available information on which growth parameter estimates are based. As a result, fishing has the potential to directly affect the accuracy of growth estimates derived from either length or age data.

Fishing can also affect growth (and hence the parameters used to describe it) indirectly, through 'density dependent growth' (Beverton and Holt, 1957). Here, individual growth is assumed to be limited by population density (*e.g.* through competition for food resources). Decreases in population density due to fishing may therefore allow growth rates to increase (Gulland, 1983). Since density dependent growth has been identified in both marine and freshwater fish populations, the assumption of static life history parameters in fish stock assessment models may be inappropriate.

The use of uncertain growth parameters may have serious effects on the outputs of assessments, resulting in either over-exploitation of the resource, or under-exploitation, leading to a loss of jobs or reduction in food supply.

1.1 PROJECT AIMS

This project aimed to answer a number of questions.

Currently, length-based growth estimation methods are the only methods available in the study fisheries. However, the accuracy and precision of these methods, and the effects of fishing upon the resulting estimates, is currently unknown for long-lived, slow-growing species. The first question to answer, therefore, is:

- **How accurate, and how precise, are growth parameters estimated using length-based methods, when applied to data from lutjanids and lethrinids?**

Age-based methods of growth assessment are likely to be more accurate than those resulting from length-based methods. A number of snapper and emperor species have been successfully aged using otoliths. However, a detailed examination of otoliths from the study species has not been performed. Therefore, the next question to answer is:

- **Can age-based methods be used for species of these families? If so, are these more expensive methods of growth assessment more accurate than length-based methods?**

Once the underlying accuracy and precision of the two growth estimation methods, and the impacts of the direct effects of fishing on these estimates, has been established for snappers and emperors, the question arises:

- **What effects does density dependent growth have on the ability to estimate growth parameters accurately and precisely?**

If density dependent growth has a notable effect, then the identification of its presence in populations becomes important. Therefore:

- **Are either length-based or age-based methods sufficiently precise to detect changes in growth due to fishing?**

Growth parameter estimates are seldom assessed in isolation. As stated, the general aim is to use such estimates to derive further parameters, through which the status of the stock can be assessed. If both the growth estimation method used, and the direct and indirect effects of fishing, affect growth parameter estimates:

- **How important for appropriate management are accurate and precise growth estimates, and identification of changes in growth through density dependence?**

Age-based methods may be the most appropriate growth estimation methods for these species. However, such methods are considered to be more expensive than the estimation of growth through length-based methods. This has great importance for fisheries institutions in developing countries. Therefore:

- **If age-based methods provide more appropriate management information for an exploited stock, are these benefits outweighed by the cost of the methodology?**

Both practical and simulation studies are undertaken to answer these questions. The studies described in this report concentrate on three study species; the lutjanids *Pristipomoides filamentosus* and *Aprion virescens*, and the lethrinid *Lethrinus mahsena*. Data were obtained from three locations in the central and western Indian Ocean; Mauritius, Seychelles, and the British Indian Ocean Territory (BIOT; Chagos Archipelago).

It was originally intended that species from the Serranidae would also be examined during this project. However, the practicalities of obtaining specific specimens for both length frequency and age-based examinations of the stocks from the majority of locations proved unfeasible. The study therefore concentrates on species of the Lutjanidae and Lethrinidae.

Background information on the study locations, and their associated fisheries, is presented in Section 1.2. Section 1.3 summarises the available information on the biology of the study species. Background information on the two main topics of this report (*viz.*, the effects of fishing on the structure and growth of fish populations, and the estimation of growth parameters) is presented in Sections 1.4 and 1.5.

1.2 STUDY LOCATIONS AND THEIR ASSOCIATED FISHERIES

1.2.1 Study locations

Background to the study locations is available from MRAG (1996b, 1996c, 1996d). The following section therefore provides a limited background of the study locations, concentrating on points of relevance to the current study.

Seychelles and Mauritius are islands in the western Indian Ocean (Figure 1.1), positioned on the limestone Mascarene Plateau, which runs from 4°S to 21°S. The features of this plateau vary from ancient granitic islands (such as Seychelles) and younger volcanic islands (such as Mauritius), through to sand cays and atolls, emerged and submerged coral reefs, algal ridges and sea mounts. The shelf of the plateau is 200m deep. However, it features several shallow banks, which form the basis for the study fisheries of Mauritius (see Figure 1.1, below). The coraline Chagos Archipelago is centred at 6°S, 72°E, on the southernmost part of the Chagos-Laccadive Ridge. The archipelago consists of five atolls, and a number of submerged banks, the largest of which is the Great Chagos Bank.

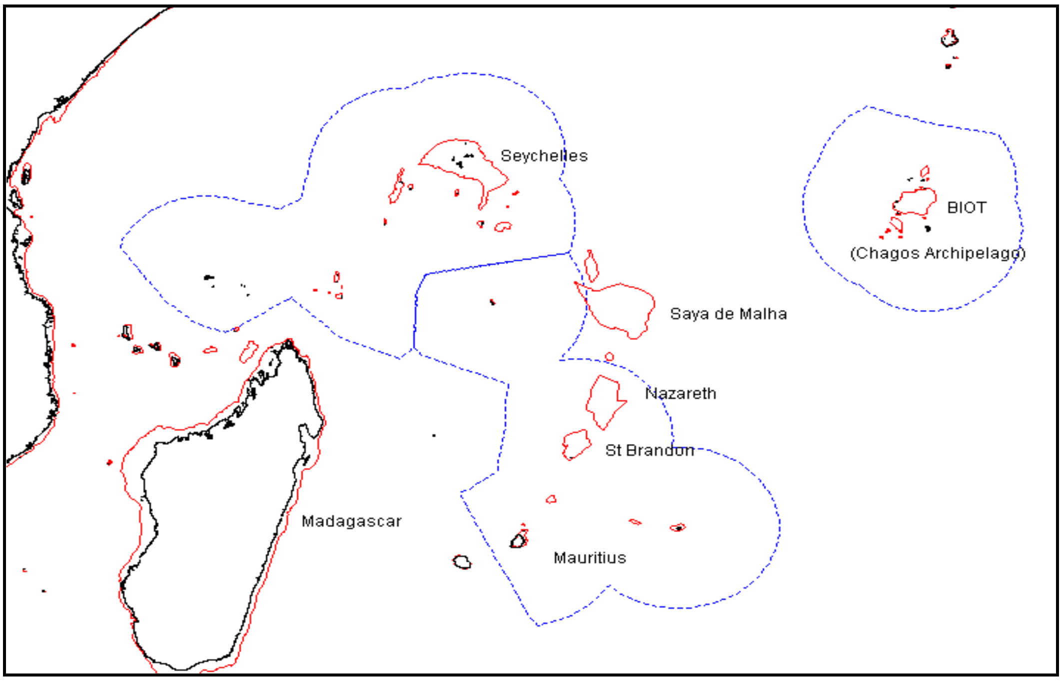


Figure 1.1 Chart of the western Indian Ocean, showing the relative position of the study locations, and 200m depth contour. Seychelles and Mauritius are surrounded by their Exclusive Economic Zones, BIOT (Chagos Archipelago) surrounded by its Fisheries Conservation and Management Zone.

The coraline banks of Seychelles and Chagos experience distinct bathymetric differences to the banks north of Mauritius ('Mauritian banks': Nazareth and Saya de Malha). The former are influenced by the east flowing Equatorial Counter Current, while the Mauritian banks lie in the west flowing South Equatorial Current. Seychelles and Chagos are largely unaffected by cyclones, whilst the Mauritian banks are frequently subject to cyclonic depressions and severe sea states from mid-November to mid-March. The South East trade winds affect the whole area from the end of May to October. This commonly limits fishing opportunities both in the Seychelles and on the Mauritian banks. In the latter fishery, vessels frequently move further northeast to the Chagos Archipelago in order to continue fishing.

Throughout this report, the term 'location' is used to describe the major regions from which the data are collected (*i.e.* the Seychelles, BIOT (Chagos Archipelago), and each of the Mauritian banks - Nazareth, south Saya de Malha, north Saya de Malha). The term 'area' describes the smaller statistical areas into which the Seychelles and BIOT (Chagos Archipelago) have been divided historically, for more convenient data analysis (see below).

1.2.2 Study fisheries

1.2.2.1 Seychelles

The islands of the Seychelles were populated in the eighteenth century, and fishing was initially limited to coastal areas near centres of population. Currently, fishing remains largely concentrated in a region within 10 nautical miles of the Mahé/Praslin island group, although fishing has now expanded to encompass the surrounding Mahé Plateau and more distant banks. Concern has been expressed over the inshore resources, while exploitation of the outlying islands remains sporadic; they are still considered to be lightly exploited.

The banks and plateaux of the region have been stratified into fishing sectors (Figure 1.2, Table 1.1). This stratification was performed for statistical and analytical convenience, and was not based on distinct populations of species (MRAG, 1996d). Throughout subsequent text, the sector numbers in Table 1.1 will be used. In that table, area estimates for shallow (0-75m) and intermediate (75-150m) depth strata were derived from Admiralty charts. Area of intermediate depths were calculated from length of the 100m contour, assuming an average width of 250m for this shelving depth band. The exception was the Mahé Plateau, for which this area was calculated by Seychelles Lands and Survey Division (MRAG, 1996d). Fishable areas (those suitable for handline fishing) were calculated as 60% of total area (Mees, 1992).

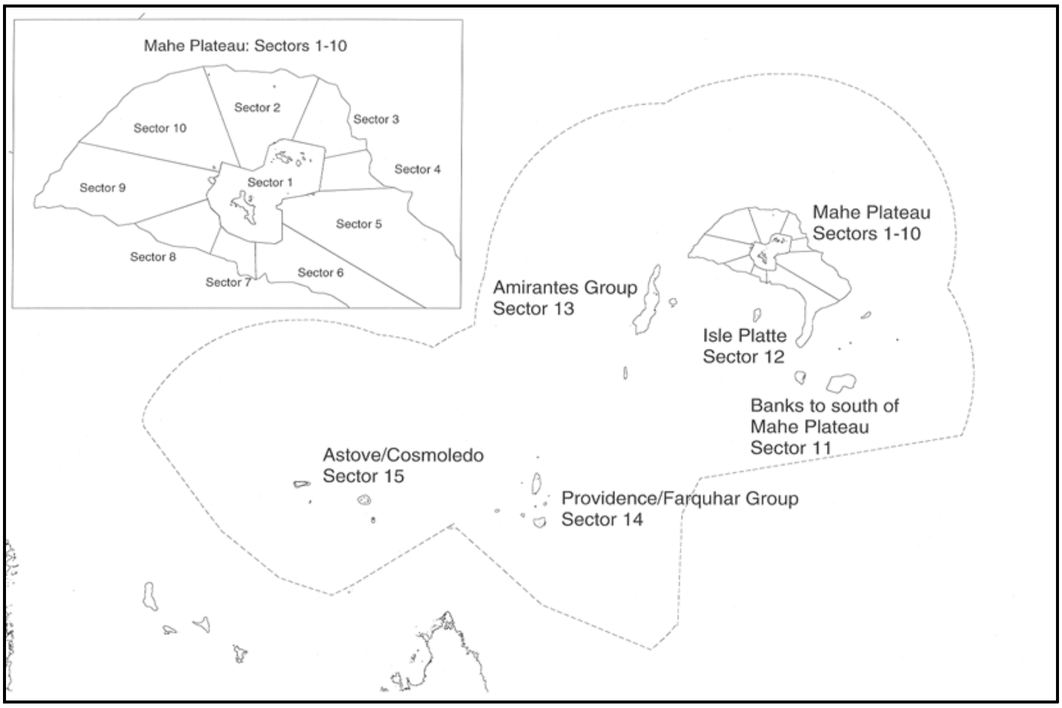


Figure 1.2 Statistical fishing sectors of the Seychelles. Insert displays the sectors of the Mahé Plateau in detail. Figure also shows the Exclusive Economic Zone.

The Seychelles artisanal fishery is described by Lablanche *et al.* (1988), Mees (1989) and Mees *et al.* (1998). It is a complex fishery, exploited by a number of vessel types and gears. For schooners (decked inboard powered vessels), whalers (undecked inboard powered vessels) and mothership ventures, species of the Lutjanidae, Lethrinidae and Serranidae contribute over 85% of the landed catch. Fishing from these vessels involves hook and line, since trawl nets are prohibited. The ‘small boat’ class of vessel (a group including fishers on foot, pirogues and outboard powered vessels) catch a smaller proportion of demersal species.

Between 1985 and 1994, the demersal fishery contributed between 20% and 40% of the 5,000t landed annually (Seychelles Fishing Authority, 1995). There is a high local demand for fish, particularly during the SE trade wind period, when adverse weather restricts fishing operations. Catches of *P. filamentosus* by schooners peaked in 1990 (28% of schooner catches; Seychelles Fishing Authority, 1991), but have since declined (Seychelles Fishing Authority, 1998). This may result from perceived declines in resource abundance, and hence changes in targeting by schooner vessels. *A. virescens* also forms a large proportion of total catches (15% of total whaler catch, 17% of schooner catch; Seychelles Fishing Authority, 1998). *L. mahsena* is the most common lethrinid in the catch. This family comprised 5% of the total landed catch in 1997.

The export market generates valuable foreign exchange (Mees, 1992). Demersal species constituted around 77% of exports between 1985 and 1994. 24% of the exported demersal catch comprised ‘job fish’ (*Pristipomoides filamentosus* and *Aprion virescens*), while lethrinid species comprised 16%.

Table 1.1 Fishing grounds and statistical sectors of the Seychelles.

Fishing Grounds	Description	Sector	Area (Km^2)		
			0-75m	0-75m fishable	75-150m
MAHÉ PLATEAU AND ASSOCIATED BANKS			**41,338.0**	**26,500**	**374**
OUT	10 mile radius of Mahé/Praslin	1	4,544.0	-	-
N, NNE, NNW	Birds, Denis, North Edge	2	4,794.0	-	44.3
NE	North East Edge	3	1,604.0	-	24.2
E, ENE	Topaze Bank	4	2,913.0	-	30.3
ESE	La Junion Bank	5	8,041.0	-	50.7
SE	South East Edge	6	5,405.0	-	79.9
S, SSE	South Edge	7	818.0	-	25.5
SW	South west Edge	8	1,876.0	-	46.8
W, WNW,	Owen Thor Roberts Banks	9	5,715.0	-	34.9
NW	North West Edge	10	5,628.0	-	37.4
BANKS TO SOUTH OF MAHE PLATEAU			**2,198.6**	**1,619.6**	**135.3**
ADE	Adelaide Bank	11	6.6	-	2.7
COE	Coetivy	11	420.0	-	20.8
CON	Constant	11	590.0	-	28.7
COR	Correira	11	17.4	-	8.3
FOR	Fortune	11	600.0	-	30.1
SAV	Bar Savat	11	48.0	-	12.5
SCO	Small Constant	11	170.0	-	13.8
M20	Seamount marked ‘20'	11	6.6	-	2.7
PLA	Platte	12	340.0	-	15.7
OUTLYING ISLANDS AND PLATEAUX					
AMI	**AMIRANTES GROUP**	**13**	**3,999.0**	**2399.4**	**135.8**
AFR	African Banks - all atolls	13	240.2	-	5.9
ALP	Alphonse	13			
BIJ	Bijoutie	13			
BOU	Boudeuse	13			
DEN	Desnoeufs	13	377.3	-	9.2
DES	Desroches Atoll	13	40.0	-	19.4
ETO	Etoile	13	553.9	-	13.8
FRA	St. Francois	13	59.3	-	7.7
IDS	Ile Du Sud	13			
JOS	St Joseph	13	869.3	-	21.8
MAR	Marie Louise	13	376.1	-	8.3
POI	Poivre	13	655.9	-	11.3
REM	Remire	13	371.1	-	16.5
	All others		95.9	-	22.0
PROVIDENCE/FARQUHAR GROUP			**1,621.7**	**927.7**	**131.7**
FAR	Farquhar Group - Unspecified	14	316.5	-	31.5
PRO	Providence Group - Unspecified	14	316.5	-	11.4
CER	Cerf Island	14			5.7
WIZ	Wizard Reef	14	100.0	-	14.0
BUL	Bulldog Bank	14	285.8	-	18.4
MCL	McLeod Bank	14	240.9	-	18.4
M17	Bank marked ‘17'	14	81.7	-	12.3
M25	Bank marked ‘25'	14	279.7	-	20.1
ASTOVE/COSMOLEDO GROUP (Excl. Aldabra)			**398.1**	**238.9**	**32.4**
AST	Astove	15	79.6	-	9.6
COS	Cosmoledo	15	318.5	-	22.8
	TOTAL		**49,554.9**	**31,799.6**	**809.2**

Current management regime

The National Development Plan, 1990-1994 (Anon, 1989) detailed the objectives related to domestic fisheries. In no particular order, these were to:

- enhance its contribution to nutrition
- create the maximum amount of work opportunities
- maximise foreign exchange earnings
- create optimum linkages with other sectors
- ensure stable development in the industry
- conserve marine resources, ensuring long term industry viability

High exploitation rates in near-shore areas resulted in a Government policy to limit the numbers of outboard-powered craft, and promote larger inboard-powered vessels capable of fishing further offshore. However, progress towards this has been limited for a number of reasons, including the high investment required to purchase such craft. A number of plans were subsequently instigated, including provision of loans, and promotion of demersal fisheries in the outer islands (Anon, 1989). A recent FAO study (Mees *et al.*, 1998) recommended that the shift to offshore fishing areas be continued, with the aim of ensuring sustainable management of fish stocks and conservation of bio-diversity. The report recommended ”a balance of regulatory measures, fiscal and economic incentives and disincentives” for appropriate management and resource development. Improvements to the management and enforcement system (including the data collection system) were recommended (see also Flewwelling *et al.*, 1992).

The Seychelles Fishing Authority (SFA) is tasked with collecting and analysing data on fisheries, and, in the light of such data, preparing and reviewing plans for fisheries development and management. Assessments for the demersal fisheries are performed through routine length-based total mortality assessments, using growth parameters derived through length-based methods (*e.g.* Mees, 1992; Mees and Rousseau, 1997). Assessments have also been performed using yield-per-recruit and length-based cohort analysis.

Management measures including closed seasons, closed areas or gear specifications, can be implemented by the Minister of Agriculture and Fisheries through the Fisheries Act, 1986. However, regulations specific to demersal fish species do not currently exist. While the instruments of management are in place, there is at present little direct management, and no demersal fishery management plan.

1.2.2.2 Mauritius

The Mauritian fishery is based on fishing on the relatively shallow banks to the north of Mauritius: Cargados Carajos (St Brandon), Nazareth and Saya de Malha banks. Saya de Malha (commonly shortened to ‘Saya’) is strictly in international waters, although Mauritius exercises traditional fishing rights there. This bank has been divided into north and south Saya de Malha for statistical purposes (Table 1.2). In this report, Nazareth and Saya de Malha are termed ‘Mauritian Banks’. Specific codes for these locations will be referred to as described in Table 1.2.

Fishing began in the eighteenth century, with salted fish coming from the copra islands of St. Brandon, Agalega and Chagos Archipelago. More extensive exploitation of the banks began in the mid 1960s (Samboo and Mauree, 1988). Fishing currently occurs from refrigerated mothervessels (commonly converted tuna longline vessels) which carry up to twenty 6-8m pirogues or ‘dories’. Three fishermen operate from each dory, using handlines rigged with between three and eight baited hooks (Samboo, 1983). Up to 1,000 fishermen are currently employed, 500 of whom are regularly active, spending up to 150 days at sea per annum.

Table 1.2 Areas (km²) of Mauritian fishing banks. Areas (0-75m and 75-150m) computed from Admiralty Charts. Fishable areas estimated based on a comparison of historical estimates (MRAG, 1996c).

Bank	Fishing Ground	Code	Area (km²)		
			0-75m	0-75m fishable	75-150m
Saya de Malha	Saya North	SMN	4,965	4,000	93
	Saya South	SMS	37,151	8,500	257
	TOTAL		**42,116**	**12,500**	**350**
Nazareth	Nazareth	NAZ	**22,814**	**10,000**	**187**
St Brandon	Albatross	ALB	4,606	3,000	51
	St Brandon	STB	4,606	3,000	50
	TOTAL		**9,212**	**6,000**	**101**

The banks fishery contributes in excess of 60% of the marine catch in Mauritius. In 1993 and 1994, catches from the Mauritian banks reached 5,000t, but still failed to meet domestic demand. Fish exports are therefore controlled, since it is necessary to import the deficit in order to meet requirements (Morel, 1989).

Catches from the banks are primarily demersal species. The main component of the catch is species from the family Lethrinidae, particularly *L. mahsena*. This is the dominant species on Saya de Malha, comprising around 90% of the total catch weight (Ardil, 1986; Bertrand *et al.*, 1986), and over 50% on the other banks (MRAG, 1997a). The majority of the remainder of the catch comprises species of the families Lutjanidae and Serranidae, including *A. virescens*. This species is a valued, if generally uncommon, feature of the catch. Until recently, *P. filamentosus* was not targeted by Mauritian vessels. In 1997, however, a Mauritian fishery for *P. filamentosus* was initiated, comprising a single mothervessel and five modified dories equipped with electric reel fishing gear.

Current management regime

The objective of Mauritian Government policy was to increase fish production to 20kg *per capita* (in excess of 10,000t in total), to stimulate frozen fish consumption, and develop the fishery to a level sufficient to replace fish imports (MRAG, 1996b). Overall, the goal was to provide a source of protein at an affordable price.

Current Mauritian legislation for the banks fishery relates to species prohibition (due to their potential for ciguatera), minimum sizes for certain fish species, price controls on frozen banks fish, and to a total allowable catch (TAC) quota system, which forms the main management tool.

The restrictions on ciguatoxic fish apply to shallower water species, and do not affect the study species. Discarding undesirable fish has the potential to result in increased mortality which will not be identified through catch data analysis. However, the impact on Mauritian banks is felt to be minimal; targeting of desired species, through selection of fishing location or hook size, is believed to be effective and the fishery is relatively monospecific. It presents a greater problem in Chagos, as this area sustains a more multi-species fishery.

Legislation on minimum length relates principally to the artisanal coastal fishery (Table 1.3). However, there has been some confusion over whether these size limits also apply to banks fish species. A number of fishing companies are now paying a reduced rate for what they consider undersized fish, or refusing to purchase them, due to both difficulties in selling small individuals on return to port, and the perceived size limits (A. Talbot, *pers. com.*). The author was told of incidents where catches of 'undersized fish' were seized on return to port, although these were not verified.

Price controls on the banks fishery were initially introduced for social reasons, to ensure that fish were available to all social classes. Price controls have since proved useful as a management tool to reduce effort; when controls were removed between 1981 and 1987, both prices and fishing effort increased.

Table 1.3 Minimum size of demersal species in Mauritius. From the fifth schedule of Mauritian fisheries legislation.

Scientific Name	Local name	Minimum size (cm)
Lethrinus sp.	Capitaines	30
Parupeneus barberinus	Rougets	20
Lethrinus mahsena	Dame Berri	30
Polysteganus baissaci	Guelles Pavees	30
Naso unicornis	Licornes	30

In 1994, a non-transferable quota system was introduced for Mauritian banks fisheries. Maximum sustainable yields for each bank were estimated through the Thompson and Bell method (Thompson and Bell, 1934). These estimates were reduced by 10% in order to determine the Total Allowable Catch (TAC) from each bank. The TAC (no reference to individual species) was initially allocated on a per vessel basis, based on historical performance. The system was amended in 1995, with the catch quota applied to companies rather than individual fishing vessels. Quotas reflected the historical performance of each company. This was a single quota, allocated for the whole of the Mauritian banks, rather than by individual bank. TAC in 1995/96 was set at 4,750t (MRAG, 1996c).

The management rule currently in place calls for an annual 5% decrease in TAC until 'consistent signs of stock recovery' are identified. Such signs include increases in catch rate and catch mean length. These are monitored annually. Routine assessments are also performed; for example, using length-based methods of total mortality estimation.

1.2.2.3 British Indian Ocean Territory (Chagos Archipelago)

The Chagos Archipelago consists of five atolls and a number of submerged banks. The atolls of Nelson, Peros Banhos, Salomon and Diego Garcia were originally inhabited, and were minor producers of salt fish. Some handlining for shark and predatory teleost fish also occurred. In the early 1970's, the atolls were evacuated, with the exception of Diego Garcia, which is now a US naval facility. Mauritian mothership-dory fishing ventures are licenced to fish within the Fisheries Conservation and Management Zone (FCMZ) of BIOT (Chagos Archipelago) during April to October. During this period, fishing on the Mauritian banks is commonly limited due to bad weather in the South East trade wind season.

For statistical purposes, the region has been divided into a number of areas (Figure 1.3, Table 1.4). Throughout this report, area codes will be referred to as described below.

Table 1.4 Statistical fishing areas within the Chagos Archipelago. Areas (0-75m and 75-150m) were computed from Admiralty Charts.

	Code	Area (km^2)	
		0-75m	75-150m
GREAT CHAGOS BANK		**6,044**	**190**
Central Chagos Bank 1	CH1	262	0
Central Chagos Bank 2	CH2	75	0
Eastern Chagos Bank	ECH	445	57
Northern Chagos Bank	NCH	1,343	25
Nelson Island	NEL	1,181	40
Southern Chagos Bank	SCH	1,181	23
South East Chagos Bank	SEC	895	15
Western Chagos Bank	WCH	662	30
OTHER BANKS / ATOLLS		**2,543**	**149**
Blenheim Reef	BLE	42	7
Cauvin Bank	CAU	56	7
Centurion Bank	CEN	29	6
Colvocoresses Reef	COL	14	6
Egmont Islands	EGM	48	6
Ganges Bank	GAN	16	4
Peros Banhos	PBA	442	25
Pitt Bank	PIT	1,296	49
Salomon Islands	SAL	17	7
Speakers Bank	SPK	562	27
Victory Bank	VIC	21	5
TOTAL		**8,587**	**339**

The fishery is less monospecific than that on the Mauritian banks; while the majority of the catch comprised of species from the Lethrinidae, species from the Lutjanidae and Serranidae are also common (Mees *et al.*, 1999). Fishing commonly occurs on the shallow bank, where lethrinids such as *L. mahsena* and *L. rubrioperculatus* predominate (46% and 32% of bank catch weight respectively; MRAG, 1997b). Fishing may also occur in deeper water on the ‘drop-off’ at the bank edge, where *P. filamentosus* dominates (55% of drop off catch weight). *Aprion virescens* is caught when fishing in both habitats (4% of catch weight from bank and drop-off catches).

Both *P. filamentosus* and *A. virescens* are ‘top grade’ fish in Mauritius. They fetch high prices, and are either exported, or more often sold to large hotels on the island. In particular years, company fish pricing structures may offer a premium for catches of *P. filamentosus*, making the additional effort involved in handlining for this species worthwhile. During such years, this species can contribute up to 15% of the total catch (MRAG, 1997b).

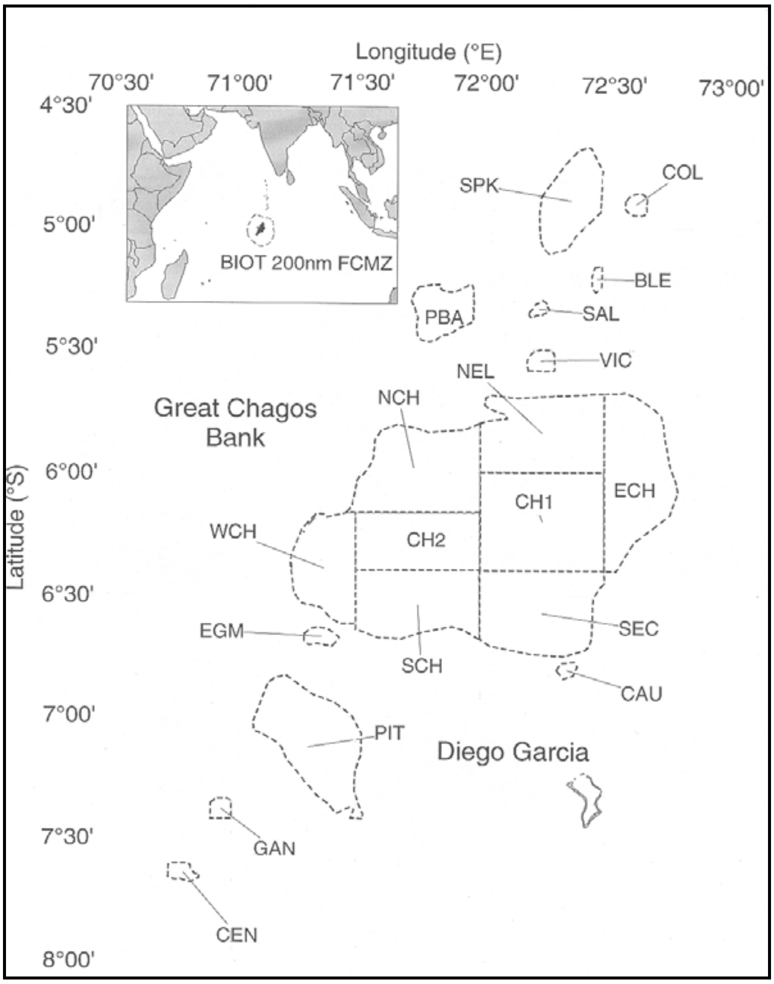


Figure 1.3 The Chagos Archipelago, indicating the statistical fishing sectors.

Current management regime

The BIOT (Chagos Archipelago) inshore fishery is controlled by the BIOT Authorities. As defined in The Fisheries (Conservation and Management) Ordinance, 1991, the main objective is conservation, rather than maximisation of any benefits from the fishery, while allowing Mauritian vessels to fish as they have previously done. The policy is to ensure that all fishing occurs with due regard and concern for the stability of fish stocks, conservation of bio-diversity, and appropriate management of resources for the long term benefit of users.

Effort controls are the principal management instrument. This is implemented through limited licensing, closed seasons, and restricting fishing areas. A maximum of six 80 day licences are issued each year for fishing within the set season from 1 April to 31 October. Fishing (which is only permitted using hooks and lines) is prohibited within lagoons (Mees *et al.*, 1999).

The fishery is monitored and evaluated annually, providing feedback to enable the management plan, or any specific instruments therein, to be revised. Such monitoring occurs through data obtained from logbooks, and the annual observer programme. The relationship between current fishing mortality (estimated using length-based total mortality estimates and empirical natural mortality estimates) and biological reference points (*e.g.* $F_{0.1}$, or comparisons of estimated length of capture and length at maturity, and the relationship between fishing and natural mortality; Mees *et al.*, 1999), are examined for signs of potential localised overfishing. Catch rates are also analysed for evidence of both long-term and short-term depletion.

1.3 STUDY SPECIES

In this report, studies concentrate on two lutjanid species (*P. filamentosus* and *A. virescens*; Figures 1.4 and 1.5), and one lethrinid species (*L. mahsena*; Figure 1.6). These are species of significant commercial importance for the study fisheries. This section provides an overview of the biological features of the two families, and reviews the information presently available specifically for the study species.

1.3.1 Lutjanidae ('Snappers')

There are 17 genera and 103 species of Lutjanidae (Allen, 1985), the majority of which are marine and reef dwelling. Snappers are active predators, feeding mainly at night. Fish are dominant in the diet of most species, although as a result of their opportunistic nature, the diet may also include zooplankton, crustacea, molluscs and benthic urochordates.

Many species show sexually dimorphic growth rates and sizes at maturity. They generally reach first maturity around 43% to 51% of the maximum total length. All snappers are said to be gonochoristic, showing no indications of hermaphroditism. Spawning is generally prolonged, with peaks during certain times of the year. During spawning, aggregations of individuals may occur. Juveniles are generally found in shallower water than the adults (Thompson and Munro, 1974).

There are four subfamilies of the Lutjanidae. Both of the study lutjanid species, *P. filamentosus* and *A. virescens,* (Figures 1.2 and 1.3) belong to the subfamily Etelinae. Members of this subfamily are classed as relatively elongate fish, with a lunate to deeply forked caudal fin.

1.3.1.1 *Pristipomoides filamentosus* (Valenciennes, 1830)

This species is called 'Batrican' in Seychelles, and 'Sacre Chien' in Mauritius.

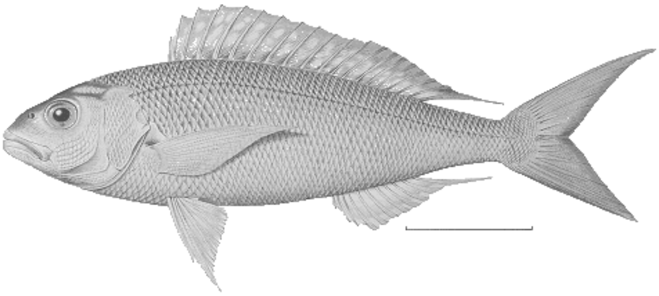


Figure 1.4 *Pristipomoides filamentosus*. Drawing by P. Opic, from Opic *et al.* (1994). Scale bar represents 10cm.

Juveniles are found on flat, featureless shallow banks and sediment bottoms close to sources of drainage, avoiding high relief areas where adults occurred (Haight *et al.*, 1993a; Parrish *et al.*, 1997). Juveniles move into deeper waters as they mature. Adult individuals are found on rocky seabeds, and shoaling around outcrops and promontories (Ralston *et al.*, 1986; Haight *et al.*, 1993b). This species occurs at intermediate depths, from 70 - 350 m, while the actual depth range varies between locations. No correlation has been found between size and depth in adult fish (Ralston and Williams, 1988b; MRAG, 1996b).

Studies in Hawaii showed that this species was primarily a zooplanktivore (Ralston *et al.*, 1986; Haight *et al.*, 1993b). Fish, crustaceans, molluscs and pelagic urochordates also feature in the diet.

In Seychelles, this species exhibits a protracted spawning period. Spawning peaks between February and May, and in November (Mees, 1993; MRAG, 1996d). The length at which 50% of females were mature (Lm_{50}) was approximately 51cm.

1.3.1.2 *Aprion virescens* (Valenciennes, 1830)

This species is called 'Job Gris' in Seychelles, and 'Vacoa' in Mauritius.

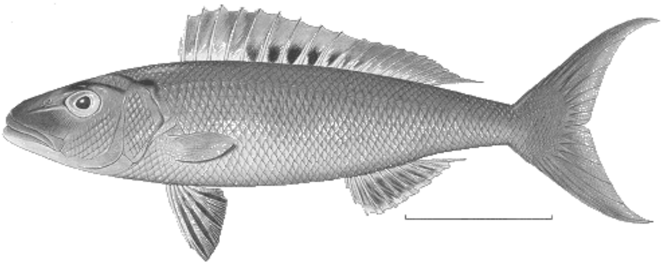


Figure 1.5 *Aprion virescens*. Drawing by P. Opic, from Opic *et al.* (1994). Scale bar represents 10cm.

A. virescens generally inhabits inshore reef areas on sandy seabeds or around coral. It is not constrained by substrate type, however, and can be caught both close to the bottom, and in the water column. Its depth range is extensive; individuals have been caught at depths down to 100m. *A. virescens* is carnivorous, feeding mainly on fish (Haight *et al.*, 1993b), while crustaceans, molluscs and plankton also feature in the diet.

Biometric data from Seychelles indicated this species has a protracted spawning period. Spawning peaks from October to February and April to May (MRAG, 1996b). A number of estimates of Lm_{50} have been derived at different locations. Overall, this species appears to mature around 45cm (Talbot, 1960; Brouard and Grandperrin, 1985; Everson *et al.*, 1989; MRAG, 1996d).

1.3.2 Lethrinidae ('Emperors')

The emperor family (Lethrinidae) are tropical and sub-tropical bottom feeding carnivorous fish of the Indo-Pacific Ocean (Fischer and Bianchi, 1984). They are generally found either on coral reefs and rocky areas or soft substrates. Species are not thought to be territorial, and generally form small shoals. Spawning aggregations also occur.

Lethrinids are carnivorous, feeding on crustaceans, echinoids, molluscs, and small fishes. They are generally caught close to the bottom as they search for food.

1.3.2.1 *Lethrinus mahsena* (Forsskal, 1775)

In both Mauritius and Seychelles, this species is known as 'Dame Berri' (Figure 1.4).

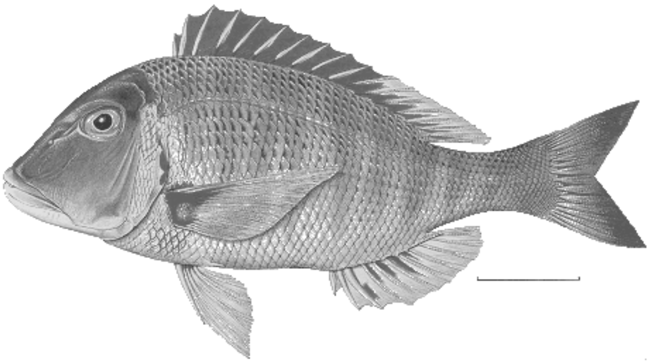


Figure 1.6 *Lethrinus mahsena*. Drawing by P. Opic, from Opic *et al.* (1994). Scale represents 5cm.

L. mahsena is generally found associated with the sea bed in areas of sand or coral, and is commonly caught at depths ranging from 25 - 50m. The species feeds primarily on benthic crustaceans, molluscs and echinoderms (Kulbicki, 1988).

L. mahsena is described as a protogynous hermaphrodite (Bertrand, 1986). Few females are said to exceed 35cm in fork length (FL), and few males are less than 20cm FL. Sex reversal occurs around 5-6 years of age, approximately 2 to 3 years after the earliest onset of sexual maturity (Bautil and Samboo, 1988). On Saya de Malha bank, the species has a single spawning season from October to February (Bertrand, 1986).

1.4 THE EFFECTS OF FISHING ON POPULATIONS

Fishing can act either directly at the level of the population or community through the removal of individuals, or indirectly through effects on growth, the removal of predator or prey species, or the modification of habitats.

For lutjanids and lethrinids, their slow growth rate, low rates of recruitment and natural mortality, and prolonged attainment of sexual maturity make them particularly sensitive to overfishing (Russ, 1991). Since these species are favoured for consumption or sale, they are commonly targeted by fishermen (Munro, 1983b; Koslow *et al.*, 1988), while their aggressive nature and relatively large size also make them particularly vulnerable to fishing gears (Munro and Williams, 1985).

The effects of fishing may be observed as changes in the relative abundance of a species in a fish community (changes in species composition, or 'ecosystem overfishing'; *e.g.* Russ, 1991; Watson *et al.*, 1996; Russ and Alcala, 1998). However, this section aims to provide the reader with a background to those effects of fishing which will be studied in this report; impacts on size and age composition, and growth.

1.4.1 Effects on size and age structure

Since fishing is commonly directed at larger, older individuals (Bohnsack, 1982; Munro, 1983b; Thompson and Munro, 1983b; Polovina, 1986; Koslow *et al.*, 1988; Ralston and Kawamoto, 1988; Samoilys, 1988; Russ and Alcala, 1989; Gulland and Rosenberg, 1992), it is expected to affect both the length structure and age structure of an exploited fish population (Craik, 1981; Russ and Alcala, 1989; Russ, 1991; Jennings and Lock, 1996). When fish are caught before they grow to the optimum marketable size (*i.e.* before that required to maximise yield), it is termed 'growth overfishing' (King, 1995).

Visual census studies have identified decreases in the mean size of predatory fish populations associated with exploited reefs (*e.g.* Bohnsack, 1982; Craik, 1981; Russ, 1985). Reduction in mean length have also been identified in the length structure of the exploitable phase of the population. In Australian waters, Rowling and Reid (1992) found a decreasing trend in mean length of Gemfish (*Rexea solandri*) over six years. Thompson and Munro (1983b) showed substantial shifts in mean size and size structure in both lutjanids and serranids on Jamaican reefs subjected to differing levels of fishing effort. Cuellar *et al.* (1996) identified a decline in mean length over time in an exploited population of the snapper *Rhomboplites aurorubens*, in the southeast USA. A compensatory decline in the length at maturity was also identified. Ralston and Kawamoto (1988) found a substantial difference in the modal size of *P. filamentosus* between areas of high and low fishing pressure in Hawaii. Langi and Langi (1989) also related size reductions in *P. filamentosus* to fishing pressure through spatial data from the Tongan seamounts, although MRAG (1994) found no evidence of this from time series data.

While a number of studies have identified changes in catch length structure, studies of the effects of fishing on age structure are limited. The removal of larger individuals due to gear selectivity may result in 'juvenescence' (Ricker, 1963). This is the successive elimination of older, more fecund size classes, and will result in a decrease in mean age. From the limited studies of exploited age structures, the results have been somewhat equivocal. Ralston and Kawamoto (1985) demonstrated that a decrease in the age of entry of *P. filamentosus* to the fishery in Hawaii from 4 yrs to 1.8 yrs was related to an increase in fishing mortality. However, Russ *et al.* (1995) showed no significant differences in the size or age structure of the coral trout *Plectropomus leopardus* within and outside closed areas of the Great Barrier Reef. This was attributed to the short duration of the closure (3 to 4 years) relative to the longevity of the species (14+ years). The lack of studies investigating the effects of fishing on the age structure of exploited tropical fish populations may be a result of the perceived or real difficulties in ageing tropical species (Russ, 1991). This indicates a gap in the knowledge of the effects of fishing on tropical fish populations.

1.4.2 Effects on growth

Two mechanisms have been suggested through which fishing can affect growth. The first hypothesis suggests that, over time, fishing has an effect on the genetic structure of an exploited population. The second mechanism is based on the release of competitive influences on growth through the removal of individuals by fishing.

Parma and Deriso (1990) postulated that due to differences in growth rates between individuals, (which have some genetic basis) fishing will selectively remove larger (and in theory, faster growing) individuals. Selection against faster growing individuals would result in a fished population containing a larger proportion of slower growing fish (Backiel and LeCren, 1978; Favro *et al.*, 1979; Laevastu, 1992). Zhao *et al.* (1997) found such a temporal decrease in size-at-age in a fished population of the vermillion snapper *R. aurorubens*. Through simulation, however, Martinez-Garmendia (1998) implied that while evolutionary changes in growth may occur, the impacts of these changes may be modest. Such changes were likely to be overshadowed by other density dependent responses.

Gulland (1983) hypothesised how the von Bertalanffy growth parameters L_∞ and K would vary with stock density, and hence with fishing pressure. Such 'density dependent growth' is thought to arise due to competition either between individuals of the same species (intraspecific competition), or between species (interspecific competition). Since growth is critically dependent on food supply, competition for food resources leads to a reduction in individual growth, compared to the growth of a single isolated individual able to command the same food supply. The removal of individuals through fishing would result in a decline in population density (biomass or numbers), leading to an increase in the growth rate of remaining individuals. As a result, size-at-age would increase, the opposite effect to that suggested by Parma and Deriso (1990). For competition to become important, therefore, density must reach the level at which the amount of food available is insufficient to allow growth at the maximum rate.

Fishing has been shown to reduce the biomass of lutjanids and lethrinids (Russ, 1985; Polunin and Roberts, 1993; Jennings *et al.*, 1996). A detectable decrease in abundance can occur over a short time. Russ and Alcala (1989) showed that the initiation of fishing on a previously unfished reef in the central Philippines resulted in a 94% decrease in the density of lutjanids and lethrinids after 18 months. In the Marianas, Polovina (1986) estimated a 48% reduction in lutjanid abundance after only 13 days of heavy fishing. Declines in abundance can also be detected through declines in the level of the catch per unit effort (CPUE; *e.g.* Munro, 1983). The potential for increased growth rate through density dependence therefore exists in these species.

Competition has been identified within and between cohorts in tropical fish species. Changes in competitive intensity among individuals of different sizes has a large effect on the variance in growth rates, and therefore on the size structure of populations (Doherty, 1982; Doherty, 1983; Polovina, 1986; Jones, 1987a). Where competition for food arises, larger more aggressive individuals are likely to grow at a faster rate than subordinates (Weatherly and Gill, 1987). A reduction in the growth rate of juvenile stages due to increased density (possibly during good recruitment years) may lead to juveniles growing through a vulnerable size range over a longer period, increasing the risk of mortality, and reducing the number of juveniles reaching maturity (Jones, 1991).

Several authors have shown that the state of development of the fishery (either a virgin resource, or an established resource at equilibrium) can significantly affect the overall growth of fish (*e.g.* Filipsson, 1989; Ross and Nelson, 1992). Commonly, these have been temperate freshwater species in enclosed experimental systems (*e.g.* Barlow, 1992) and environments such as fish culture ponds and lakes (*e.g.* Le Cren, 1958; Bowen *et al.*, 1990; Klein, 1992; Lorenzen, 1996; Salvanes and Balino, 1998). In culture-based fisheries, the manipulation of population density and nutrients in the environment, and hence growth, are the basis of maximising yield.

Studies in marine ecosystems have shown that density dependent growth also operates in this larger environment. For example, density dependent growth relationships have been identified in plaice (*Pleuronectes platessa*) and haddock (*Melanogrammus aeglefinus*) in the North Sea (Beverton and Holt, 1957); in silver hake (*Merluccius bilinearis*), haddock and yellowtail flounder (*Pleuronectes ferrugineus*) in the Northern Georges Bank-Gulf of Maine (Ross and Almeida, 1986; Ross and Nelson, 1992; Helser and Alimeida, 1997), in juvenile Atlantic Salmon (*Scomber scombrus*) in the northwest Atlantic (Overholtz, 1989) and in juvenile Atlantic Herring (*Clupea harrengus*) in Maine (Anthony, 1971).

Density dependent growth has also been identified in tropical marine fish species (*e.g.* Doherty, 1982; Jones, 1984a, 1987a, 1987c). Jones (1991) stated that "the effect [of density dependent growth] may be large enough to have a major impact on the structure of reef fish populations". Booth (1995) observed a reduced growth rate in large groups of damselfish (*Dascyllus albisella*) compared with that in smaller groups. Munro (1983b) indicated that snappers (Lutjanidae) must compete both amongst themselves and with other species for food and space. This suggests that a reduction in the level of competition would lead to an increase in growth rate at certain biomass levels, although Parrish (1987) stated that the diversity of potential prey might reduce the impact of competition among snappers.

The effects of fishing on the growth of snappers and emperors, and in particular the three species to be studied, has not been reported. Although density dependent growth may occur, a lack of accuracy and precision in growth and abundance assessments may mask any relationship (Backiel and Le Cren, 1978). Current growth estimates for these species are derived through length-based methods, which are not considered sufficiently accurate to identify changes in growth resulting from the effects of fishing (MRAG, 1996b). The use of otoliths and other hard parts for ageing may go some way to rectify this problem.

The study of population age structure and growth rate are important in the assessment of the potential productivity of exploited fish stocks (Rowling and Reid, 1992). The biology of a species, including its growth rate, determines the way in which individuals and populations are affected by fishing. An understanding of the effects of fishing on a species is therefore vital for the appropriate monitoring of exploited stocks, and the incorporation of fishery induced changes into stock assessment criteria and methods.

The effects of fishing on length and age structure, or changes in growth rate due to density dependence, will also have direct effects on growth estimates derived using either length- or age-based methods. A background to growth estimation methods is provided in the next section.

1.5 ASSESSMENT OF AGE AND GROWTH

Growth parameters can be determined through a number of methods (as defined by Morales-Nin, 1992):

- *Anatomical method*: the counting of regular growth marks formed in hard tissues;
- *Length-frequency analysis*: studying the progression of identifiable modal size classes through time;
- *Direct estimate*: extrapolating direct measurements of growth rate from individual specimens to the stock as a whole. For example, this can be achieved through mark and recapture studies or direct monitoring of the growth of captive fish of known age.

The ‘direct estimate’ method is frequently open to ‘tagging artefacts’ (Brothers, 1982), where the stress of the tagging event subsequently causes a period of reduced growth. For the current study, this method was not feasible due to the limited time available, the depths inhabited by the study species, and the general failure of tagging studies on related species (Parker, 1990b), due to evisceration and high subsequent mortality (DeMartini *et al.*, 1996). The ‘anatomical method’ and ‘length frequency analysis’ were therefore employed.

1.5.1 Anatomical method

The anatomical method involves counting regularly formed marks on hard tissues (Manooch, 1987). Such growth units are simple structures composed of protein-rich and protein-poor layers embedded in a calcium carbonate (aragonite) crystal lattice, forming a bipartite structure composed of discontinuous and continuous zones. These are thought to relate to regular/seasonal changes in the environment or biology of the fish.

Anatomical ageing methods were first used in 1759, when vertebrae were used to age a number of species, including eels and pike (Henderstrom, 1959). Vertebrae have since been used to age a number of species (*e.g.* Edwards, 1985; Liu and Yeh, 1991). Scales have been used for ageing since 1898 (*e.g.* Van Oosten, 1923, 1929; Carlander, 1987). However, scales are frequently difficult to read, and may underestimate ages (Beamish and McFarlane, 1987). They are subject to reabsorption during periods of starvation and stress (Mugiya and Watabe, 1977), and are commonly lost and regenerated during the life of a fish (Thompson and Munro, 1983b). As a result, scales have seldom been used successfully to age adult snappers and emperors (Manooch, 1987) Other hard tissues, such as urohial bones (Espinosa and Pozo, 1982) and spines (Edwards, 1985), have also been used for ageing. For snappers and emperors, however, the most common hard part used for ageing is the otolith. These structures have been used since Reibisch identified annual ring formation in Plaice (*Pleuronectes platessa*) in 1899 (reported in Ricker, 1975).

Otoliths are structures in the membranous labyrinth of the inner ear of fish which respond to linear acceleration and tilting (Gauldie, 1988), and integrate auditory and vestibular stimuli

(Radtke and Shafer, 1992). Of the three otoliths present, the largest (sagitta) is usually employed in ageing assessments (Bach, 1989).

The use of both whole or sectioned otoliths for ageing fish is now a common research tool in the study and stock assessment of temperate fish species (Gulland, 1983). Until relatively recently, however, they had not been employed on a large scale for tropical species. This was related to two factors. Fisheries in tropical regions are frequently less developed when compared to their temperate counterparts, attracting a lower research effort. Perhaps more importantly, there has been a historical perception that the tropical marine environment was relatively constant. Fish were assumed to respond to this by growing and spawning continuously throughout the year. Hence, they were thought to lack 'growth checks' from which an incremental otolith structure would arise (Fowler, 1995).

The discovery of daily increments in otoliths of tropical fish by Panella (1971) altered this perception. The existence of daily rings has since been confirmed in a number of tropical species (Panella, 1974; Brothers *et al.*, 1976; Brothers and Mathews, 1987; Morales-Nin, 1989). The study of otolith microstructure requires either a powerful light microscope or Scanning Electron Microscopy (SEM). SEM has been recognised as a successful technique for ageing both larval, juvenile and adult fish (Brothers and McFarland, 1981; Ralston and Miyamoto, 1981; Brouard and Grandperrin, 1984; Radtke, 1987; Smith and Kostlan, 1991; Bach and Chauvelon, 1994). However, the method is generally confined to areas of the otolith corresponding to faster-growing juveniles; decreased growth rates in older individuals result in closely spaced or merged daily bands that cannot be separated (Manooch, 1987). Although the time spent exhaustively counting individual daily rings can be reduced by certain techniques (Ralston and Miyamoto, 1981; Ralston and Miyamoto, 1983; Ralston and Williams, 1988a; Smith and Kostlan, 1991; Williams and Lowe, 1997), the costs in both equipment (*e.g.* SEM) and time involved in this method are potentially prohibitive both for long term assessment programmes and for developing countries. The use of annual rings offer the only real method for ageing large numbers of relatively long lived fish, and thus offers the best basis for stock assessment and management.

Increased confidence in the use of tropical otoliths for ageing purposes led to a number of studies assessing annual rings (Lou, 1992; Newman, 1995; Williams *et al.*, 1995; Fowler, 1995). Loubens (1978) investigated the legibility of annual rings using low power light microscopy in a number of families of tropical species, including Lutjanidae and Lethrinidae. Annual rings have since been identified in a number of snappers, groupers and emperors (Loubens, 1980; Mason and Manooch, 1985; Manooch, 1982; Manooch and Drennon, 1987; Morales-Nin, 1988; Moralez-Nin and Ralston, 1990; Ferreira and Russ, 1992; Francis *et al.*, 1992; Sadovy *et al.*, 1992; Rocha-Olivares and Gomez-Munoz, 1993; Milton *et al.*, 1995; Manickchand-Heileman and Philipp, 1996); see also Manooch (1987) and Fowler (1995) for reviews).

Few studies have examined otoliths from snappers and emperors at the low latitudes examined in the current study. In Seychelles, preliminary studies were performed by SFA in the early nineteen nineties to examine the potential for using otoliths to age common snapper and emperor species. Examinations indicated that structures and patterns similar to those observed in temperate water fish were present. However, sample sizes examined were too small to allow validation (Bedford, *pers com.*, results reported in Mees, 1992). An otolithometry unit was established at SFA in 1992. Subsequent studies, which used a number of sectioning techniques for several species, failed to indicate consistent growth rings which could be related to annual or seasonal events. It was concluded that whilst rings were evident in about 75% of otoliths studied, they lacked homogeneity, and the precision of results was low. These techniques were considered inadequate for ageing Seychelles species (Orts, pers com). However, the study was not performed by an expert in the field, an there was some criticism of the sections studied (MRAG, 1996b).

During the FMSP project R2584, further investigations were undertaken, Otoliths of *P. filamentosus* were sent to the Centre for Tropical Coastal Management studies at Newcastle, UK, as the basis for a BSc study. In contrast to previous examinations, this study identified evidence of clear annual-type banding, together with what appeared to be strong monthly bands (Hardman-Mountford *et al.*, 1997). However, the sample size was very small, and establishing the time scale proved difficult. These studies indicate that banding does occur in otoliths from Seychelles demersal species. However, the question of whether otoliths of snapper and emperor species in these locations can be used for ageing was not answered conclusively. The interpretation of growth rings in otoliths of these species is clearly not straightforward, and needs to be performed by experts in the field with considerable experience with which to interpret their observations. Such examinations are to be undertaken in the current study.

1.5.2 Length Frequency Analysis

When compared to direct assessment of growth using hard tissues, length-based methods have a number of advantages (Pauly, 1987);

- sampling is generally cheaper than that for age-based methods, since this method does not require fish to be purchased for data collection;
- direct ageing methods are labour intensive. Large amounts of data for length-based methods can be collected in a short time;
- ageing methods require experienced trained personnel to perform the work. The skills and training necessary for collecting length frequency data are minimal;
- large amounts of historical length frequency data are commonly available;
- a number of models are size rather than age related (*e.g.* food conversion efficiency (Pauly, 1981), gear selection (*e.g.* Hamley, 1975; Pope *et al.*, 1975), recruitment to fishing grounds (Pauly and Morgan, 1987), maturity (Gulland, 1987) and marketability and price).

Given these points, length-based methods have become common in all types of fisheries, including those for snappers and emperors.

1.5.2.1 Basis for length-based methods of growth assessment

Length-based methods of growth assessment are based on the theoretical ability to relate modes in length frequency distributions to cohorts. Hence, methods assume no large variations in individual growth rate, or in recruitment (Gulland, 1987). Based on this assumption, a growth curve can be fitted to modes in a single length frequency distribution, or to modes tracked through a time series of length frequency data.

The majority of work has used the growth curve developed by von Bertalanffy (1934). This takes the form:

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

where	L_∞	'asymptotic maximum length' of the fish (the maximum length a fish could theoretically achieve)
	K	growth rate of the fish
	t_0	theoretical age at which a fish has zero length

If the assumption of limited individual growth rate and recruitment variation holds, growth can be described by a single set of von Bertalanffy growth parameters which best describes the pattern of modes in the length frequency data.

One of the first uses of length frequency based methods was by Petersen (Petersen, 1891; Petersen, 1892) on length data for the eel-pout *Zoarces viviparus*. Using a single length frequency distribution, different relative ages were attributed to individuals comprising prominent modes in the sample. Subsequently, methods of assessment progressed to graphical (*e.g.* Harding, 1949), and then to computer-based methods (*e.g.* Hasselblad, 1966). Increases in computer processing power allowed the estimation of parameters using more complex models (*e.g.* the parametric models of Sparre (1987) and Pope (1987)).

As defined in Majkowski *et al.* (1987), there are two general groups of von Bertalanffy growth parameter estimation methods using length frequency data: 'parametric' and 'non-parametric' methods.

1.5.2.2 Parametric methods

Parametric methods such as MIX (MacDonald and Pitcher, 1979), require information on the shape of modes in length frequency data. Early methods assumed that age class peaks could be approximated through normal distributions (*e.g.* Bhattacharya, 1967), converting length frequency distributions into a series of age frequency distributions. More complex parametric models are no longer constrained by this assumption, which a number of studies found to be invalid (*e.g.* Morgan, 1987).

Improvements to parametric techniques have been devised (*e.g.* Schnute and Fournier, 1980; Sparre, 1987; Pope, 1987). For example, samples can be weighted using catch per unit effort data, and related to the von Bertalanffy growth function. If mortality rate and initial cohort strength are assumed, the likely position and relative strength of each cohort in subsequent samples can be calculated. Expected and observed frequencies are then compared statistically. A large number of assumptions are required for these improvements and, in turn, a large number of parameters must be estimated.

A more feasible approach is represented by the computer program MULTIFAN (Fournier *et al.*, 1990). This method assesses growth through the analysis of multiple length frequency data sets, using a maximum likelihood estimation procedure. By using a number of length frequency distributions to produce global parameter estimates, the number of significant age classes that can be resolved (and, hence, analysis sensitivity) is increased. The model again assumes that lengths in each age class can be described by normal distributions. However, the method is robust to limited deviations from the models hypothesis of where and how individuals should be distributed in the length frequency data.

Parametric methods have not reached the prominence of non-parametric methods in tropical fisheries. In part, this may be a result of the data intensive nature of these methods. Alternatively, it may represent a lack of availability; methods such as ELEFAN (see below) have been incorporated into a number of stock assessment computer packages, including FiSAT (Gayanillo *et al.*, 1994) and LFDA (Holden *et al.*, 1995). These packages are readily available to tropical fisheries institutions, and are capable of running on relatively basic computer equipment.

1.5.2.3 Non-parametric methods

Non-parametric methods, such as the Electronic LEngth Frequency ANalysis (ELEFAN, Pauly and David, 1981; Pauly, 1987) use the number and positions of peaks in a single or series of length frequencies to estimate growth. Growth curves, derived through a specified growth model and using growth parameter sets selected from a specified range, are fitted. The coincidence between observed and expected modes in length frequency distribution(s) is used to indicate the suitability of that growth parameter set.

Throughout this report, the 'Length Frequency Data Analysis' package (LFDA; (Holden *et al.*, 1995) is used. This package incorporates three non-parametric length-based methods of growth assessment; Shepherd's Length Composition Analysis ('SLCA'; Shepherd, 1987a), PROJection MATrix Method (‘Projmat’; Rosenberg *et al.*, 1986; Basson *et al.*, 1988), and ELEFAN (Pauly and David, 1980; Pauly, 1987; Brey *et al.*, 1988). Basic descriptions of the methods are presented below.

Shepherd’s length composition analysis (SLCA)

This method estimates the best-fitting L_∞ and K parameter set by maximising a goodness-of-fit function. This function, which is based on a sine wave, is positive at predicted modal lengths, and negative at predicted inter-modal lengths. To score the fit, a correlation coefficient between the data and test function is calculated; test function values for each length class are weighted by the square root of the number of individuals present in that length class, and summed across all examined length classes. Growth parameters which best describe the length distribution therefore maximise the resulting score function.

Projection matrix method (PROJMAT)

PROJMAT uses a modification of a method originally used to forecast catch at length by projecting length compositions forward in time (Shepherd, 1987b). In this method, a ‘projection matrix’ is derived to project length classes through time, using a given set of growth parameters and growth equation.

This method requires more than one length frequency distribution. An initial distribution is projected forward to the time of the second distribution, based on the growth parameters and matrix. The resultant frequency distribution is then be compared to the true sampled distribution, through an unweighted least-squares score function. The most appropriate growth parameters therefore provide the best fit between observed and expected distributions.

Electronic length frequency analysis (ELEFAN)

To assess the fit of growth parameters, ELEFAN first restructures the length distribution. This restructuring, using a ‘moving average frequency’ (Pauly, 1987), denotes peaks (above the moving average) and troughs (below the moving average) in the distribution. Peaks receive a positive value, while troughs are assigned a negative value. A growth curve is then derived, based on a selected set of L_∞ and K values, and compared to the restructured length distribution. That growth curve is then scored by summing the restructured values for each length class the growth curve passes through (‘explained sum of peaks’; ESP). Hence, it is a function of the proportion of available peaks hit and troughs avoided by that curve. The ‘available sum of peaks’ (ASP) for the distribution represents the maximum score which could be obtained by a single growth curve, being the sum of maximum restructured values for each peak. The ratio ESP/ASP is then maximised by varying the growth parameter set, to identify the best fitting growth parameters.

Fitting growth curves within LFDA

The following explanation is taken from the LFDA manual (Holden *et al.*, 1995). Each of the growth parameter estimation methods described above allow the calculation of a score function. When assessing growth, this score is calculated for a user-specified number of equally-spaced values of L_∞ and K, within specified ranges. A table of the scores resulting from this ‘grid search’ identifies peaks in the score function within that range.

Precise identification of the L_∞ and K values that correspond to identified local maxima in the score function can then be achieved using a numerical maximisation procedure. This is based on the ‘Amoeba’ simplex method described in Press *et al.* (1986). In essence, this maximisation procedure works by starting at a specified point, and then trying to move away from that point in an ‘uphill’ direction on the score function surface. Once a point is identified for which heading away from it in any direction means going ‘downhill’, this point is taken to be the local maximum. This process is repeated from five points within the selected area. The maximum point is then overlaid on a two-dimensional contour plot of the score function.

It is then up to the user to identify whether maximisation has been successful, and that this maximum represents the L_∞ and K combination which fits the data most appropriately.

1.5.2.4 Estimation of growth in tropical species

As described in previous text, otoliths have been used to age an increasing number of tropical species. However, in the study locations, and for many other tropical locations, growth assessments are performed using non-parametric length-based methods (*e.g.* Posada and Appledorn, 1996).

Such assessments are suitable where there is evidence of discrete modes in the length data (Shepherd *et al.*, 1987; Gulland and Rosenberg, 1992). Such modes are favoured where growth is rapid (generally correlating with a short lifespan), and spawning season is restricted (MacDonald, 1987). In such cases, length-based methods have been used with great success.

As a result of these factors, the methods are considered to have limited applicability for long-lived, slow growing species (Mees and Rousseau, 1997). The biology of such species results in the superimposition of successive modal classes, reducing the information available with which to estimate growth parameters. Furthermore, modes in the data, which are assumed to represent individual cohorts, may actually represent a number of age-classes.

Langi (1990) noted difficulties in deriving growth parameter estimates using ELEFAN for three species of deepwater snapper, including *P. filamentosus*. Reservations over the use of length-based methods for assessing growth in slow growing individuals were also expressed by MRAG (1996b). In that study, there was no evidence of modal progression in any of the length data collected from a number of tropical reef species in Seychelles. On analysis, length-based methods indicated a number of possible parameter combinations were valid, resulting in considerable uncertainty over the growth estimates.

Although a number of simulation studies have examined the accuracy of length-based growth parameter estimates (*e.g.* Hampton and Majkowski, 1987; Rosenberg and Beddington, 1987; Basson *et al.*, 1988; Isaac, 1990), these studies have generally concentrated on data for relatively fast growing species, for which these methods are considered more appropriate. Such studies have not been performed explicitly for slow growing species. Furthermore, such studies have examined the impacts on growth parameter estimates alone. Given the potential for uncertainty in growth parameters to be transferred into further parameter estimates, and hence stock assessments and management, it is prudent to examine this potential ‘knock-on’ effect. Such studies are of particular interest for snappers and emperors, given that length-based growth estimates are generally used for such species, and that fisheries based upon them require accurate management to remain sustainable.

1.6 REPORT STRUCTURE

To answer the questions posed in this chapter, both theoretical (simulations) and field work studies were undertaken. Before practical studies could be undertaken, increments seen in the otoliths of the study species needed to be validated. This process is described in Chapter 2. To render the individual-based simulations performed in these studies realistic, a measure of individual variability in growth was required. The methods used to estimate this level are presented in Chapter 3.

The work performed in Chapters 2 and 3 allowed the remaining studies to be undertaken; the examination of the effects of fishing, and the resultant effects on the outputs of growth parameter estimation methods. Methods common to a number of these chapters, including the derivation of three models for density dependent growth, and the methods used to estimate growth parameters, are presented in Chapter 4.

In Chapter 5, the effects of the three models of density dependent growth on the yield-effort curves of the study species are examined. One model is then selected for use in further simulations examining the direct and indirect effects of fishing on the catch length structure. In Chapter 6, comparisons of length data between and within the study fisheries are presented, with the aim of identifying whether trends indicated in Chapter 5 are found in actual fisheries data. Using otoliths validated in Chapter 2, age data are also examined both to identify trends in the catch age structure between locations subjected to different levels of fishing pressure, and for evidence of density dependent growth.

While a significant amount of literature is available on the accuracy and precision of length-based growth estimates, this has not been related specifically to long-lived, slow-growing species. Through the simulations described in Chapter 7, the accuracy and precision of length-based and age-based growth parameter estimation methods is examined for such species, using Monte-Carlo methods. The effects of fishing, including density dependent growth, on the growth parameter estimates are examined. In turn, outputs of these growth assessments are used to assess further biological and fisheries parameters. In Chapter 8, these outputs are used within management strategy simulations. These simulations examined the effect on management performance of uncertainty in growth parameter inputs to the management process, and the indirect effects of density dependent growth for an $F_{0.1}$ management strategy. Management performance was assessed against conservation measures and fleet performance.

In Chapter 9, the application of both length-based and age-based growth estimation methods to actual length and age data from the study locations is described. This examines whether trends identified in the previous chapters hold in actual fisheries data. In this chapter, the first age-based estimates of growth and mortality are derived for the study species. Mortality estimates are also derived using age frequency distributions derived directly from otolith assessments, and through the use of age-length keys. The feasibility of using otolith weight to assess age and mortality is also examined. This method has significant benefits for relatively poor fisheries institutions. Using derived estimates, the status of the study fisheries is examined.

It is frequently stated that age-based growth assessment methods are more expensive (in both time and effort) than length-based methods. However, the potential advantages of age-based methods may outweigh these additional costs. To examine this, a cost-benefit analysis is performed for each growth assessment method. This is described in Chapter 10. Costs involved in each growth estimation methodology are described, and compared with benefits obtained, in terms of increased sustainable revenue from the fishery.

The outputs of these studies combined to answer the questions posed in Section 1.1. These, and the guidelines for stock assessment and management arising from these results have been presented in the Final Technical Report.

It should be noted that, since data continued to be collected throughout the study, some of the analyses described in the earlier chapters could not be conducted on the full dataset.

2. Validation of the increments seen in the otoliths of the study species

2.1 INTRODUCTION

Examination of sectioned hard tissues, such as otoliths, frequently reveals the presence of ‘rings’. Laid down incrementally (whether daily, monthly or annually), these structures provide a means of ageing fish.

The physiological basis for the formation of distinct zones in the calcified structures of tropical species has not yet been established conclusively (Ferreira and Russ, 1994). They have commonly been associated with abiotic (*e.g.* regular seasonal variations in water temperature or photoperiod) and biotic (*e.g.* feeding, reproduction, or spawning period) factors (*e.g.* Reay, 1972; Panella, 1980; Morales-Nin and Ralston, 1990; Beckman and Wilson, 1995).

‘Indeterminate increments’ (increments not related to a regular time scale) are found in all hard tissues. These need to be distinguished from increments formed at regular intervals (Fowler and Doherty, 1992). Before increments can realistically be used for ageing, they need to be ‘validated’ to ensure that structures, such as the otoliths used in this study, can be used as accurate chronometers (Beamish and McFarlane, 1983). They must therefore fulfill a number of criteria (Fowler and Doherty, 1992);

- the otolith must grow throughout the lifespan of individual fish;
- the otolith must show an internal structure of increments; and
- this structure must correspond to a regular time scale.

Local fisheries institutions at each of the study locations are, to date, limited to the use of length-based growth assessment methods. Estimates from such methods are considered potentially biased when applied to long-lived, slow-growing species such as snappers and emperors, owing to modal overlap and a general absence of modal progression (*e.g.* Langi, 1990). The work described in this study aimed to validate the increments seen in the otoliths of the three study species, so that age-based methods of assessment could be applied to these commercially important species.

The study was divided into two phases. The first phase was undertaken by otolith experts at the Centre for Environment, Fisheries and Aquaculture Science (CEFAS). Based on the results of that study, the second phase was undertaken by the researcher, with the assistance of CEFAS staff.

The initial (phase 1) study examined historical otolith collections from a number of lutjanid and lethrinid species caught in Seychelles, and of *L. mahsena* from Mauritius. Otoliths were examined to assess the clarity of the increment structure and consistency of ‘age’ assessments, the latter through between-reader count comparisons. Additionally, the most suitable technique for preparing otoliths was determined.

Based on the results of the phase 1 study, and the species’ commercial importance, three species were selected for further study. In the second phase of the study, validation of the increments seen in the otoliths of these species was attempted.

The study concentrated on macro-increments (annuli). Ageing through micro- (daily) increment counts, such as performed in Hawaii for *P. filamentosus* (Ralston and Miyamoto, 1983) requires considerable investment in time and equipment, and is generally constrained to younger ages, where daily increments remain distinct. Ageing through annuli, using low-power light microscopes, remains the most practical and convenient way for ageing large numbers of relatively long-lived fish, and hence the best basis for stock assessment and management (Fowler, 1995).

2.2 PHASE 1

2.2.1 Methodology

The initial study aimed to investigate the legibility and consistency of rings seen in the otoliths of a number of snapper and emperor species, and their potential suitability for use as tools in ageing studies. Due to their experience in the field of otolithometry, CEFAS were retained to perform this initial study on a historical collection of otoliths donated by Seychelles Fishing Authority (SFA). This historical collection comprised samples from the following species;

the Lutjanidae	*Pristipomoides filamentosus*,
	Aprion virescens,
	Aphareus rutilans,
	Lutjanus bohar,
and the Lethrinidae	*Lethrinus variegatus*,
	Lethrinus crocineus.

Since there was no historical collection of *L. mahsena* otoliths available, a monthly port sampling regime was undertaken by Albion Fisheries Research Centre (AFRC) in Mauritius. The fishery on the Mauritian banks is seasonal, with vessels being constrained in their fishing activities on the more southerly banks by changes in the weather systems during certain months of the year. The first two month's samples (July and August) were obtained from St. Brandon. Subsequent monthly samples were obtained from Nazareth bank, as vessels were forced further north due to bad weather and declining catch rates. Otoliths were sent to CEFAS for sectioning and were examined by the researcher, with the assistance of the CEFAS staff.

A number of methods were utilised during the preliminary examination. These methods, and the results arising from them, are now detailed.

2.2.1.1 Examination of the whole otolith

Otoliths were immersed in water in a black cavity block, and examined under reflected light using a Leica MZ6 light microscope. Faint ring patterns were visible, but the ring structure could not be determined in all areas of the otolith. It was felt that this method would lead to the underestimation of age in older specimens, and was therefore rejected (see also (Rocha-Olivares and Gomez-Munoz, 1993; Ferriera and Russ, 1994).

2.2.1.2 Breaking and burning

One otolith from each pair was broken transversely through the centre, and the exposed surface heated in a flame from a spirit burner. For temperate species, this process enhances the appearance of the ring structure, since proteinaceous rings carbonise more readily than other areas of the otolith. A slight improvement in ring contrast was seen in Seychelles specimens. However, the improvement was insufficient to persevere with the method. The rings in otoliths of *L. mahsena* from Mauritius were enhanced through this method. This indicated that staining might have a more consistent clarifying effect.

2.2.1.3 Viewing thin sections

One otolith from each fish was embedded in black polyester resin, and two 0.5mm transverse sections taken through the centre (‘nucleus’) of the otolith using a diamond cutting blade (Bedford, 1983). One section was mounted on a microscope slide in clear resin, and the second was stained using acidified neutral red (Richter, 1990). Otoliths were examined using a Zeiss optical microscope with zoom lens and up to x60 magnification. Both reflected and transmitted light were used to identify and count increments.

The clearest pattern of rings in the Seychelles samples was evident in sections mounted in clear resin using transmitted light. In *L. mahsena* from Mauritius, staining proved the best method for clarifying the ring structure, with a discrete band stained in the otolith. Although the clarity of the staining effect in *L. mahsena* was variable, an overall improvement in mark legibility was seen. The type of growth found at the tip of the large lobe of the otolith - the fastest growing area for the majority of the ages studied, and hence the area in which a growth zone would first develop - was more easily identified. Appropriate sections were mounted in clear resin, and a detailed examination of the ring pattern undertaken.

2.2.1.4 Ring counts

Each otolith was examined independently up to three times by two experienced readers. The same section was then aged by the readers working together on two separate occasions.

2.2.2 Results

A pattern of opaque and transparent rings were evident in all species, although the contrast between bands varied considerably both within and between species. Rings were more widely spaced closer to the nucleus, becoming narrower and more even toward the edge. Such a pattern is typical of annual rings, reflecting the expected decrease in growth rate as a fish aged.

In all species, rings could not be traced completely around the otolith section. Counts were therefore made in a number of limited zones within the otolith. Such zones were usually consistent within species. For example, in *P. filamentosus* otoliths, rings were most easily counted running beside the groove of the *sulcus acousticus*. The number of ring counts generally increased with fish length.

The consistency of ring counts between readers was best for *Aprion virescens* (44% of readings were in agreement, 76% within one ring). Ring counts for *Pristipomoides filamentosus* and *L. crocineus* produced similar results (61% within one ring, 80% within two rings). The remaining species were more difficult to read, and ages were less consistent. For *A. virescens* and *P. filamentosus*, the variation in counts within reader were also reasonable, with readings in agreement in approximately 50% of the examinations (CEFAS, 1997a). For *L. mahsena*, age estimates from 49 stained sections read using reflected light were compared with their corresponding unstained sections read using transmitted light, to ensure comparability between methods. Excellent agreement was obtained between the two methods, with identical ages in 76% of cases, and ages within one year in 94% of cases.

Interpreting the position of the first growth ring was difficult. Due to the extended spawning period found in these species (Mees, 1993), the amount of growth occurring before the first ring was laid down would vary in individuals spawned at different times of the year.

Problems were also experienced in interpreting the type of new growth at the otolith edge in samples from Seychelles. Readers could not be certain whether the current years’ growth had commenced, and therefore whether an additional year should be added to the age. This would lead to bias in ageing the unstained sections, with fish being under or over aged in relatively equal numbers.

Based on the results of the initial study, the likely availability of specimens from port collections, and the commercial value of each species, the lutjanid species *Aprion virescens* and *Pristipomoides filamentosus* were chosen for further study alongside *L. mahsena*. The second phase of the study was then initiated to attempt to validate the periodicity of the increments seen in the otoliths of the three species from the study locations.

2.3 PHASE 2

2.3.1 Methodology

Otoliths of the study species were obtained from commercial fish catches through both port collections and observer programmes. *L. mahsena* samples were obtained from the Mauritian mothership-dory ventures fishing on the Mauritian banks (Nazareth, Saya south, Saya north) and BIOT (Chagos Archipelago), and from port collections in Seychelles. For *A. virescens* and *P. filamentosus*, samples were obtained from both Seychelles and BIOT (Chagos Archipelago).

Sagittal otoliths were selected for validation, since a number of studies have successfully used these structures to age snapper and emperor species elsewhere (*e.g.* Manooch, 1982; McPherson and Squire, 1992; Morales-Nin, 1989; Newman *et al.*, 1996; see also Appendix 1), including *A. virescens* and *P. filamentosus* (Loubens, 1980; Ralston and Miyamoto, 1981; 1983). However, the work of Ralston and Miyamoto on *P. filamentosus* concentrated on daily rings, which are unsuitable for routine ageing in tropical countries. Studies which have examined annual rings in *P. filamentosus* (*e.g.* Hardman-Mountford *et al.*, 1997) have achieved equivocal validation. Doubt remains over the existence of annual rings in this species. The extent of validation of *A. virescens* otoliths by Loubens in New Caledonia was unclear (Appendix 1). However, even if validation had been successful in New Caledonia, it cannot be used as a justification to assume validation in the current study locations. Despite the work performed on these species in other locations, validation was still required.

Two methods were used to determine whether otoliths fulfilled the three requirements for ageing; a) back-calculation of growth using otolith increments; and b) marginal increment analysis and edge analysis. A general description of the methodologies are provided in Blacker (1974) and Williams and Bedford (1974).

The initial study by CEFAS indicated that thin otolith sections resulted in the most consistent readings (CEFAS, 1997a). Otoliths were therefore prepared as described in Section 2.2.1.3.

In this study, terminology is based on that recommended in Secor *et al.* (1995). The term ‘opaque zone’ refers to the area within a suspected annual increment which appeared milky under reflected light, or dark under transmitted light in unstained samples. The accompanying zone, with the opposite optical qualities, was termed the ‘translucent zone’. Opaque zone deposition is thought to occur during periods of increased growth, while the corresponding translucent zone is formed during periods of low metabolic activity (Beckman and Wilson, 1995). In sections prepared with neutral red, a band was stained on the border between the end of the translucent zone and the start of the next opaque zone.

Initial validation studies were undertaken using commercial samples of *A. virescens* and *P. filamentosus* from Seychelles, and *L. mahsena* from Nazareth bank. The subsequent text describes the validation techniques employed on these samples. These techniques were subsequently used for samples from the other locations, as and when they became available.

Preliminary studies were undertaken by CEFAS, examining the microstructure of *P. filamentosus* and *A. virescens* otoliths (CEFAS, 1997b). A number of studies have validated ageing by relating the microincrements seen under SEM with the pattern of annual rings seen under the optical microscope. In most studies, the microincrements are assumed to be daily increments and annula increments counts validated by counting approximately 200-360 increments within each opaque and translucent band (Brothers and Mathews, 1987; Radtke, 1987; Morales-Nin, 1989). This study was limited in scope, and hence is not described in detail in this section. The results described in CEFAS (1997b) are discussed in Section 2.4.

2.3.1.1 Back-calculation of growth using otolith increments

For back-calculation, snapper otoliths were most easily assessed unstained, while *L. mahsena* otoliths were assessed stained. Only otoliths which showed clear ring patterns were used for measurements. As a result, seven *A. virescens* otoliths, in which it was difficult to distinguish the first or second ring, were omitted from the samples. Measurements of total otolith radius, from nucleus to outside edge, and the distance along the selected growth axis between suspected annual increments were made using the tools described in Millner and Whiting (1996). After mounting the sample on an optical microscope, images of the sections were displayed on a colour monitor. The distance along the selected growth axis between suspected annual increments was then measured using a digitiser pad and 'VIDS' software (see Millner and Whiting, 1996).

Unstained *P. filamentosus* and *A. virescens* otoliths were assessed along a growth axis close to the *sulcus acusticus* (see Figures 2.1 and 2.2), this area providing the most consistent and easily interpreted ring pattern. Measurements on stained *L. mahsena* otoliths were performed out to the tip of dorsal lobe, at approximately 90° to the *sulcus* (Figure 2.3). In all species, when the ring structure became too closely spaced to measure individual increments accurately, the thickness of further increments was estimated by interpolation. This was based on the remaining distance from the last measured increment to the outside otolith edge, the number of years expected in this zone, and the pattern found in the previous increment widths.

Following the recommendations of Francis (1990) and Ricker (1992), the geometric mean regression (GMR) of fork length at capture from otolith radius at capture was calculated for each species. Using lines relating the length at capture (Fl_c) to the intercept point (b), back-calculated lengths-at-age (Fl_i)for each individual were derived using the following equation (Ricker, 1992):

$$Fl_i = (\frac{Fl_c - b}{O_c} \cdot O_i) + b$$

where		
	Fl_i	estimated fork length at age *i*
	Fl_c	fork length at capture
	O_c	otolith radius at capture
	O_i	otolith radius at age *i*
	b	intercept of the GMR calculated using the Ricker procedure

For each species, a von Bertalanffy growth curve was fitted to the back-calculated mean length-at-age through least squares estimation.

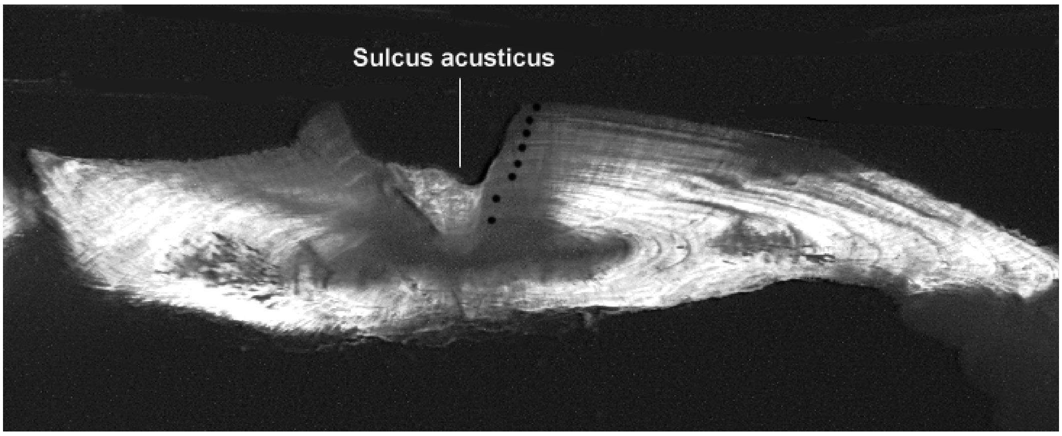


Figure 2.1 Unstained transverse 0.5mm section through the sagittal otolith of *P. filamentosus* from Seychelles, viewed under transmitted light. Magnification x16. Black dots along sulcus acusticus mark suspected annual increments.

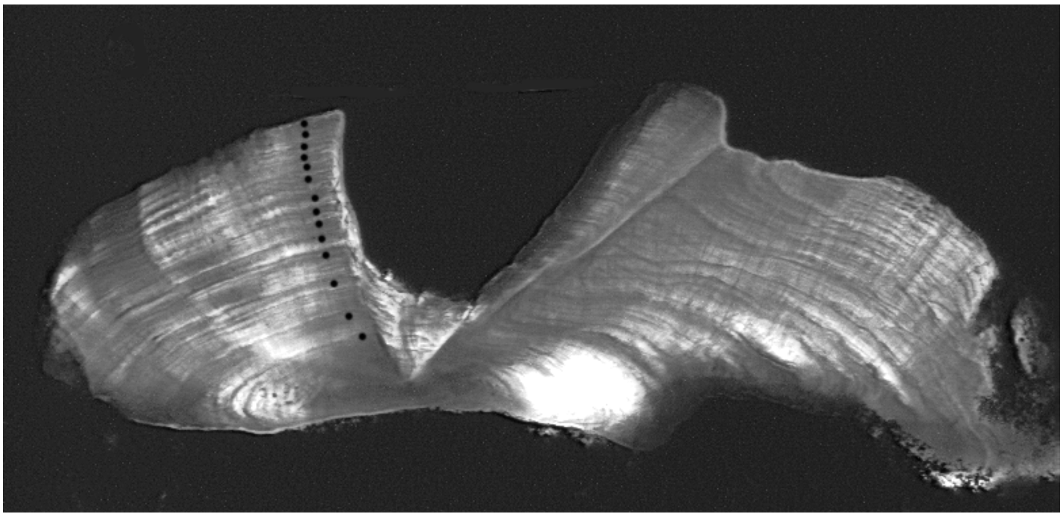


Figure 2.2 Unstained transverse 0.5mm section through the sagittal otolith of *A. virescens* from Seychelles, viewed under transmitted light. Magnification x32. Black dots along sulcus acusticus mark suspected annual increments.

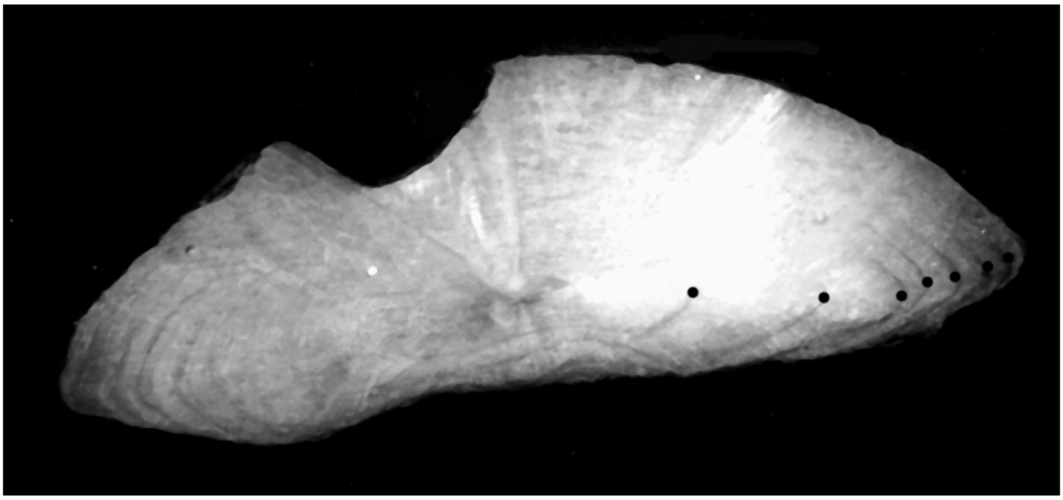


Figure 2.3 Transverse 0.5mm section through the sagittal otolith of *L. mahsena* from Mauritius (Nazareth bank), viewed under reflected light. Magnification x23. Black dots mark suspected annual increments.

2.3.1.2 Marginal increment analysis

The thickness of the outer zone in otolith sections was measured using the image analysis system employed for back-calculation (see Millner and Whiting, 1996). Measurements were taken from the inside edge (start) of the last opaque band (the last stained ring in *L. mahsena*) and the edge of the otolith. Since rings at the edge of sections taken from the otoliths of both snapper species were indistinct, an average was calculated from four measurements taken in the region of the *sulcus acusticus* (where rings were more easily distinguished). Rings at the edge of stained *L. mahsena* otolith sections were clearly visible, and it was therefore possible to obtain a single measurement, along the same growth axis as that used for the purposes of back-calculation.

The pattern expected in the marginal increment resulting from the development of an annual ring would be a minimal marginal increment at the start of the growth period. The measure would then increase with time, until it fell to a minimum again at the formation of the next period of growth.

The size of the growth zone will vary both with the time of sampling during the year and the age of the fish. Since younger fish grow faster than older individuals, a larger marginal increment is expected. As a result, quantitative marginal increment analyses should be standardised for age. The study was therefore carried out by age class. Due to the wide range of ages encountered, however, there were insufficient samples to accomplish this fully. It was necessary to combine ages into two or three groups representing fast, moderate and slow growing individuals (Table 2.1). These classes were based on the growth curves derived from back-calculation, and hence on the assumption that the increments represented annual growth.

Table 2.1 ‘Age groups’ selected for marginal increment analysis, by species.

Species	Growth Group	Age Class (years)
L. mahsena	Fast	1-5
	Slow	6+
A. virescens	Fast	3-5
	Slow	6+
P. filamentosus	Fast	3-5
	Moderate	6-10
	Slow	11+

Due to poor sample sizes and temporal distribution, data for *P. filamentosus* were grouped into bi-monthly time periods. Sufficient *L. mahsena* and *A. virescens* samples were obtained to allow the analysis to occur on a monthly basis. For all three species, a mean marginal increment for each time period and growth category was calculated.

2.3.1.3 Edge analysis

The type of zone (‘opaque’ or ‘translucent’) at the growing edge of the otolith was identified in each month of the year. Annuli would be traceable as the development of a single translucent and opaque zone on the otolith edge during that growth year.

Problems were encountered in identifying the edge type in unstained *P. filamentosus* and *A. virescens* from Seychelles. This was due to poor resolution of the banding in the otoliths, and what appeared to have been the seepage of resin either under or through the edge of the otolith. Staining trials were performed in an attempt to clarify the growth type at the edge of the otolith in these species.

For all three species, thin sections of the stained otoliths were assessed for the presence of the band of stain on the growing tip of the dorsal lobe. Since the region between translucent and opaque zones took up the stain, the presence of the stained area would indicate the start of opaque zone formation. The percentage of otoliths with a stained band at the growing tip was calculated for each month. Although an extended data set was available for edge analysis, as a result of the seasonal nature of the Seychelles and Mauritius fisheries, samples remained either low, or unavailable in certain months.

2.3.1.4 Examination of other study locations

Based on the results of the above validation studies, further edge analyses were carried out for both *L. mahsena* and *A. virescens* specimens from the other study locations. Again, samples were assessed for the presence of the stained zone at the edge of the otolith in each month.

2.3.2 Results

Based on the assumption that the increments seen in otoliths were annual, the length and age range of individuals from each species examined during each method is presented in Table 2.2. Sample size is also shown.

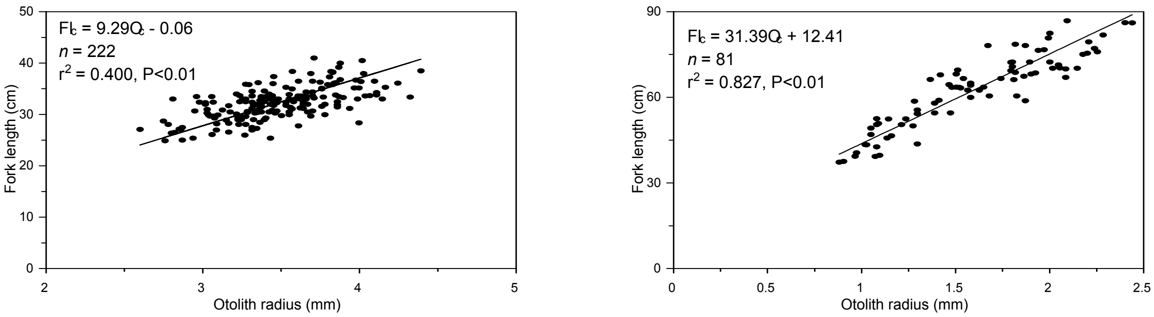
Table 2.2 The length range, age range and sample size of individuals of each species examined, by method. Ages based on the assumption that increments identified in the otoliths are annuli.

Species	Range	Back-calculation	Marginal increment analysis	Edge analysis
L. mahsena	Length	22-42cm	22-42cm	20-50cm
	Age	3-14yrs	3-14yrs	3-16yrs
	n	222	220	558
A. virescens	Length	37-87cm	37-87cm	30-99cm
	Age	3-19yrs	3-19yrs	3-27yrs
	n	60	141	1259
P. filamentosus	Length	22-73cm	22-73cm	-
	Age	3-30yrs	3-30yrs	-
	n	60	242	-

2.3.2.1 Back-calculation

A linear relationship existed between fork length and otolith radius in all three species, to which the geometric mean regression (GMR) of fork length from otolith radius was fitted (Figures 2.4 a to c).

a. *L. mahsena* b. *A. virescens*



c. *P. filamentosus*

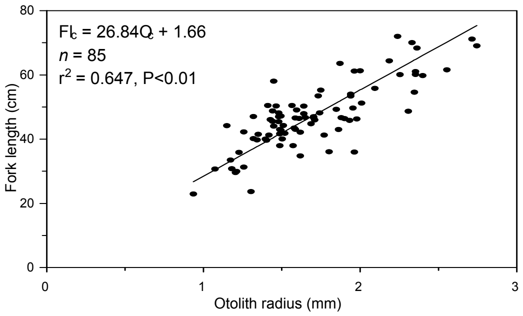


Figure 2.4 Geometric mean regressions of fork length (cm) from otolith radius (mm).

Individual back-calculated lengths-at-age were used to calculate a mean length-at-age. Von Bertalanffy growth parameters were then derived from the mean back-calculated length-at-age data (Table 2.3). Initial L_∞ estimates for *L. mahsena* (34cm) were low compared to the maximum lengths seen in length frequency distributions from the region (52cm). L_∞ was therefore constrained to the maximum length found in the catches, and the remaining von Bertalanffy growth parameters re-estimated.

Table 2.3 Von Bertalanffy growth parameters estimated from back-calculated length data and reference. L = parameters derived using length-based methods, O = otoliths.

Species	K	L_∞ (cm)	*n*	Method	Reference
L. mahsena	0.38	34.1	222	O	This study
	0.09	52.0	222	O	This study, L_∞ = 52cm
	0.1	61.7	-	L	Bautil and Samboo (1988)
	0.32	58.9	-	L	Dalzell *et al.* (1992)
P. filamentosus	0.11	62.3	60	O	This study
	0.29	81.7	7,060	L	Mees (1993)
	0.24	75.8	2,432	L	Mees and Rousseau (1997)
	0.146	78	-	O	Ralston and Miyamoto (1983)
	0.33-0.36	78-86	-	O	Hardman-Mountford *et al.* (1997)
A. virescens	0.13	79.0	60	O	This study
	0.32	95-104	-	L	Mees (1993)
	0.31	65.6	-	O	Loubens (1980)

2.3.2.2 Marginal increment analysis and edge analysis

The number of samples analysed for marginal increment analysis are presented in Table 2.4.

Table 2.4 Numbers of individuals examined for marginal increment analysis by monthly or bi-monthly interval.

	L. mahsena		*A. virescens*		*P. filamentosus*		
Age Class	1-5 yrs	6+ yrs	3-5 yrs	6+ yrs	3-5 yrs	6-10 yrs	11+ yrs
Jan	14	8	-	4	95	29	20
Feb	13	5	-	-			
Mar	19	5	4	8	-	16	18
Apr	-	-	3	15			
May	15	9	10	17	-	-	-
Jun	4	11	6	11			
Jul	15	8	10	-	8	-	4
Aug	21	4	5	6			
Sep	-	-	-	8	11	19	5
Oct	-	17	-	4			
Nov	-	19	6	16	-	7	10
Dec	13	20	-	8			

L. mahsena

The analysis indicated an overall increase in marginal increment between January and May, falling in August (Figure 2.5). This pattern was clearest in the younger, faster growing age class. A unimodal distribution was found in the plot of the proportion of stained edges found in each month, with a high proportion of individuals showing opaque growth commencing between May and October (Figure 2.6).

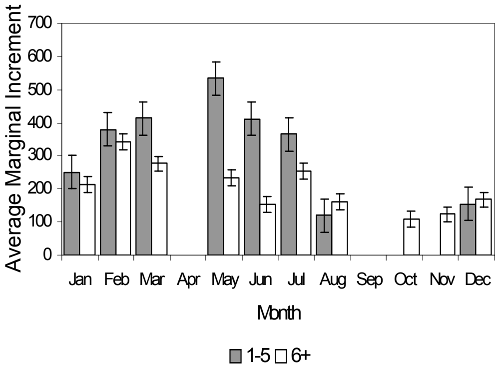


Figure 2.5 Marginal increment plot by month for *L. mahsena*. Marginal increment measured in 'VIDS units' (pixels). Data segregated as in Table 2.1. Error bars denote one standard error.

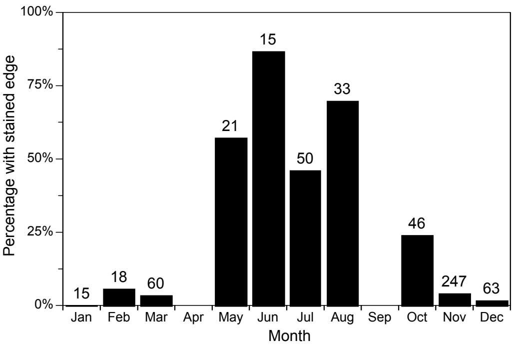


Figure 2.6 Proportion of *L. mahsena* otoliths with stained edge on the growing tip of the dorsal lobe, by month. Numbers denote sample size.

A. virescens

With relatively few samples from certain key times during the year, patterns in the marginal increment of this species could not be identified clearly (Table 2.4). The width of the marginal increment increased until June in younger, faster growing individuals, but showed no decrease in subsequent months (Figure 2.7). No pattern was found in the marginal increment of older individuals. Staining improved the clarity of the type of growth present at the otolith edge. The edge analysis plot of the percentage of stained edges by month showed a unimodal distribution. A high proportion of individuals exhibited opaque zone formation in the period between October and March (Figure 2.8).

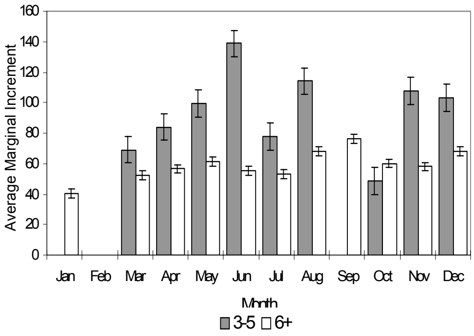


Figure 2.7 Marginal increment plot by month for *A. virescens*. Marginal increment measured in 'VIDS units' (pixels). Data segregated as in Table 2.1. Error bars denote one standard error.

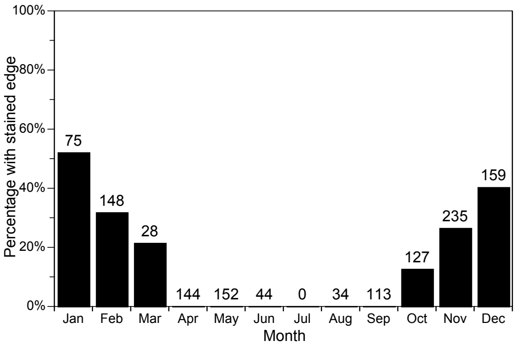


Figure 2.8 Proportion of *A. virescens* otoliths with stained edge on the growing tip of the dorsal lobe, by month. Numbers denote sample size.

P. filamentosus

No overall pattern of increase in the marginal increment was found (Figure 2.9). This was partly the result of a lack of samples from the months of May and June. The legibility of increments in the unstained otoliths of this species was poor, but staining failed to improve their clarity. The identification of edge type was confused by indeterminate increments formed in the translucent growth period. Their presence on the edge of the otolith at the time of capture led to the mis-identification of opaque zone formation, confusing the pattern.

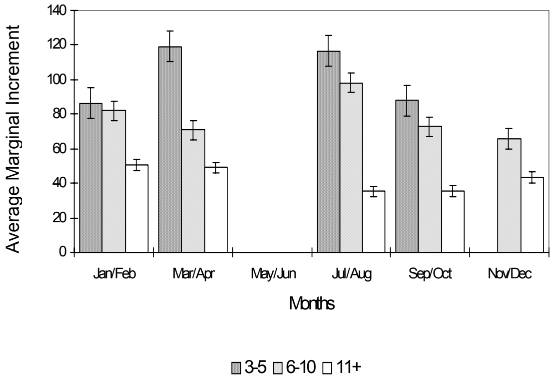


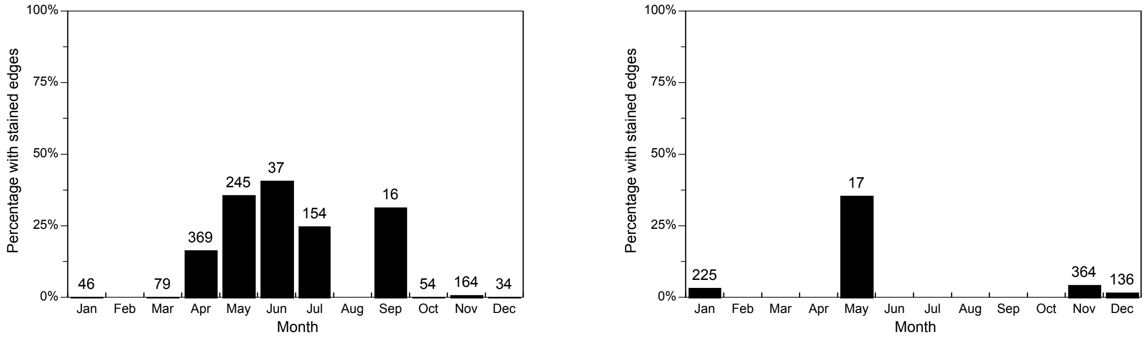
Figure 2.9 Marginal Increment plot by month for *P. filamentosus*. Marginal increment measured in 'VIDS units' (pixels). Data segregated as in Table 2.1. Error bars denote one standard error.

2.3.2.3 Examination of other locations

Based on the results obtained for *L. mahsena* and *A. virescens* from Nazareth bank and Seychelles respectively, further edge analysis studies were undertaken for the other study locations. The pattern in the percentage of otoliths with a stained zone present at the growing tip of the otolith each month are presented in Figures 2.10 and 2.11.

a. Saya south

b. Saya north



c. Seychelles

d. BIOT (Chagos Archipelago)

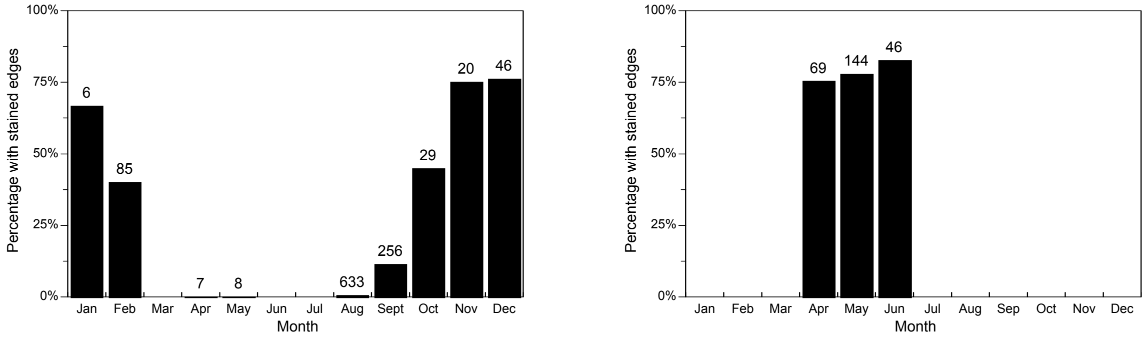


Figure 2.10 Percentage of *L. mahsena* otoliths with a stained zone present at the growing tip of the otolith in each month, by location. Numbers denote the sample size.

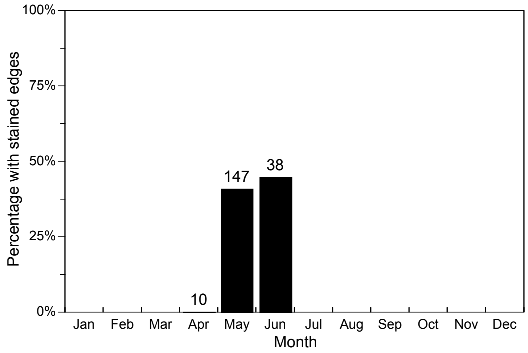


Figure 2.11 Percentage of *A. virescens* otoliths from BIOT (Chagos Archipelago) with a stained zone present at the growing tip of the otolith in each month. Numbers denote the sample size.

Where sampling was achieved throughout the majority of the year, such as at Saya south and Seychelles for *L. mahsena*, a unimodal distribution of the percentage of otoliths with a stained edge was identified. The pattern found for in Seychelles followed that identified for *A. virescens* at this location (Figure 2.8).

In BIOT (Chagos Archipelago) and Saya north, the sampling programme was limited by vessel activities. In BIOT (Chagos Archipelago), this limited sampling to three months of the year. However, the patterns seen in the edge analyses were consistent with those found in related locations from where a more complete sampling programme was achieved. Edge analysis for *L. mahsena* from Saya north and BIOT (Chagos Archipelago) showed the same pattern as that found at Nazareth; stained edges were present in the middle of the year. BIOT (Chagos Archipelago) *A. virescens* samples also showed stained edges in this period.

2.4 DISCUSSION

The results of back calculation indicated that there was a direct linear relationship between fork length and otolith radius. The otoliths of each species also showed an internal structure, with increments widely spaced near the nucleus leading to narrower and more evenly spaced increments toward the outer edge. Growth curves derived from back-calculated length-at-age indicated an exponential decrease in increment width with increasing assumed age. Over the age range observed in the samples, otoliths grew throughout the life of the fish, and showed an internal increment structure. Otoliths of the three species therefore fulfilled the first two criteria for their use in ageing. However, the pattern in *P. filamentosus* was confused by the presence of indeterminate increments.

Confirmation of the third criteria (*i.e.* observed increments corresponded to a regular time scale) was not demonstrated so readily. Validation could not be achieved through methods such as tetracycline injection, due to practical limitations imposed by the fisheries, and the biology of the species. *P. filamentosus*, for example, is caught below 75m depth. The majority of specimens would either be dead or heavily stressed through barotrauma on reaching the surface (DeMartini *et al.*, 1996), and therefore useless for tagging programmes. Marginal increment analysis and edge analysis were therefore used.

Some evidence for the annual nature of increments in *L. mahsena* otoliths was found in the pattern of marginal increments through the year. This was confirmed by the unimodal distribution resulting from edge analysis, indicating that opaque band formation was initiated once a year, during May to August. To some extent, the observed range of months in this distribution was due to the combination of data from different age classes. The initiation of opaque zone formation is not expected to be identical between individuals from different age classes, due to relative differences in growth rate (Vilizzi and Walker, 1999).

The pattern of marginal increments found in *A. virescens* was confused by the poor resolution of the unstained sections and relatively low sample sizes, rendering the results inconclusive. However, the unimodal plot resulting from edge analysis on stained specimens indicated that the transition between translucent and opaque bands did occur once a year, between October and March.

Based on this evidence, there were sufficient data to indicate that the increments seen in the otoliths of both *L. mahsena* from Mauritius and *A. virescens* from Seychelles were annual.

The timing of opaque zone initiation in *L. mahsena* from the Mauritian banks (May to August) corresponded to the rough weather of the South East trade wind season. The timing of opaque zone deposition in *A. virescens*, initiated between October and March, coincided with the Seychelles' North West monsoon season.

Reviews of otolith studies in tropical latitudes found that, for the majority of species studied, the period of opaque growth coincided with spring and summer months, as seen in *L. mahsena* (Beckman and Wilson, 1995; Fowler, 1995). Both *A. virescens* and *L. mahsena* from Seychelles appear to contradict this general pattern, with opaque zone formation being initiated during winter months. Of the twenty nine tropical species reviewed by Fowler (1995), only four showed opaque zone formation in winter. If opaque zone formation were linked with high food availability, the monsoon periods experienced in Seychelles at this time may improve local productivity and feeding conditions.

The results of marginal increment analysis for *P. filamentosus* were inconclusive, since problems were experienced in identifying and measuring the outer zone in the otolith. Staining did not improve the clarity of the zones due to the frequent appearance of 'indeterminate increments'. Validation was therefore considered to be unsuccessful for *P. filamentosus* in Seychelles, and contrasts with that achieved in Hawaii using microincrements (Ralston, 1981; Ralston and Miyamoto, 1983; Radtke, 1987). In this study, an initial examination of *P. filamentosus* otoliths was performed by CEFAS using Scanning Electron Microscopy (CEFAS, 1997b), in an attempt to validate 'suspected' annuli through microincrement counts (see Brothers and Mathews, 1987). Unlike the results reported from Hawaii, no consistent pattern of microincrements was found, although it should be noted that the CEFAS study was very limited in scope (*n*=4). The study of Hardman-Mountford *et al.* (1997), also using specimens from the Seychelles, related assumed 'monthly increments' to assumed annuli, finding approximately 12.4 monthly increments within each annual ring. Consistent banding of this type could not be found during the current study for specimens collected from the same region, even though there was a larger sample size.

The lack of consistent annual increments in *P. filamentosus* may be a result of the biology of this species. Spawning occurs throughout the year, with two peaks (Mees, 1993), and may not provide a sufficient stimulus for zone formation. *P. filamentosus* is found at greater depth (between 75 and 150m) than the other study species (around 30m), in conditions which may be buffered against environmental change. Hardman-Mountford *et al.* (1997), however, indicated that the 20 to 24.5°C temperature range at this depth is sufficient to leave increments on scales in some species (Chey, 1933; in Panella, 1980). If this species is sensitive to relatively small changes in temperature, currents, food supply or quality, relatively short periods of fluctuation in these factors may result in a high number of 'indeterminate increments'. Even if validation had been achieved, *P. filamentosus* otoliths would be unsuitable for routine ageing due to the difficulties in differentiating periodic increments from indeterminate increments.

These difficulties highlight the dangers in assuming the periodicity of increments in otoliths, based on validation of that species, or a similar species, in another location (*e.g.* Smith and

Kostlan, 1991), and also identify the need for thorough validation studies. For example, the present study has indicated that the assumption of annual, and possibly daily periodicity for increments in otoliths of *P. filamentosus* in Seychelles, based on published data, would have proved unfounded.

Due to the success of edge analysis in validating the annuli seen in the otoliths of *L. mahsena* from Nazareth and *A. virescens* from Seychelles, otoliths from the other study locations were analysed using this method. The results were most conclusive where samples were available from the majority of months in the year. Samples for *L. mahsena* in Saya south and Seychelles showed unimodal distributions, indicating that, as for Nazareth bank, the increments seen in the otoliths of these species were annuli.

Validation through edge analysis became less conclusive as the range of sampled months during the year was truncated. This was particularly notable in the samples from BIOT (Chagos Archipelago) and Saya north. In these locations, the use of otoliths for ageing requires the assumption that the increments present are annuli. Such an assumption appears justifiable from the limited data available for BIOT (Chagos Archipelago; both species) and Saya north (*L. mahsena*). The ring structure was similar to that seen in areas where validation was successful, with increments more widely spaced towards the nucleus and narrowing towards the edge, the typical pattern for annual increments. The pattern in the edge type observed in the months for which data were available also matched that seen in the validated locations of the Mauritian banks.

Interestingly, the timing of opaque zone deposition in BIOT (Chagos Archipelago) matched that of the Mauritian banks, and not of Seychelles which is on a similar latitude. Current systems do not explain this difference; both Seychelles and BIOT (Chagos Archipelago) are affected by the east flowing Equatorial Counter Current, while the Mauritius banks lie in the west flowing South Equatorial Current. Similarly, there appears to be no relationship with mean surface water temperature patterns during the year. However, there may be some link between the weather systems that affect each region. The Mauritian banks are affected by cyclones, which form to the south and east of BIOT (Chagos Archipelago). Seychelles is out of the path of such systems. If such climatic systems were linked with increased productivity, they might trigger the changes seen in the otolith zonation.

Published work (Sparre and Venema, 1998) suggests that consistent periodic rings do not form in otoliths of tropical species, particularly in the case of low-latitude species (*e.g.* Munro and Williams, 1985). The validation results obtained within this study prove a sharp contrast to this view; indeed, the results obtained add to the expanding number of tropical species for which the validation of annual increments has been successful.

The use of accurate growth parameter estimates is important in many fisheries assessments; the output of models such as analytical yield-per-recruit (Beverton and Holt, 1957) are sensitive to uncertainty in the estimates of growth (Mees and Rousseau, 1997). For the study species, uncertainty arises through the use of length-based growth estimates, the only estimates previously available. However, successful validation of the use of otoliths for ageing *L. mahsena* and *A. virescens* means that, where funds allow, the use of reliable age-based methods of assessment (Hilborn and Walters, 1992) becomes a real possibility for these locations.

The back-calculated growth parameters derived in the current study allow a preliminary comparison of length- and age-based growth estimates for the study species. Although not definitive, they suggest that for *A. virescens*, current length-based growth estimates may have over-estimated both mean growth rate and asymptotic length. For *L. mahsena*, growth rate may have been under-estimated, and asymptotic length over-estimated. However, constraining the value of L_∞ to levels in keeping with the maximum size found in length distributions from the region (52cm) resulted in a similar growth rate to that identified by Bautil and Samboo (1988).

If the study Lutjanidae do indeed have a longer life-span than previously indicated by length-based assessments, they may be more vulnerable to overfishing than previously thought.

3. Calculation of individual variability in growth

3.1 INTRODUCTION

Variation in growth between individuals results from the influences of both genetic and environmental factors. While an individual may be genetically predisposed toward faster growth, the ability to achieve this growth may be limited by the availability of food within the environment. In turn, interactions between these factors can be modified through the effects of fishing. For example, the influence of growth limiting factors such as food availability may be decreased as fish are removed, producing density dependent growth effects. Fishing may also have direct selective influences on the genetic structure of the stock (Parma and Deriso, 1990).

Most fisheries models assume that population growth can be described adequately through mean growth parameters (Sainsbury, 1980). Indeed, the overwhelming majority of growth parameter estimates in the literature describe such 'average' growth. However, considerable variation around this mean growth pattern can be identified from most length-at-age plots; an individual's growth trajectory may be quite different from the population average.

The expected effect of variability in the von Bertalanffy growth parameters on length-at-age was described in Rosenberg and Beddington (1987). Where L_∞ was the only source of variability, variation in length-at-age increased monotonically with age. This is the pattern said to be identified most frequently in actual fish populations (*e.g.* Schnute and Fournier, 1980). Where variation occurred in K alone, length-at-age variability initially increased with age, then decreased. Such a pattern has been identified in a number of fast-growing pelagic fish species, and in many molluscs (Isaac, 1990; Erzini, 1991). If t_0 were the only parameter varying in the growth equation, length-at-age variation would be high for younger age groups, decreasing rapidly with increasing age.

Simulation studies described in Rosenberg and Beddington (1987) and Isaac (1990) indicated that individual growth variability can seriously affect the precision of both length-based growth estimates, and the outputs of other length-based stock assessment methods. For example, with individual variability in L_∞, CV=30%, bias in ELEFAN K estimates was 41% (Isaac, 1990). Variability in length-at-age is also important when estimating age frequency distributions from length distributions or when fitting growth curves to length-at-age data (Erzini, 1991).

While a knowledge of individual growth variability is important when applying fisheries models, it is also important when deriving models to simulate exploited fish stock behaviour at an individual level (*e.g.* Kristiansen and Svarsand, 1998; Lowerre-Barbieri *et al.*, 1998). Where such models include a growth component, the use of mean growth parameters to describe individual growth is erroneous. For example, the simulation of realistic length frequency distributions requires some measure of individual growth variability.

Individual-based simulations have generally modelled growth variability through independent growth parameter distributions (*e.g.* Isaac, 1990). However, other studies have taken the perceived negative correlation between L_∞ and K explicitly into account. In the simulations described in Hampton and Majkowski (1987), this was done by assuming that the correlation between L_∞ and K was -0.8. Other authors have assumed that all three growth parameters are correlated (*e.g.* Martinez-Garmendia, 1998). In the latter study, the absence of information on individual variability led the authors to assume a parameter covariance matrix which resulted in realistic size-at-age distributions.

Individual growth trajectories in snappers have been described as 'highly variable' (Pauly *et al.*, 1996a), and therefore have the potential to significantly affect growth parameter estimates. To examine the accuracy of growth assessments, individual-based simulations of both length frequency distributions and length-at-age are to be carried out in this report. An accurate assessment of individual growth variability is therefore required.

There are a number of methods by which individual variability in growth could be estimated.

Where modes representing individual cohorts are present in length frequency data, the distribution of sizes around the mean length can be assumed to result from individual growth variability. In practice, the modal structure in length frequency distributions is usually complicated by other factors. For example, modes will be affected by the duration of the spawning period and by gear selectivity, confusing estimates of individual growth variation. Furthermore, due to the long-lived, slow growing nature of the study species, modes in length frequency data are seldom distinct, and are likely to be comprised of a number of age classes, rather than a single one. For these species, therefore, this method cannot be employed.

The study described by Rosenberg and Beddington (1987) estimated the coefficient of variation (CV) in L_∞ for a number of temperate species. L_∞ estimates (or mean size-at-age for the oldest group) were compared either between years, or between populations. This method assumed that the population was well sampled, and that L_∞ was the only source of variability in length-at-age. In a similar manner, the level of individual variability in L_∞ may be approximated by the variation in length-at-age of extremely old fish (Sainsbury, 1980). In both cases, however, obtaining suitable sample sizes of extremely old fish for such assessments may be complicated by the selectivity of the gear, or the state of stock exploitation.

A more appropriate methodology is to assess the growth of individual fish directly, throughout their lives. Such measurements, usually achieved through captive studies or tagging programmes, allow a growth curve to be assessed for each individual. However, the results of such programmes may be confounded by additional stresses incurred during tagging, captivity, or through density dependence. These factors will alter individual growth rates from their natural state, biasing assessments.

An alternative method to obtain information on individual growth histories is to back-calculate length-at-age using increment width information contained in validated otoliths. Such data has been derived to estimate mean growth parameters for the study species (Chapter 2).

Considering the potential importance of individual growth variability in fisheries assessments (*e.g.* Sainsbury, 1980), the number of published studies which have quantified this variability for populations is extremely low. However, the increasing number of species reared for aquaculture (*e.g.* Sirois *et al.*, 1998), examined through tagging programmes (*e.g.* Nash *et al.*, 1994; Kristiansen and Svarsand, 1998), or for which otolith or scale increments have been successfully validated has resulted in an increasing number of studies assessing individual growth rates (*e.g.* Millner and Whiting, 1996; Yamamoto and Nakano, 1996; Fukuwaka and Kaeriyama, 1997). At present, however, such studies have concentrated on changes in length-at-age through time, or comparisons of growth in different sexes or developmental stages (*e.g.* Kingsford and Atkinson, 1994; Bertram *et al.*, 1997), rather than the assessment of individual growth variability.

The only notable assessment of individual growth variability was described in Isaac (1990). In that study, von Bertalanffy growth curves were fitted to length-at-age data obtained from individual captive reared guppy (*Lebistes reticulatus*) and Tilapia (*Oreochromis sp.*). The variation in the individual growth parameters was then assessed. This method will be employed within the current study ('Isaac's method'). Isaac (1990) reported a CV for L_∞ of between 5% and 26%, and for K of 11% to 30%, depending on the species examined.

Isaac's method has a potentially serious source of bias: estimates of individual growth variability incorporate errors inherent in the method used to estimate the individual growth parameters. Where data are confined to young ages, and growth is slow, there is little information on the true value for L_∞. As a result, L_∞ is likely to be overestimated, and K and t_0 underestimated. Alternatively, where data are lacking from the early years of life, estimates of K, and hence the other parameters, will be flawed. Such estimation errors will strongly influence the individual growth variability estimates. The degree to which these errors influence the estimates will vary, depending on the data set examined. However, the degree of variability resulting from individual growth and estimation error cannot easily be separated.

In the current study, an alternative method was also employed, based on a non-linear random effects model (Walker, 1996). The advantage of this model was that the mean and variance of each of the von Bertalanffy growth parameters could be estimated, while minimising error inherent in the growth parameter estimation process.

Nonlinear random effects models have been used in a number of fields, including the assessment of individual and population growth in humans (*e.g.* Abidi *et al.*, 1996; Susman *et al.*, 1998). The model used in this study was originally developed for the field of population pharmacokinetics, the statistical analysis of pharmaceutical trials (Smith and Wakefield, 1994). In such studies, the profile of drug concentrations over time are modelled following their administration to individual subjects. Observed concentrations are modelled as departures from the underlying profile, as characterised for each individual by a set of parameters. In a population, inter-individual variation is modelled by drawing individual profile parameters from the population distribution. The latter is described by a mean population profile and individual variation around it (random effects). Such models can be analysed using Bayesian hierarchical modelling, with computations carried out through Markov Chain Monte-Carlo 'Gibbs sampling' techniques (see Smith and Wakefield, 1994).

The outputs from each method allowed the level of correlation between the three growth parameters, and in particular between L_∞ and K, to be estimated. These two parameters are frequently believed to be negatively correlated (*e.g.* Hampton and Majkowski, 1987). However, correlation between parameters will result automatically from the non-linear nature of the von Bertalanffy growth equation. Indeed, estimates of L_∞ and K derived using this model frequently show a large negative correlation. There is therefore no direct evidence to suggest that such a correlation is biologically correct. This was tested using outputs from the random effects model. The estimate was compared with that derived using the outputs of Isaac's method, which incorporated additional correlation resulting from the use of the von Bertalanffy growth equation.

The aim of the work described in this chapter was to assess the level of growth variability in individuals of *L. mahsena*. This will allow realistic simulations of catch and population length frequency distributions and length-at-age data to be performed, as described in later chapters. Using individual back-calculated length-at-age data derived for this species in Chapter 2, two methods were employed to assess this variability: Isaac's method (Isaac, 1990), and a modified non-linear random effects model (Walker, 1996). The correlation between L_∞ and K was also assessed from the outputs of both methods.

3.2 METHODOLOGY

This section is divided into three parts. The first briefly describes the back-calculated length-at-age data used within this study. The subsequent two sections describe the two methods used to calculate individual growth variability.

3.2.1 Length-at-age data

In Chapter 2, length-at-age data were back-calculated over the lifespan of a number of individuals from each of the study species. Increment measurements from *A. virescens* and *P. filamentosus* were open to some uncertainty, due to variable clarity in the increment structure. However, *L. mahsena* otoliths generally exhibited clear, consistent marks, and hence the use of these otoliths resulted in the most precise increment measurements. Back-calculated length-at-age data derived from otoliths of this species alone were selected for the current assessment.

The effect of measurement errors on estimates of individual growth variability was reduced further by using data obtained from specimens sampled at Nazareth bank; otoliths from this location exhibited the clearest increment structure.

3.2.2 Isaac's method

This method was based on the procedures described in Isaac (1990). A von Bertalanffy growth curve was fitted to the back-calculated length-at-age data set for each *L. mahsena* individual, using the nonlinear method described in Allen (1966). Allen's method produced least-squares estimates of both the von Bertalanffy growth parameters, and the standard errors of the parameter estimates. For each growth parameter, an average value was calculated from the individual estimates. The variance of these parameter estimates was also assessed, and hence the coefficient of variation (standard deviation/mean). Based on the individual estimates of L_∞, K and t_0, a covariance matrix was derived.

3.2.3 Non-linear random effects model

The back-calculated length-at-age data represented lengths L_{ij} at ages T_{ij}, $j=0,1,2,...n_i$ measurements in $i=1,2,...n$ fish. The basic model to fit to these data was:

$$L_{ij} = L_{\infty i} \cdot (1 - e^{(-K_i \cdot (T_{ij} - t_{0i}))}) + E_{ij}$$

where $L_{\infty i}$, K_i, and t_{0i} were the three von Bertalanffy growth parameters for the i^{th} fish, and E_{ij} was a normally distributed random error term. The model therefore corresponded to the form of a non-linear random effects model.

Assistance was sought from Dr S. Walker of the Imperial College Mathematics Department, who had experience with non-linear random effects models. Dr Walker kindly agreed to modify and employ both a model and computer program which he had previously used to assess pharmacokinetic data (Walker, 1996). Assuming there are n_i observations available for each individual i, the model was parameterised in the following way:

$$l_{ij} = \log\left(\theta_{3i} + e^{\theta_{1i}}\,[1 - e^{-t_{ij}\,e^{\theta_{2i}}}]\right) + \varepsilon_{ij} \quad for\ j = 1...,n_i$$

where:

$$\varepsilon_{ij} \sim N(0,\sigma^2)$$

and the growth parameters for each individual were assumed to be sampled independently from a trivariate normal distribution:

$$\boldsymbol{\theta}_i = \begin{pmatrix} \theta_{1i} \\ \theta_{2i} \\ \theta_{3i} \end{pmatrix} \sim N_3(\mu,\Sigma) \quad : i=1...,n$$

Using the computer program, μ and Σ for each parameter (θ_{1i}, θ_{2i}, θ_{3i}) were estimated from the individual length-at-age data.

Initial analyses were performed using the maximum likelihood estimation method. However, the results suggested that this estimation method could still produce large estimates of variability in the growth parameters. This implied that implausible growth parameter estimates were consistent with the data. Given this, an alternative Bayesian approach was used, which allowed prior information on the likely ranges of the parameter values to be used.

A range of plausible L_∞, K and t_0 values were obtained, based on published von Bertalanffy growth parameter estimates for lethrinid species, and information on the length and age structure of the study stocks available at that time. From these ranges, prior probability distributions for σ, μ and Σ were developed:

- the prior distribution for σ (specifically $\frac{1}{\sigma^2}$) was taken to be a gamma distribution, with parameters ½, ½;
- the prior for μ was a non-informative multivariate normal distribution, with zero mean and covariance matrix with diagonal elements equal to 200, and off-diagonal elements equal to zero;
- the prior for Σ was an inverse Wishart distribution (*e.g.* VonRosen, 1997), with precision parameter 3, and prior mean:

$$\begin{bmatrix} 0.1 & 0.0 & 0.0 \\ 0.0 & 0.2 & 0.0 \\ 0.0 & 0.0 & 0.1 \end{bmatrix}$$

Using these prior distributions, individual back-calculated length-at-age data were fitted to the random effects model. Posterior distributions for the parameters were calculated using Markov Chain Monte-Carlo methods, through a Gibbs sampler (Wakefield *et al.*, 1994). This estimated μ, Σ and σ simultaneously by sampling from posterior distributions of these parameters.

Outputs from the program represented estimates of the parameters θ_{1i}, θ_{2i}, and θ_{3i}, and their covariance matrix. Von Bertalanffy growth parameter estimates were then derived from the θ_i estimates using the following transformations:

$$K = e^{\theta_{2i}}$$

$$L_\infty = \theta_{3i} + e^{\theta_{1i}}$$

$$t_0 = \frac{(\theta_{1i} - \ln[\theta_{3i} + e^{\theta_{1i}}])}{e^{\theta_{2i}}}$$

So that results from the nonlinear model could be compared with those from Isaac's method, an estimate of the coefficient of variation for each von Bertalanffy growth parameter estimate was desired. An EXCEL™ spreadsheet was devised to sample individual θ_{1i}, θ_{2i} and θ_{3i} values, using their estimated means and covariance matrix. Sampled parameter sets were then converted into von Bertalanffy growth parameters, using the equations described above. The Crystal Ball™ spreadsheet add-in was employed to sample 10,000 growth parameter sets in this fashion. From the resultant set of von Bertalanffy growth parameter estimates, their means and covariance matrix were calculated.

3.3 RESULTS

3.3.1 Length-at-age data

Historical lengths-at-age were successfully obtained for seventy two *L. mahsena* individuals from Nazareth bank. Table 3.1 indicates the resultant average length-at-age, and variation between individual measurements.

Table 3.1 Mean back-calculated length-at-age, variance, and coefficient of variation by age, for *L. mahsena* sampled from Nazareth bank.

Age (yrs)	*n*	Mean fork length (cm)	Variance	CV (%)
1	72	11.3	6.3	22.3
2	72	17.7	6.9	14.8
3	72	22.1	7.1	12.1
4	72	25.3	7.0	10.5
5	68	27.6	7.5	9.9
6	60	29.6	7.0	8.9
7	43	30.6	7.5	8.9
8	27	31.5	8.1	9.0
9	15	32.0	11.4	10.6
10	8	31.4	11.3	10.7
11	3	33.1	19.2	13.2
12	2	36.2	15.3	10.8

Overall, the variance in length-at-age increased with age. The CV in length-at-age, however, was highest at age 1, decreasing to around 9% by age 6 years. The CV in length-at-age then increased slightly with further increases in age. In part, the latter increase may be a result of the decrease in the sample sizes. This may confound the true age-related variability to some extent.

3.3.2 Isaac's method

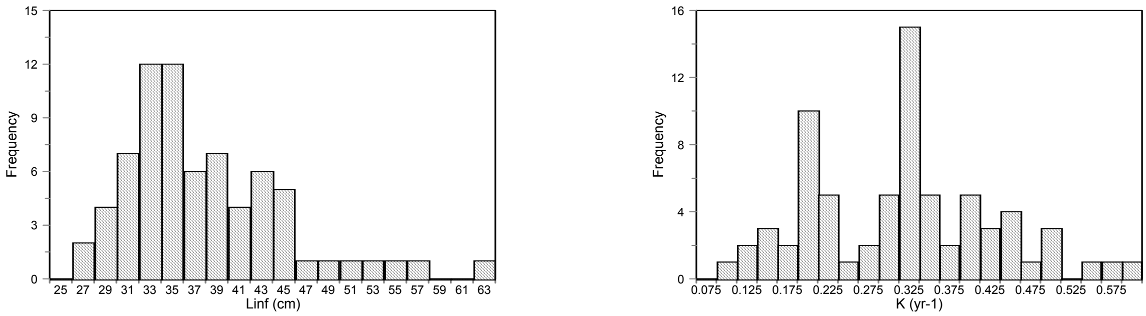
The mean, variance, and hence CV of the individual von Bertalanffy growth parameter estimates derived through Isaac's method are presented in Table 3.2. The frequency distributions from the 72 individual growth parameter estimates are presented in Figure 3.1.

Table 3.2 Mean von Bertalanffy growth parameters for *L. mahsena*, variance, and coefficient of variation (CV, %) calculated using Isaac's method.

Parameter	Mean	Variance	CV(%)
L_∞ (cm)	36.8	50.5	19.3
K (yr^{-1})	0.30	0.01	37.2
t_0	-0.40	0.35	149.4

a) L_∞ (cm)

b) K (yr^{-1})



c) t_0

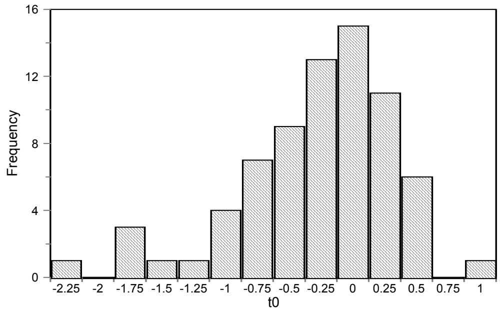


Figure 3.1 Frequency distributions of individual growth parameter estimates resulting from the application of Allen’s estimation method to 72 sets of individual length-at-age data.

Based on the von Bertalanffy growth parameter sets obtained from the 72 individuals, a covariance matrix was derived:

$$\begin{bmatrix} 50.5 & -0.55 & -1.62 \\ -0.55 & 0.01 & 0.04 \\ -1.62 & 0.04 & 0.36 \end{bmatrix}$$

From this covariance matrix, the correlation between L_∞ and K was calculated as:

$$\frac{-0.55}{\sqrt{(50.5 * 0.01)}} = -0.69$$

3.3.3 Non-linear random effects model

The individual θ_i estimates output from the Bayesian nonlinear model were used to assess the mean θ_i values. Individual estimates were also converted into von Bertalanffy growth parameter estimates, and a mean calculated (Table 3.3).

Table 3.3 Mean growth parameter estimates output by the Bayesian nonlinear model.

θ estimates		von Bertalanffy estimates	
θ_{1i}	3.50	L_∞ (cm)	36.0
θ_{2i}	-1.28	K (yr^{-1})	0.28
θ_{3i}	2.85	t_0	-0.30

The resulting covariance matrix for the θ_i estimates was:

$$\begin{bmatrix} 0.06 & -0.04 & -0.26 \\ -0.04 & 0.13 & -0.10 \\ -0.26 & -0.10 & 7.61 \end{bmatrix}$$

Figure 3.2 presents the distributions of 10,000 individual growth parameter estimates sampled from the estimated population parameter distributions, as calculated using the EXCEL^{TM} spreadsheet. The mean, variance and coefficient of variation calculated from these sample growth parameter distributions are presented in Table 3.4.

a) L_∞ (cm)

b) K (yr^{-1})

c) t_0

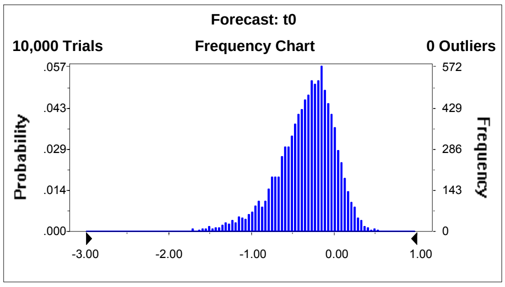


Figure 3.2 Distributions of 10,000 L_∞, K and t_0 values sampled from Bayesian estimates of θ_i and accompanying covariance matrix.

Table 3.4 Mean growth parameter estimates and coefficient of variation from the sampled growth parameter distributions.

Parameter	Mean	CV (%)
L_∞ (cm)	36.9	20.3
K (yr^{-1})	0.30	36.2
t_0	-0.34	105.9

Based on the von Bertalanffy growth parameter sets simulated for the 10,000 individuals, a covariance matrix was derived:

$$\begin{bmatrix} 59.5 & -0.43 & 0.09 \\ -0.43 & 0.01 & 0.01 \\ 0.09 & 0.01 & 0.14 \end{bmatrix}$$

From this covariance matrix, the correlation between L_∞ and K was calculated as:

$$\frac{-0.43}{\sqrt{(59.5*0.01)}} = -0.56$$

3.3.4 Comparison of methods

The mean growth parameter estimates, and corresponding CV (%), output from the two estimation methods are compared in Table 3.5.

Table 3.5 Comparison of mean growth parameter estimates and CV (%) derived using Isaac's method, and the nonlinear random effects model.

Parameter	Isaac's method		Random effects model	
	Mean	CV (%)	Mean	CV (%)
L_∞	36.8	19.3	36.0	20.3
K	0.30	37.2	0.28	36.2
t_0	-0.40	149.4	-0.30	105.9

Overall, mean von Bertalanffy growth parameter estimates were comparable between methods. Estimates from the non-linear random effects model were slightly lower than those estimated by Isaac's method. Estimates of CV (%) for the individual L_∞ and K distributions were also comparable. The random effects model estimated a slightly higher CV in L_∞ estimates than that from Isaac's method, and correspondingly a slightly lower CV for K. The CV for t_0 was notably lower when estimated through the random effects model.

3.4 DISCUSSION

The main aim of this chapter was to obtain an estimate of the variation in von Bertalanffy growth parameters between individuals of *L. mahsena*. Two methods were used. The first, that described in Isaac (1990), calculated growth parameters from individual length-at-age data, and assessed the variation between these individual growth estimates. This can be viewed as the current 'standard' method for estimating individual variability in growth. The second method, derived for this report, employed a non-linear random effects model, based on a model previously used in population pharmacokinetics. Individual length-at-age data were fitted to the latter model through Bayesian methods.

The main drawback with Isaac's method is that error resulting from the growth parameter estimation method used is incorporated into the estimates of von Bertalanffy growth parameter variability. The random effects model does not suffer from this problem. In theory, therefore, the use of the latter method should result in more reliable, and probably lower, estimates of growth parameter variability. In practice, the mean growth parameter estimates and coefficient of variation for L_∞ and K distributions calculated through Isaac's method and the Bayesian random effects model were comparable. This was somewhat surprising. However, since the back-calculation method interpreted growth back to age one, and each data set also included individuals of sizes close to the estimated mean L_∞, any additional error resulting from the growth parameter estimation method may have been minimal. From a cursory glance, there would appear to be little advantage in the additional computations required for the random effects model over Isaac's method. However, the advantage of the random effects model, the elimination of additional errors resulting from the estimation methods used, results in growth variability estimates of greater certainty. In other data sets, the effects of growth estimation error may be more significant, resulting in biased growth variability estimates from Isaac's method.

The level of individual variability in *L. mahsena* von Bertalanffy growth parameters calculated through the Bayesian nonlinear model was generally greater than that calculated for guppies and Tilapia using Isaac's method (Isaac, 1990). The coefficient of variation in L_∞ estimated in Rosenberg and Beddington (1987) from population growth parameter estimates was below 10%, notably less than that calculated in this study. As noted in Pauly *et al.* (1996a), tropical species show 'highly variable' individual growth trajectories compared to the temperate species examined by Rosenberg and Beddington (1987). In turn, the wild *L. mahsena* individuals examined were exposed to increased environmental influences compared to the reared species examined by Isaac (1990). The result is therefore not unexpected. Using the random effects model, further examinations of other wild tropical fish species would indicate whether the level of individual growth variability estimated for *L. mahsena* was consistent with that for other species.

The correlation between L_∞ and K estimated from outputs of the random effects model (-0.56) was lower than that from Isaac's method (-0.69). This too was not unexpected, since the latter estimate included additional negative correlation due to that resulting from the use of growth parameters estimated directly through the von Bertalanffy growth function. The estimate from the random effects model appears to represent the first assessment of this correlation using actual growth data. While the correlation is negative, as expected, the value is lower than the general perception of this relationship identified in the literature. For example, the correlation selected for the length frequency simulations of Hampton and Majkowski (1987) was -0.8. Further studies would be required to examine whether this correlation was consistent between species.

The variation in *L. mahsena* back-calculated length-at-age increased with age. Other studies have noted that such increases can be modelled by individual variation in L_∞ alone (*e.g.* Jones, 1987b; Rosenberg and Beddington, 1987). However, these studies assumed that the growth parameter distributions were independent. As indicated by the current study, all three parameters are in fact correlated. As a result, it is impossible to identify which parameter contributes most significantly to the variability in length-at-age. However, it is clear that all three parameters contribute to some extent. It is therefore unrealistic to base such variation on a single growth parameter.

Overall, the nonlinear random effects model offers a number of advantages over Isaac's method. Theoretically, it minimises additional error resulting from the growth parameter estimation method (and hence deficiencies in the data examined), although this advantage could not be confirmed in the current study. The method also outputs a covariance matrix, describing the relationship between growth parameter estimates, which unlike that derived from Isaac's method, is not influenced by the negative correlation in parameter estimates derived directly from the von Bertalanffy growth function. This covariance matrix allows realistic individual-based simulations to be performed (see Chapter 4), and a less biased correlation between L_∞ and K to be calculated. Although the computations involved in the method are notably more complex, computer programs such as that used in the current study makes the routine use of such models feasible.

4. Methodology

4.1 INTRODUCTION

The studies described in Chapters 2 and 3 provided both techniques and information required for the studies described in subsequent chapters. In the current chapter, both general methodologies and data common to these subsequent studies are described. Those used during the examination of the effects of fishing are presented first. Secondly, those used in the estimation of growth parameters are described. Methods used to estimate further biological and fisheries parameters using these growth parameters are then presented. Specific methodologies are described in the relevant chapters.

4.2 ASSESSMENT OF THE EFFECTS OF FISHING

The effects of fishing on the catch length, age and growth rate of exploited fish populations were examined using both simulation studies, and assessments of data from the case study populations. In the following section, the simulation studies, incorporating a model for density dependent growth, are first described. Subsequently, data used to assess the effects of fishing on the case study species are presented.

4.2.1 Simulations

This section describes the methods used to simulate the potential effects of fishing and density dependent growth on both the yield and catch length structure of simulated lutjanid and lethrinid populations.

A model to simulate the indirect effects of fishing through density dependent growth was derived, based on the study species' biology. The model was incorporated into the age-based simulation program 'MIDAS' (developed in the FMSP project R5484). Using this model, the effects of density dependent growth on the simulated yield-effort curves of the study species were examined. This was performed for three sub-models of increasing complexity. Based on these studies, one model for density dependent growth was selected for use in further simulations.

A model to generate length frequency data was also incorporated into the MIDAS program. To ensure that the output length frequency distributions were as accurate as possible, the level of individual growth variability estimated in Chapter 3 was employed. The algorithm for length frequency simulation was then used to examine the direct and indirect effects of fishing on the length structure of catches from exploited populations.

In the following section, the potential for density dependent growth in the study species is discussed. A background to the simulation of density dependent growth in fish species is then presented. The model to simulate density dependent growth, based on the study species' biology, is then described. The settings used within MIDAS to examine the effects of density dependent growth on the yield-effort curves of the study species are presented. Finally, the model used to simulate catch length frequency distributions, and the biological parameters required to perform these simulations, are presented.

4.2.1.1 Potential for density dependent growth in the study species

Although density dependent growth has been identified in a number of marine fish species, including coral reef species, it has not been studied in either the Lutjanidae or Lethrinidae. Practical studies on these species are limited by their biology. For instance, *P. filamentosus* in the Seychelles is found at depths between 75 - 150 m (Mees, 1993), limiting the ecological studies which can be performed. Studies are also limited by the remote location of the fishing grounds, and nature of the fisheries. However, the limited information available on their behaviour, biology and life histories indicates a number of factors which may result in density dependent growth. These are discussed below.

Diet

Since density dependence results from competition between individuals, it may be influenced by the dietary habits of these species. All three species are carnivores (Myers, 1989b; Haight *et al.*, 1993b; Newman, 1995). Competition for food is likely in carnivorous species, whose dietary range is constrained by the physiological adaptions required by their feeding habits.

The diet of Lutjanidae changes little with age (Parrish, 1987) indicating that if competition occurred, it would affect a considerable size range of the population. However, intra-specific competition is only likely at high densities, since Lutjanidae and Lethrinidae are capable of switching prey items (Parrish, 1987; Haight *et al.*, 1993b), and would therefore tend to avoid its consequences (Weatherly and Gill, 1987). A review of the general trophic biology of Lutjanidae and Lethrinidae concluded that intra-specific competition was unlikely to be significant (MRAG, 1996b).

Shoaling

L. mahsena may form both shoals and spawning aggregations (MRAG, 1996c). Observations of Lutjanidae in general indicate that species may spawn in groups (Thompson and Munro, 1983b). *P. filamentosus* is commonly found in large aggregations (Grandcourt, 1995; Newman, 1995), and congregates up-current and around submerged promontories (Ralston *et al.*, 1986). *A. virescens* is occasionally found in small shoals (Newman, 1995), while large catches can be achieved in one localised area, indicating that a high density of individuals can occur (A. Venkatasami, *pers. com.*). Shoaling in all three species is more common in juveniles (MRAG, 1996b).

Substrate Distribution

Since the distribution of suitable substrates for species such as *L. mahsena* is patchy, isolated groups of fish are likely to result. Such groups may exhibit little lateral exchange or adult migration, depending on the distance between them. Lutjanidae are also said to show high ‘site fidelity’ (Pauly *et al.*, 1996a). Such groupings may enhance competitive effects.

Juvenile/Adult Separation

Juveniles of all three species are more commonly found in shallow waters, mangrove areas and other inshore locations, spatially separated from the adults in deeper water. For example, according to Haight *et al.* (1993a), Parrish (1987) and Parrish *et al.* (1997), juvenile *P. filamentosus* in Hawaii remain in the relatively nearshore areas until about 1 to 2 years old. Such spatial separation reduces the level of competition between juveniles and adults.

4.2.1.2 Modelling density dependent growth

A number of models have been developed to simulate density dependent growth. Commonly, these have been based on data from closed systems such as aquaculture ponds or lakes. However, a number have also been derived for marine fish species.

Beverton and Holt (1957) examined the growth response of North Sea plaice and haddock to changes in population density. It was concluded that variations in growth due to density could be described by a von Bertalanffy growth function, with the asymptotic length L_∞ defined as a linear declining function of population density. Similar linear models have been proposed by Lorenzen (1996) for pond-reared common carp (*Cyprinus carpio*), by Barlow (1992) from experimentally reared guppy populations, and Salojaervi and Mutenia (1994) for whitefish lake stocks, while Helser and Brodziak (1998) used a linear density dependent growth model to simulate the management of recovering U.S. silver hake (*Merluccius bilinearis*) stocks. The distinct advantage of the linear model is its simplicity.

A number of more complex models have been developed. Backiel and LeCren (1978) reviewed growth data on pond reared carp (*e.g. Cyprinus carpio*), brown trout (*Salmo trutta*) reared in streams, and haddock (*Melanogrammus aeglefinus*) at different population densities in the North Sea. An inverse relationship between numbers and the change in weight (Δw) was proposed, with changes in density at low population numbers being associated with greater changes in average growth rate than similar changes at high numbers. Walters and Post (1993) developed a hyperbolic model to predict density dependent growth depression in juvenile pond stocked fish through the analysis of food production, feeding and the bioenergetics of growth. Unfortunately, the model required a large number of parameters to be estimated, limiting its use.

The majority of density dependent growth models (*e.g.* Beverton and Holt, 1957; Barlow, 1992; Lorenzen, 1996) have related changes in population density to changes in the von Bertalanffy growth parameter L_∞ (or the related asymptotic weight, W_∞), rather than to changes in K.

The von Bertalanffy growth function describes growth as the net result of anabolism (the build up of body materials, related to L_∞) and catabolism (the breakdown of existing body materials, related to K). Catabolism (K) is presumed to be affected by the amount of body material to be broken down (weight of the organism, level of metabolic activity) and therefore independent of population density. Anabolism (L_∞), or the build up of body materials, is dependent on the food resources available to individual fish, and therefore population density.

Estimates of L_∞ and K for a data set are strongly negatively correlated, and thus as the estimates of L_∞ decreases, that of K increases, and *vice versa*. The direct effect of density on metabolism (K) is still uncertain. Reiman and Myers (1990) found that the metabolic costs for the salmonid *Oncorhynchus nerka* increased with density. By contrast, fish may become more active (*i.e.* metabolic rate increases) when densities are lower and feeding rates higher (Kerr, 1982). In shoaling species, search time and thus metabolic rates may indeed be reduced as a function of shoal density (*e.g.* Wootton, 1976; Pitcher *et al.*, 1982).

4.2.1.3 The density dependent growth model

In this section, the basic density dependent growth model used within the simulations is derived.

Where a precise series of growth rate observations at different population density levels are available, density dependent growth can be quantified (Backiel and Le Cren, 1978). Such data were not available for the study species. A simple density dependent growth model was therefore developed, based on the biology of the study species.

In this model, the results of density dependent growth acted on either L_∞ or K, the specific parameter being selected by the user. On theoretical grounds, it is understood that population density should affect the value of L_∞. However, the arguments for changes in metabolic activity (K) with shoal density are relevant to the study species, since they form both shoals and spawning aggregations. The effect of changes in both growth parameters was therefore examined.

Based on the biology of the study species, three density dependent growth models of increasing complexity were devised. The computer program ‘Multi-species Interactive Dynamic Age-structured Simulation’ (MIDAS; Mees, 1997, FMSP project R5484) was updated by J. Rousseau to include a comprehensive intra-species density dependent growth model (Appendix 2), to the authors specifications. MIDAS itself is an update of the 'Age-Structured Population Dynamics' model (ASPD; Kirkwood *et al.*, 1994).

To simulate density dependent growth, changes in the growth parameter were linearly related to population biomass. Changes in the biomass of either the whole, or part, of the population were related to changes in either L_∞ or K, depending on the growth parameter specified by the user:

The relationship for L_∞ took the form:

$$L_\infty = L_{\infty 0}[1 - \frac{g(L)}{100}.\frac{B_0(L)-B(L)}{B_0(L)}]$$

while the relationship for K took the form:

$$K = K_0[1 - \frac{g(L)}{100}.\frac{B_0(L)-B(L)}{B_0(L)}]$$

where:

B	total biomass, averaged over the previous year
B_0	equivalent biomass at unexploited equilibrium
L_∞	asymptotic length (cm) at biomass B
$L_{\infty 0}$	asymptotic length (cm) at unexploited equilibrium (before changes due to density dependent growth)
K	von Bertalanffy growth parameter at biomass B
K_0	von Bertalanffy growth parameter at unexploited equilibrium (before changes due to density dependent growth)
g	gradient of the density dependent growth relationship, specified by the user
$B(L)$	sum of the biomass from all sizes greater than or equal to the length specified (L). Where this length was 0cm, changes in the total population biomass affected growth

The gradient of the linear relationship was set by the user. The model therefore assumed that density dependent growth occurred with equal strength at all population densities. Increases or decreases in growth due to density dependence may well reach an asymptote, since there will be biological limits to maximum or minimum size. Therefore, at extremes of the potential biomass levels, a sigmoid relationship might be more appropriate. Since no information was available on which to set such boundaries, it was felt that, for the potential biomass ranges in the field, density dependent changes in growth were adequately described by the linear relationship.

The initial von Bertalanffy growth parameter values ($L_{\infty 0}$, K_0) were those at unexploited equilibrium, *i.e.* before any changes due to density dependent growth. The gradient (*g*, specified as a percentage) was negative since reductions in biomass led to increases in L_∞ or K. The magnitude of *g* defined the limit to the change in the growth parameter, since when B*(L)* = 0, L_∞ (or K) increased by *g*%.

Gradients for the density dependent growth model

For these species there were no data from which to estimate the likely limits to the gradient of density dependent growth for each growth parameter (L_∞ or K). Literature studies on other marine species from which gradients could be calculated proved limited. The study of Beverton and Holt (1957) on haddock and plaice from the North Sea represented some of the few data available. A 30% gradient for the relationship with L_∞ in haddock (a ten fold change in population numbers resulted in a three-fold change in growth rate) and 25% for plaice (a two-fold change in density resulted in a 50% change in growth rate) was indicated.

An alternative method to calculate a possible limit to the density dependent growth gradients specifically for tropical Lutjanidae and Lethrinidae was investigated. A range of L_∞ and K estimates for a number of snapper and emperor species were obtained from the literature. For each species, the smallest and largest L_∞ and K estimates were noted, regardless of the location at which the estimate was derived (Appendix 3). The percentage difference from the smallest to the largest L_∞ and K estimate was calculated for each species, and these differences were then averaged (Table 4.1). Since the precision of growth parameters estimated through length-based methods is uncertain, parameters estimated through the use of hard tissues were employed where possible.

Table 4.1 Percentage difference between growth parameter estimates for a number of lutjanid and lethrinid species. The minimum and maximum values for growth parameter estimates (L_∞ (cm) and K) found in the literature, and the percentage difference between these values, are shown.

Species	Min L_∞	Max L_∞	% difference	Min K	Max K	% difference	*n*
Aprion virescens	65.8	104.0	59%	0.26	0.31	19%	5
Pristipomoides filamentosus	58.0	97.1	67%	0.15	0.31	112%	9
Etelis carbunculus	54.0	127.0	135%	0.13	0.36	186%	2
Etelis corruscans	82.0	116.0	41%	0.12	0.13	6%	7
Lutjanus bohar	52.0	81.7	57%	0.11	0.33	200%	4
Lutjanus kasmira	21.1	40.0	90%	0.21	0.38	79%	7
Lutjanus sebae	72.0	102.5	42%	0.13	0.31	136%	5
Lutjanus synagris	42.2	71.0	68%	0.20	0.27	34%	4
Lutjanus vitta	24.0	42.5	77%	0.26	0.37	45%	3
Lethrinus mahsena	58.9	61.7	5%	0.10	0.32	220%	4
Lethrinus miniatus	45.7	83.0	82%	0.10	0.27	170%	10
Lethrinus nebulosus	48.0	99.9	108%	0.10	0.34	237%	7
Avg. Difference			69%			120%	
SD			34%			83%	

The average difference in L_∞ was approximately 70%, while that in K was 120%. These values were viewed as the likely *maximum* increase in the growth parameters. The differences could be caused by a number of factors. For example, habitat effects, density dependent growth, individual growth variability, and estimation errors resulting from the methodology used. The parameters were also selected from a number of locations, where growth might be affected by local differences in temperature or food availability. There were insufficient estimates within locations to be able to negate this problem. However, while these average differences should not be viewed as the average level of density dependent changes alone, they do provide an idea of the relative scale of changes in L_∞ and K.

The density dependent growth gradients identified by Beverton and Holt (1957) were approximately half the total percentage difference calculated for L_∞ in Table 4.1. Assuming similar magnitudes of density dependent growth for temperate and tropical species, approximately half of the average variation in the lutjanid and lethrinid growth parameters might be attributed to density dependent growth. Using the relative scale of changes for L_∞ and K seen in Table 4.1, simulation runs were therefore performed with gradients of -35%

for L_∞ (half of 70%), and -60% for K (half of 120%). Due to uncertainties in the level of density dependent growth, simulations were also performed with density dependent growth at a range of gradients.

The population could be divided into size classes by the user. Density dependent growth could then be varied with size to simulate, for example, the spatial separation of juveniles and adults. Density dependent growth affected individuals within each size class at the specified gradient, as suggested by Beverton and Holt (1957). Here, however, the biomass influencing growth was calculated as the sum of biomass from all sizes greater than or equal to the size specified (B(*L*)). It was envisaged that individuals could not easily consume larger food items and would consequently shift to the target food items of smaller individuals. The biomass of larger individuals would therefore contribute to the density dependent growth rate of the smaller. There was one exception to this rule. Juveniles were modelled as spatially separated from the adult population. Therefore, density dependent growth acting on juveniles was not influenced by adult biomass directly.

The density dependent growth models

Three density dependent growth models of increasing complexity were defined for each of the study species. The action of density dependent growth on a population was constrained to specific size classes to mimic the effects of spatial separation and mating behaviour.

- Model 1 was the simplest simulation of the effects of density dependent growth on populations. Changes in L_∞ or K were related to changes in *total* population biomass. Therefore, total population biomass was assumed to represent the effects of competition on individual growth accurately, regardless of size or age.

- Model 2 simulated density dependent growth acting independently within two separate size classes. This simulated the spatial separation of individuals on the nursery grounds from those recruited to the adult fishery. The division length was based on the length of a 2 year old individual. This is the age at which *P. filamentosus* is said to recruit to the fishery in Hawaii (Haight *et al.*, 1993a). In the absence of data for *L. mahsena* and *A. virescens*, this age determined the division length for these species, based on the von Bertalanffy growth parameters.

- Model 3 was similar to model 2. However, in model 3 the adult population of model 2 was divided into two size classes, representing ‘small adults’ and ‘large adults’. The division length between these classes was based on the length at maturity (Lm_{50}). In the adult size classes, small adult growth was influenced by the biomass of the large adults. Growth in large adults was only influenced by the biomass within that size class. Density dependent growth gradients were specified for each size class.

The models, and the simulations performed using them, are described in detail in Chapter 5.

4.2.1.4 Effect of density dependent growth on the yield-effort curve

MIDAS was modified to estimate MSY under the conditions specified by the model inputs. The density dependent growth model derived above was employed within MIDAS, and the effect of density dependent growth on MSY and the shape of the yield-effort curve of the three study species examined (see also Beverton and Holt, 1957). In Table 4.2, the biological parameters required by MIDAS to simulate yield-effort curves for the study species are presented. These values, obtained from the literature, represented the best estimates of these biological and fishery parameters for the study locations at that time.

Table 4.2 Values for biological parameters required by MIDAS. Lengths in centimetres.

Parameter	Species		
	L. mahsena	*A. virescens*	*P. filamentosus*
Growth (non-seasonal)			
L_∞	61.7	94.7	75.8
K	0.100	0.321	0.244
t_o	-0.710	-0.190	-0.260
Length-Weight			
a	0.0000806	0.00002704	0.00004283
b	2.740	2.831	2.757
Reproduction			
Lm_{50} (females)	37.0*	55.0	51.0
Lm_{75} (females)	37.0*	74.0	59.0
Mortality			
M	0.220	0.560	0.480
Length at capture			
Lc_{50}	29.5	67.0	37.1
Lc_{75}	31.2	69.2	39.8
Stock Recruitment Relationship			
Type	Shepherd SRR through unexploited equilibrium, with density dependence		
Density Dependence in SRR (*d*)	0.8		
Source	Bautil & Samboo, (1988) - Mauritius	MRAG (1996) - Seychelles	

* no estimates for this parameter were available from the literature. The value used is an estimate based on data from other Indian Ocean banks species (MRAG, 1996b)

Maturity was assumed to relate to size and not age (*e.g.*; Jones, 1984; Gulland, 1987; Jones, 1987c). Length at maturity therefore remained constant with fishing pressure (*e.g.* Russ *et al.*, 1995), while age at first maturity depended on growth rate. Decreased growth rate would therefore imply increased mortality before reaching maturity.

Data on the stock-recruitment relationship in these species did not exist. Therefore, a stock-recruitment relationship of the functional form proposed by Shepherd (1982) was selected (see Appendix 2). This relationship could be adjusted as required, using the level of density dependence in the stock recruitment relationship (*d*; Kirkwood *et al.*, 1994). This dictated the number of individuals born at the start of each year, based on the average spawning stock biomass during the previous years' spawning season. A comparison of stock and recruitment data for similar species (Myers *et al.*, 1995) showed a range for *d* from 0.6 to 1 was suitable. Constant recruitment (*d*=1) was considered inadequate to represent stock effects at low biomass (Mees and Rousseau, 1997), and so a degree of density dependence *d* = 0.8 was selected. At this level, where the spawning stock biomass had been reduced by 20% of initial levels, recruitment would decrease by 5%.

4.2.1.5 The simulation of catch length frequency distributions

Both direct and indirect effects of fishing are likely to be detected as changes in the catch length structure. This section describes the simulations performed to examine these effects. Simulations were performed based on parameter settings for the emperor *Lethrinus mahsena*. An estimate of individual growth variability was derived for this species in Chapter 3. Density dependent growth was simulated using the most appropriate model identified through the simulations described in Chapter 5.

The simulation model used in these studies was also employed in the studies of the effects of fishing on the accuracy and precision of growth parameter estimates (Chapters 7 and 8). In that study, simulations were performed to mimic the fishing practices in two locations: Nazareth bank, and BIOT (Chagos Archipelago). Parameter estimates required for these simulations are presented.

Generation of length frequency distributions

A length frequency distribution simulation program was incorporated into MIDAS. The main features were:

- Both population and catch length distributions were simulated;
- Distributions were output either at equilibrium, or as a specified series of transient length frequency distributions;
- Distribution length class could be specified. This was set at 1cm for all simulations;
- The sample size and frequency of catch length frequency distributions was specified;
- Period, or periods, of recruitment during a year were specified as a normal distribution. Recruitment variability was specified with lognormal distribution;
- To incorporate the effects of density dependent growth, fish were simulated individually; and
- von Bertalanffy growth parameters were specified using mean values, and a covariance matrix (see below).

Cohorts were simulated from time t = - maximum age. This was the earliest time from which survivors might remain in the population at $t = 0$. Individuals were randomly assigned values from growth and recruitment parameter distributions at birth. These parameters remained constant throughout the lifetime of the individual, except where modified by density dependent processes.

The simulation time step was set to 0.1 of a year (approximately one month). For each simulation time step, whether an individual fish had survived or died was calculated, based on the level of natural and fishing mortality. Where an individual died within that time step, the probability that it had been caught, given that it had died, was calculated:

$$P(caught) = \frac{F}{F+M}$$

If caught, the length was stored in the catch length frequency. All lengths were stored for the population length frequency distribution.

Input parameters for *L. mahsena*

Table 4.3 describes the parameter values used to simulate length frequency distributions for *L. mahsena*, and their source. An estimate of individual variability in growth was derived for this species in Chapter 3. It will be noted that the parameters used in these simulations are different to those used in the simulations of the yield/effort curves (Table 4.2). This results from the improved parameter estimates derived from work performed subsequent to those initial studies.

Table 4.3 Biological parameters required by MIDAS for *L. mahsena*, and their source.

Parameter Group	Parameter	Value	Source
Growth	L_∞ (cm)	48.5	This chapter
	K (yr^{-1})	0.14	
	t_0	-0.78	
Length-weight	a	0.0000806	Samboo (1987)
	b	2.74	
Mortality	M (yr^{-1})	0.4	Pauly's equation
Reproduction	Lm_{50}	27.5cm	Lebeau and Cueff (1976)
	Lm_{75}	27.5cm	
Stock-recruitment relationship (SRR)	Type	Shepherd SRR, with density dependence (*d*)	Lebeau and Cueff (1976), MRAG (1996b), Mees and Rousseau (1997)
	d	0.8	
Recruitment	CV (Nazareth/Chagos)	61% / 25%	This chapter
	Recruitment peak	Oct. to Feb.	Samboo and Mauree (1988)
Age/Length at capture	Tc_{50} (Lc_{50})	3.75yrs (22.8cm)	This chapter
	Tc_{75} (Lc_{75})	4.17yrs (24.3cm)	

Von Bertalanffy growth parameters and individual variability

The level of individual variability in von Bertalanffy growth parameters of *L. mahsena* was estimated in Chapter 3. The analysis provided mean growth parameter estimates, and a covariance matrix describing the relationship between those parameters. Since the aim of this study was to provide an indication of the likely effects of fishing and density dependent growth on the length structure of long-lived, slow growing populations (Chapter 5), and on growth parameter estimates (Chapter 7), it was felt justified to concentrate on *L. mahsena* alone.

The suitability of the mean growth parameter estimates derived in Chapter 3 (L_∞ = 36.0, K=0.28, t_0=-0.3) for use in the current simulations was first tested. The parameters and covariance matrix were used to simulate length frequency distributions using MIDAS. These distributions were then compared to those sampled from the fishery. In turn, a simple age-cohort model incorporating the covariance matrix was also derived within an Excel^{TM} spreadsheet. Age-at-length distributions were simulated using the growth parameters, and compared to those distributions identified from Nazareth Bank otolith data.

Using the mean growth parameters estimated in Chapter 3, the resultant simulated length frequency distributions were not comparable to those sampled from Nazareth bank catches. In addition, the underlying age-at-length distribution did not resemble that identified from otolith samples. The back-calculated mean growth parameters were therefore unsuitable for use in the simulations. This may be a result of the relatively small sample size of the back-calculated length-at-age data set.

As an alternative, length-at-age data from 949 individuals sampled from Nazareth bank were used to estimate growth parameters through least-squares estimation. These growth parameter estimates (L_∞ = 56.1, K = 0.07, t_0 = -4.4) suffered from a lack of small individuals in the sample. While the resulting simulated length frequency distribution was comparable to that from Nazareth Bank, length-at-age distributions were poorly correlated with the true distributions at younger ages, due to the underestimation of K and t_0.

The feasibility of combining back-calculated length-at-age and individual age-at-length estimates was examined. Where data overlapped, the length-at-age data from the two sources appeared comparable (Figure 4.1). Growth parameter estimates were therefore obtained from the combined data set (Table 4.3). The length frequency distribution and underlying age-at-length distribution resulting from these growth parameters and the covariance matrix, were comparable to those found in the Nazareth fishery.

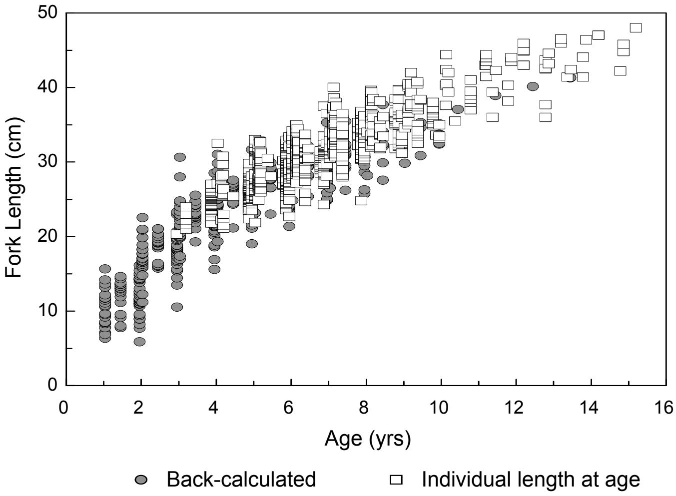


Figure 4.1 Age-at-length data for *L. mahsena* from combined and back-calculated sources.

Studies of the effect of density dependence on the yield-effort curves described in Section 4.2.1 were performed before the growth parameter estimates derived from the otolith data were available. Growth parameters used in the simulation of length frequencies (Table 4.3) are therefore different from those used in Section 4.2.1 (Table 4.2). However, brief analyses of the yield-effort curves using growth parameters derived from otoliths indicated that, while the curve for *L. mahsena* was different, general trends in the yield-effort curve resulting from density dependent growth were similar. Re-examination of the effects of fishing on the yield-effort curve using the new growth parameters was therefore not pursued.

Natural mortality

Literature estimates of natural mortality for this species have been based either on Pauly's formula (*e.g.* MRAG, 1997b), or through iterative use of length-based cohort analysis (Bautil and Samboo, 1988). The value used in simulation (M=0.4 yr^{-1}) was derived from the application of Pauly's equation to those growth parameters given in Table 4.3. This estimate agreed well with other natural mortality estimates for Lethrinidae (Table 4.4).

Table 4.4 Natural mortality estimates for lethrinid species available in the literature.

Species	Location	Natural Mortality Estimate (yr^{-1})	Reference
Lethrinus enigmaticus	Seychelles	0.2	Lebeau and Cueff (1975)
Lethrinus nebulosus	Fiji	0.51	Carpenter and Allen (1989)
	Kuwait	0.36	

Annual variation in recruitment

The literature did not provide estimates of the level of recruitment variation in Lutjanidae and Lethrinidae. An estimate of relative year class strength for *L. mahsena* was therefore derived from the numbers of individuals-at-age, determined from otolith samples. The level of annual variation in recruitment was estimated for both Nazareth bank, and for BIOT (Chagos Archipelago), the two locations examined in Chapter 7.

A catch curve was derived from the age frequency data obtained from random otolith samples from Nazareth and BIOT (Chagos Archipelago). Deviations from the regression line of the descending limb were assumed to represent variations in year class strength (Doherty and Fowler, 1994). Total mortality was estimated from the gradient of the catch curve descending limb. On the assumption of constant total mortality for all age classes, the total mortality estimate was used to back-calculate the numbers of individuals present at year zero required to account for the numbers found at each age (Table 4.5), based on a derivation of the exponential decay model:

$$n_0 = \frac{n_i}{e^{(-Z \, . \, i)}}$$

where n_0 = numbers at age zero
n_i = numbers at age i years
Z = total mortality

The coefficient of variation (CV, %) for numbers at age zero was then calculated.

Table 4.5 Numbers at age zero back-calculated from numbers at age (*i*) for Nazareth bank and BIOT (Chagos Archipelago), assuming constant total mortality across all ages (Z = 0.7 and 0.4, respectively).

Age *i* (yrs)	Nazareth		BIOT (Chagos Archipelago)	
	No. at age *i*	No. at age zero	No. at age *i*	No. at age zero
6	185	12,147	-	-
7	137	18,067	-	-
8	79	20,925	87	2,847
9	38	20,217	72	3,643
10	12	12,823	41	3,208
11	7	15,024	23	2,783
12	8	34,487	18	3,369
13	5	43,293	18	5,210
14	2	34,783	10	4,476
15	-	-	5	3,461
16	1	70,161	2	2,141
Mean		28,193		3,460
Standard Deviation		17,200		868
CV (%)		**61.0**		**25.1**

The variability seen in estimates of numbers-at-age is due to a combination of factors. These include variations in the size of the spawning stock biomass, and subsequent level of success in recruitment to juvenile grounds. The use of this estimate as the basis for annual recruitment variability ignores the contributions of spawning stock biomass. The latter is modelled using a separate variable (*d*).

Period of recruitment (spawning period)

The main spawning period for *L. mahsena* was from October to February (Samboo and Mauree, 1988). In the simulation, recruitment was therefore described by a normal distribution, with a mean (as a proportion of the year) of 0.96, and the standard deviation 0.10 of a year.

Age-at-capture

Age-at-capture (Ac_{50}) was calculated from the age-based catch curve derived for Nazareth bank. This catch curve was also used to calculate total mortality and the coefficient of variation (CV) in recruitment, as described above. Through the extrapolation of the total mortality regression line to younger ages, expected numbers at age were estimated. The shortfall when compared to the actual numbers at age found in the catch was assumed to result from gear selectivity. By dividing actual numbers at age by expected numbers at age, gear selectivity was described as a function of age. Linearisation of this selectivity function (*e.g.* Sparre and Venema, 1998) allowed Ac_{50} to be assessed through regression (Ac_{50} = intercept/-gradient).

Fishing mortality levels

To obtain a range of fishing mortality levels for the simulations, historical length-based assessments of *L. mahsena* populations were examined. Annual fishing mortality assessments for both the Mauritian banks and BIOT (Chagos Archipelago) have been based on the subtraction of natural mortality (calculated using Pauly's formula) from estimates of total mortality (generally through the length converted catch curve). The distribution of these estimates is shown in Table 4.6.

Table 4.6 Frequency of fishing mortality estimates (yr^{-1}) obtained through Z - M, by location (BIOT = BIOT, Chagos Archipelago).

F estimate	BIOT	NAZ	SMN	SMS	F estimate	BIOT	NAZ	SMN	SMS
0.05	3	0	0	0	0.65	0	0	0	0
0.1	3	0	0	0	0.7	1	0	0	0
0.15	1	0	0	0	0.75	0	0	0	0
0.2	2	3	0	1	0.8	0	0	0	0
0.25	3	4	1	2	0.85	1	0	0	0
0.3	2	0	0	0	0.9	0	0	0	0
0.35	0	0	0	3	0.95	1	0	0	0
0.4	0	1	2	0	1.0	0	0	0	0
0.45	0	0	1	1	1.05	0	0	1	0
0.5	0	0	0	0	1.1	0	0	0	0
0.55	0	0	0	0	1.15	0	0	0	0
0.6	0	0	0	1	1.2	0	0	0	1

Based on these distributions, four levels of fishing mortality were selected (Table 4.7)

Table 4.7 The four levels of fishing mortality selected for simulation.

Level of fishing mortality (F yr^{-1})	Basis for this value
0.05	Lowest estimate
0.25	Mode of estimates
0.7	Upper limit of frequent mortality estimates
1.2	Largest estimate

These four annual fishing mortality levels were used in all simulations examining the effects of fishing on catch structure and growth parameter estimation.

4.2.2 Assessments of the effects of fishing in the case study fisheries

4.2.2.1 Introduction

This section describes the data used to assess the effects of fishing on the catch length and age structure, and growth rate, of the case study species. The methods used to collect and process these data are described.

4.2.2.2 Methodology

This section is divided into three parts. The first describes the catch and effort data used in the study to calculate both cumulative effort and catch per unit effort (CPUE). In the second, the length frequency data, and the methods used to collect them, are described. The third describes the sampling methodologies used to collect otolith specimens in the study locations, and the techniques used to assess age-at-length. This section also details the biological information collected from individuals sampled for otoliths.

Since the otoliths of *P. filamentosus* could not be validated (Chapter 2), data collection for this species was halted early in the sampling regime. Analyses performed in this chapter therefore concentrate exclusively on assessments of *L. mahsena* and *A. virescens* data.

Factors such as temperature, or localised productivity levels can result in differences in growth rate or population structure between locations. To minimise these effects, trends were also examined within locations (*i.e.* between statistical areas).

Catch and Effort Data

To examine the effects of fishing, trends in the assessed characteristics were compared with either the level of cumulative fishing pressure applied, or CPUE obtained, in that location or statistical area. This section describes the sources of effort data used.

In FMSP project R4584, effort data for Seychelles and Mauritius was standardised for the relative fishing power of each vessel (boat-gear type), and both depth and season fished, using a generalised linear model (GLIM4, Francis *et al.*, 1993). Effort was standardised relative to one man day fishing by handline from a dory in the depth range 0-75m, during the period of the SE trade winds (model: boat, season, depth). The relative fishing power of the Seychelles mothership was assumed to be equivalent to that of the average Mauritian vessel. BIOT (Chagos Archipelago) effort data could not be standardised since the data lacked sufficient spatial and temporal homogeneity; vessels in a statistical area varied from year to year, while different vessels fished at different times and locations (Mees *et al.*, 1999). Therefore, the relative fishing power of each Mauritian mothervessel calculated for the Mauritian banks was assumed to apply to the same vessels when operating in BIOT (Chagos Archipelago) (Mees *et al.*, 1999). Mauritian and Seychelles effort data had been previously standardised up to 1994 (MRAG, 1996c; MRAG, 1996d, respectively). Standardisation of data from subsequent years for Mauritius and Seychelles, and from all years for BIOT (Chagos Archipelago), was performed using the relative fishing powers previously calculated. This was felt valid since no major technological changes had occurred in the fishing fleet during the intervening period.

Mauritian Banks

Catch and effort data, in the form of the number of men fishing each day (man days), was available for each vessel from Mauritian fishing logbook returns from 1988. Prior to this period, unstandardised data were available from a number of sources: 1969-1977 Ardil (1979), FAO/SWIOP (1983); 1977-1988 Samboo (1989); 1977-1986 Ardil (1986). These were reconciled in MRAG (1996c). The latter data could not be standardised since it lacked specific vessel information.

Seychelles

Catch and effort data were collected by SFA through the stratified Seychelles Catch Assessment Survey (CAS; Seychelles Fishing Authority, 1990). Data were available by boat and gear type from 1985.

BIOT (Chagos Archipelago)

From 1991, catch and effort data (in man days) were available by location and statistical area within the British Indian Ocean Territory from inshore fishing logbooks (Mees *et al.*, 1999).

It was noted that cumulative effort did not provide information on the temporal pattern of fishing. If a location had been unexploited and then fished heavily for a limited number of years, a similar cumulative effort could result to that in an area which had been lightly fished over a longer period. However, the effects on the stock structure would be different. An examination of data for each location over time indicated no large changes in the annual effort level. Cumulative effort assessments for the study locations would therefore relate to similar effects on the exploited populations.

The period over which cumulative effort could be assessed varied. For example, accurate effort data was only available from BIOT (Chagos Archipelago) since 1991, although fishing had occurred previous to this year. For comparisons between locations, cumulative effort was assessed over the period for which data were available from all locations. Where stock structure was assessed within locations over time, effort data were assessed as far back as the maximum age of the fish from the first year of stock data, or as far back within this period as data allowed. From Chapter 2, maximum age for *L. mahsena* was 16 years, while that for *A. virescens* was 27 years (see Section 2.3).

For comparisons between or within locations, effort in man days was standardised to a unit bank area (km^2) for each location. Effort was therefore calculated as man days km^{-2}. Area estimates are detailed in Chapter 1. Where available, estimates of fishable area were used. Otherwise, total area was used. The area used was consistent within comparisons.
Assuming constant catchability, CPUE is an index of resource abundance (Hilborn and Walters, 1992). Estimates of CPUE were therefore used to assess mean length-at-age data for the presence of density dependent growth (Section 6.2.2.2). Since detailed data on individual species were not available from Seychelles and Mauritius, total demersal catch and effort were used to calculate CPUE for each specific year. Seychelles and BIOT (Chagos Archipelago), and to a lesser extent the Mauritian banks, are multispecies fisheries. Hence, such assessments did not represent the abundance of the study species alone. However, total demersal CPUE was assumed to provide a reasonable approximation of the strength of both inter- and intra-species competitive interactions. Both these influences are likely to affect growth.

Examination of catch length structure

This section describes the length frequency data available from each study location, and the methods used to collect and process them.

Mauritian Banks

The collection of length frequency data from commercial catches of *L. mahsena* for each of the Mauritian banks was initiated by the staff at Albion Fisheries Research Centre in the fourth quarter of 1988. Since the fishery is largely monospecific (Ardil, 1986; Bertrand, 1986), length frequency data collection concentrates exclusively on this species. Prior to this period, limited length frequency data between 1977 and 1987 were available for Nazareth bank from Bautil and Samboo (1988).

The numbers of individuals sampled by year and bank are presented in Appendix 4. Due to the seasonality of the fishery, monthly samples for certain locations were not always available. For analysis, data were grouped into quarters of the year.

Limited data were also available from the 1996 and 1998 BIOT (Chagos Archipelago) inshore observer programmes. In these years, vessels fished on the Mauritian banks either before proceeding to, or on the return journey from, BIOT (Chagos Archipelago).

Seychelles

Length frequency data collection in Seychelles was initiated in late 1989 (Mees, 1993). Data were collected for the main species found in the commercial catches, including *A. virescens*, but not *L. mahsena*. Data were mainly collected from schooners landing fish to the

Seychelles Marketing Board (SMB, now Oceana Pty. Ltd.) at Port Victoria, and from SFA research cruises (MRAG, 1996d). From 1990, gear type and fishing location (Sector number) were noted. The number of *A. virescens* individuals sampled each year, by statistical sector, are presented in Appendix 4.

Through the otolith sampling programme, a limited quantity of length frequency data was also available for *L. mahsena* from 1997 and 1998.

British Indian Ocean Territory

Length frequency data collection in BIOT (Chagos Archipelago) began with the initiation of the joint British-Mauritian observer programme in 1994. The observer programme generally lasts for a period of around three months, around the beginning of the April-October fishing season. Data are noted by statistical fishing area within BIOT (Chagos Archipelago). The number of *A. virescens* and *L. mahsena* individuals sampled each year are presented in Appendix 4.

During 1997 and 1998, small emperor individuals were commonly separated from the main catch, since they were purchased by the company at a different price. Care was taken to ensure that such individuals were included in the length frequency sample.

Examination of catch age structure and growth

The marks seen in the otoliths of *L. mahsena* and *A. virescens* were validated as annual in Chapter 2. This allowed direct studies of the effects of fishing on population age structure and growth. This section describes the collection of otoliths from the study locations in the Indian Ocean. The sampling regime, and methodologies involved in otolith preparation and assessment, will be described. The methods used to derive and analyse catch age structure and length-at-age for the effects of fishing are detailed.

The sampling regime

An otolith sampling programme was initiated through port collections in Mauritius (by Albion Fisheries Research Centre) and Seychelles (by Seychelles Fishing Authority) and during the 1997 and 1998 BIOT (Chagos Archipelago) inshore observer programmes. For Seychelles and BIOT (Chagos Archipelago), otoliths were sampled from both *L. mahsena* and *A. virescens* catches. Due to the relatively mono-specific nature of the Mauritian fishery, only *L. mahsena* samples were taken.

Two sampling regimes were specified: random sampling and targeted sampling. Random sampling programme was designed to develop a catch age structure (Chapter 6), and to allow the age-based assessment of mortality and age-at-capture (Chapter 9). Based on initial assessments of the range of ages in catch samples, at least 250 fish were requested from each location for this purpose. The structured sampling programme was designed to improve age-based assessments of growth rate (Chapter 6), and allow age-based estimation of von Bertalanffy growth parameters (Chapter 9). It supplemented the random sample with otoliths from the extremes of the available size range. These were generally under-represented, but are highly influential in the estimation of growth parameters (*e.g.* Ferreira and Russ, 1994). Samples sizes were still limited by the selectivity characteristics of the gear, and actual population structure present.

The progress of otolith collection in each location was monitored on a ‘Collection of Otoliths’ form (Appendix 5). This form specified the number of fish required for structured sampling, by size class and sex. As otoliths from each fish were collected during the random sample, that individual was marked on the form. Once sufficient random samples had been obtained in each location, the sheet was examined. Any under-represented size classes were targeted until sampling for that class was complete.

Due to the removal of otoliths, collection of biological information and sample sizes required, un-gutted fish were purchased from fishermen and fishing companies in Seychelles and Mauritius, respectively. In BIOT (Chagos Archipelago), sampling during the observer programme was carried out on gutted fish specimens as they were returned to the mothervessel. Details on the location of fishing, (by statistical area in Seychelles and BIOT (Chagos Archipelago), by bank in Mauritius), fishing method, hook size, and the depth fished were obtained from the fishing master or fisherman.

The following information was collected from each fish specimen sampled for otoliths:

• Length	Total, fork and standard length were collected from each unfrozen fish. Lengths were measured to the nearest centimetre in BIOT (Chagos Archipelago) and to the nearest millimetre in Mauritius and Seychelles. Where the tail of the fish was damaged, total length was not taken.
• Weight	Whole and/or gutted weight was measured to the nearest gramme. Generally, fish sampled in BIOT (Chagos Archipelago) had been gutted before sampling.
• Sex	The sex of the fish (male, female, unknown) was assessed for all whole specimens. If necessary, microscopic interpretation of the reproductive organs was performed.
• Maturity	The maturity stage was assessed on a five point scale in the Seychelles (Mees, 1992), while an eight point scale was used in both Mauritius and BIOT (Chagos Archipelago) (MRAG, 1996a).
• Gonad weight	Where feasible, gonad weight was assessed to the nearest hundredth of a gramme in both Seychelles and Mauritius. No gonad weights were taken during the BIOT (Chagos Archipelago) inshore observer programme.

Once the biological data had been collected, the pair of otoliths were removed from each sampled fish. Each fish was identified with a unique ‘fish number’, comprised of the number of that fish in the sample, and the date. This code was noted on both the otolith envelope and corresponding data sheet, along with the species and sample location.

Preparation and ageing

Otoliths were forwarded to CEFAS for sectioning and staining (Chapter 2). The corresponding biological data was incorporated into the master database. The researcher was trained in the techniques of otolithometry by CEFAS. Sectioned and stained otoliths prepared by CEFAS were then read by the researcher using a Leica MZ6 compound light microscope at x16 to x32 magnification.

Integer ages were used during all age-based studies described in Chapter 6. Age determinations were performed with reference to a designated birthday (Holden and Raitt, 1974; Vilizzi and Walker, 1999). For both species, an arbitrary birthday of 1st January was set, following the convention for most Atlantic species. This corresponded with the spawning periods identified for these species in the study locations (Bertrand, 1986; MRAG, 1996d). In *A. virescens*, this period corresponded with the period of stained ring formation. For *L. mahsena*, stained rings are laid down in the middle of the year. Therefore, to ensure that the age corresponded with the correct year class, the last ring at the edge of the otolith section was not counted between the period of deposition and the 1st of January in the following year. The year-class of a fish could then be established simply by subtracting assessed age from the year of capture.

In otoliths where indeterminate rings were present, ages were potentially uncertain. Two ages classes were therefore noted. The first was the age considered to be the most appropriate, while the second was the potential alternative age. For example, 5?6 denoted a fish that was most likely five years old, but was potentially six years old. The more certain (first) age was used. Where both ages were considered equally likely, fish could not be aged accurately. As a result, no age was noted.

4.3 ESTIMATION OF GROWTH

In simulations and assessments for the study species, von Bertalanffy growth parameters were estimated through both length- and age-based methods. In the first section, the methods used to simulate the estimation of von Bertalanffy growth parameters through both methods are described. The subsequent section describes those methods used in the actual assessment of growth parameters for the case study species.

4.3.1 Simulated assessments of growth

4.3.1.1 Length-based estimation of von Bertalanffy growth parameters using LFDA

The estimation methods available within LFDA were used to obtain growth parameter estimates, based on the time series of catch length frequency data simulated by MIDAS. Normally, fitting a growth curve to length frequency data involves a degree of subjective assessment by the user. Since the process was automated, fits could not be assessed visually. The score function of each method was therefore used to select the 'best-fitting' growth curve. The sequence used to obtain these growth parameters is described in the flow chart presented in Figure 4.2. Notes applying to this figure are provided below.

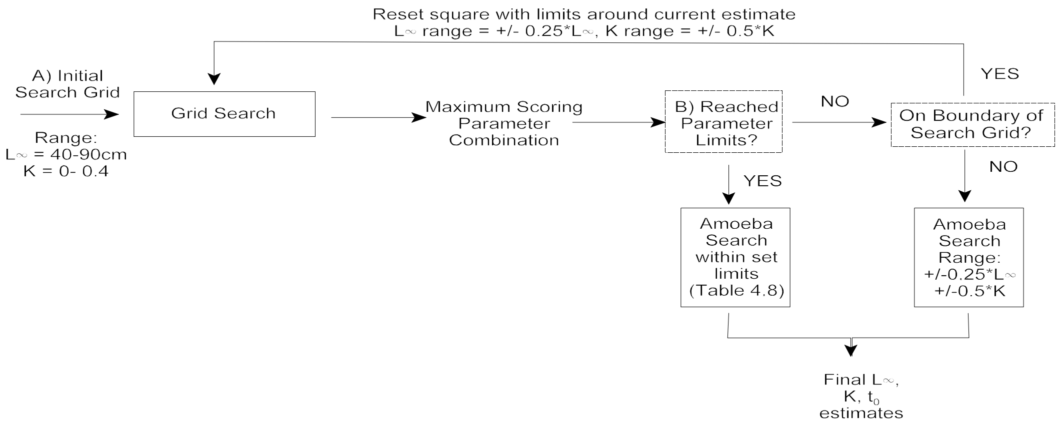


Figure 4.2 Decision tree applied to the length-based growth parameter estimation process performed using LFDA.

- An initial 'grid search' was carried out for values of K from 0 to 0.4 (step size 0.025) and L_∞ from 40 to 90 (step size 2.5). The boundaries of this search were set based on manual searches performed by the author.

- If the resultant parameter estimates were on the boundary of the search grid, the grid was adjusted as described in Figure 4.2. If this occurred a number of times, growth parameter estimates may have reached non-feasible levels ($0 \le K \le 1$, $0 \le L_\infty \le 150$). In this case, initial searches ceased, and a subsequent amoeba search (Chapter 1, Section 1.5.2) was performed within set limits (Table 4.8).

Table 4.8 Search limits for K and L_∞ set when grid search reached unrealistic values.

Parameter	Limit breached	Parameter range set: from	to
K	≤ 0	0	0.2
K	≥ 1	0.8	1
L_∞	≤ 0	0	40
L_∞	≥ 150	110	150

The maximum scoring output of the amoeba search through either route described in Figure 4.2 was accepted as the best fitting growth parameter set of L_∞, K and t_0 for that data.

4.3.1.2 Age-based estimation of growth parameters

In simulations described in Chapter 7, age-based methods of growth parameter estimation were carried out to compare the performance of this assessment method with that of length-based methods.

Age frequency data were not simulated within MIDAS. At the time this program was modified to output length frequencies, the aims of the project were to assess the effects of fishing and density dependent growth on growth parameter estimates derived through length-based methods alone. However, it became clear from initial assessments that length-based growth estimates were significantly more biased than expected from studies described in the literature. It was therefore decided to examine the effects of fishing on age-based growth parameter estimates. MIDAS could not be restructured to output age-at-length data within the timescale required. Age-at-length was therefore simulated within an EXCEL^{TM} spreadsheet. The simulation was designed to mimic the procedures used within MIDAS as closely as possible.

Simulation of length-at-age data

To summarise, individuals were simulated in an EXCEL^{TM} spreadsheet throughout their lives. This was modelled based on individual growth parameters selected from the mean and covariance matrix, as used within MIDAS. Based on their probability of survival to a given length (which incorporated the effects of gear selectivity) individuals were randomly 'sampled' from the population. The resultant age-at-length data were used to estimate growth parameters. This process is now explained in more detail, as follows:

This simulation used a modification of the EXCEL^{TM} spreadsheet derived in Chapter 3 (Section 3.2.3). Within this spreadsheet, 500 separate growth parameter combinations were simulated, based on the mean growth parameters (L_∞ = 48.5, K=0.14, t_0=-0.78) and the covariance matrix derived in Chapter 3.

For the 500 individuals, age-at-length data were simulated in 2cm length classes between 6cm and 48cm. This was the size range found in the combined back-calculated and individual length-at-age data sets, as used to calculate the mean growth parameters used within MIDAS (Section 4.2.1.5). Each individual was assigned a length within the boundaries of that 2cm size class, based on a uniform distribution. Using each individual's growth parameters, the age at this length and at L_{min} was calculated. L_{min}, the length at which fish first entered the fishery, was set at 13cm (the smallest fish found in the catch from Nazareth bank was 13.5cm).

To simulate the sampling programme, 10 individuals were randomly selected from each two centimetre size class. The exception was the 46-48cm size class, from which five individuals were selected. The selection of individuals was based on the probability of their survival to that length (P_{surv}), calculated from the natural and fishing mortality experienced up to that length:

$$P_{surv} = e^{(-(M*t_1)-(F*t_2))}$$

where t_1 was the current age, and t_2 was the difference in years between t_1 and the age at L_{min}. Natural mortality was set at M=0.4 (Table 4.3), while fishing mortality was set at the level required for the simulation (Table 4.7).

The assumption of constant fishing mortality from L_{min} did not accurately mimic the simulation process used within MIDAS, since the latter included the effects of gear selectivity. Consequently, gear selectivity was accounted for as follows.

The selectivity ogive for the gear (S_i) followed the age-based equation:

$$S_i = \frac{1}{[1 + e^{(a-b*L_\infty*(1-e^{(-K*(t-t_0))}))}]}$$

where *a* and *b* were constants. From the growth parameters and values of Lc_{50} and Lc_{75} presented in Table 4.3, the equation was solved simultaneously for these points on the selectivity ogive, to estimate values for the constants; *a*=16.70 and *b*=0.73.

The age-based selectivity equation accounted for the fact that different levels of total fishing mortality would be experienced by individuals with different growth rates; the selectivity ogive was contracted or expanded depending on the growth parameters of each fish. By multiplying the resultant age-based selectivity ogive by the fishing mortality rate, the area under the ogive up to current age (t_i) was equivalent to the total fishing mortality experienced. This area was calculated for each individual within each exploited length class (*i.e.* where current length was greater than L_{min}) using Simpson's Rule. The calculation was performed within a Visual Basic program, based on the algorithm found in Press *et al.* (1996).

P_{surv} was therefore based on the combination of cumulative natural mortality (*i.e.* the product of 0.4 and age at the stated length) and fishing mortality.

By dividing each individual's P_{surv} by the summed P_{surv} from all 500 individuals in that length class, a relative probability of survival was obtained for each fish. These relative probabilities were ranked in ascending order, and a cumulative probability calculated. Individuals were then sampled based on this cumulative probability, and a set of random numbers selected from a uniform distribution between zero and one. Individuals were sampled where the random number just exceeded their cumulative probability.

Samples from each length class were grouped to develop the overall age-at-length sample. Growth parameter estimates were then calculated from each overall data set using least squares methods. This process was repeated one hundred times.

Assessment of the mean population growth parameters

Mean population growth parameters initially used in the simulation of age-at-length data were identical to those used in the MIDAS length frequency simulation (L_∞=48.5, K=0.14, t_0=-0.78). The suitability of these mean parameters was first tested.

The mean growth parameters were estimated using otolith samples from Nazareth bank (Table 4.3). Therefore, mean growth parameters estimated from simulated age-at-length data, using identical sampling methods, should be similar to those mean population parameters. Growth parameters were therefore estimated from age-at-length data simulated at F=0.25yr^{-1} (current best estimate of fishing mortality at Nazareth bank).

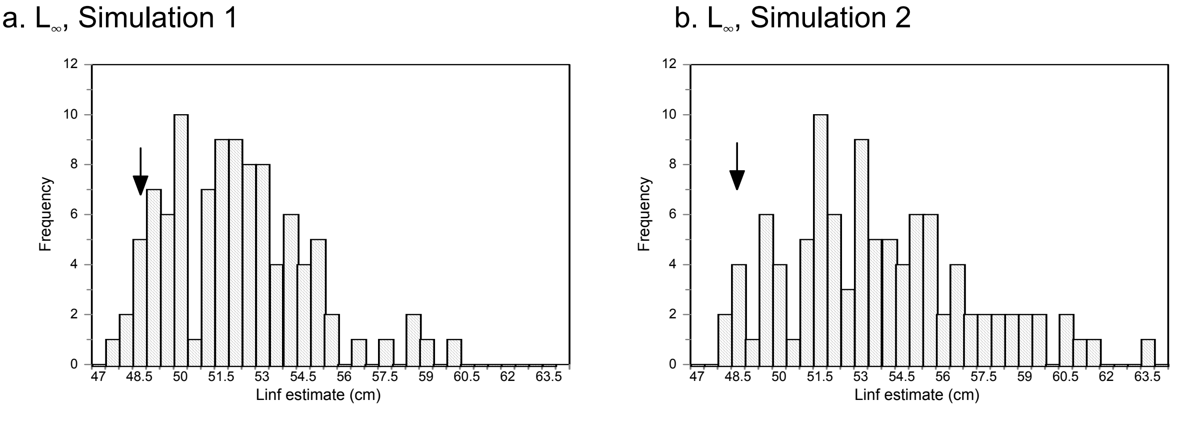
Mean growth parameters estimated from the simulated age-at-length data (Table 4.9, simulation 1) were positively biased. 'True' values were at the lower end of the parameter estimate distributions (Figure 4.3). Mean growth parameters used in the simulation therefore required proportional adjustment, to improve the comparison with actual Nazareth growth parameter estimates. Two caveats were placed on this adjustment; both ages-at-length distributions and length frequencies derived with adjusted growth parameters should remain comparable with actual Nazareth samples.

The mean sample estimates suggested a decrease in both population growth parameters to L_∞=43.9, K=0.12. When these mean parameters were used, output L_∞ estimates were again positively biased. However, the mean estimate of K was greatly improved (Table 4.9, simulation 2). The 'true' value of L_∞ (48.5) remained at the lower end of the L_∞ estimate distribution, although the distribution of estimates was now skewed toward this value. The 'true' estimate of K was central in the estimate distribution.

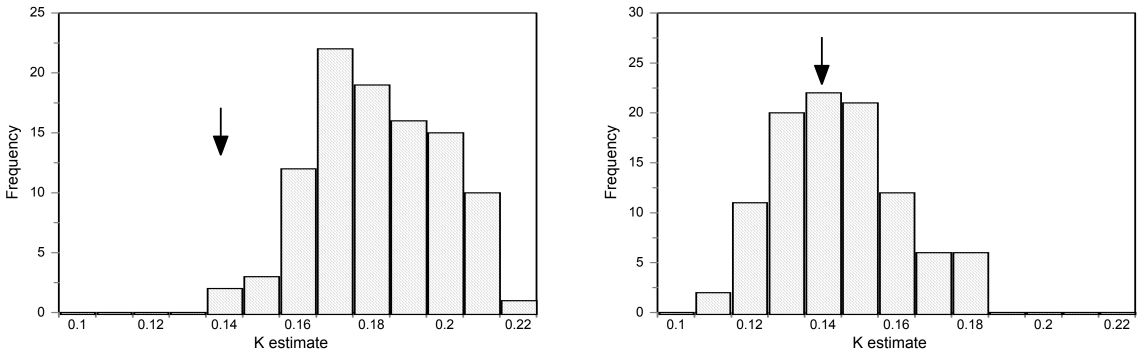
Table 4.9 Adjustment of mean population parameter estimates to obtain the required mean parameter values resulting from sampling (L_∞=48.5, K=0.14).

		Population mean	Resultant sample mean	Suggested population parameters
Simulation 1	L_∞	48.5	54.0	43.9
	K	0.14	0.17	0.12
Simulation 2	L_∞	43.9	53.4	-
	K	0.12	0.14	-

The age-at-length and length frequency distributions calculated from the adjusted population parameters remained comparable to those seen in Nazareth. Length frequency distributions based on these adjusted parameters were not significantly different from those where the original population parameters were used (Kolmogorov-Smirnov test, $D_{0.05}$ = 0.096, D = 0.081).


a. L_∞, Simulation 1

b. L_∞, Simulation 2


c. K, Simulation 1

d. K, Simulation 2

Figure 4.3 Distribution of L_∞ and K estimates resulting from simulation 1 (pre-population growth parameter adjustment) and simulation 2 (post-population growth parameter adjustment). Arrows denote 'target' values.

Further adjustments to the population parameters failed to improve the mean sample L_∞ estimates. Extremely low population L_∞ estimates (*e.g.* L_∞ = 35.1cm) resulted, while the age-at-length and length frequency distributions no longer resembled the Nazareth sample. L_∞=43.9 and K=0.12 were therefore used as the population mean growth parameters in the simulations.

The non-linearity in the relationship between population and sample L_∞ estimates seen in the adjustments was a result of the covariance matrix. Decreasing the population L_∞ decreased the numbers of individuals surviving to larger size classes. Individuals that did survive had L_∞ and K combinations selected from the extremes of the growth parameter distributions. At larger sizes, therefore, individuals present were unrepresentative of the true growth parameter distribution. This had a significant effect on the resulting growth parameter estimates.

In theory, the adjusted growth parameters should also have been employed within the MIDAS simulation of length frequency distributions. However, the use of these growth parameters resulted in length frequency distributions which were not significantly different from those where the original population parameters were used (see above). Given this similarity, the inaccuracy and imprecision of length-based growth parameter estimates, and the practical consideration that a number of length-based simulations had already been performed, the mean population parameters used within MIDAS were not adjusted.

4.3.2 Practical assessments of growth

Using data from the study fisheries, von Bertalanffy growth parameters were estimated through both length- and age-based methods. In the following sections, the methods used to estimate these parameters are detailed.

4.3.2.1 Length-based methods

Time series of length frequency data were available from all locations (Appendix 4). Data from BIOT (Chagos Archipelago) were only available from the observer programmes. The resulting three month data sets were amalgamated by year. Due to the small quantities of data for *L. mahsena* from Seychelles in 1997 and 1998, data were also amalgamated by year. Data for *A. virescens* for this location, and *L. mahsena* from the Mauritian banks, were grouped by quarter of the year. Data were examined by gear type.

Each time series was examined for modal separation and progression. Von Bertalanffy growth parameters for each data set were estimated using the three growth parameter estimation algorithms provided in LFDA4 (Holden *et al.*, 1995); SLCA, PROJMAT, and ELEFAN.

Where sample sizes for particular time periods within a data set were low (less than 50 individuals), and represented isolated data within the time series, those samples were discarded. Such samples would otherwise have had a disproportionate influence on the growth parameter estimation processes (Hoenig *et al.*, 1987). Estimates were initially derived using the full time series. Where the time series was discontinuous, sub-sets of data were subsequently examined individually.

An initial range of L_∞ and K values was selected for the grid search procedure (Section 4.3.1.1), based on growth parameter estimates from related species, sizes observed in the length frequency distribution, and information obtained from the simulations performed in Chapter 7. This range is presented in Table 4.10. This initial search area was left deliberately wide to ensure that the search was not unduly constrained around the 'expected' parameter values.

Table 4.10 The range of parameter estimates searched using the 'score function grid'.

Species	L_∞ (FL, cm)		Number of Evaluations	K (yr^{-1})		Number of Evaluations
	From	To		From	To	
L. mahsena	40	80	21	0.05	0.5	10
A. virescens	60	120	31	0.1	0.5	9

Maxima identified within this grid search were used to concentrate the subsequent contour plot search. Potential maxima, as identified by the score function, were focussed on in turn and the fit of the resulting growth curve to the length data examined. As noted in MRAG (1996d), the selection of the most appropriate growth parameters involved a combination of the score function details, the plotted fit of the growth curve to the data, and experience.

Initially, non-seasonal growth curves were fitted to the length frequency data. However, seasonal growth was evident from the pattern of increment deposition in the otoliths of these species. Therefore, seasonal growth curves were also applied, using this facility within LFDA, to investigate whether the fit to the data was improved.

4.3.2.2 Age-based methods

Age-based von Bertalanffy growth parameter estimates were calculated from individual age-at-length data obtained from otolith assessments.

Age determinations were performed with reference to a designated birthday (January 1st). Integer ages were assigned as described in Section 4.2.2.2. For the growth assessment, a 'partial age' was then calculated. Individuals caught on 1st January were assigned an integer age. For fish caught during the year, a decimal age was computed as:

integer age + (days from January 1st to date of capture/365)

For each location, a von Bertalanffy growth function was fitted to assessed length-at-partial age using likelihood methods (Kimura, 1980). The log-likelihood was maximised using the Quattro Pro™ 'optimiser', by varying the values of L_∞, K, t_0 and ε_u. Where it was felt valid, based on visual assessments, seasonal two-phased growth curves of the type described in Soriano *et al.* (1990) were fitted by least squares methods. The seasonal growth curve equation takes the form:

$$L_t = L_\infty (1 - e^{-KA(t-t_0)})$$

where:

$$A = 1 - \frac{h}{(t-t_h)^2 + 1}$$

t_h	the age at which the transition between the two growth phases occurs
h	determines the magnitude of the maximum difference between the seasonal and non-seasonal curves

4.4 ESTIMATION OF FURTHER BIOLOGICAL AND FISHERY PARAMETERS

To allow stock assessments to be performed, and hence management actions to be derived, the growth parameter estimates obtained through length- and age-based methods were used to estimate further biological and fishery parameters. This was performed in both the simulations (Chapter 7), and during the study fishery assessments (Chapter 9). In each case, total, natural (and hence fishing) mortality, length-at-capture, and yield-per-recruit (and hence both F_{MYPR} and $F_{0.1}$) were estimated.

In the following section, the methods used to estimate these parameters during the simulations are described. Where the methods used to calculate these parameters were different in the assessment of the study fisheries, they are detailed in Section 4.6.2.

4.4.1 Methods used in the simulations

4.4.1.1 Estimation of Mortality

Total mortality (Z) was estimated using two length-based methods; the Beverton-Holt Z estimator (Beverton and Holt, 1956), and the length-converted catch curve method (*e.g.* Pauly, 1983). Natural mortality (M) was estimated using the empirical methods of Pauly (Pauly, 1980) and Ralston (Ralston, 1987). From these estimates, fishing mortality (F) estimates were derived (F=Z-M).

Beverton-Holt's total mortality (Z) estimator

This method was available within the LFDA package. The Lc_{50} estimate derived from the first year of length frequency data through the length converted catch curve (see below) was used for L_c.

Length-converted catch curve

Within an EXCEL^{TM} spreadsheet, the length frequency distribution representing the last year of simulated data was transformed into numbers caught at age, as described in Sparre and Venema (1998). In summary, the mid-point of a length class (bounded by lengths *L1* and *L2*) was converted into age using the inverse of the von Bertalanffy growth equation. This represented the *x*-axis of the catch curve plot (x = *t*((*L1*+*L2*)/2)). For the *y*-axis of this plot, numbers caught in that length class were divided by the time taken to grow through the length class (Δ*t*), as defined by the growth parameters. The natural log of this value was then taken:

$$y = \ln \frac{C(L1,L2)}{\Delta t(L1,L2)}$$

The selection of points defining the regression on the catch curve descending limb thus derived normally involves a subjective assessment by the user. However, since the Monte-Carlo simulations were automated, these points were selected using a standard set of criteria.

The peak of the catch curve was identified by iteratively assessing points from the start of the data. The peak was assumed to have been reached when the values in a series of three adjacent cells declined (*i.e.* cell 1>cell 2, cell 2>cell 3). However, due to the inconsistency of declines in the catch curves, this process did not always identify the correct peak. A further decision rule was therefore added. If cell1>cell2, but cell2<cell3, a peak was still declared if cell3>cell4 *and* cell 1>cell4. In both cases, the start point for the Z regression was taken as one point past the peak (*i.e.* cell 2).

The end point of regression was based on the L_∞ estimate. If L_∞ was larger than the largest individual in the length frequency, the end point was taken as the last cell after the assessed peak with a non zero catch (a zero value in the regression would result in an error). Manual assessments using simulated data showed that this point generally lay on, or close to, the line of the descending limb. If the estimate of L_∞ was smaller than the largest individual found in the catch, the end point was taken as $0.95*L_\infty$. In both cases, the process avoided using points close to L_∞. Using the start and end points identified, a regression of *y* against *x* was carried out, the gradient of which was -Z.

Pauly's empirical formula for natural mortality ('Pauly's M equation')

Using the von Bertalanffy growth parameter estimates, and an estimate of the average annual habitat temperature T (°C), Pauly's estimate of natural mortality was obtained:

$$Ln(M) = -0.0152 - 0.279*Ln(L_\infty) + 0.654*Ln(K) + 0.463*Ln(T)$$

In Pauly's analysis, the temperature used for shallow water benthic species, such as the study species, was the sea surface temperature (Pauly, 1980). An average annual sea surface temperature of 27°C was used for both the Mauritian banks and BIOT (Chagos Archipelago) (obtained from the Nautical Almanac for the Indian Ocean).

Ralston's empirical formula for natural mortality (Ralston, 1987)

Using the estimated von Bertalanffy growth parameter K, Ralston's M estimate was obtained:

$$M = 0.0189 + 2.06*K$$

Calculation of Fishing Mortality

The current level of fishing mortality (subsequently called F_{curr}) was estimated using the two values of total and natural mortality calculated above. This resulted in four different F_{curr} estimates.

4.4.1.2 Estimation of length-at-capture and yield-per-recruit

Length-at-capture (Lc_{50})

The spreadsheet derived to estimate total mortality from the length converted catch curve was extended to estimate length-at-capture (see Sparre and Venema, 1998). A standard set of criteria selected the points for the regression on the ascending limb. The start of the regression was selected using an iterative process which searched backwards in the data until the first non-zero length frequency was identified. From this starting cell, the value of the observed over expected frequency (*i.e.* selectivity ogive) was assessed until it reached, or exceeded the value of one (100% selectivity). The end point of the regression was taken as the cell within this range that contained the largest value of the selectivity ogive that was still less than one.

t_{50} was estimated from the regression (t_{50} = intercept/-gradient). Lc_{50} was then calculated using the growth parameters estimates. Lc_{50} was assessed for the first year of data; when fishing mortality was increased, the first year would most closely represent the actual selectivity of the gear.

Beverton and Holt's yield-per-recruit equation (Beverton and Holt, 1957)

The maximum yield-per-recruit was assessed within an Excel ™ spreadsheet. T_c, the age at first capture, was calculated during the estimation of the length-at-capture (Lc_{50}). T_r, the age of recruitment to the fishing grounds, was calculated from a fork length of 13cm (L_{min}). Both Pauly and Ralston M estimates were used in each assessment. W_∞ (asymptotic weight), was calculated for *L. mahsena* using the estimate of L_∞ and the length-weight equation presented in Samboo (1987):

$$W_\infty = 0.0000806*(L_\infty^{2.74})$$

Microsoft Excel Solver™ was used to maximise yield-per-recruit by varying fishing mortality. The resultant level of fishing mortality (F_{MYPR}) was noted. $F_{0.1}$, the fishing mortality at which the gradient of the yield-per-recruit curve was 10% of that at F=0 (Caddy and Mahon, 1995), was also calculated. The gradient of the yield-per-recruit curve was iteratively assessed at F=0.01 intervals, starting at F=0.01. $F_{0.1}$ was identified where the difference between the current gradient and 10% of the initial gradient was minimised.

4.4.2 Methods used in the assessment of the study fisheries

Using the catch length frequency distributions collected from the study fisheries, and the catch age frequency distributions derived through otolith assessments, both total mortality and length- and age-at-capture were estimated through length- and age-based methods. For the study fisheries, the use of otolith weight as a measure of age, and hence as a method to calculate total mortality, was also examined. The latter is detailed in Chapter 9. Following the estimation of these parameters, natural mortality and yield-per-recruit (and hence fishing mortality and $F_{0.1}$) were estimated using the methods described in the previous section.

4.4.2.1 Length-based estimation of mortality and length at first capture

Length-based estimates of total mortality and length at first capture were derived from the 1997 length frequency distribution for each location. This was the only year in which both length and age data were available from all study locations.

Total mortality was estimated using the Beverton and Holt Z estimator (Beverton and Holt, 1956); calculated in an EXCEL™ spreadsheet), and from the length-converted catch curve procedure contained within the FAO - ICLARM Stock Assessment Tool (FiSAT; Gayanillo *et al.*, 1994). In the latter method, points for regression of the catch curve descending limb were selected such that the start was the point following the catch curve's peak (highest point). The regression was then fitted to the range of points that formed the most suitable straight line from this start (assessed visually). Points representing individuals close to L_∞ were excluded.

Length-at-first-capture estimates were derived through FiSAT from the ascending limb of the catch curve constructed to estimate total mortality. A three-point moving average was selected within FiSAT to smooth the probability of capture series. Ac_{50}, and through the growth parameters Lc_{50}, were interpolated.

Both the length- and age-based growth parameter estimates derived in this chapter were used in the estimation of total mortality and length/age at first capture.

4.4.2.2 Age-based estimation of mortality and age at first capture

To assess total mortality, age frequency distributions were derived through individual otolith assessments, and through the conversion of length frequency data using an age-length key.

Age-at-length data

Individual integer ages assessed from randomly collected otolith samples were organised into numbers at age, forming an age frequency distribution for each location.

Age-length key

Age-length keys, describing the number of individuals of each age at each length, were constructed using the age-at-length data. If the age-length key derived for a location encompassed the range of length classes present in the length frequency distribution of that year, the age-length key was used to convert the length frequency into an age frequency.

The numbers-at-age in each one centimetre length class of the age-length key were converted into proportions-at-age; each cell in that length stratum was divided by the total number of individuals aged at that length. The age-length key was then applied to the length frequency, distributing the numbers-at-length over the age groups in the proportions dictated by the key. By summing the resultant numbers of individuals in each age class, an age frequency was derived.

Estimation of total mortality and age at first capture

The age frequency distributions derived through each method were used to construct an age-based catch curve. The natural log of the numbers at age was plotted against the integer age in years, in a Quattro Pro^{TM} spreadsheet. Points for the regression on the descending limb of the catch curve (which estimated total mortality) were selected using the criteria described in the length-based estimation of total mortality (Section 4.4.2.1).

The age at which 50% of individuals were vulnerable to the gear (Ac_{50}) was estimated from the ascending limb of the age-based catch curve, as described in Section 4.4.1.2. Age at first capture was calculated from the ascending limb of the catch curve. From a linear regression of $x = t$ (age, years) and $y = \ln(1/S_t-1)$ (where S_t is the observed selectivity ogive; see Sparre and Venema, 1998), Ac_{50} was obtained by dividing the constant of the regression by the gradient; Ac_{50} = intercept/-gradient.

5. Simulating the effects of fishing on growth and length structure of fish populations

5.1 INTRODUCTION

Within tropical artisanal fisheries, length-based methods are commonly used to assess stock status. Clearly, mechanisms which affect the underlying length distribution of a population introduce potential uncertainty into the estimation processes; length-based estimates of growth and mortality may be significantly affected by fishing. In this context, fishing represents the removal of individuals from the population (direct effects). Such removals may affect the suitability of current management practices and any future strategies developed as a reaction to the results from stock assessments. It is therefore important to understand the effects of fishing on target species in order to incorporate 'fishery induced' effects into stock assessment methodologies.

For example, density dependent growth, the limitation of growth rate through the competition for resources, will be influenced by the removal of individuals through fishing (an indirect effect of fishing). Such removals would increase the rate of growth as more resources become available to an individual. Such growth rate increases may result in a population capable of withstanding a greater level of fishing mortality. This is of particular interest if fisheries are being managed on the basis of total allowable catches or effort controls. Alternatively, if catch length structure is being monitored for changes in length as an indicator for management (as in Mauritius) density dependent growth might confound such changes, while the underlying age structure is significantly affected. Knowledge of the potential effects of density dependent growth is therefore important.

Simulation studies allow rapid estimation of the potential effects of fishing on a fish population. They allow the level of fishing pressure, type of gear used, or fishery regulations (such as minimum size limits) to be controlled individually. The effects of such changes on the potential yield from the fishery, its long-term viability, and on characteristics of the population and catch, such as length structure, can be studied. Having identified the likely effects of fishing in simulation studies, it is possible to examine the actual condition of the fishery in the light of these results.

In Chapter 4, a basic model describing density dependent growth was derived for the study species (*L. mahsena*, *A. virescens* and *P. filamentosus*). Three models of increasing complexity were derived, providing increasing levels of realism in the light of the biology of the study species. In the current study, these models are used to examine the effects of density dependent growth on the maximum sustainable yield (MSY) and yield-effort curve (see Beverton and Holt, 1957) of the three study species. The results of the three models will be compared, and one model selected for use in further simulation studies.

Through gear selectivity, fishing is commonly directed at larger individuals in a population. A number of studies have related changes in the mean or modal size of fish in populations to different levels of fishing pressure (*e.g.* Langi and Langi, 1989). The second part of this chapter will present a simulation of the direct effects of fishing on the catch length structure of *L. mahsena*, using Monte-Carlo methods and the length frequency simulation program described in Chapter 4. It will examine the indirect effects of fishing on exploited fish population length structure, using the most appropriate density dependent growth model identified previously.

5.2 METHODOLOGY

The basic model simulating density dependent growth was derived in Chapter 4 (Section 4.2.1.2). Three models of increasing complexity were then derived, based on the biology of the study species. The simulations performed using these models to examine the effects of density dependent growth on the yield-effort curves of the study species are described in the following section.

5.2.1 The density dependent growth simulation runs

For each of the three density dependent growth models, the simulations performed to examine the effects of that model on the yield-effort curve are described.

5.2.1.1 Model 1

Model 1 was the simplest simulation of the effects of density dependent growth on populations. Changes in L_∞ or K were related to changes in *total* population biomass. Therefore, total population biomass was assumed to represent the effects of competition on individual growth accurately, regardless of size or age. Simulations were designed to study the following;

a) The effect on the yield-effort curve of density dependent growth relationships based on L_∞ or K.
Runs were performed both with and without density dependent growth operating, and compared. For density dependent growth, gradients were set at -35% for L_∞ and -60% for K (Chapter 4, Section 4.2.1.3).

b) The effect of increasing the degree of density dependent growth in both L_∞ and K.
Due to the uncertainty over the level of density dependent growth, simulations examined the effects of increasing the gradient of the relationship to either L_∞ or K. The gradient was varied by a fixed percentage (Table 5.1).

Table 5.1 Gradients of density dependent growth simulated for each growth parameter, model 1.

Run	L_∞ gradient	or	K gradient
1	-20%		-30%
2	-35%		-60%
3	-50%		-90%
4	-65%		-120%

5.2.1.2 Model 2

In model 2, density dependent growth acted independently within two separate size classes (Table 5.2). This simulated the spatial separation of individuals on the nursery grounds from those recruited to the adult fishery. The length selected for the division between juveniles and adults was based on the length of a 2 year old individual.

Table 5.2 Length classes representing juveniles and adults in model 2.

	Size Class (cm)	
	Juveniles	Adults
L. mahsena	5 - 15	15.1 - L_∞
P. filamentosus	5 - 25	25.1 - L_∞
A. virescens	5 - 30	30.1 - L_∞

Juvenile or adult growth was only affected by the biomass within that size class, since juveniles and adults were spatially separated. The density dependent growth gradient was specified for each of the two size classes, and remained constant within each size class. The following simulations were performed:

a) **The effect of splitting the population into two discrete groups, with identical density dependent growth relationships in each size class, when compared to model 1.**
The gradient of density dependent growth in L_∞ or K was set equally within both size classes (-35% or -60% respectively). Yield-effort curves were compared with those from model 1.

b) **The effect of varying density dependent growth with size class.**
Density dependent growth in either L_∞ or K was enabled in one size class at a time (Table 5.3).

Table 5.3 Runs for model 2, varying the density dependent growth by size class. Gradient (%) settings for density dependence in L_∞ presented.

	Size Class	
Run	Juveniles	Adults
1	-35%	-35%
2	-35%	0%
3	0%	-35%

5.2.1.3 Model 3

This model was similar to model 2. In model 3, however, the adult population of model 2 was divided into two size classes of 'small adults' and 'large adults' (Table 5.4). The division length between small and large adults was based on the length at maturity (Lm_{50}). In the adult size classes, small adult growth was influenced by the biomass of large adults. Growth in large adults was only influenced by the biomass within that size class. Density dependent growth gradients were specified for each size class.

Table 5.4 Division of the population into three size classes in model 3.

	Size Class (cm)		
	Juveniles	Small Adults	Large Adults
L. mahsena	5 - 15	15.1 - 37	37.1 - L_∞
P. filamentosus	5 - 25	25.1 - 51	51.1 - L_∞
A. virescens	5 - 30	30.1 - 55	55.1 - L_∞

The following simulations were performed:

a) **The effect of splitting the population into three groups, with identical density dependent growth relationships in each, compared with models 1 and 2.**
The density dependent growth gradient was set equal in all three size classes (L_∞=-35%, K=-60%). Yield-effort curves were compared with the results of models 1 and 2.

b) **The effect of varying density dependent growth with size class.**
Density dependent growth in either L_∞ or K was enabled in one size class at a time (Table 5.5).

Table 5.5 Runs for model 3, varying the density dependent growth by size class. Gradient settings for density dependent growth in L_∞ presented.

	Size Class		
Run	Juveniles	Small Adults	Large Adults
1	-35%	-35%	-35%
2	-35%	0%	0%
3	0%	-35%	0%
4	0%	0%	-35%

5.2.2 Simulations examining the effects of fishing on the catch length structure

Simulations examining the effects of fishing on the catch length structure of *L. mahsena* were performed using the computer simulation program incorporated into MIDAS. This program, and the values of the MIDAS input parameters were described in Chapter 4 (Section 4.2.1.5). Two sets of simulation runs were performed:

- Simulation of equilibrium catch length structure at a range of fishing pressures.
- Simulation of the transient effect of fishing on catch length structure.

In both sets of simulations, runs were performed at a range of fishing pressures, with and without density dependent growth operating. The gradient of the density dependent growth relationship was varied as in Section 5.2.1.1.

Due to the stochastic nature of the length frequency generation process, 100 length frequencies were simulated within each run. These frequencies were combined, and the mean length and standard deviation of the resulting distribution calculated.

To examine the significance of differences between length frequencies, mean length estimates were compared using the GT-2 test (Hochberg, 1974; Sokal and Rohlf, 1995). This test statistically compares the means of samples with unequal sizes and variances. Critical values from the 'studentised maximum modulus' are use to calculate the minimum significant difference for the means (standard error for the GT-2 test x critical value). This is then compared to the difference between the means. Gabriel's method (Gabriel, 1978) was used to calculate upper and lower 95% comparison intervals around each mean for display purposes. These should not be confused with 95% confidence intervals. Gabriel's plots were used to present the results.

The form of two length frequency distributions were also compared statistically using the non-parametric Kolmogorov-Smirnov test (Sokal and Rohlf, 1995). The null hypothesis assumed that the two samples were distributed identically. If the observed maximum unsigned difference between cumulative frequency distributions derived from the two frequencies was larger than the expected critical value, the null hypothesis was rejected, and the two distributions were considered significantly different.

5.2.2.1 Simulation of the equilibrium catch length structure at a range of fishing pressures

Simulations were first performed with no density dependent growth operating in the population. Catch length structures were simulated from populations at equilibrium with the level of fishing mortality. Simulations were performed for fishing mortality levels between F=0yr^{-1} (unexploited equilibrium) and F=1.5yr^{-1}, at intervals of F=0.1.

Catches from populations at equilibrium with the level of fishing mortality were then simulated with density dependent growth acting on L_∞ or K. The gradient of the density dependent growth relationship was initially set at -35% for L_∞ runs, and -60% for K runs (Section 4.2.1). The gradient of the relationship was then increased to -70% for L_∞ runs, and -120% for K runs. These runs were performed at the four levels of fishing mortality identified in Table 4.7 (Chapter 4). Comparisons were made between the mean length and form of the length frequency distributions simulated with and without density dependent growth.

5.2.2.2 Simulation of the transient effects of fishing on the length structure of catches

To examine the transient effects of fishing, populations were simulated at unexploited equilibrium up to time zero. Fishing mortality was then applied at a constant level from time zero for the next ten years, at each of the four levels of fishing mortality. Catch length structure was output at the start of each simulated year. Runs were then repeated with density dependent growth operating in L_∞ or K, at the gradients used in the equilibrium simulations.

5.2.2.3 Examination of the effects of variation in recruitment

Due to an error within the MIDAS computer program, annual variability in recruitment was not enabled during the simulation of length frequency distributions. This was noted after completion of the simulation runs. The computer program was subsequently modified to enable this feature, and runs were performed to examine the importance of the effect of annual recruitment variability on catch length structure.

Catch length frequencies were simulated at F=0.25yr^{-1} with recruitment based either purely on the spawning stock biomass and the level of density dependence in the stock recruitment relationship (recruitment CV=0%), or with additional variability around this recruitment (recruitment CV=61%).

5.3 RESULTS

The results are divided into two sections. The first (Section 5.3.1) presents the results of studies examining the effects of density dependent growth on the yield-effort curve of the study species. The second (Section 5.3.2) describes the results of simulations examining the direct and indirect effects of fishing on catch length structure.

5.3.1 Effect of density dependent growth on the yield-effort curve

Initial runs showed that results from *L. mahsena* data were the most informative, since the complete yield-effort curve was displayed over a reasonable range of fishing mortalities (F=0 to 1.5yr^{-1}). This species was therefore used to illustrate results from the majority of runs. The yield effort curves calculated using *P. filamentosus* and *A. virescens* parameters exhibited similar trends to those found simulating *L. mahsena*. The curves for the snapper species are displayed for the comparison of the three main models.

5.3.1.1 Standardising the results

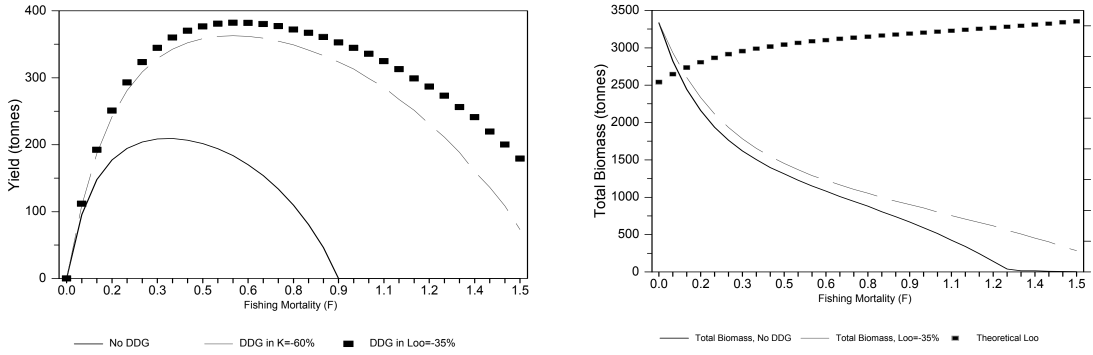
The results are interpreted as the yield, in tonnes, which can be extracted at a sustainable level at a given fishing mortality. Comparison of populations with different initial biomass (due to different input parameters) required scaling to the initial (unexploited) total population biomass. Yield is therefore expressed either in tonnes, or as a percentage of initial total population biomass. Where this standardisation could not be used (*e.g.* in runs with varying L_∞), results were compared using the fishing mortality level required to achieve MSY (F_{MSY}).

5.3.1.2 Results of model 1

Model 1 related changes in total population biomass to L_∞ or K.

a) The effect of modelling density dependent growth based on L_∞ or K.

Density dependence in L_∞ or K increased both the value of MSY and F_{MSY}. The results for *L. mahsena* are displayed as an example (Figure 5.1a). Fishing decreased population density allowing increases in growth rate (Figure 5.1b). Length-at-age, and hence weight-at-age, increased. Yield per individual therefore increased. Individuals also matured at a younger age (as length at maturity was constant), bolstering the spawning stock biomass. The overall result was an increase in biomass at exploitable lengths, thereby increasing yield.


a. Yield-effort curve

b. Theoretical value of L_∞ at F

Figure 5.1 Effect of density dependent growth on a) the yield-effort curve of *L. mahsena*, b) total biomass and the theoretical value of L_∞. Density dependent growth operating in L_∞ at -35%.

Where density dependent growth was operating, stocks were more robust to higher fishing mortality levels, being able to withstand increased levels of mortality before collapse. Due to increased growth rates resulted from fishing, a greater number of fish reached maturity, and reproduced before capture. Fish also reached exploitable lengths faster, becoming available to the fishery at an earlier age.

Results from density dependent growth operating in L_∞ or K were very similar. This was examined further in the following investigation.

b) Effect of increasing the degree of density dependent growth in L_∞ or K.

Increasing the gradient of the density dependent growth relationship for either L_∞ or K increased the numbers of individuals reaching both exploitable and reproductively active sizes, and decreased the age at which they did so. As a result, increasing the degree of density dependent growth increased the value of both MSY, and F_{MSY} (Table 5.6, Figure 5.2). The robustness of the population at high fishing mortalities was also increased.

Table 5.6 Effect of increasing density dependent growth in L_∞ and K (as shown by DDG affects column, at gradient specified) on MSY for *L. mahsena*.

DDG affects	Gradient	MSY			
		Yield (tonnes)	% increase	Fishing Mortality	% increase
NONE	-	209	-	0.33	-
L_∞	-20%	298	42%	0.45	36%
	-35%	361	73%	0.50	52%
	-50%	423	103%	0.60	82%
	-65%	484	131%	0.69	112%
K	-30%	289	39%	0.45	36%
	-60%	363	73%	0.54	64%
	-90%	432	108%	0.61	85%
	-120%	498	139%	0.74	114%

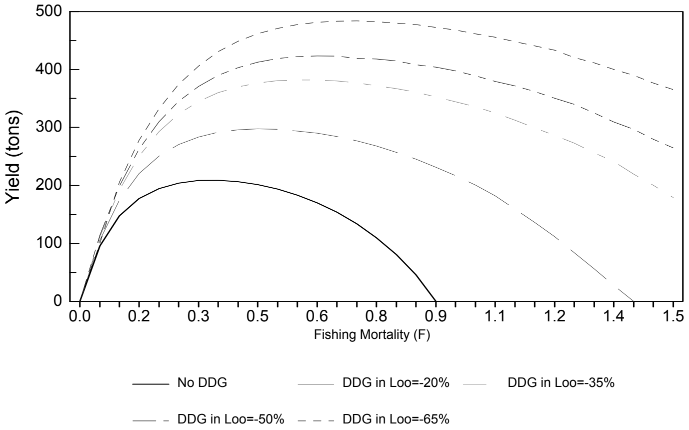


Figure 5.2 Effect of varying the gradient of the density dependent growth relationship for L_∞ on the yield-effort curve of *L. mahsena*.

Due to the similarity between the effects of density dependent growth in L_∞ or K of equivalent gradients (*e.g.* L_∞ = -35%, K=-60%, Table 5.11), L_∞ was used to illustrate the results of remaining simulations.

5.3.1.2 Results of model 2

Model 2 simulated density dependent growth acting independently within juvenile and adult size classes.

a) Effect of splitting the population into two discrete groups.

Compared to no density dependent growth, model 2 resulted in increases in both MSY and F_{MSY}. The increase in yield was slightly less than that resulting from model 1 (Figure 5.3). Yield-effort curves for the two models converged at higher fishing mortalities.

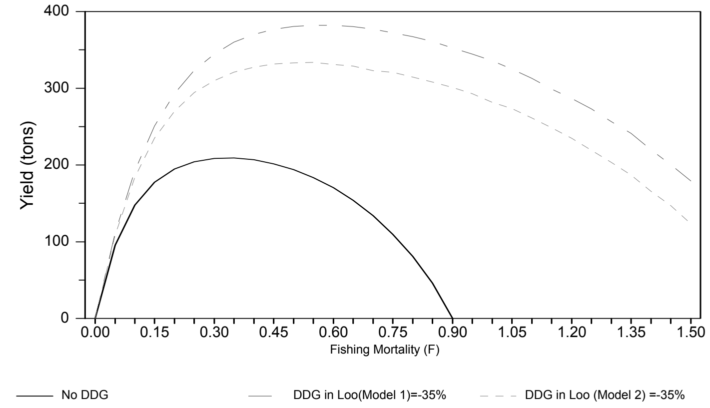


Figure 5.3 Effect of the density dependent growth model (acting on L_∞ at -35%) on the yield-effort curve of *L. mahsena*. Size class division in Model 2 at 15cm.

In model 2, reductions in adult density through fishing did not directly affect juvenile growth, and hence over yield was lower. Fishing did reduce the spawning stock biomass, and therefore recruitment. In turn, this reduced recruitment caused a limited increase in juvenile growth rate and earlier entry to the fishery, an effect which was more pronounced at higher fishing mortalities. However, increased juvenile growth rate had a limited effect on yield, since individual growth rate reverted to that of adults upon recruitment to the fishery.

As fishing mortality increased, populations became dominated by smaller individuals. Yields were comprised of individuals growing into the exploitable length classes, decreasing the difference between the two curves.

b) Varying the density dependent growth gradient between size classes.

Enabling and disabling density dependent growth in each size class (Figure 5.4) indicated that most of the increased yield resulted from density dependent growth acting in the adults (greater than 15cm). Adults contributed the majority of the population biomass, and their growth was directly affected by fishing mortality. At higher fishing mortalities, where depletion of the spawning stock led to declines in recruitment, the impact of higher growth rates in the juveniles became slightly more significant.

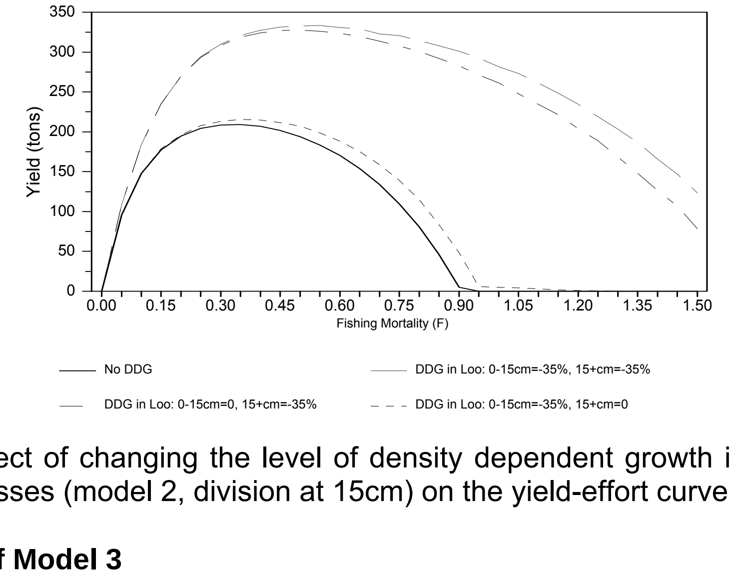


Figure 5.4 Effect of changing the level of density dependent growth in L_∞ between size classes (model 2, division at 15cm) on the yield-effort curve of *L. mahsena*.

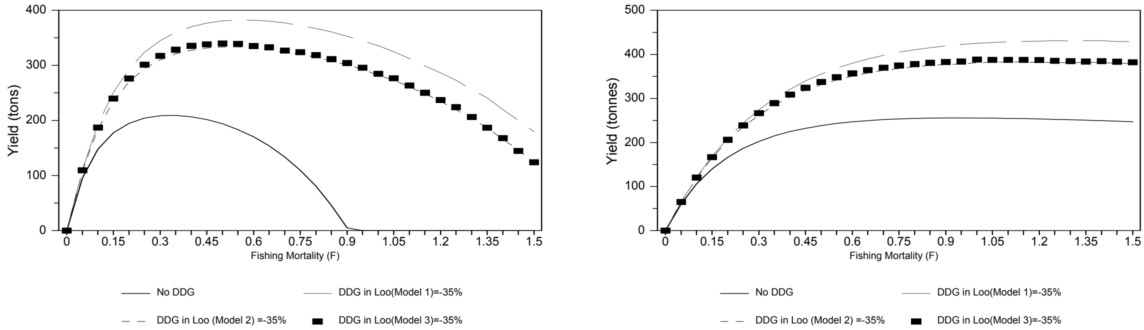
5.3.1.3 Results of Model 3

Model 3 divided the population into three size classes; juveniles, small adults and large adults. Density dependence acted independently within juveniles and large adults, while small adult growth was affected by total adult biomass.

a) Dividing the population into three size classes.

Where the density dependent growth gradient was equal in each size class, yields were similar to those of model 2 (Figure 5.5). Most of the density dependent growth effect was therefore due to one of the adult size classes only. The three yield-effort curves again converged at higher fishing mortalities.

a. *Lethrinus mahsena* b. *Pristipomoides filamentosus*



c. *Aprion virescens*

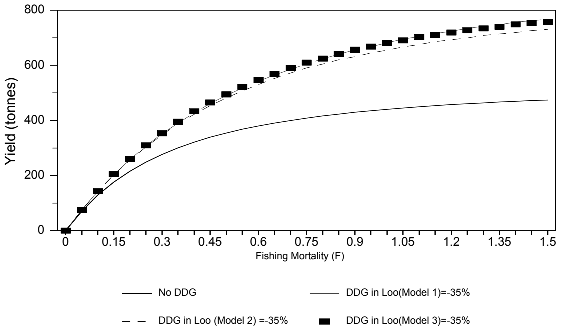


Figure 5.5 Comparison of the three density dependent growth models (acting on L_∞ at -35%), using the yield-effort curve from each of the three study species. Size class divisions as in Table 5.2 for model 2, and Table 5.4 for model 3.

b) Effect of varying the density dependent growth effect between size classes.

Density dependent growth operating in the small adult size class contributed most of the increase in yield (Figure 5.6). This size class also contributed the majority of the total biomass (Table 5.7). Hence, growth changes in these individuals had a significant impact on the yield; faster growth increased both the number of mature individuals (size at maturity was reached at a younger age) and the average size (and weight) of exploitable individuals.

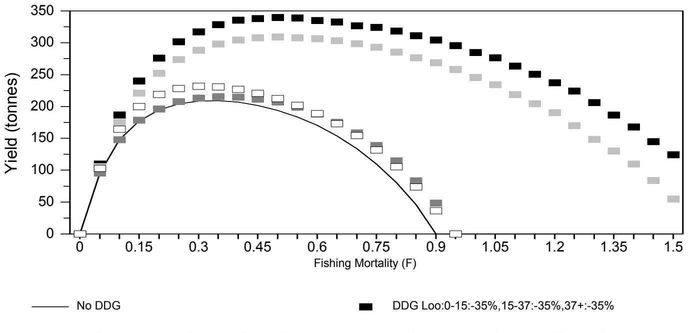


Figure 5.6 Effect of varying the level of density dependent growth (L_∞) in length classes of model 3 on the *L. mahsena* yield-effort curve. Length classes at 15cm and 37cm.

Table 5.7 Percentage of total population biomass within each size class at MSY (F_{MSY} = 0.33).

Class	Size Range (cm)	Percentage of population biomass
Juveniles	5 -15	15%
Small Adults	15.1 - 37	74%
Large Adults	37.1 - L_∞	11%

Changes in juvenile and large adult growth rate had minor effects on maximum sustainable yield. Both size classes contributed a relatively small proportion to total biomass, while juvenile growth was not directly affected by fishing mortality. The latter was influenced by the level of the density dependence in the stock recruitment relationship (*d*). At the setting used in the simulations (*d*=0.8), changes in spawning stock biomass had a relatively small effect on the level of recruitment. When the value of *d* was decreased to 0.6, density dependence in the juveniles and large adults had an increased effect on the yield.

Density dependent growth acting on L_∞ had a greater effect on large adult growth than that operating in K. Individuals in the large adult size class had already reached a length over half the L_∞ (Figure 5.7, 'normal' curve). Density dependent growth in K resulted in individuals reaching the set L_∞ earlier (Figure 5.7, K=0.16). With changes in L_∞ (Figure 5.7, L_∞=83.3), however, fish grew to both a greater maximum size, and greater mass.

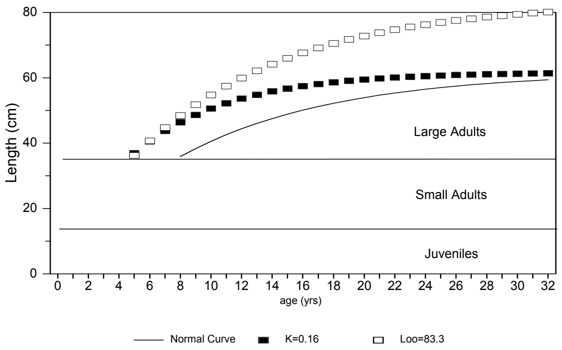


Figure 5.7 Effect of increasing L_∞ or K in the 'large adult' size class on the *L. mahsena* growth curve.

5.3.2 Effect of fishing on the catch length structure

MIDAS was used to simulate catch length frequency distributions at a range of fishing mortality levels. The effects of fishing were examined both with and without density dependent growth.

5.3.2.1 Simulation of catch structure at equilibrium with fishing mortality

Where density dependent growth was not operating, increasing the level of fishing mortality resulted in a decrease in both the mean and standard deviation of the equilibrium length frequency distribution (Figure 5.8).

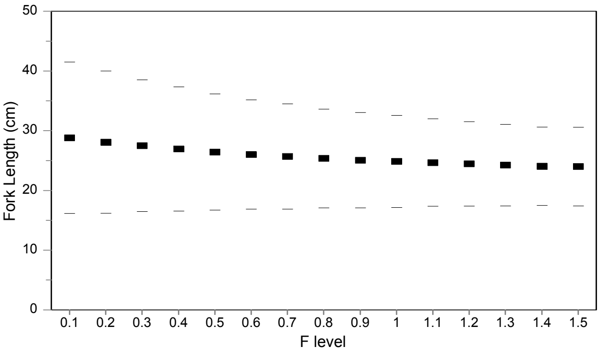
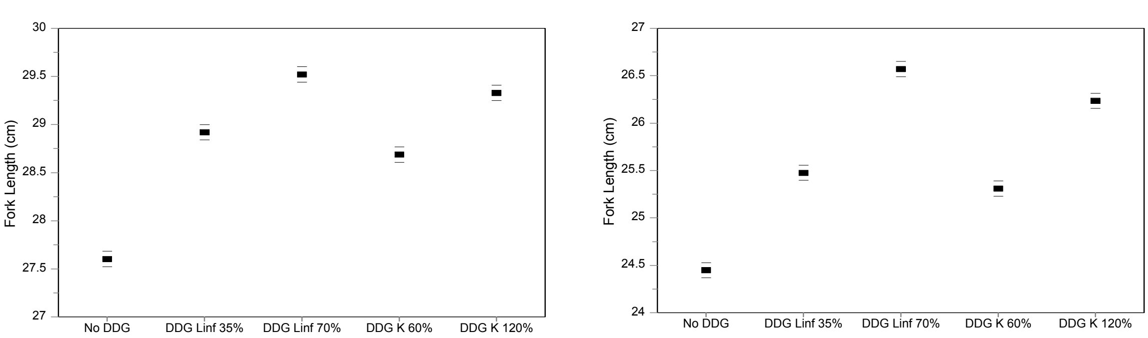


Figure 5.8 Mean length +/- two standard deviations from length frequency distributions at equilibrium with the simulated level of fishing mortality (F level).

The rate of decline in mean length and standard deviation was fastest at lower effort levels. Through gear selectivity, fishing mortality acted most strongly on larger individuals. These less common individuals, which strongly influenced the mean and standard deviation, were removed at low fishing mortality levels. Relatively small increases in effort therefore had a large effect on the mean length. Further increases in effort affected size classes at which individuals were relatively common, and where sufficient small individuals were present to grow into those exploited size classes. At this point, increases in effort had a reduced impact on mean length.

Density dependent growth increased the mean length of the equilibrium distribution at the four study fishing mortality levels (see Figure 5.9). Increasing the gradient of the density dependent growth relationship resulted in significant increases in mean length. This was particularly emphasised at higher fishing mortality levels. Density dependence in L_∞ tended to result in larger mean lengths than those in K. While density dependence in K caused individuals to grow toward their individual L_∞ values faster, density dependence in L_∞ increased the maximum potential length (*e.g.* Figure 5.7). This resulted in an increased number of large individuals in the length frequency, which had a disproportionately large impact on mean length.



a. F=0.25yr^{-1}

b. F=1.2yr^{-1}

Figure 5.9 Gabriel's plot of the effect of different levels of density dependent growth on the mean length of catch length frequencies at different fishing mortality levels. F=0.25 and F=1.2yr^{-1} presented as examples.

Changes in mean length were the result of a combination of increased growth rates due to density dependence, and decreased mean length due to the level of fishing mortality (Table 5.8). As the level of density dependence increased, growth rate was sufficient to counteract decreases in mean length at increasing fishing mortality levels.

Table 5.8 Percentage increase in mean length at different levels of density dependent growth (DDG), by fishing mortality level.

F level (yr^{-1})	% increase in mean length over situation with no DDG			
	DDG L_∞ at		DDG K at	
	-35%	-70%	-60%	-120%
0.05	1.7	3.1	1.6	1.6
0.25	4.8	6.9	3.9	6.3
0.7	4.4	9.0	3.8	7.3
1.2	4.2	8.7	3.5	7.3

The structure of length frequency distributions with no density dependent growth were compared to runs with density dependent growth (in either L_∞ or K) at the maximum gradients (Figure 5.10). At these levels of density dependence, differences were amplified.

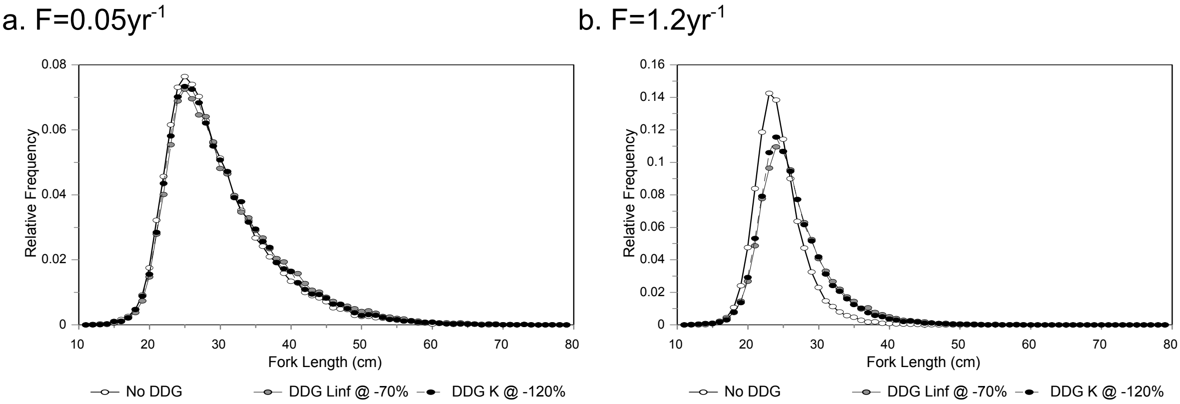


Figure 5.10 Length frequency distributions at F level with and without density dependent growth. F=0.05 and F=1.2yr^{-1} presented as examples.

The effects of density dependence were limited at low fishing mortality levels, since the population biomass was relatively unaffected. Length frequencies showed reduced impacts from fishing where density dependent growth was operating, with increased numbers of relatively large individuals present in the catch. Large individuals were still present at low frequencies in the density dependent distributions at high fishing mortalities (Figure 5.11).

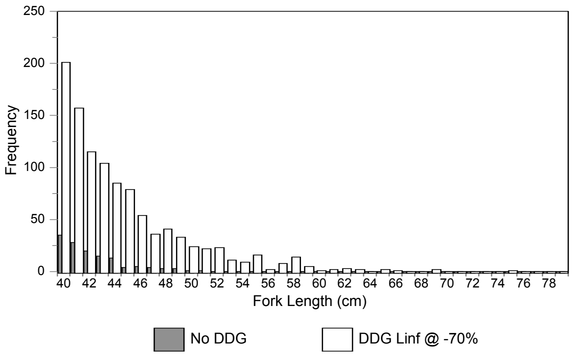
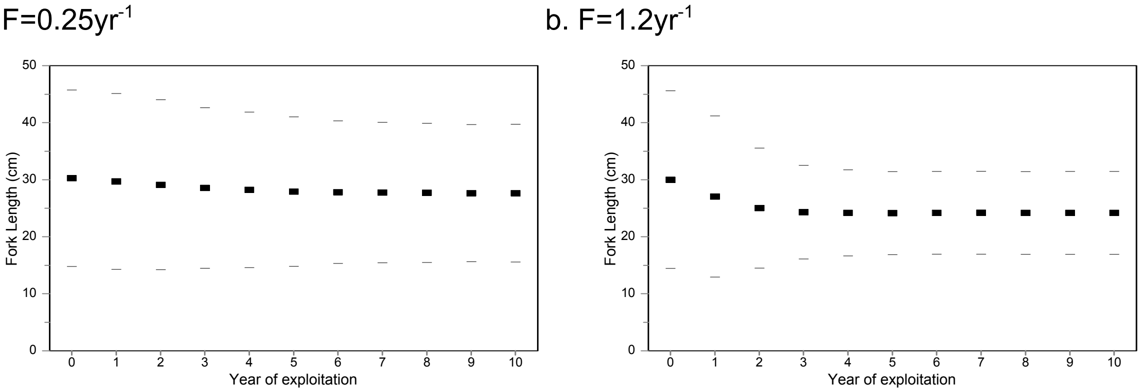


Figure 5.11 Length frequency distribution at F=1.2yr^{-1} over a limited length range. Distributions shown without density dependence, and with density dependence operating in L_∞ at -70%.

5.3.2.2 Simulation of the transient effects of fishing

Transient fishing runs were performed over 10 years. Prior to this time, the fishery was simulated at unexploited equilibrium. Due to the stochastic nature of the simulation, runs were repeated 100 times, and an average taken across these runs.

Initiation of fishing at time zero in a fishery without density dependent growth resulted in a decrease in both the mean length and standard deviation with time (Figure 5.12).

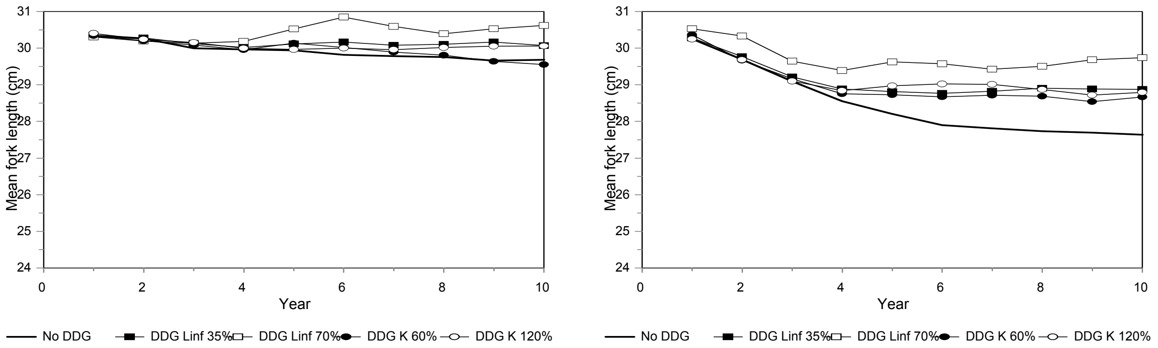

a. F=0.25yr^{-1}

b. F=1.2yr^{-1}

Figure 5.12 Effect of application of fishing effort on the mean length ± two standard deviations of a previously unexploited *L. mahsena* population. F=0.25yr^{-1} and F=1.2yr^{-1} are displayed to illustrate the general decline, and the effects of different fishing mortality levels.

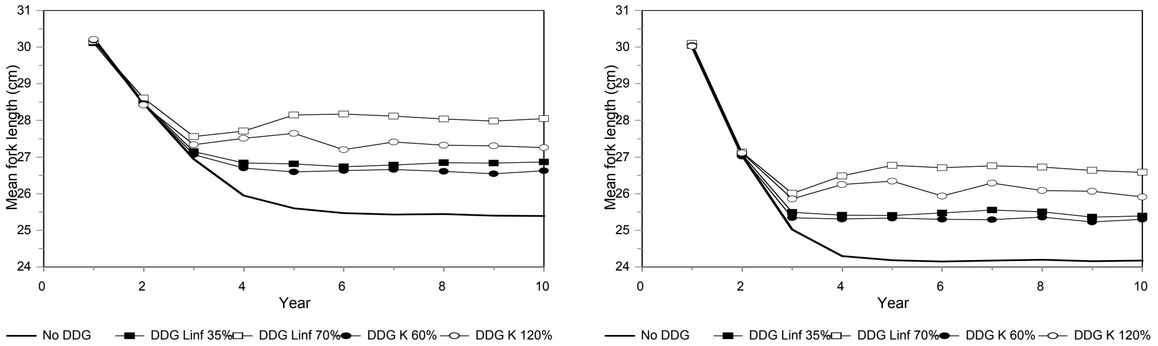
The rate of decline in mean length and time taken to reach exploited equilibrium varied with the level of fishing mortality. At F=1.2yr^{-1}, the decline occurred for four to five years after the onset of fishing mortality, before reaching a relatively constant mean length. At lower mortality levels, the decrease was slower, but extended. At such levels, relatively few individuals were removed each year. However, the slow growth rate meant that individuals were not replaced by fish growing into those size classes. Fishing therefore progressed to smaller sizes until a balance between the removal and growth of individuals was reached. At higher fishing mortality levels, the effect was more marked.

Density dependent growth reduced the rate of decline in mean length and standard deviation with time (Figure 5.13). There was an increase in mean length at exploited equilibrium, while the rate at which it was achieved decreased.



a. F=0.05yr^{-1}

b. F=0.25yr^{-1}



c. F=0.7yr^{-1}

d. F=1.2yr^{-1}

Figure 5.13 Transient simulations of the effect of fishing mortality (at four levels) on mean length of a previously unexploited *L. mahsena* population, both with and without density dependent growth. Populations simulated for ten years after the initiation of fishing.

Patterns in the mean length in each year showed notable fluctuations over time where density dependent growth was operating. This was the result of the transient nature of the simulation, and the effects of density dependent growth. Increased growth due to density dependence in one year resulted in an increased biomass in the following year, compared to the situation without density dependent growth. As a result, growth rate slowed, and fishing mortality had a more significant effect on length structure in the following year.

At high fishing mortalities, where density dependent growth was operating at high gradients, mean length initially declined below the level at which equilibrium was later reached. This was a result of the delay between the effects of fishing and compensatory effects of density dependent growth. At high density dependent gradients, the growth parameter increase resulting from fishing was sufficient to counteract fishing effects in subsequent years, increasing mean length. At lower gradients, the increase in growth was insufficient to fully counteract fishing effects, and no recovery was found.

5.3.2.3 The effects of recruitment variability

Due to an error in the MIDAS programme, recruitment variability was not enabled in the previous simulations. Therefore, runs were performed to examine the effect that this variability had on the catch length structure.

Where recruitment variability was enabled, output catch length frequencies were not significantly different from those where recruitment variability was due solely to the level of spawning stock biomass (Kolmogorov-Smirnov test, $D_{0.05}$=0.10, D=0.09; Figure 5.14). The impact of recruitment variability was insignificant.

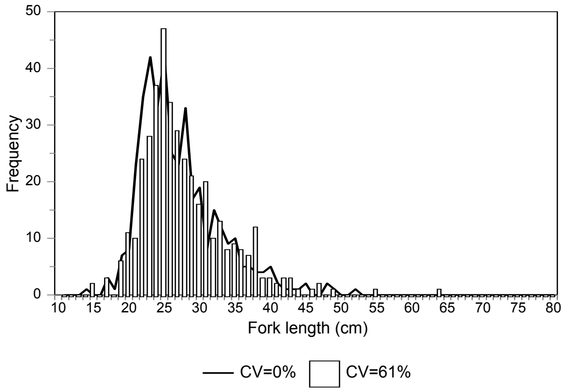


Figure 5.14 Comparison of catch length distributions where annual recruitment variability was solely due to spawning stock biomass (CV=0%) or combined with additional inter-annual variability (CV=61%).

5.4 DISCUSSION

5.4.1 Effect of density dependent growth on the yield-effort curve

This study examined the effect of density dependent growth using three models of increasing complexity. In model 1, total population biomass acted on the density dependent growth relationship. For model 2, the population was divided into juveniles and adults, simulating the spatial separation found in the study fisheries. Model 3 was an extension of model 2, with the adult size class divided into two further classes at the length of maturity.

5.4.1.1 Simulation results

Density dependent growth increased the yield available at a given level of fishing mortality. In these simulations, the majority of this increase in yield was a result of increased growth in the small adult size class.

There was little difference between the yield estimates whether density dependent growth models 1, 2 or 3 were used (Figure 5.5). Given this similarity, the increased complexity of model 3 did not appear warranted. From the purely practical viewpoint, model 1 would be preferred for further investigations since, although simple, it produced comparable results to more complex models. However, basing density dependent growth on total biomass does not conform to the biology of the three study species. Studies in Chapter 7 involve the estimation of growth parameters through length frequency distributions generated by MIDAS. The use of model 1, which ignored the species biology, would therefore affect the structure of the length frequency outputs and, potentially, growth parameter estimates. For these reasons, model 2 will be used in further simulations.

5.4.1.2 The importance of density dependent growth in natural populations

The simulations indicate that density dependent growth could have a significant effect on lutjanid and lethrinid populations. As stated in the introduction, no studies have been performed to identify density dependent growth in these families. However, certain biological characteristics suggest that density dependent growth could occur in the study species.

Data from the study fisheries will be assessed in an attempt to identify whether signs of density dependent growth exist (Chapter 6). Length-based methods of growth estimation are felt too inaccurate to detect changes in growth resulting from fishing (MRAG, 1996b). However, the studies undertaken in Chapter 2 validated the annuli in the otoliths of two of the study species.

These structures will be used to provide a more accurate estimation of growth rate. These estimates will then be assessed for indications of density dependent growth.

5.4.1.3 The effect of density dependent growth on management

In a lightly exploited fishery, where effort is likely to be increased, the cautious approach is to assume that density dependent growth is not occurring. If this assumption were made for *L. mahsena*, for example, F_{MSY}=0.33 (yield=209 tonnes). If density dependent growth were operating in L_∞ with a gradient of -35%, as in model 2, fishing at F=0.33yr^{-1} would produce an unexpectedly high yield of 320 tonnes. The actual MSY with density dependent growth operating (at F_{MSY}=0.52) was only 4% greater (MSY = 333 tonnes). If, by contrast, density dependent growth was assumed to be operating where it was not, and fishing mortality were set at F_{MSY}=0.52, overfishing would occur. The yield obtained (190 tonnes) would be 10% less than that achieved at the MSY level where no density dependent growth was operating. A small loss in yield would therefore result by taking the cautious approach over the situation where perfect information was available.

In contrast, in a heavily exploited fishery, where there is a need to decrease the level of effort, the cautious approach is to assume that density dependent growth is occurring. As fishing effort is decreased, biomass will increase. As a result of density dependent growth, both K, L_∞, and hence MSY, are decreased. Fishing at the previously calculated MSY therefore results in over-exploitation. Based on the assumption of density dependent growth, however, the growth parameters will require re-calculation. Where the decrease in the growth rate is detected, MSY and F_{MSY} will be decreased.

In a similar way, most estimates of growth come from an exploited population. As a result, where density dependent growth is operating, parameter estimates will not equal $L_{\infty 0}$ or K_0, but the value of these parameters at the population biomass relating to the level of fishing pressure applied ($L_{\infty B}$ and K_B). Increases in fishing mortality would result in higher yields than expected, following the same pattern as described above, and managers should again assume no density dependent growth was operating. Where density dependent growth was not taken into account and fishing mortality *decreased*, yields would be less than expected, while fishing at the assumed MSY would result in overfishing. In this situation, some knowledge of the degree of density dependence is required.

Management advice based on depletion models will be affected by density dependent growth. Fishing will increase the growth rate and individual weight-at-age. Density dependent growth would therefore result in an artificially high CPUE (if based on catch weight). Such increases might mask, or reduce, declines in population numbers. The use of such CPUE data in depletion models would lead to an erroneously high estimates of unexploited population numbers.

The Mauritian banks fisheries are managed through Total Allowable Catches (TACs). Density dependent growth can have significant impacts on yield-effort curves. Hence, additional research to establish the presence and strength of density dependent growth is required where the aim is to maximise the resource harvest, or effort (for employment). Where maximisation is not required, management should again assume that no density dependent growth occurs.

Currently, TAC in Mauritius is reduced by 5% per annum until a consistent recovery in the stock (identified as an increase in the catch mean length and an increase in catch rate) is identified. Both of these indicators will be affected by density dependent growth. Declines in mean length due to fishing may be limited by the increased rate of growth (Section 5.3.2). However, where density dependent growth is operating, increases in mean length and CPUE in a recovering population may be slower than expected, since increases in population size and biomass will decrease the growth rate. The time over which stock recovery is expected must be evaluated, taking such compensatory responses into account (Helser and Brodziak, 1998).

5.4.2 Effects of fishing on the population length structure

This study examined the effect of fishing on the length structure of simulated *Lethrinus mahsena* populations. Populations were subjected to different levels of simulated fishing mortality, and the mean and standard deviations in the catch length structure were assessed. The structure was initially examined where the population was at equilibrium with the level of fishing mortality applied. Transient effects, where populations were adjusting to the onset of fishing mortality, were also examined through a time series of catch length structures. The effects of density dependent growth on the catch length structure in both these situations were examined using model 2.

Fishing resulted in a decline in both mean length and standard deviation of the catch length structure. The decline was dependent on the level of fishing mortality applied. This was a result of selective removal of larger individuals due to gear selectivity. Density dependent growth reduced the impact of fishing on catch length structure, since increased growth rates resulting from decreased population biomass counteracted the removal of individuals through fishing.

Changes in the length structure took a number of years, depending on the level of fishing mortality. Declines in mean length occurred rapidly where fishing mortality was high, while an extended decline was found where fishing mortality was low. The time taken to reach this relative equilibrium was decreased where density dependent growth was operating, while the mean length at equilibrium was increased.

Annual variability in recruitment was not operating in the majority of length frequency simulations. Subsequent analysis showed that the inclusion of this variability did not have a significant effect on catch length structure. The slow growth and low natural mortality rate of this species, combined with the effects of gear selectivity, reduced variations in numbers at length resulting from high or low years of recruitment. The potential effect of recruitment variation on the outputs of length-based growth assessment methods will be examined during the study described in Chapter 7.

5.4.2.1 The effect of fishing on management

Catch length frequency samples will be affected through fishing; by decreases in mean length, the effects of density dependent growth, and the selectivity of the gear. Fishing will remove larger individuals from the population, and may reduce the information available to estimate L_∞ (Sparre and Venema, 1998). Fishing may also affect modal signals of growth in catch distributions, through both the removal of individuals and changes in growth rate. The application of length-based growth assessment methods to such distributions may result in erroneous growth parameter estimates.

Fishing can result in 'juvenescence' (Ricker, 1963), *i.e.* the reduction in the numbers of older individuals in a population. Density dependent growth will result in younger individuals attaining a greater size-at-age than that found in an unexploited population. Length frequency distributions will not indicate such effects, as they reveal little of the underlying age structure of populations, particularly in long-lived, slow growing species, where the length distributions of cohorts rapidly overlap with increasing age.

In Chapter 6, catch length and age structure from the study fisheries will be examined for the effects of fishing identified in the current chapter. Growth rate will also be examined, to identify whether changes resulting through density dependent growth can be found in actual populations.

The importance of the effects of fishing mortality and density dependent growth on both length- and age-based growth parameter estimates will be assessed through simulations in Chapter

7. Given the results derived from the current study, density dependent growth will be simulated at the highest gradient examined. At this level, effects of density dependence will be most prominent.

6. The effects of fishing on the structure and growth of the study fish populations

6.1 INTRODUCTION

Through the selectivity of gears and effects of competition for bait, fishing will affect the length structure of exploited populations (Ricker, 1969). As gears generally select for larger individuals, if the level of fishing mortality is sufficient, catch mean length will decrease over time (Chapter 5). Such reductions in average size are likely to be mirrored by decreases in the average age of fished populations (Russ, 1991).

If density dependent growth is operating, the effects of fishing on length structure may be confounded by the resulting increased individual growth rate. Density dependent growth has the potential to maintain a relatively stable length frequency distribution under increasing fishing pressure, while the underlying age structure may be severely altered.

While a number of studies have related declines in the size structure of a population to fishing pressure (*e.g.* Langi and Langi, 1989; Ralston and Kawamoto, 1988), few have utilised ageing methods to assess the effects of fishing on the age structure of tropical fish populations. Of those that have examined changes in age structure over time, the resulting trends have varied. Russ *et al.* (1995) attributed a lack of significant differences between the size and age structures of *Plectropomus leopardus* populations in fished and unfished (closed) areas of the Great Barrier Reef to the short duration of the closure (3 to 4 years) relative to the species' longevity (14+ years). When assessing *Pristipomoides filamentosus* stocks in Hawaii, however, Ralston and Kawamoto (1985) described a decrease in the age at first capture from 4 yrs to 1.8 yrs over time, indicating a shift in catch age structure. This trend was related to an increase in fishing mortality.

This chapter will investigate the effects of fishing on both the length and age structures of snapper and emperor populations from the study locations in the Indian Ocean. The banks of Mauritius, Seychelles, and the British Indian Ocean Territory (Chagos Archipelago), have all been subjected to a range of fishing pressures. BIOT (Chagos Archipelago) is considered to be a moderately fished location (Mees *et al.*, 1999), as is the Seychelles (dependent on the location and species to be studied; MRAG, 1996d), while the banks of Mauritius are considered to be relatively heavily exploited (MRAG, 1996c).

Length frequency data have been routinely collected from commercial catches in all three study locations. Data were therefore available to identify the indicators of exploitation described in Chapter 5; declines in mean length and standard deviation of the catch length structure either over time, or through comparisons of length structure both between and within locations.

Fishing is expected to reduce the mean age of catch samples. Otoliths from *Lethrinus mahsena* and *Aprion virescens* were validated for the study locations in Chapter 2. Age data derived from otoliths allowed the catch age structure from each location to be assessed. Differences in mean age between and within locations were related to the historical exploitation level.

Studies to identify density dependent growth in closed systems have commonly used direct measurements of length or weight over time to discern the growth rate of populations, and related such measurements to population density (*e.g.* Backiel and LeCren, 1978). While such studies are feasible in pond experiments, these techniques cannot be used to assess growth in the study species. Tagging is also unfeasible, due to the high level of mortality at capture resulting from barotrauma, the nature of the fishing operations (*e.g.* fishing may not occur in the same location in consecutive years), and limited time available to the project. Growth increments could be assessed through the back-calculation of individual growth using otoliths (Chapters 2 and 3). However, the involved procedure used to measure otolith increment width was not feasible for the large numbers of otoliths examined in each location. Length-at-age provides a summary of the growth rate over the life of each individual (*e.g.* Shackell *et al.*, 1997), acting as a proxy for growth. Increased growth rates resulting from density dependent growth would be expected to increase mean length-at-age (*e.g.* Weatherly and Gill, 1987; Ross and Nelson, 1992; Landa, 1999). Length-at-age data were therefore compared both between and within locations to assess whether density dependent growth operated in the study species.

The direct comparison of length-at-age data between and within locations avoided the problems inherent in the comparison of growth parameter estimates derived from samples with varying ranges of length-at-age data (Zivkov *et al.*, 1999). As noted by Rowling and Reid (1992), the length composition of samples can strongly affect the estimated growth parameters. A comparison of parameters derived from samples with different ranges of length and age may therefore produce false indications of changes in growth rate due to fishing.

Density dependent growth may also result in changes in the length-weight relationship. Increased growth through density dependence may be at the expense of body mass, resulting in a loss of condition. Therefore, assessments of the condition factor, calculated using the biological information collected during otolith data collection, were compared.

This chapter therefore describes studies investigating whether the expected fishing induced changes in length structure, age structure and growth (through density dependence) occurred in the study snapper and emperor populations.

6.2 METHODOLOGY

The data used in this study, and the methods used to collect it, were described in Chapter 4 (Section 4.2.2). The methods used to analyse this data for the expected effects of fishing are described in the current section. Those used to assess the length frequency data for declines in mean length are first described. Those used to assess the age data for declines in catch mean age, and increases in mean length-at-age (as a proxy for growth) are then presented. Finally, the examination of the biological data for the effects of fishing are described.

6.2.1 Spatial analysis of length frequency data

Length frequency data were compared on two spatial scales; that of the location, and that of statistical areas within each location. For each comparison, mean fork length and standard deviation of the catch length frequencies were calculated. These values, along with the form of the length frequency distributions themselves, were examined for significant differences.

The Kolmogorov-Smirnov test (Sokal and Rohlf, 1995) was used to assess the significance of differences in the form of two length frequency distributions. Mean fork length and standard deviation of distributions were also assessed for significant differences. Welch's approximate *t*-test (Sokal and Rohlf, 1995) was used for comparisons with only two samples. For comparisons with more than two samples, the GT-2 test (Hochberg, 1974) was used. For the latter, upper and lower 95% comparison intervals around each mean were calculated through Gabriel's method for display purposes (Gabriel, 1978).

Length frequency data were first examined within each location over time, to identify significant changes indicating the temporal effects of fishing, and whether several years of data could be amalgamated to increase sample sizes. Comparisons between locations were then performed. Since the level of data collection for the study species was influenced by their relative importance in the catch at each location, comparisons were frequently limited. For all years up to 1997, *L. mahsena* comparisons were limited to those between the Mauritian banks and BIOT (Chagos Archipelago). In 1997 and 1998, data were also available from Seychelles. For *A. virescens*, comparisons between locations were limited to data from Seychelles and BIOT (Chagos Archipelago). Data were not collected for this species from the Mauritian banks, since this species is rarely found in the catch (<0.1% of catch weight; MRAG, 1997a). All comparisons were made within gear types (Seychelles), to eliminate the effects of gear selectivity, and where necessary within years, to eliminate between year differences. Where sufficient data were available (n>50), length frequency data from different statistical areas within a location were examined to identify local differences in population structure.

Mean length was related to the level of cumulative fishing effort applied. Regressions relating cumulative effort (man days; Section 4.2.2.2) to mean fork length or standard deviation were performed. A student's one-tailed t-test was used to assess the significance of the trend identified by the regression. The null hypothesis for this test was that the gradient of the regression line was not significantly different from the horizontal in a negative direction (*i.e.* this specifically tested whether the expected significant decline with increasing cumulative fishing effort was identified).

6.2.2 Spatial analysis of mean age and growth

Age data were organised to estimate the catch age frequency for each study location and statistical area. With the corresponding length data, mean length-at-age was calculated, as a proxy for growth.

6.2.2.1 Age frequency distributions

Age frequency distributions were developed using assessed integer ages from all randomly sampled individuals. Data were examined within years both by location, and by statistical area within location. Age frequency distributions were compared using the Kolmogorov-Smirnov test. Mean age was calculated from each distribution and compared for significant differences using the GT-2 test. Significant differences were related to the level of cumulative fishing pressure through regression.

6.2.2.2 Length-at-age data

Density dependent growth would result in an increased population growth rate, and hence increased length-at-age with increasing fishing pressure. To identify density dependent growth, mean length-at-age in different locations or statistical areas within locations were related to measures of local population density (CPUE or cumulative effort).

A spatial comparison of standardised mothervessel dory catch rates for all demersal species (MRAG, 1996c) noted that the catch rate indicated for Chagos was lower than expected from the level of prior fishing effort. This was attributed to discarding and targeted fishing practices (species avoidance), due to certain potentially ciguatoxic lutjanid species. Hence CPUE in this location was not an accurate measure of demersal species abundance. Examinations of length-at-age were therefore performed both with and without BIOT (Chagos Archipelago) data.

In the light of the problems in using CPUE as a measure of abundance for these species, mean length-at-age was also related to the cumulative level of standardised fishing effort expended. Since growth was felt to be related to total (or exploitable) population biomass, cumulative effort over an extended period was felt to represent the effects of fishing on the population more closely than shorter (*e.g.* annual) periods of effort. The use of fishing mortality as a measure of abundance required a number of assumptions, including that the level of recruitment, natural mortality, immigration and emigration were constant over time. No data were available to incorporate such additional variation into assessments.

Mean length in each integer age class was calculated for each study location, and statistical area within location. Some additional variability will have resulted from the use of integer ages, since further growth will have occurred in the period between January 1st and the time of capture. However, the effect was minimised by the relatively slow growth rate of the study species. Mean lengths-at-age were compared for significant differences using the GT-2 test. Significant differences between or within locations were related to CPUE, or total cumulative fishing pressure, through linear regression. Since higher CPUE was assumed to relate to increased abundance, a smaller length-at-age would result through density dependent growth. In contrast, higher cumulative fishing mortality levels were assumed to relate to lower species abundance, and hence larger length-at-age. To test the significance of the trend in mean length-at-age with CPUE and cumulative effort, a one-tailed *t*-test examined whether the gradient of the regression was significantly different from the horizontal in a negative or positive direction, respectively.

6.2.3 Examination of other biological data

Information on weight, sex, maturity stage and gonad weight were collected from individuals sampled for otoliths (Chapter 4, Section 4.2.2.2). These data were used to calculate length-weight relationships, sex ratios, and reproductive parameters such as Lm_{50} (length at which 50% of individuals were mature). Biological data were examined at the resolution of study location only. Dis-aggregation of data to the scale of statistical area within location reduced samples sizes, to the extent that trends frequently resulted due to the limited sample sizes. In this chapter, only length-weight relationships are examined, due to their relevance in studies of density dependent growth. The results of the examination of sex and maturity data are described in Appendix 6. While the latter information is of relevance to fisheries assessments (Chapter 7), they have little bearing on the effects of fishing on length structure, age structure, and growth.

6.2.3.1 Length-weight relationships

The weight of fish increases approximately in proportion to the cube of the length. The relationship takes the form:

$$W_i = q.L_i^b$$

The natural logarithm of fork length (cm) and corresponding weight (ungutted or gutted, kg.) were taken, and a regression performed on these log transformed values. The resultant regression parameters were then converted into parameters for the length-weight relationship, where *b* was the gradient of the regression, and *q* was the exponent of the regression intercept.

The GT-2 test was used to compare regression coefficients (*b* parameter) from length-weight relationships. In summary, this method used the minimum significant differences obtained by the GT-2 method, analogous to the method used to test the significance between two means. However, in this case the slope of the regression was tested (Sokal and Rohlf, 1995), using standard errors of the regression coefficients. Gabriel's method was then used to construct comparison intervals.

6.3 RESULTS

The examination of trends in length, age and growth data is described by species. Data were examined both between and within locations.

Seychelles length frequency data were collected from catches of a number of gear types. Comparisons were therefore made within gears to avoid any bias due to gear selectivity. A brief analysis of the effects of gear selectivity on length frequency distributions was also undertaken.

6.3.1 *Lethrinus mahsena*

Data were collected for this species from the Mauritian banks, BIOT (Chagos Archipelago), and Seychelles. Data from the Mauritian banks could not be subdivided into smaller areas; comparisons by statistical area were confined to those within BIOT (Chagos Archipelago) and Seychelles.

6.3.1.1 Assessment of mean length and age

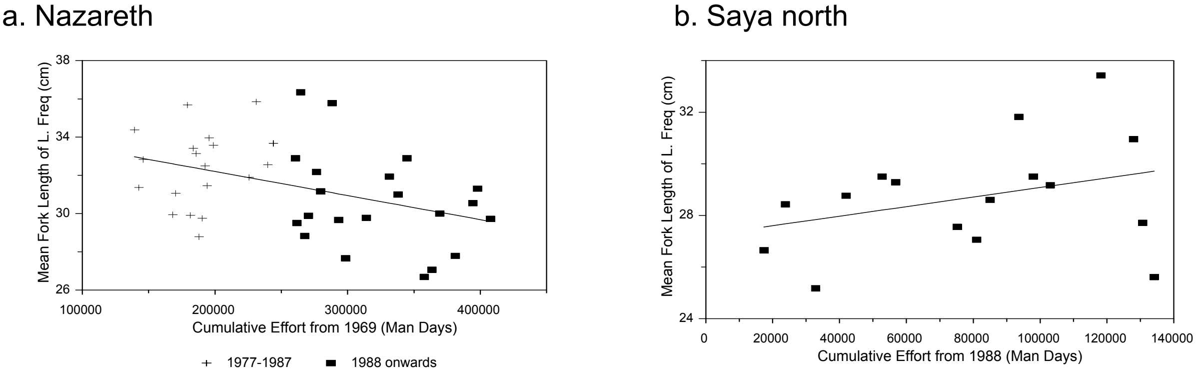
Catch mean length and standard deviation were first examined within each location over time, to identify temporal effects of fishing. Data were then analysed for significant differences both between and within locations, and related to the level of cumulative historical fishing pressure. From Seychelles, only two years of data were available for this species and hence an assessment of trends over time could not be performed. For this location, analyses were limited to those between and within locations.

Trends at location over time

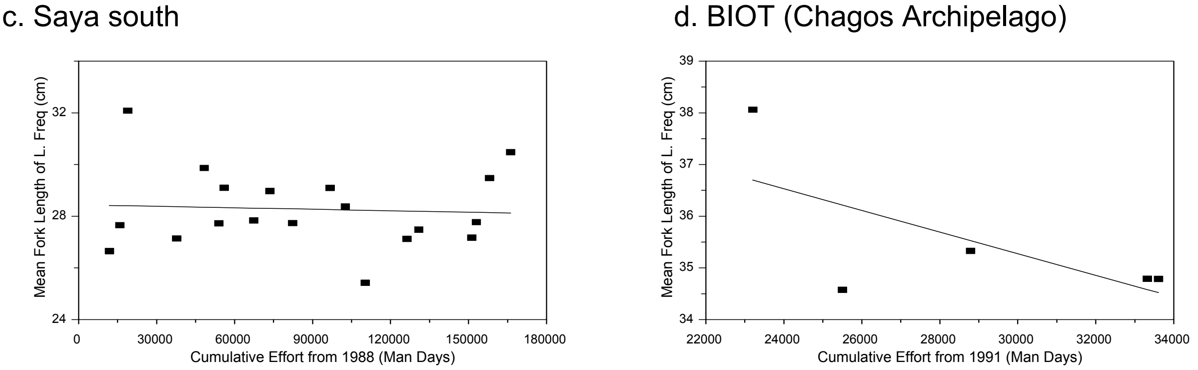
At each of the Mauritian banks, significant differences between consecutive samples were found in catch mean length. In contrast, mean lengths from BIOT (Chagos Archipelago) between 1995 and 1998 were not significantly different, with an exception in 1994. 1994 was the first year of the observer programme, when length frequency data collection was not a priority. It is possible that the measuring technique may not have been standardised, resulting in the significant difference.

A decreasing trend in catch mean length and standard deviation was found at Nazareth bank between 1989 and 1997. When mean lengths were related to the level of cumulative fishing pressure through linear regression, the decline of the regression approached significance (Table 6.1). Extension of the data set with mean fork length data from 1977-1987, computed from length frequency data presented in Bautil and Samboo (1988), resulted in a significant decline in mean length when related to unstandardised effort over this period (Table 6.1, Figure 6.1a).

Although a slight decline in mean length over time was observed at Saya south, the regression gradient was not significantly different from zero (Table 6.1, Figure 6.1c). An increasing trend in the mean length with fishing pressure was identified at Saya north (Figure 6.1b). Again, the regression gradient was not significantly different from zero (Table 6.1). Mean length in BIOT (Chagos Archipelago) remained relatively constant between years after 1994 (Figure 6.1d), and was not related to fishing pressure. No significant relationships were found between the standard deviation from the mean and increasing fishing pressure in each location (Table 6.1), although trends for BIOT (Chagos Archipelago), Saya south and Nazareth (1989 onwards) approached significance.


a. Nazareth

b. Saya north


c. Saya south

d. BIOT (Chagos Archipelago)

Figure 6.1 Mean length of *L. mahsena* by quarter (Mauritian banks) or year (BIOT, Chagos Archipelago) against cumulative effort. Effort data for BIOT (Chagos Archipelago) summed from 1991, and for Mauritian banks from 1988, or 1969 (NAZ). Note differences in scale.

Table 6.1 Regression analyses relating mean length or standard deviation to cumulative effort, by location.

	Regression of			
Location	Mean Length vs. Effort		Standard Deviation vs. Effort	
	r^2	*t*-test *P*	r^2	*t*-test *P*
Nazareth 1989 onwards	0.128	0.056	0.109	0.072
Nazareth 1977 onwards	0.168	0.004**	0.001	0.571
Saya south	0.004	0.401	0.097	0.097
Saya north	0.109	0.894	0.029	0.736
BIOT (Chagos)	0.444	0.110	0.606	0.060

** regression gradient significantly different from zero at the 5% level, as assessed using the *t*-test.

While general trends in mean length were described by the regressions, r^2 values indicated that cumulative effort generally described relatively little of the between quarter/year variability in mean length.

Comparison between locations within years

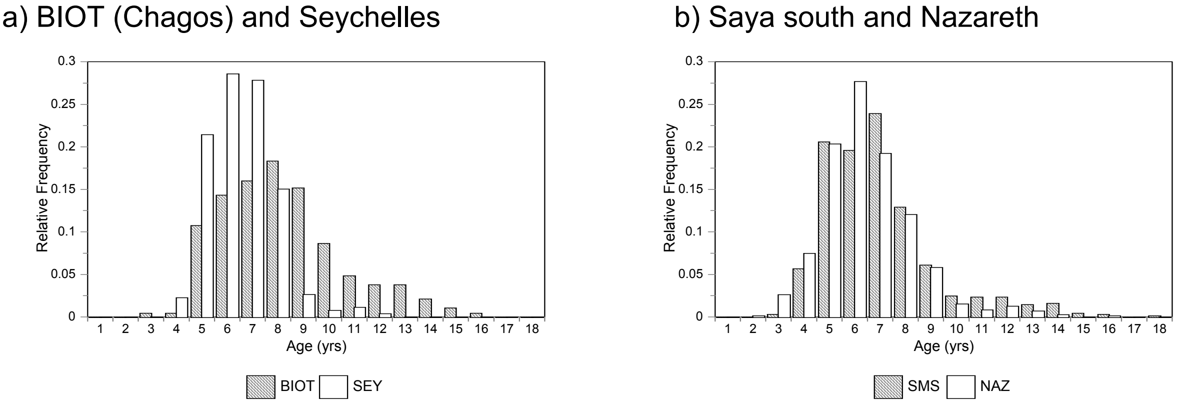
Due to the level of between-year variation, comparisons of mean length and age between locations were performed within years. The majority of samples collected from Saya north were targeted; an age frequency could not be derived for this location.

In all years, *L. mahsena* mean length from BIOT (Chagos Archipelago) was significantly larger than that at each of the Mauritian banks. For 1997, data were available from all study locations (Table 6.2). Catch age frequency distributions in 1997 were also significantly different (Kolmogorov-Smirnov test).

Table 6.2 Catch mean length and age of *L. mahsena*, by bank, in 1997. Cumulative effort (man days km^{-2}) also shown.

Location	Length (cm)		Age (yrs)		Cum. Effort (man days km^{-2})
	Mean	SD	Mean	SD	
BIOT (Chagos)	35.0	5.5	8.2	2.42	3.9
Nazareth	30.7	5.5	6.4	1.82	14.7
Saya south	29.3	4.6	7.0	2.26	17.7
Saya north	26.6	4.7	-	-	29.2
Seychelles	32.0	3.4	6.5	1.30	4.2

Catches from BIOT (Chagos Archipelago) contained a greater proportion of larger, and older individuals than those from other locations (Figures 6.2 and 6.3). Mean length for *L. mahsena* from Seychelles in 1997 was smaller than that calculated for BIOT (Chagos Archipelago), but larger than that calculated for the Mauritian Banks. The age frequency for Seychelles, however, was similar to that for the Mauritian banks (Figure 6.2).


a) BIOT (Chagos) and Seychelles

b) Saya south and Nazareth

Figure 6.2 Catch age frequency distributions for *L. mahsena* from four study locations.

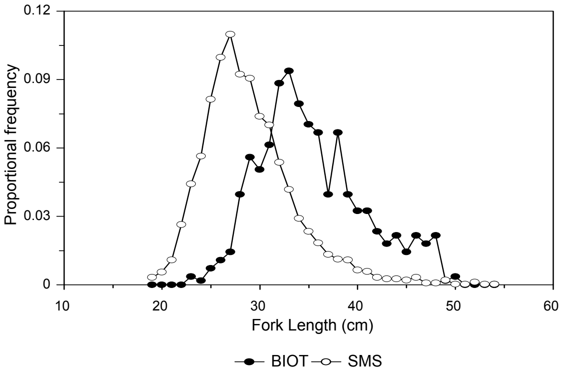


Figure 6.3 Comparison of *L. mahsena* catch length structure from BIOT (Chagos Archipelago) and south Saya de Malha (SMS). Data from 1996 BIOT (Chagos Archipelago) inshore observer programme. Data were unaffected by gear selectivity, seasonality, vessel/crew characteristics.

Mean length by location in 1997 was related to the cumulative fishing pressure in man days km^{-2} since 1991 (Figure 6.4).

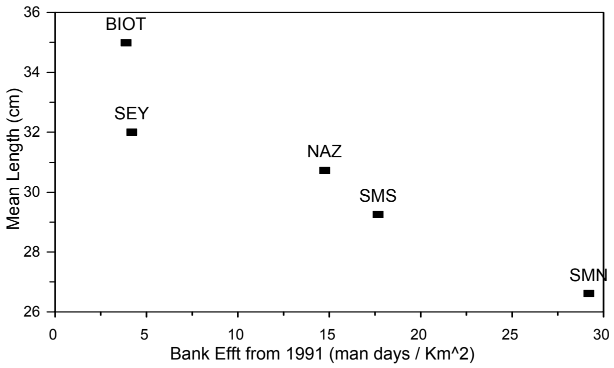


Figure 6.4 1997 mean fork length (cm) of *L. mahsena*, by location, against cumulative fishing effort since 1991 (man days km^{-2}).

A significant decline in mean length was identified with increasing cumulative effort per unit area (r^2 = 0.885, *t*-test of regression, *P*=0.009). It was noted that in 1998, the length frequency distribution for Seychelles was significantly different from that for 1997 (mean length in 1998 = 26.3cm, *n*=893). Insufficient effort and length data were available from all locations to test whether the relationship remained significant in this year.

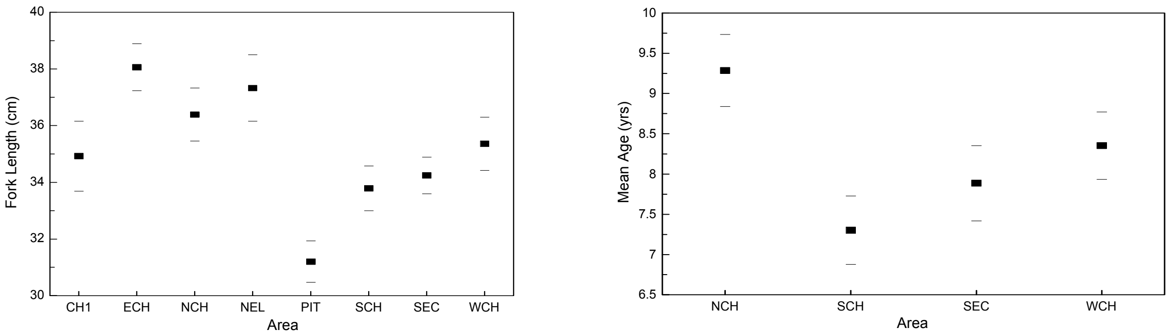
Although mean ages between locations were significantly different (GT-2 test, not shown), the decline with increasing fishing mortality was not significant (regression, r^2=0.116, *t*-test *P*=0.296). This was due to the low mean age identified in Seychelles. The mean age was only slightly greater than that calculated for Nazareth, and younger than that identified for Saya south. Where the mean age from Seychelles was excluded from the regression, fishing effort since 1991 explained 75% of the variation in mean age (regression, r^2=0.746). However, the decline in mean age with increasing fishing pressure remained insignificant (*t*-test *P*=0.168).

Comparison of length and age structure within locations

For BIOT (Chagos Archipelago), significant differences between successive years were found in length frequencies within a statistical area. On the assumption that this was also true for Seychelles, comparisons between statistical areas within these locations were performed within years. For BIOT (Chagos Archipelago), 1997 and 1998 data sets enabled the comparison of a number of statistical areas with suitable sample sizes (where *n*>50). In Seychelles, comparisons were limited to 1998.

Significant differences in mean length were found between specific statistical areas within BIOT (Chagos Archipelago) in 1997 (Figure 6.5a). Mean length at Pitt Bank was significantly lower than that from catches in statistical areas on the Great Chagos Bank. Within the Great Chagos Bank, fish from the south (SCH) and southeast (SEC) were significantly smaller than those found in the east (ECH), north and northeast (NCH, NEL) of the bank. Although the actual mean lengths were different, an identical trend was found in the subsequent year (1998). Within the 1998 data set, information was also available from Cauvin bank (CAU, to the southeast of the Great Chagos Bank). Mean length in this area was not significantly different from that at the south and southeast of the Great Chagos Bank, areas to which this bank is adjacent.

The Komogorov-Smirnov test indicated significant differences in *L. mahsena* age structure between statistical areas within BIOT (Chagos Archipelago). These were confirmed through the examination of mean age in each area using the GT-2 test (Figure 6.5b). Since assessments were made only for areas with more than 50 aged individuals, the total number of statistical areas examined was limited. However, the overall trend in mean age by statistical area was identical to that found in the mean lengths.

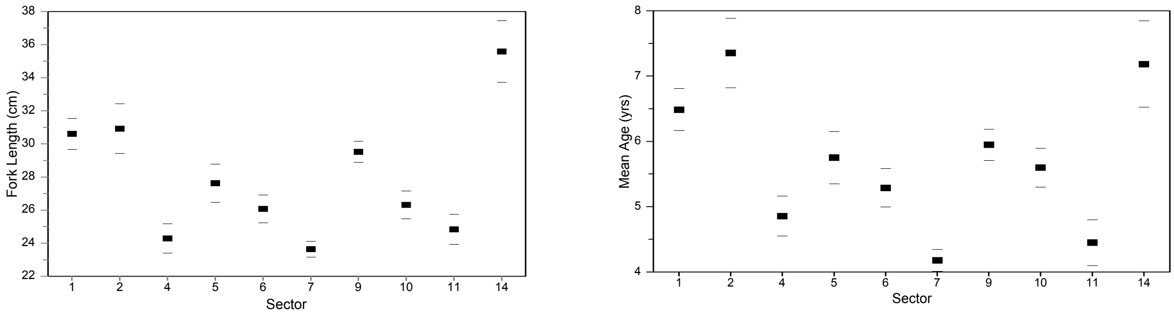

a) Mean length

b) Mean age

Figure 6.5 Gabriel's Plot of 95% comparison intervals by the GT-2 method for a) mean fork length and b) mean age of *L. mahsena* for different statistical areas within BIOT (Chagos Archipelago) during 1997.

There was no significant relationship between mean fork length in a statistical area of BIOT (Chagos Archipelago), and cumulative effort since 1991 (*t*-test for regression, 1997 data: *P*=0.891, 1998 data: *P*=0.698). While mean age in 1997 increased with cumulative fishing pressure, this increase was not significant (*t*-test of regression, *P*=0.797).

For Seychelles, sufficient data were collected during the otolith sampling programme in 1998 to compare *L. mahsena* mean length and age between sectors (Figure 6.6).


a) Mean length

b) Mean age

Figure 6.6 Gabriel's plot of 95% comparison intervals by the GT-2 method for a) mean fork length and b) mean age of *L. mahsena* by sector within Seychelles, 1998.

Mean lengths in Sectors 1, 2, 9 and 14 were significantly larger than those in all other sectors. Mean age followed similar patterns, with ages in sectors 2 and 14 being significantly older than those in all other sectors, bar sector 1 (Figure 6.6 b).

When related to the level of cumulative effort since 1985, both mean fork length and age by sector tended to decline with increasing effort (Figure 6.7). The decline in mean length approached statistical significance (regression r^2 = 0.286, *t*-test *P*=0.056). The decline in mean age with increasing cumulative fishing effort was significant, with fishing effort explaining 41% of the variation in mean age between statistical areas (r^2 = 0.408, *t-test* of gradient, *P*=0.023). Sector 7 was very influential in both relationships. When data for this area were excluded, the variation explained by cumulative effort was reduced (length; r^2=0.195, age: r^2=0.266), while the significance of the decline indicated by the regression gradient was also reduced (*t*-test of regression; length: *P*=0.117, age: *P*=0.078).

a) Mean length

b) Mean age

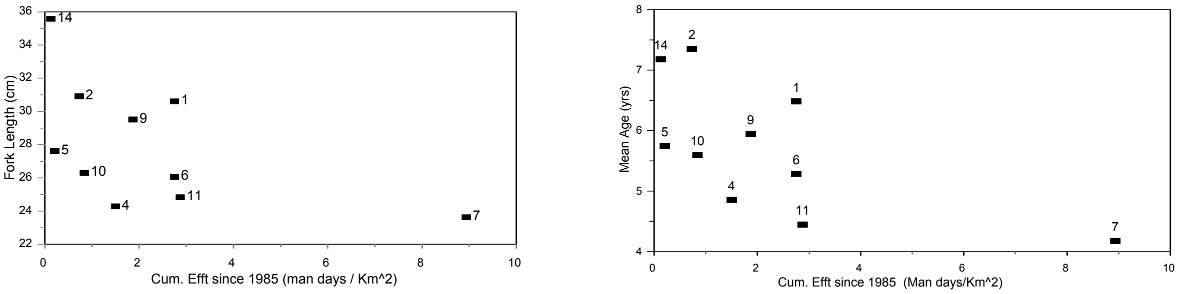


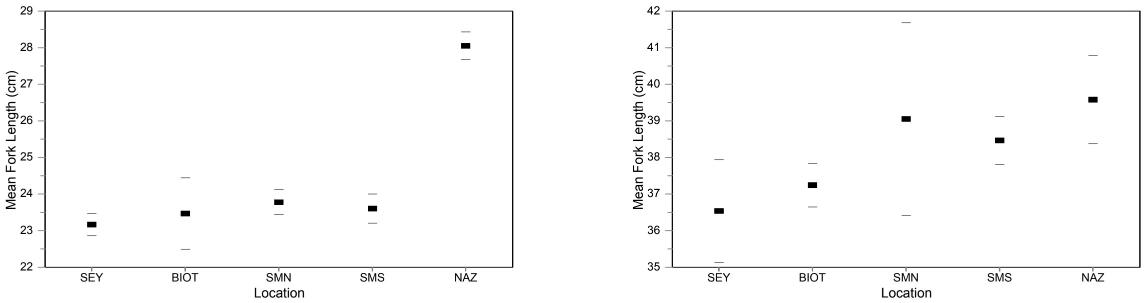
Figure 6.7 Relationship between a) 1998 mean length and b) 1998 mean age in sector (label) and the level of cumulative effort experienced since 1985.

6.3.1.2 Comparison of length-at-age and condition factor

Length-at-age data were available both within and between locations. There were insufficient data to assess condition factor by statistical area. Comparisons of length-weight relationships were limited to those between locations.

Comparison between locations within years

Mean length of *L. mahsena* from Nazareth was significantly larger than that from the other locations from ages 2 to 5 years (Figure 6.8a). Mean length in this location remained significantly larger than that in BIOT (Chagos Archipelago) and Seychelles up to age 9 years (Figure 6.8b). Above this age, there were no significant differences in mean length by location.



a) Age 4

b) Age 9

Figure 6.8 Gabriel's plots of 95% comparison intervals by the GT-2 method for *L. mahsena* mean length-at-age by location. Data for ages 4 and 9 years presented for illustration.

For each age, mean length by location was related to CPUE (kg man day^{-1}) and cumulative fishing pressure (man days km^{-2}) applied since 1991, through linear regression. At young ages, there was no overall relationship between CPUE or fishing mortality and mean length at that age by location (Table 6.3). However, as fish grew older (6+ years), mean length-at-age increased with increasing cumulative effort, and decreased with increasing CPUE (Figure 6.9). As ages increased further (>13 years), the strength of these relationships declined. The trend in mean length-at-age with CPUE, where BIOT (Chagos Archipelago) was excluded, was significant at ages 6 and 11 years (Table 6.3), while that for fishing mortality was significant at age 11 years, and approached significance for ages 8 to 12 years (excluding age 10 years). The exclusion of BIOT (Chagos Archipelago) data from the relationship between CPUE and mean length also improved the fit of the regression.

a) CPUE (kg man day^{-1}), age 11 years

b) Cum. effort (man days km^{-2}), age 11 years

Figure 6.9 Relationship between *L. mahsena* mean length-at-age and a) CPUE or b) cumulative fishing effort since 1991, by location, at age 11 years.

Table 6.3 Regression of mean length-at-age against CPUE (Kg man day^{-1}) or cumulative fishing mortality since 1991 (man days km^{-2}), by age and location. BIOT = BIOT (Chagos Archipelago)

Age (yrs)	CPUE (kg/man day)				Cumulative effort (since 1991)	
	Including BIOT		Excluding BIOT			
	r^2 of regression	*t*-test *P*	r^2 of regression	*t*-test *P*	r^2 of regression	*t*-test *P*
4	0.09	0.316	0.204	0.274	0.018	0.414
5	0.247	0.197	0.291	0.230	0.015	0.422
6	0.619	0.057	0.884	0.030**	0.395	0.128
7	0.392	0.129	0.634	0.102	0.276	0.182
8	0.418	0.119	0.733	0.072	0.574	0.069
9	0.236	0.203	0.618	0.107	0.590	0.065
10	0.527	0.082	0.572	0.122	0.265	0.188
11	0.500	0.091	0.826	0.046**	0.659	0.048**
12	0.257	0.192	0.555	0.127	0.567	0.071
13	0.215	0.268	0.706	0.182	0.232	0.259

** denotes significant trend at the 5% level

Since GT-2 tests of the length-weight relationships by sex within each location indicated no significant differences (not shown), data were amalgamated. There were insufficient data from BIOT (Chagos Archipelago) to perform this comparison. Data in this location were amalgamated based on the results from the other locations. The resultant length-weight relationship parameters for each location are presented in Table 6.4.

Table 6.4 Length-weight relationship parameters for *L. mahsena* by location. Both whole weight- and gutted weight-length relationship parameters are presented.

Location	Whole weight				Gutted weight			
	q	SE	b	SE	q	SE	b	SE
Nazareth	0.000027	0.102	2.92	0.022	0.000025	0.087	2.91	0.021
Saya south	0.000024	0.090	2.94	0.012	0.000024	0.098	2.92	0.012
Saya north	0.000020	0.083	3.00	0.019	0.000018	0.089	3.01	0.013
BIOT (Chagos)	-	-	-	-	0.000006	0.119	3.41	0.114
Seychelles	0.000041	0.117	2.84	0.023	-	-	-	-

The GT-2 test comparison of length-gutted weight regressions indicated that BIOT (Chagos Archipelago) was significantly different from all other locations (Figure 6.10). From the length-whole weight regressions, Seychelles was also significantly different from the Mauritian banks (GT-2 test, not shown). From plots of the length-weight relationships, individuals from BIOT (Chagos Archipelago) and Seychelles were significantly heavier at length than individuals from the other locations. Since the Mauritian banks are considered to be relatively heavily fished, this would imply a decrease in condition factor with increasing fishing pressure.

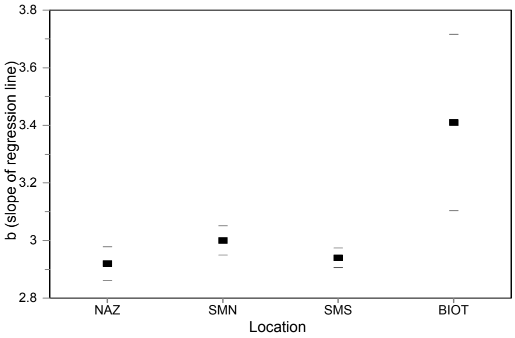
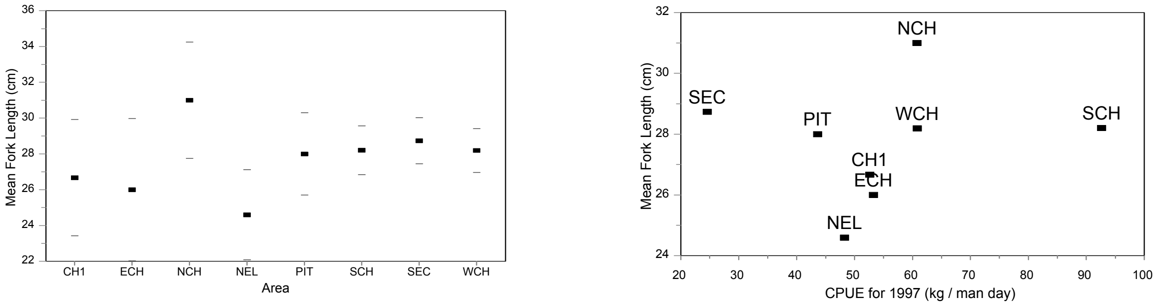


Figure 6.10 Gabriel's plot of the 95% comparison intervals for the 'b' parameter of length-gutted weight regressions by location. Gutted weight data were not available for Seychelles.

Comparisons within locations

Comparisons within Seychelles and BIOT (Chagos Archipelago) were limited to the examination of mean length-at-age data.

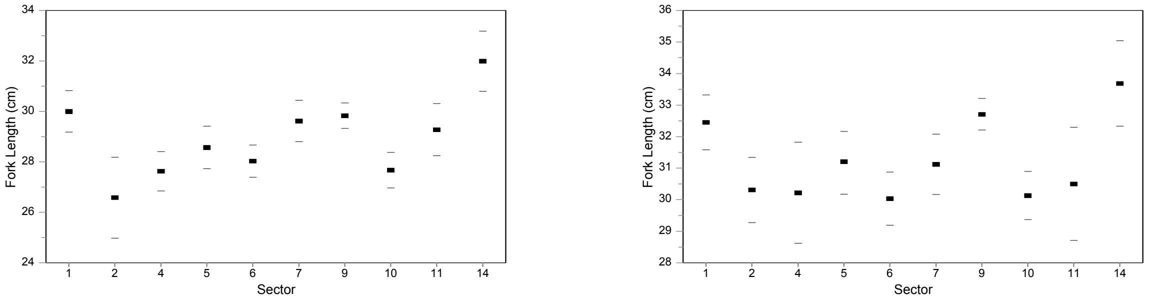
For BIOT (Chagos Archipelago), comparisons of mean length-at-age (GT-2 test) indicated that although certain statistical areas showed significant differences at individual ages (Figure 6.11 a), patterns were not consistent between ages. There appeared to be no significant difference in overall growth rate of *L. mahsena* between different statistical areas of BIOT (Chagos Archipelago). Mean length at each age by statistical area showed no consistent pattern when related to the level of CPUE or cumulative fishing pressure applied per unit area since 1991 (Figure 6.11 b). Only when mean length at age 12 years was related to CPUE by statistical area was a significant (decreasing) relationship found (regression, r^2=0.950; *t*-test, *P*=0.012).


a) Mean length at age 5 yrs, by area

b) Mean length at age 5 years vs CPUE

Figure 6.11 a) Gabriel's plot of the 95% comparison intervals by the GT-2 method for mean length at age 5 years by statistical area within BIOT (Chagos Archipelago). b) Corresponding pattern in mean length at age 5 years with CPUE (kg man day^{-1}) for 1997.

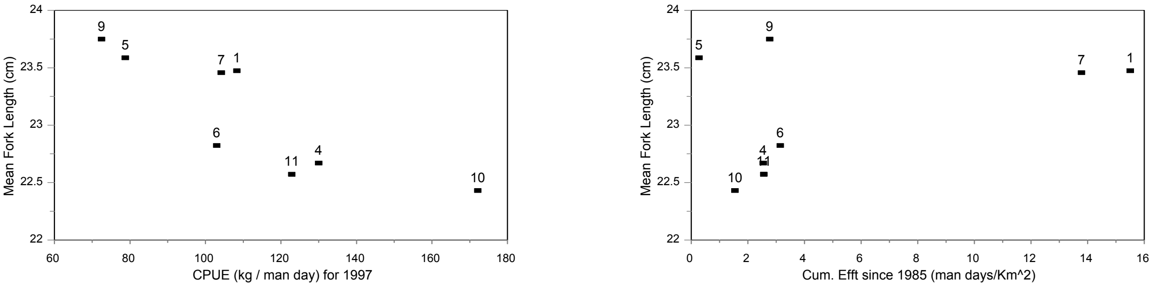
In Seychelles, mean length-at-age plots indicated differences between specific sectors at certain ages. Mean length-at-age in Sectors 1, 9 and 14 tended to be significantly larger than those from other sectors for ages 6 and 7 years (Figure 6.12). However, although significant differences in growth rate were identified between sectors in Seychelles, patterns were inconsistent between ages.


a) Age 6 years

b) Age 7 years

Figure 6.12 Gabriel's plots of 95% comparison intervals by the GT-2 method for mean length-at-age of *L. mahsena* by sector in Seychelles for ages 6 and 7.

A general decreasing trend in sector mean length-at-age with increasing CPUE, and an increasing trend with increasing cumulative fishing mortality was found (Table 6.5, Figure 6.13). Trends were strongest in younger age classes. When compared to cumulative effort, the relationship was significant at ages 4 and 5 years. The pattern was strongly influenced by the data from Sectors 1 and 7.


a) CPUE, 1997 (kg man day^{-1}), age 4 yrs

b) Cum. effort (man days km^{-2}), age 4 yrs

Figure 6.13 Mean length for *L. mahsena* in sector related to the level of a) CPUE for 1997, b) cumulative fishing pressure from 1985, at age 4 years.

Table 6.5 Regression of mean length-at-age against CPUE (Kg manday^{-1}) or cumulative fishing mortality since 1985 (man days/km^2), by age and sector.

Age (yrs)	CPUE (kg/man day)		Cumulative effort (since 1985)	
	r^2 of regression	*t*-test *P*	r^2 of regression	*t*-test *P*
3	0.253	0.155	0.263	0.149
4	0.157	0.166	0.718	0.004**
5	0.280	0.089	0.400	0.047**
6	0.150	0.134	0.047	0.727
7	0.097	0.190	0.002	0.548
8	0.184	0.145	0.266	0.095
9	0.710	0.079	0.675	0.089

** denotes significant trend at the 5% level.

Length-at-age data were available from Sector 14 for ages six years onwards. As indicated in Figure 6.12, growth in this location was significantly faster than that in the majority of other locations, while the cumulative fishing effort at this location was low. This was the opposite pattern expected from density dependent growth. When relationships were re-assessed for ages 6-9 years with Sector 14 excluded, both the fit of the regressions and significance of the trends with CPUE and effort were improved. The trend with increasing CPUE at age 6 years became significant (r^2=0.356, *t*-test *P*=0.045), while trends at age 7 years approached significance (CPUE: r^2=0.225, *P*=0.098; cumulative effort: r^2=0.293, *P*=0.066).

6.3.1.3 Summary of results for *L. mahsena*

- The expected decreasing trend in catch mean length over time was found at Nazareth bank. This decline was significant in a data set including extended historical data. In the other locations, no significant trends were identified. A significant decline in mean length by location in 1997 was identified when related to cumulative effort from 1991 (*P*=0.009). However, declines seen in mean age were not significant.

- Individuals from Nazareth showed significantly faster growth (larger mean length-at-age) than all other locations for ages 2-5 years, and for BIOT (Chagos Archipelago) and Seychelles up to age 9 years. Mean length-at-age by location increased with increasing cumulative fishing mortality, and decreased with increasing CPUE for ages between 6 and 12 years. However, trends were significant at a limited number of ages. Condition factor in BIOT (Chagos Archipelago) and Seychelles was greater than that at the Mauritian banks.

- Significant differences in mean length were identified between statistical areas within BIOT (Chagos Archipelago) and Seychelles. In BIOT (Chagos Archipelago), these differences were consistent between years. No trends were found where mean length and age by statistical area within BIOT (Chagos Archipelago) were related to cumulative effort. In Seychelles, however, the declining relationship with length approached significance (*P*=0.056), while that with age was significant (*P*=0.023).

- No significant differences in growth (mean length-at-age) were found between statistical areas of BIOT (Chagos Archipelago). In Seychelles, however, significant differences were found. These differences were positively related to increasing cumulative fishing effort, and negatively related to increasing CPUE. Sector 14 was influential on the trends at ages 6 years or greater, reducing their significance.

6.3.2 *Aprion virescens*

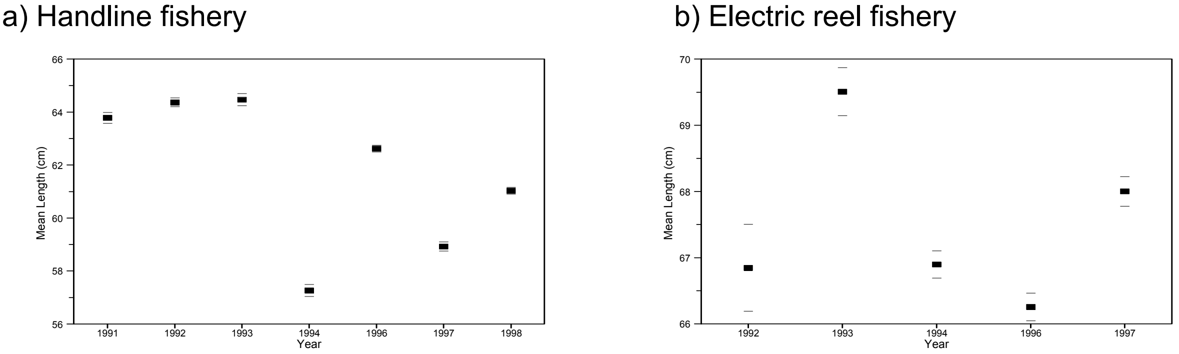
The assessment of length, age and biological data from *A. virescens* are described in this section. Data for this species were available from both BIOT (Chagos Archipelago) and Seychelles.

6.3.2.1 Assessment of mean length and age

Length frequency data were first examined within each location over time, to discern trends in mean length and standard deviation which might indicate the expected temporal effects of fishing. Data were then compared between and within locations, and between successive years.

Trends within location over time

The comparison of catch length structures between years in Seychelles were performed for data from handline and electric reel fisheries. Mean lengths of the handline length frequency distributions were significantly different to all other years, bar those from 1992 and 1993 (Figure 6.14 a). For the electric reel fishery, mean length in 1992 was not significantly different from those in 1994 and 1996, while those in 1993 and 1997 were significantly larger than the other years (Figure 6.14 b). In both cases, there was a notable degree of between year variability in catch mean length.


a) Handline fishery

b) Electric reel fishery

Figure 6.14 Gabriel's Plot of 95% comparison intervals by the GT-2 method for *A. virescens* mean fork length caught in Seychelles using a) handlines, b) electric reels, by year.

There was evidence of a decline in handline catch mean length with increasing cumulative fishing pressure. However, the regression gradient relating mean length from either handline or electric reel catches to standardised demersal cumulative fishing pressure was not significantly different from the horizontal (*t*-test, handlines: $P = 0.110$, electric reels, $P=0.394$).

For BIOT (Chagos Archipelago), only the 1994 and 1997 data sets contained sufficient samples to warrant examination. Mean fork length was significantly larger in 1997 than in 1994 (Welch's Approximation, $t_{0.05} = 1.98$, $t_s = 4.49$).

Comparison between locations within years

Length frequency comparisons between Seychelles and BIOT (Chagos Archipelago) were limited to handline catches in 1994 and 1997 (Table 6.6). Mean length for Seychelles handline catches in 1994 was significantly larger than that from BIOT (Chagos Archipelago) (Welch's Approximation, $t_{0.05} = 1.97$, $t_s = 3.19$), while there was no significant difference in the mean lengths in 1997 (Welch's Approximation, $t_{0.05} = 1.97$, $t_s = 0.03$).

Table 6.6 Comparison of mean length of *A. virescens* from BIOT (Chagos Archipelago) and Seychelles in 1994 and 1997, related to cumulative fishing pressure per unit area from 1991 (man days km^{-2}).

	1994		1997	
	SEY	BIOT	SEY	BIOT
Mean length (cm)	57.3	55.0	58.9	58.9
Cum. effort/km^2	2.3	2.7	4.2	3.9

Age frequencies resulting from the analysis of 281 randomly sampled individuals in BIOT (Chagos Archipelago) and 1,275 individuals in Seychelles (Figure 6.15) were significantly different (Kolmogorov-Smirnov test, $D_{0.05} = 0.09$, $D_{max} = 0.15$). The distribution in Seychelles contained a greater proportion of older individuals compared to that from BIOT (Chagos Archipelago).

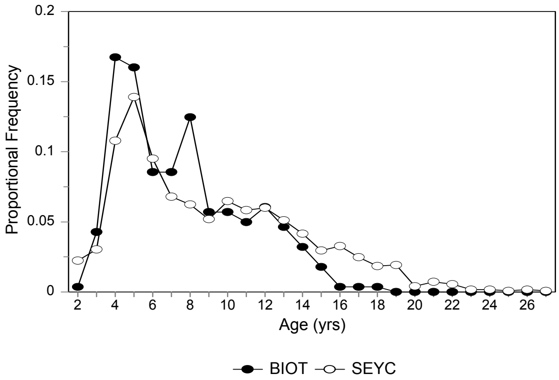


Figure 6.15 Comparison of *A. virescens* age frequency distributions from Seychelles and BIOT (Chagos Archipelago).

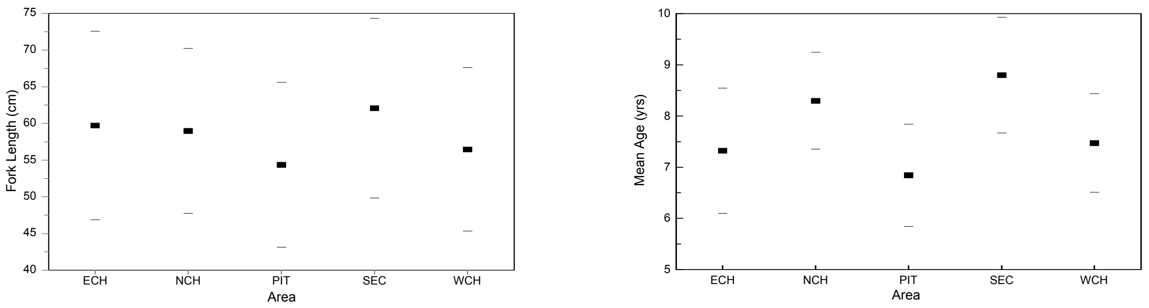
Mean age was compared statistically using Welch's approximate *t*-test. Mean age in Seychelles (9.1 years) was significantly larger than that found in BIOT (Chagos Archipelago) (7.6 years; $t_{0.05} = 1.97$, $t_s = 6.44$).

Different hook sizes were used in the two locations, which added to variation resulting from any differences in habitat conditions. In BIOT (Chagos Archipelago), *A. virescens* was caught using Limerick type 3/0 or 4/0 hooks. In Seychelles, larger 'ringed blued' 5/0 hooks, and size 12/0 and 13/0 tuna circle hooks were used.

Hook size may influence catch length and age structure. Data for *A. virescens* was insufficient to identify changes in catch length structure between gears. Studies of *L. mahsena* length data from BIOT (Chagos Archipelago) observer programmes, however, showed significant differences in mean length with hook size. Mean catch length from 3/0 hooks (34.3cm) was significantly smaller than that found in catches from larger 4/0 hooks (36.2cm; Welch's Approximation, $t_{0.05} = 1.97$, $t_s = 5.58$).

Comparison of length and age structure within locations

Due to the relatively low frequency of *A. virescens* in catches from BIOT (Chagos Archipelago), comparisons of length and age frequency distributions within this location were limited to 1997. No significant differences were found between mean length or mean age in any of the five statistical areas for which sufficient data were available (Figure 6.16).


a) mean length

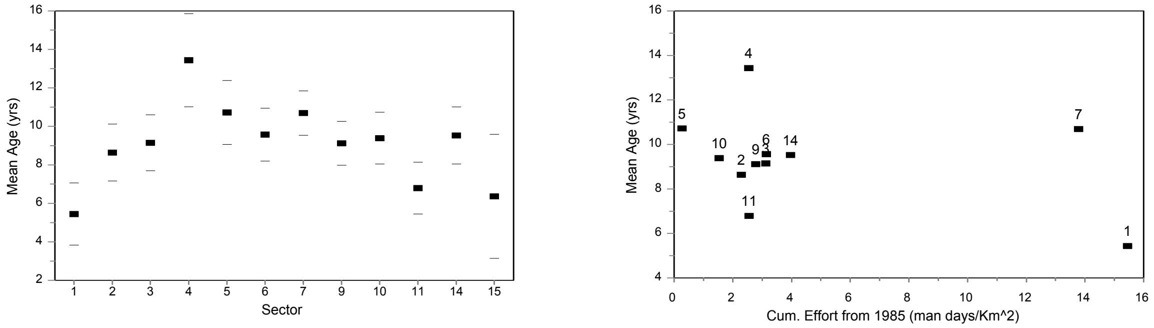
b) mean age

Figure 6.16 Gabriel's plot of 95% comparison intervals by the GT-2 method for a) mean fork length and b) mean age of *A. virescens* caught in statistical areas of BIOT (Chagos Archipelago) in 1997.

No relationship was found between either mean length or mean age and the cumulative fishing mortality exerted in each statistical area since 1991 (regression of effort vs mean length, r^2 = 0.026, *t*-test *P*=0.399; regression of effort vs mean age, r^2 = 0.209, *t*-test *P*=0.849).

For Seychelles, significant differences in *A. virescens* mean length from each sector were found within years. In 1991, 1996 and 1997 there were sufficient data to perform regressions of mean length against cumulative effort (since 1985) per unit area. No significant relationship was found in any year (*t*-test of regression; 1991 *P*=0.670, 1992 *P*=0.673, 1997 *P*=0.479). A comparison of trends in mean length between sectors common to the three years indicated that the pattern in sector mean length was not consistent between years.

The Kolmogorov-Smirnov and GT-2 tests identified significant differences in *A. virescens* age frequency distributions in different statistical areas of the Seychelles (Figure 6.17 a).


a) Mean age by sector

b) Mean age by sector vs cumulative effort

Figure 6.17 a) Gabriel's plot of 95% comparison intervals for *A. virescens* mean age (yrs) by sector within Seychelles. b) Plot of mean age in sector against cumulative fishing effort (man days km^{-2}) since 1985. Sector numbers shown.

Mean age in Sector 1 was significantly lower than the majority of other sectors bar Sectors 11 and 15. Therefore, the mean age in Sector 1 was significantly lower than that found in all other statistical areas of the Mahé Plateau (Sectors 2-10). Mean age in Sector 4 was significantly greater than that in the majority of sectors. There was no significant trend in mean age from each sector with the level of cumulative fishing mortality since 1985 (Figure 6.17 b; regression, r^2 = 0.088, *t*-test, *P*=0.188). Data for Sector 15 was not included since no effort data were available for this location.

6.3.2.2 Comparisons of length-at-age and condition factor

Comparisons of length-at-age data were made both between and within locations. Since there were insufficient length-weight information available when data were dis-aggregated by statistical area, condition factor was only compared between locations.

Comparison between locations within years

The GT-2 test indicated there were no significant differences between the mean length-at-age distributions from BIOT (Chagos Archipelago) and Seychelles at any sampled age (Figure 6.18).

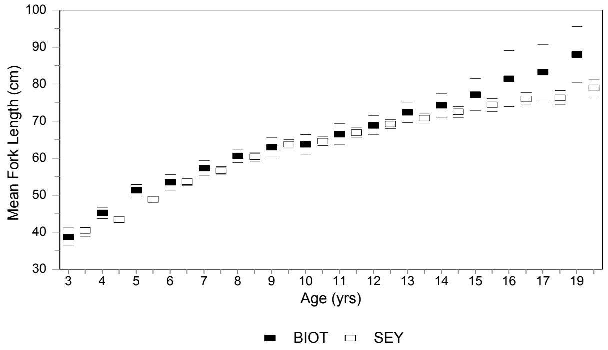


Figure 6.18 Gabriel's plot of 95% comparison intervals by the GT-2 method for *A. virescens* mean length-at-age from Seychelles and BIOT (Chagos Archipelago).

Mean length-at-age diverged in the older age classes, with that from BIOT (Chagos Archipelago) being larger than that in Seychelles. However, this divergence was not significant, as indicated by the overlapping comparison intervals. This may result from low sample sizes in BIOT (Chagos Archipelago).

Since the length-weight relationships for male and female *A. virescens* in Seychelles were not significantly different, as identified by the GT-2 test, data were combined for the calculation of an overall relationship. There were insufficient sex data for BIOT (Chagos Archipelago) to perform a corresponding comparison. Data were amalgamated based on results from Seychelles. The length-weight parameters are shown in Table 6.7, by location.

Table 6.7 Length-weight relationship parameters for *A. virescens* by study location. Both whole and gutted weight-length relationships are shown.

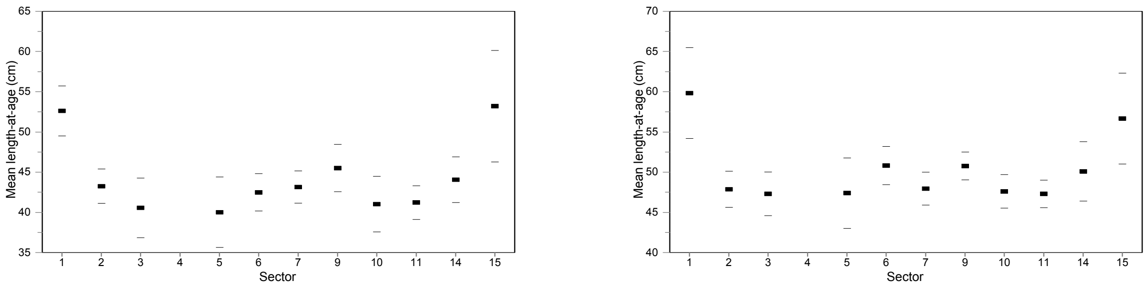
Location	Whole weight				Gutted weight			
	q	SE	b	SE	q	SE	b	SE
BIOT (Chagos)	-	-	-	-	0.000030	0.112	2.82	0.043
Seychelles	0.000031	0.113	2.79	0.021	0.000032	0.177	2.74	0.026

GT-2 test comparisons indicated that length-weight regression parameters were not significantly different between locations. There was therefore no significant difference in condition factor between the two locations.

Comparisons within locations

For BIOT (Chagos Archipelago), GT-2 test comparisons of mean length-at-age by statistical area identified only one significant difference. At age 4 years, mean length at Pitt Bank (PIT) was significantly lower than that at east Great Chagos Bank (ECH) and northeast Great Chagos Bank (NEL). This species appears to grow at a similar rate in all the statistical areas of BIOT (Chagos Archipelago) examined. No significant relationships were found between mean length-at-age by statistical area and either CPUE in 1997, or cumulative fishing mortality since 1991. Exceptions were age 6 years for CPUE (regression; r^2=0.857, *t*-test *P*=0.012), and age 12 years for cumulative effort (regression r^2=0.997, *t*-test *P*=0.016).

Mean length-at-age plots indicated significant differences in *A. virescens* growth between sectors of the Seychelles. Mean length-at-age in Sector 1 was significantly larger than all other sectors, bar Sector 15, at ages 4 and 5 years (Figure 6.19), and all sectors bar 9 and 15 at age 6 years.



a) Age 4 years

b) Age 5 years

Figure 6.19 Gabriel's plot of 95% comparison intervals by the GT-2 method for mean length-at-age of *A. virescens* in sectors of Seychelles, by age. Ages 4 and 5 years presented as examples.

Mean length-at-age for each sector was related to CPUE in 1997, and cumulative fishing pressure (man days km^{-2}) applied since 1985, through linear regression. Data for Sector 15 were not included due to the lack of effort information for this location. Decreasing trends in mean length were found with increasing CPUE, while increasing trends were found with increasing fishing mortality (Table 6.8; Figure 6.20).

Table 6.8 Regression of mean length-at-age for *A. virescens* by sector in Seychelles against CPUE for 1997 (kg man day^{-1}) and level of cumulative fishing mortality since 1985 (man days km^{-2}), by age and statistical area.

Age (yrs)	CPUE for 1997		Cumulative effort from 1985	
	r^2 of regression	*t*-test *P*	r^2 of regression	*t*-test *P*
4	0.004	0.432	0.531	0.008**
5	0.002	0.453	0.433	0.019**
6	0.113	0.189	0.290	0.054
7	0.461	0.022**	0.054	0.726
8	0.213	0.076	0.191	0.090
9	0.410	0.023**	0.365	0.032**
10	0.359	0.026**	0.268	0.063
11	0.264	0.053	0.173	0.102
12	0.251	0.070	0.003	0.556
13	0.183	0.109	0.001	0.535
14	0.242	0.089	0.224	0.099
15	0.370	0.041**	0.001	0.526
16	0.454	0.049**	0.007	0.573

** denotes significant trend with effort at 5% level

a) CPUE, 1997 (kg man day^{-1}), age 9 yrs

b) Cum. Effort (man days km^{-2}), age 9 yrs

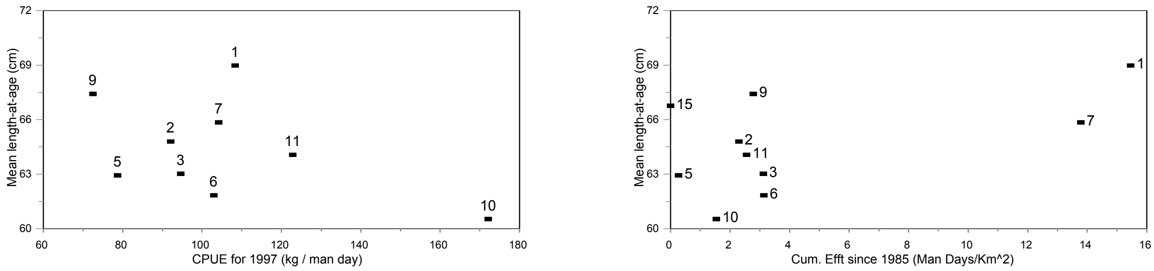


Figure 6.20 Pattern in mean length-at-age by sector (labels) when related to a) CPUE (kg man day^{-1}) for 1997, b) cumulative fishing effort (man days km^{-2}) since 1985. Patterns in mean length by sector at age 9 years presented.

Trends were significant, or approached significance, at a number of ages when related to either cumulative effort or CPUE.

6.3.2.3 Summary of results for *A. virescens*

- No significant trends in mean length over time were found in Seychelles, while data from BIOT (Chagos Archipelago) were too limited to perform such assessments. For comparisons between these locations, while mean length was not significantly different, mean age in Seychelles was significantly larger than that from BIOT (Chagos Archipelago). Gear selectivity may have influenced these patterns; hook sizes used in Seychelles were larger than those in BIOT (Chagos Archipelago).

- There were no significant differences in mean length-at-age or condition factor between Seychelles and BIOT (Chagos Archipelago).

- No significant differences in mean length or age were found between statistical areas within BIOT (Chagos Archipelago). Significant differences were found by statistical area in Seychelles. For example, mean age in Sector 1 was significantly lower than that in all other areas of the Mahé Plateau (Sectors 2-10). However, the relationship with cumulative effort was not significant.

- Growth rate was comparable between statistical areas within BIOT (Chagos Archipelago). In Seychelles, growth rate in Sector 1 was significantly faster than that for all other sectors on the Mahé Plateau for ages 4 and 5 years, and all bar Sectors 9 and 15 at age 6 years. Mean length-at-age by statistical area in Seychelles increased with increasing cumulative fishing mortality, and decreased with increasing CPUE between ages 4 and 12 years. Trends were significant for specific ages within this range (Table 6.8).

6.4 DISCUSSION

This chapter examined the length, age and growth of exploited *L. mahsena* and *A. virescens* populations for evidence of the effects of fishing. Characteristics were compared both between and within the study locations. In the following sections, the results of these studies are discussed.

From the studies performed in Chapter 5, fishing was expected to result in a decrease in the mean length of catch length frequency distributions with increasing fishing pressure. Mean lengths were first assessed over time in each location. Both mean length and age were then compared between and within locations. Trends were related to the level of cumulative fishing pressure applied per unit area.

To examine the effects of fishing on growth, mean length-at-age for the study species was compared between and within locations. Where population density was related to CPUE, density dependent growth would result in a decrease in mean length-at-age with increasing CPUE. When related to fishing effort, an increase in mean length-at-age would result with increasing fishing effort. A further indicator of density dependent growth is a change in the length-weight relationship. Increased growth due to density dependence may divert resources from other functions, leading to a decrease in the condition factor. The level of allometry and weight-at-length were therefore assessed both between and within locations (by statistical area), and related to the level of cumulative fishing pressure.

The assessments of length, age and growth performed between locations will first be discussed. Those assessments made within locations will then be examined.

6.4.1 Examination of data between locations

6.4.1.1 Trends in length and age distributions

The expected trend of decreasing mean length over time was identified in *L. mahsena* data from Nazareth bank. Generally, however, no trend was found in either species. This lack of trends may also result from the level of fishing mortality experienced. In BIOT (Chagos Archipelago) and Seychelles, fishing effort may have been too low to significantly affect population length structure during the period examined. At more heavily fished locations such as Saya south, where historical fishing mortality has remained relatively stable over the period examined (if at a relatively high level), *L. mahsena* length structure may have reached an equilibrium with that level of effort (see Chapter 5). In turn, if density dependent growth were operating, declines in mean length over time due to fishing pressure may have been mitigated.

At Saya north, *L. mahsena* mean length appeared to increase over time, although the trend was not significant. This was the opposite trend to that expected from Chapter 5. However, such increases in catch mean length could result from the effects of fishing. A decrease in fishing effort over time may allow an exploited population length structure to recover. No such decrease in annual effort was apparent. Alternatively, under relatively constant fishing mortality, increases in growth rate due to high levels of density dependent growth may ‘over-compensate’ for the effects of fishing on the length structure. However, such increases could also result from fishing practices. Small individuals may be discarded, since fishing companies have recently begun to limit/prohibit the landing of such sizes. Where they are accepted, they are commonly separated from the main catch. As a result, port data collection programmes will not sample those size classes, leading to an increase in catch mean length. Small individuals comprise a higher proportion of the catch at Saya north compared to the other locations, as seen from the comparison between locations (*e.g.* Table 6.2). The effect of discarding on mean length may therefore be more obvious at this location. In turn, since population structure may be localised (see below) vessels may have encountered relatively unexploited populations, with larger mean length.

Evidence for the expected effects of fishing on catch mean length were identified when comparing this measure between locations within years. In 1997 a significant decline in *L. mahsena* mean length by location was identified with increasing cumulative effort (P=0.009). In 1998, however, catch mean length in Seychelles was similar to that found at the Mauritian banks. Due to a lack of effort data in this year, a relationship could not be derived. As indicated by the r^2 values of the regressions relating mean length over time, there was significant between-year variation in the catch length structures. This had the potential to obscure relationships with fishing effort; a number of other factors must also influence the sample mean length.

Catch mean age also exhibited the trends expected to result from fishing. *L. mahsena* catch age structure in BIOT (Chagos Archipelago) contained significantly more older individuals than that found in the more heavily exploited Mauritian banks. The sampled age structure from relatively lightly fished Seychelles, however, was comparable to that identified at the Mauritian banks. This may have resulted from historical fishing mortality not included in the calculation of cumulative effort from 1991. By excluding Seychelles data, cumulative fishing effort explained 75% of the variation in mean age between locations. However, the decline with increasing fishing pressure was not significant.

A. virescens catch mean age in Seychelles was significantly larger than that in BIOT (Chagos Archipelago). Given the higher historical (pre 1991) exploitation rates assumed for Seychelles, this is the reverse of the expected trend. Differences did not result from growth rate, which was comparable between the two locations. The larger mean age in Seychelles may result from gear selectivity effects. Larger hooks were used to catch *A. virescens* in Seychelles, compared to those used in BIOT (Chagos Archipelago). As shown with *L. mahsena* length frequency data, such larger hooks may result in an increased catch mean length, and hence age. Habitat influences may also affect the population structure; if natural mortality in BIOT (Chagos Archipelago) was greater than that in Seychelles, this would also explain the reduction in mean age.

Length at capture can be controlled through gear restrictions or minimum size limits. However, the latter methodology is inappropriate for the species studied, since the expansion of gas bladders and evisceration on landing results in high levels of mortality in subsequently discarded fish (*e.g.* DeMartini *et al.*, 1996; Mees and Rousseau, 1997). Although hook size and fish size have generally shown little relationship (*e.g.* Ralston, 1982; Bertrand, 1988), others have shown that the use of larger sized hooks can protect smaller individuals from fishing mortality (*e.g.* Ivo and Rocha, 1988; Cortez-Zaragoza *et al.*, 1989; Ottway and Craig, 1993). Hook size has also been restricted by companies exploiting the Mauritian and BIOT (Chagos Archipelago) fisheries to limit the number of undesirable ‘undersized’ fish (A. Talbot, *pers. com.*). Some evidence for variation in mean size with hook size has been identified in these fisheries (MRAG, 1997b). Regulation of the size at capture through gear restrictions may therefore be feasible.

6.4.1.2 Trends in growth rate

No significant differences in *A. virescens* growth rate were found between Seychelles and BIOT (Chagos Archipelago). *L. mahsena* mean length-at-age by location exhibited trends consistent with density dependent growth between ages 6 and 12 years. However, those trends were only significant for a limited number of ages. In addition, trends for CPUE were only significant where data for BIOT (Chagos Archipelago) were excluded. The latter was not unexpected, given the uncertainty over the relationship between species abundance and catch rate in this location, as a result of discarding and species avoidance. Length-weight relationships for *L. mahsena* indicated a significantly higher weight-at-length in individuals from BIOT (Chagos Archipelago) and Seychelles, compared with the Mauritian banks. Condition factor assessments therefore increased the evidence for density dependent growth in this species. However, overall the evidence for density dependent growth in this species was limited.

Trends indicating density dependent growth were not found in older age classes. At such ages, effects may be obscured by the reduction in growth rate with age, and increased variability in length-at-age. However, younger, faster growing *L. mahsena* individuals also showed no indication of density dependent growth. This may result from spatial or behavioural differences between younger and older age groups. If younger ages were feeding on an alternative resource to adults, for which density did not limit access, growth would not be affected by intra-specific competition. Interestingly, analysis of the maturity data (Appendix 6) indicated that the age at maturity (Am_{50}) in *L. mahsena* was between 5 and 7.5 years. This corresponded to the age at which trends between length-at-age and fishing effort were first noted. A relationship may exist between the formation of spawning aggregations and the onset of density dependent growth. Alternatively, increased stresses experienced due to gamete production may be offset somewhat where densities are low and food consequently more plentiful, allowing relatively faster growth.

Trends in both the population structure and growth rate could be obscured by environmental differences between locations. To minimise these impacts, data for both species were examined by statistical area within BIOT (Chagos Archipelago) and Seychelles.

6.4.2 Examination of data within locations

6.4.2.1 Trends in length and age

In BIOT (Chagos Archipelago), significant differences in *L. mahsena* catch mean length and age by statistical area did not result from fishing pressure, or differences in growth rates. This was not unexpected, given the low level of fishing mortality experienced. Patterns between areas were consistent between-years, suggesting localised ‘meta-populations’ existed (*e.g.* MRAG, 1996c). Such meta-populations may be constrained by the distribution of suitable substrate, food sources, or through spawning aggregations. Since length-at-age was comparable between areas, however, environmental factors controlling growth appear constant across the bank. Differences in the length and age structures of such localised populations may therefore result from the selection of different habitats by fish at different stages in their development, from localised differences in natural mortality, or different levels of localised annual recruitment. Specific populations may be more vulnerable to fishing as a result.

In Seychelles, significant differences in *L. mahsena* length and age structure between areas appeared to be influenced by fishing pressure. Catch mean age by area declined significantly with increasing localised cumulative fishing effort (*P*=0.023), while the trend in mean length approached significance (*P*=0.056). The relatively heavily fished Sector 7 was influential in these relationships. Without the data from this Sector, decreasing trends remained, but relationships were not significant. The fact that a relationship existed between both mean length and age and local fishing effort implies that the distribution of *L. mahsena* populations in Seychelles was also localised.

There were no significant differences in *A. virescens* mean length and age between statistical areas in BIOT (Chagos Archipelago). Growth rate was also comparable between areas across the bank. This species is a more mobile predator than *L. mahsena*, and may represent one large, dispersed population across the region. Since this species may move between statistical areas, localised fishing pressure and growth rate are unlikely to be related.

While significant differences in *A. virescens* mean length were found between statistical areas in Seychelles, no consistent indication of a localised population structure was found. Mean age of *A. virescens* in Sector 1 was significantly lower than that of all other statistical areas on the Mahé Plateau. This appeared to result from faster growth rates, rather than the direct impacts of fishing. Individuals therefore became vulnerable to gears at an earlier age. Faster growth also resulted in a length structure comparable to the other areas.

6.4.2.2 Trends in growth rate

Trends indicating density dependent growth were identified for *L. mahsena* in Seychelles. When related to increasing CPUE and fishing mortality , mean length-at-age by sector showed significant trends at ages 4 and 5 years. For older ages, the significance of trends was reduced by the influence of data from Sector 14. Individuals from this sector showed significantly faster growth at a low level of fishing mortality, the opposite trend to that expected to result from density dependence. Cumulative effort may not represent the effects of fishing in this location; effort in the period before 1994 was concentrated in 1992 (MRAG, 1996c). Short periods of heavy fishing will have greater impacts on populations, potentially resulting in the faster growth rate identified.

In contrast to Seychelles, no trends in *L. mahsena* growth were found in BIOT (Chagos Archipelago). Since fishing is thought to have occurred in Seychelles for a longer historical period compared to BIOT (Chagos Archipelago), impacts on population abundance may have been greater, resulting in visible density dependent growth effects. Alternatively, the relationship between density and growth may be more critical in Seychelles when compared to BIOT (Chagos Archipelago), over-riding other factors affecting growth rate.

Patterns consistent with density dependent growth were found when *A. virescens* mean length-at-age by sector in Seychelles was related to the level of CPUE and cumulative fishing pressure. These trends were significant, or approached significance, for a wide range of ages (Table 6.8). Given the mobility of *A. virescens* between different sectors of the Seychelles (MRAG, 1996d), the significant relationships between mean length-at-age and localised fishing mortality implies such movement between sectors may be relatively limited. The sectors in Seychelles may encompass a greater proportion of this species' range than the smaller statistical areas of BIOT (Chagos Archipelago).

The age at which trends in *A. virescens* growth were first noted was below that at which 50% of individuals were mature (Am_{50} ~ 9 years; Appendix 6). This implied that, unlike *L. mahsena*, the onset of maturity may not influence density dependence. However, as noted in Appendix 6, the maturity ogive of this species is shallow, with females first becoming reproductively active around 33cm (~ age 3 years). Reproductive stresses may play an increasingly important influence in density dependent growth from a young age.

Density dependent growth may explain the increased growth rate found in Sector 1 (Seychelles) for both species, since this area is heavily exploited. However, increased growth rate may also result from the proximity of this sector to the populated islands. If increased productivity in the surrounding waters resulted due to run-off from the granitic islands, local developments disturbing inshore water nutrients, or increased temperature from either local discharge or relatively shallow water, growth rate may increase (*e.g.* Ross and Nelson, 1992; Nash *et al.*, 1994). Therefore, the presence of islands in Sectors 2, 11, 14 and 15 of Seychelles may influence local fish population structures. Coraline atolls, such as those in BIOT (Chagos Archipelago), are likely to have a reduced effect on local production. Apart from the fact that the atolls in this location are not developed (with the exception of Diego Garcia, which is separated from the main banks), their coraline structure will filter rain water, thereby reducing nutrient run off. Other local habitat differences will also affect growth; catches from areas dominated by sea grass rather than coral, for example, may result in different growth rates due to variations in food availability or calorific content.

Biological factors may also affect population structure. For example, the young age structure found in *A. virescens* at Sector 1 may also indicate that this region forms a 'nursery area'. Due to the proximity of the islands, there are a number of mangrove areas in which juveniles could mature (as seen in *P. filamentosus*; Haight *et al.*, 1993; Parrish *et al.*, 1997). Individuals may then disperse from this area to other regions on the Plateau as they mature. It was interesting to note that statistical areas outside the Mahé Plateau in which similar young ages were found (Sector 11, Amirantes and Sector 15, Astove/Cosmoledo) also tended to contain similar island habitats. However, such findings were not consistent for all areas (for example, Sectors 2 and 14, which also contain islands), and comparable trends were not found in *L. mahsena* age structure. More detailed studies on maturity would be required to examine this further; there were insufficient maturity data in this study to identify differences at the resolution required.

6.4.3 Overall Summary

The results of this study identified a number of declining trends in *L. mahsena* and *A. virescens* mean length and age with increasing exploitation rate. A number of studies have noted the effects of fishing on length structure of tropical species, including that of snappers (*e.g.* Thompson and Munro, 1983; Langi and Langi, 1989). However, similar examinations of the effects of fishing on tropical fish age structure are rare, due to the relative paucity of age studies for such species (Russ, 1991). The results of studies which have examined the effect of fishing on age structure have been variable (*e.g.* Ralston and Kawamoto, 1985; Russ *et al.*, 1995). In a similar fashion, a number of comparisons in the current study did not show the expected decreases in mean length or age. In the majority of cases, these could still be attributed to the pattern of fishing, or fishing practices. However, trends were also obscured by the high level of between-year variation in mean length. Although it could not be confirmed by the current study, similar variation in catch mean age was likely. In part, this variation may result from fishing in different years occurring in different areas within a location, containing different population structures. Variations in sampling techniques or sampling frequency will also contribute. Such influences can be monitored and minimised. However, other sources of variation may be difficult to minimise. These include biological factors such as the annual level of recruitment, which may also affect the growth rate through density dependence.

The study identified indications of density dependent growth in *A. virescens*, and to a lesser extent in *L. mahsena* populations, by relating mean length-at-age to increasing CPUE and cumulative effort. The expected trends were identified in the majority of comparisons. Trends were significant, or approached significance, in a high proportion of cases.

However, trends were not significant at all ages. This inconsistency may result from problems in the assumption of a direct relationship between fishing effort or CPUE and population density. In addition, as both fishing and fish distribution frequently appear localised, the effects on growth may be constrained to a more local scale than the resolution of the data can identify. As stated by Backiel and Le Cren (1978), a lack of precision in estimates of abundance contributes to the difficulty in quantifying the relationship between population density and growth. Given the complex biology and ecology of the populations and meta-populations, the fact that general trends have been identified in the data may indicate that density dependence can have a considerable effect on growth.

This appears to represent the first indication of density dependent growth in large predatory tropical fish species. Previous studies on tropical species have identified density dependent growth in wrasse (Labridae; *e.g.* Jones, 1987c) and damselfish (Pomacentridae; *e.g.* Doherty, 1982), relatively small herbivores and molluscivores.

The gradient of the density dependent growth relationship in these species cannot be quantified given the present level of information. Nevertheless, some inferences can still be drawn. Although there was no evidence of density dependent growth for BIOT (Chagos Archipelago) in either species, it was noted in the relatively lightly fished areas of Seychelles for *A. virescens* and *L. mahsena*. In Seychelles, these species appears capable of significantly faster growth when released from the competitive constraints of density. In turn, the 'gradient' of the density dependent growth relationship may be steep.

Although the pattern of evidence for density dependent growth in *L. mahsena* between locations was consistent with the pattern expected from variation in K (variation in that parameter results in length-at-age variability increasing with age, and then decreasing; Chapter 3, Section 3.1), the growth parameter affected by density dependent growth cannot be conclusively assigned to an individual parameter. Indeed, it is doubtful that the transient effects of density dependent growth during the life history of an individual could be assigned to a single parameter. In both species, the effect of density dependent growth appears most prominent within the mature section of the population. However, there is insufficient information from the present study to chose between any of the density dependent growth models derived in Chapter 4.

Evidence for density dependent growth has been found in both study species, although it has been of varying significance. However, it is relevant to investigate the likely effects of density dependent growth, despite the difficulties of detecting its presence in the field.

The effects of fishing will have both direct (through density dependent growth) and indirect (through the removal of individuals) impacts on growth assessments. In Chapter 7, the effects of fishing on estimates of growth derived through both length- and age-based methods will be assessed. The impacts of using such estimates in further analyses is examined. In turn, simulations of the use of such assessments in annual stock assessments, and hence management, are described in Chapter 8. In Chapter 9, practical assessments of the growth and mortality of the study species are described.

The results described in this chapter have direct implications for the current assessment and management methods employed in the study locations.

Foremost, assessments made at the level of the study location ignore the localised population structure of these species. In the case of mortality estimates, for example, assessments for a location will not detect localised stock depletion. With the exception of *A. virescens* in BIOT (Chagos Archipelago), where assessments at the level of the location appear warranted, assessments should be made at as high a spatial resolution as possible. One drawback is that such accurate spatial data collection programmes may result in patchy data where vessels do not visit particular areas during a year.

The results have particular importance for the assessment methods used in Mauritius. Currently, the impacts of annual decreases in TAC on *L. mahsena* catches from the Mauritian banks are assessed by monitoring for increases in both CPUE and mean length (Chapter 1). This study has indicated a number of problems with this method:

- Considerable between-year variability in catch mean length has been identified. Consistent trends in mean length are unlikely to be identified over a small number of years, confounding any changes resulting from the management regime;

- CPUE assessments at the spatial level of the bank will also be affected by localised population structure. Such effects may be reduced by performing assessments at a higher spatial resolution (*e.g.* statistical grid square, as collected in the Mauritian fishing logbook);

- Density dependent growth will affect assessments. Decreases in effort through the management regime will result in increased population densities. Hence, increases in mean length through decreased fishing mortality will be reduced by decreased growth rate. CPUE may also be affected, since it is measured as catch weight-per-unit-effort. The overall effect will depend on the relationship between decreases in growth rate, and any corresponding increase in condition factor;

- Discarding of small ‘undersized’ fish, or separation from the catch before return to port may result in increases in mean length compared to previous years in which such practices were less prevalent. Such increases may be mis-interpreted as the result of annual decreases in effort.

A more appropriate measure is required to assess the effects of such reductions in TAC. Assessments of localised CPUE can now be supplemented by those of age structure. While minimising the effects of density dependent growth, such assessments would also provide additional information on growth, mortality, and localised population structure.

7. The suitability of length- and age - based methods for estimating growth parameters of long-lived, slow growing species

7.1 INTRODUCTION

Due to the perceived difficulty in ageing tropical fish, the practical problems of funding validation studies, and the subsequent time and expense involved in the use of otoliths for age assessment, length-based methods have been used extensively in the tropics (Venema *et al.*, 1988).

The results of length-based methods of growth estimation, however, are only as good as the data to which they are applied (*e.g.* Majkowski *et al.*, 1987; Shepherd *et al.*, 1987). Length-based methods are generally reported as unsuitable for tropical species such as snappers and emperors (Mathews, 1974; Morgan, 1983; Morales-Nin, 1989; Langi, 1990; Mees and Rousseau, 1997), since species of these families are commonly long-lived and slow growing (Manooch, 1987), with highly variable individual growth trajectories (Pauly *et al.*, 1996a) and protracted spawning periods (*e.g.* Thompson and Munro, 1983; Mees, 1993). Such characteristics result in the superimposition of successive modal classes, reducing the information through which length-based methods estimate growth. In the absence of other methodologies, however, length-based methods continue to be used. It is prudent, therefore, to identify the likely bias that may arise in such assessments, so that the resulting uncertainty can be incorporated into management actions based on these growth estimates.

A number of studies have examined the accuracy (the closeness of a measured or computed value to its true value) and precision (the closeness of repeated measurements to the same quantity) of length-based growth estimation methods through simulation. By controlling the input parameters which model the populations, bias in the estimates can be assessed through Monte-Carlo methods, comparing the estimates with the true input values (*e.g.* Rosenberg and Beddington, 1987; Basson *et al.*, 1988). Such methods were used in the study described in this chapter. These involved the non-parametric growth estimation methods available in the 'Length Frequency Distribution Analysis' computer package (LFDA4, Holden *et al.*, 1995): ELEFAN, PROJMAT and SLCA (see Chapter 1). In the following section, the results of previous studies which have examined the use of these methods are summarised (Hampton and Majkowski, 1987; Rosenberg and Beddington, 1987; Basson *et al.*, 1988; Isaac, 1990).

7.1.1. General trends in growth estimates derived using length-based methods

A number of individual factors can bias the results of length-based growth estimation methods. In assessments using actual fishery data, these factors are combined, resulting in an overall level of bias. In this review, the effects of specific factors will be discussed first, before the overall bias identified in the outputs of these methods is described.

7.1.1.1 Growth rate and growth variability

Studies investigating bias in growth estimation methods have generally concentrated on simulations of relatively fast growing species, for which the methods are thought to be more applicable. Both Hampton and Majkowski (1987) and Isaac (1990) simulated populations with K=0.5, while Rosenberg and Beddington (1987) examined populations where K=0.7. All three studies briefly examined the effects of a range of K values (K=0.1 to 1.8 and K=0.4 to 1.0 for the last two studies, respectively). Basson *et al.* (1988) explicitly examined a range of K values (K=0.5, 1.0 and 1.5). The growth rates used in these simulations were therefore notably higher than that used in the current study (K=0.14).

Rosenberg and Beddington (1987) found that the accuracy of K estimates from ELEFAN increased as the true K was decreased from 1.0 to 0.4. In contrast, Isaac (1990) found that ELEFAN K estimates were more accurate for small, fast growing species than for larger, slow growing species. SLCA estimates showed the opposite trend, being most accurate for larger, slow growing species. It was noted that faster growth rates tended to increase the degree of modal separation in the length frequency distributions (Basson *et al.*, 1988). However, modal separation was also affected by the level of individual growth variability.

Independent individual variability in L_∞ or K of 20% resulted in levels of bias of over 40% in mean growth parameters estimated by SLCA or ELEFAN (Isaac, 1990). L_∞ was overestimated, while K was underestimated (Rosenberg and Beddington, 1987). As a result of individual growth variability, individuals larger than the mean L_∞ were present in the simulated catch length distribution (Hampton and Majkowski, 1987; Isaac, 1990), positively biasing the L_∞ estimate. This was particularly true for the version of ELEFAN I used by Hampton and Majkowski (1987), where the estimate of L_∞ was constrained to be at least one length class larger than the midpoint of the length class containing the largest sampled fish. K estimates from SLCA were positively biased, as increased variation obscured modes in the length frequency distributions. Comparisons with the study of Rosenberg and Beddington (1987) indicated that SLCA was more robust than ELEFAN I. PROJMAT was relatively robust to increasing individual growth variability (Basson *et al.*, 1988). However, the above studies concentrated on the accuracy of K estimates. Isaac (1990) noted that the trend depended on the parameter examined; as the level of individual growth variability was increased, ELEFAN produced more accurate L_∞ estimates, and SLCA more accurate K estimates.

7.1.1.2 Sampling Problems and Gear Selectivity

For accurate length-based growth parameter estimates, a catch sample representative of the population is required. Samples from catches at different depths and localities may be un-representative, particularly where ontogenic migration occurs (Posada and Appeldorn, 1996). Sampling must also be of suitable frequency and volume; Hoenig *et al.* (1987) noted that growth estimates from ELEFAN were strongly influenced by isolated data samples.

Although the sampling regime may be appropriate, length frequencies will still be affected by gear selectivity. Shepherd *et al.* (1987) found that truncation at the lower end of the length distribution strongly affected the growth parameter estimates. As younger individuals grow at a faster rate than older individuals, their modes are often more defined. As growth slows with age, the modes of older cohorts overlap, offering less information (*e.g.* Sainsbury, 1980; Jones, 1987b). Size selectivity favouring larger fish resulted in negatively biased K estimates, and positively biased L_∞ estimates from ELEFAN (Pauly, 1987; Hampton and Majkowski, 1987), while SLCA estimates proved more accurate (Isaac, 1990). The presence of older fish in samples was, however, required to improve the estimate of L_∞ (Sparre and Venema, 1998).

7.1.1.3 Using Transient Length Frequency Data

The length-based growth assessment methods used assume that changes in the position of modes in a series of length frequencies are the result of cohort growth. Where length frequency data are taken from a fishery undergoing a change in fishing effort or stock vulnerability, the length structure of the population and catch will change over time (Chapter 5), confounding changes due to growth. Changes in gear type or size over time can also affect the catch length-structure, altering the influence of cohorts in the length frequency distribution, and confusing the growth pattern.

7.1.1.4 Variable recruitment

Between year variation in recruitment may increase the accuracy of length-based growth parameter estimates. Prominent modes from good recruitment years might be more easily tracked through time, acting as a 'marker' for growth (*e.g.* Russ *et al.*, 1996). However, Rosenberg and Beddington (1987) showed that between year recruitment variation resulted in negatively biased estimates of K from ELEFAN. Good recruitment years strongly influenced ELEFAN estimates, due to the method used to fit the growth curves. Under such conditions, SLCA estimates of L_∞ were more accurate (Isaac, 1990).

Extended periods of recruitment within each year resulted in negatively biased K estimates from ELEFAN (Rosenberg and Beddington, 1987). When combined with between year recruitment variability, this negative bias increased to over 50%.

7.1.1.5 Overall trends in growth parameter estimates

To mimic more accurately actual data from fisheries, simulation studies commonly combine the effects of individual factors.

Hampton and Majkowski (1987) showed that where K=0.5, fishing was size selective, and individual variation in the growth parameters was modelled, ELEFAN overestimated L_∞ by 11-23%, and underestimated K by 16-36%. Under similar conditions, this pattern was identified at a range of K values (Rosenberg and Beddington, 1987; Isaac, 1990). For SLCA, Basson *et al.* (1988) noted that K estimates were generally accurate (within 15% of the true value), where 'at least some peaks and troughs were distinguishable'. Accuracy deteriorated where the ability to distinguish cohorts was reduced. While estimates of K from PROJMAT were similarly affected by the ability to distinguish cohorts, this method was more robust to decreasing modal separation.

The initial search range for the growth parameters influenced the maxima selected in each of the methods examined (Basson *et al.*, 1988). Rosenberg and Beddington (1987) noted that the accuracy of ELEFAN estimates was improved if the search range of L_∞ and K was constrained to 20-25% of the true K value (in this case K=0.7). While local maxima of the ELEFAN score function often occurred near the true parameter values, other parameter combinations resulted in greater score function maxima.

For length-based methods of growth estimation to provide accurate assessments, therefore, some evidence of modes in the length frequency distributions representative of age classes is required. Modal separation is influenced by the growth rate, level of individual variability in growth, and level of recruitment variability. The structure of the length distributions is also affected by the selectivity of the gear and status of the fishery. As a result, methods are generally most successful for faster growing species with low rates of individual growth variability, in a fishery at equilibrium. Estimates are improved where some information on the true mean growth parameters is known, so that narrow search ranges can be specified.

7.1.2 Aims of the current study

As described, an extensive literature already exists on the accuracy and precision of length-based growth assessment methods. However, these studies generally concentrated on faster growing species. In this study, therefore, analyses concentrated specifically on assessments of *L. mahsena*, a relatively long-lived, slow-growing species.

Previous studies have not examined the effects of fishing on growth estimates explicitly. Fishing can affect populations both through the direct removal of individuals selected by gears, and through the indirect effects of fishing via density dependent growth (Chapter 5). Both processes have the potential to affect the catch length structure, and therefore the outputs of length-based methods of assessment (Rowling and Reid, 1992).

Through Monte-Carlo simulations, this study quantifies the effects of fishing on both the accuracy and precision of length-based *L. mahsena* growth parameter estimates. Length frequency distributions are simulated using the 'Multi-species Interactive Dynamics Age-structured Simulation' (MIDAS). Based on these, length-based growth parameter estimates are derived using the algorithms available in LFDA (see Chapter 1).

Prior to this study, age-based methods could not be used to assess growth in the study species. However, validation of otoliths in Chapter 2 now allows such estimates to be derived. Age-based assessments of growth are felt to be the most robust methodology available for such long-lived, slow-growing species. Therefore, the simulation study also examines the effects of fishing on the accuracy and precision of age-based growth parameter estimates for *L. mahsena*. These estimates are derived from simulated age-at-length data.

One of the major sources of uncertainty in tropical stock assessments is the use of potentially biased growth parameter estimates in further calculations; for example, in the estimation of mortality and yield-per-recruit (Rowling and Reid, 1992; Mees and Rousseau, 1997). The 'knock-on' effect of using estimated growth parameters in further length-based parameter estimation methods is examined during the Monte-Carlo simulations.

In Section 7.2, the methods used to perform these simulations are described. A number of preliminary simulations were carried out to define specific settings in the simulation process. These initial simulations, and the results arising from them, are described in Section 7.3. In Section 7.4, the four simulations examining the effects of fishing are described. These assess the accuracy of estimates arising under different fishery states, with and without density dependent growth operating.

7.2 METHODOLOGY

This section describes the Monte-Carlo simulations performed to test the effects of fishing on the accuracy of biological and fisheries parameter estimation methods. Figure 7.1 provides an overview of the basic simulation process. It may help the reader to refer to this flow diagram throughout the chapter.

Both length frequency data and length-at-age data were simulated. Time series of length frequency data were simulated within MIDAS (see Chapter 4, and Section 7.2.1). After modifications to the layout of the data (Section 7.2.2), the length frequency distributions were used to estimate growth parameters from each of the three methods available within LFDA. Length-at-age data were simulated within an EXCEL^{TM} spreadsheet (see Chapter 4, Section 4.3.1.2). 'Age-based' growth parameter estimates were derived from this data (Section 7.2.3). Estimates of growth parameters from both sources were then used to calculate mortality, length-at-capture and yield per recruit through length-based methods (Section 7.2.4). The bias and precision of all parameters were assessed through comparison with the true parameters used to seed the simulation.

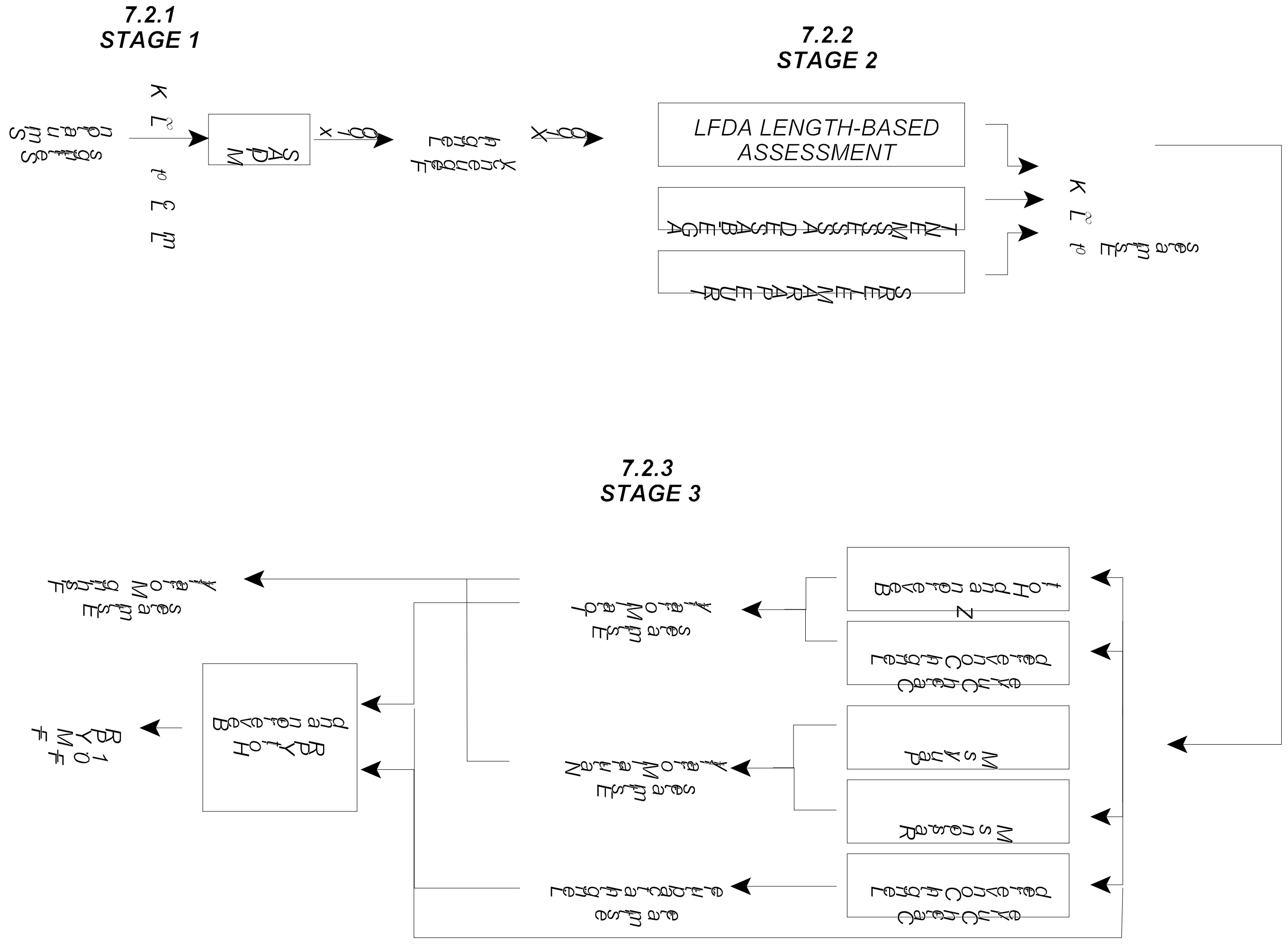


Figure 7.1 Summary of Monte-Carlo simulation to examine the accuracy and precision of length- and age-based methods of assessment.

7.2.1 Stage 1. The simulation of length frequency distributions

The simulation of *L. mahsena* length frequency distributions using the algorithms incorporated into MIDAS is described in Chapter 4 (Section 4.3.1.1).

Two regions were simulated during the study; Nazareth (Mauritian banks) and BIOT (Chagos Archipelago), representing the two main regions in which *L. mahsena* is caught. These locations are distinguished by different patterns of fishing during the year. For the Nazareth bank, fishing was assumed to occur throughout the year. Although the main fishing season at this location is generally shorter than a year, vessels fishing on more northerly banks frequently exploit Nazareth bank on route to or from these areas, extending the season. In BIOT (Chagos Archipelago), the season is limited by licence from April to October. The simulation of fishing mortality was therefore different for each location.

The simulation time step (Δt) within MIDAS was set at 0.1 years. In Nazareth, fishing mortality was simulated in each period of the year. For BIOT (Chagos Archipelago), fishing pressure was simulated between t=0.2 and t=0.8 years. In both locations, length frequencies were sampled from catches amalgamated between t=0.2 and t=0.5 years. While comparable to the sampling period in BIOT (Chagos Archipelago) during the three month observer programme, sampling from Nazareth generally occurs throughout the year. Due to the slow growth of this species, however, samples taken from other periods in the year were not significantly different (as identified using the Kolmogorov-Smirnov test).

A number of initial simulations were performed to identify the most appropriate basic settings within MIDAS. These runs identified the number of sampled individuals, and the number of years of data to be simulated. Since simulations took a considerable amount of time, the aim was to set these numbers to the minimum possible, while ensuring that the growth parameter estimates were unaffected. The simulations, and their results, are presented in Section 7.3.

7.2.2 Stage 2. Estimation of growth parameters

Growth parameters were derived using both length-based and age-based methods. The simulation of this estimation process was described in Chapter 4 (Section 4.3.1).

7.2.3 Stage 3. Estimation of other parameters

Using the length-based and age-based growth parameter estimates, further biological and fishery parameters were estimated. These were total, natural, and fishing mortality, length at first capture, and yield-per-recruit. The methods used to estimate these parameters was described in Chapter 4 (Section 4.4.1).

In this process, the ‘true’ growth parameters (those used to seed the MIDAS simulation; L_∞ = 48.5, K = 0.14) were also used to indicate the level of accuracy managers could obtain if they had ‘perfect’ knowledge. Biological and fisheries parameters were estimated using length-based methods applied to the final year of simulated length frequency data, representing estimates of the ‘current’ situation.

7.2.4 Analysis of parameter estimates

To examine the precision and accuracy of the assessment methods, a frequency distribution of the parameter estimates from the 100 runs was plotted. From the resulting distributions, a mean value for each parameter was calculated. The bias in this mean, compared to the true ‘seed’ value used to simulate the data, and the coefficient of variation (CV) of the distribution were calculated as percentages.

$$Bias = \frac{(Estimated\ parameter\ -\ True\ parameter) * 100}{True\ parameter}$$

Where required, frequency distributions were compared using the Kolmogorov-Smirnov test (Sokal and Rohlf, 1995).

7.3. INITIAL SIMULATIONS

Initial simulation runs identified the most suitable settings for the fishery simulation runs described in Section 7.4. As the simulation process took a long time, the most suitable settings represented a trade-off between those resulting in the most precise estimates, and those resulting in the shortest simulation time (the simulation of a single set of length frequency distributions could take up to 20 minutes). This was assessed using the distributions of estimated parameters. All initial runs were performed with the population at equilibrium with the selected level of fishing mortality. Due to time constraints, a limit of 100 simulated length frequency data sets was set for each run or scenario.

In the following sections, the methods used to perform each simulation are described. In each section, the results of that simulation are presented.

7.3.1 Number of individuals required in the simulated catch length sample

This run aimed to identify the number of individuals required for the simulated catch length sample in each year. This number could not be so low as to bias the growth parameter estimates derived from the length distributions. Five years of length frequency data were simulated from a fishery at equilibrium with fishing mortality level $F=0.25yr^{-1}$. 500 individuals were set as the maximum number which could be simulated within the time limitations. Runs were therefore performed with either 100, 300 or 500 simulated individuals sampled from the catch. From the results of the comparisons of ELEFAN growth parameters derived from these three runs, a further simulation run was performed with 400 sampled individuals simulated.

Preliminary analyses indicated that increasing the number of individuals sampled each year resulted in more precise ELEFAN growth parameter estimates. Growth parameter estimates based on 500 individuals was therefore taken as the benchmark against which the other simulations were compared.

Where 100 or 300 sampled individuals were simulated, the resultant growth parameter distributions were significantly different from those where 500 individuals were used (identified through the Kolmogorov-Smirnov test). Estimates were biased toward low parameter values. At such low sample sizes, small numbers of individuals were present in each length class, resulting in false modes in the distributions.

Further runs were therefore performed simulating 400 sampled individuals. The resultant parameter estimate distributions were not significantly different to those where 500 individuals were simulated (*e.g.* for L_∞, Kolmogorov-Smirnov test, $D_{0.05}=0.192$, $D=0.09$). Four hundred individuals sampled per year were therefore used in the fishery simulation runs.

7.3.2 Number of simulated annual catch length samples required

This run aimed to define the number of years of length frequency data to be simulated. Sufficient years of data were required to ensure that growth parameters were estimated by ELEFAN with a satisfactory degree of precision.

The population was simulated at equilibrium with a fishing mortality of $F = 0.25yr^{-1}$. Ten years of length frequency data were taken as the maximum number which could be simulated within the time limitations. Runs were performed with one, three, five, seven or ten years of length frequency data simulated. For each year, 400 individuals were simulated, as identified in Section 7.3.1.

Where fewer than five years of data were simulated, the growth parameter estimates derived by ELEFAN were significantly different when compared to those from the ten year runs, as identified by the Kolmogorov-Smirnov test ($D>D_{0.05}$, where $D_{0.05} = 0.192$). However, the distribution of growth parameter estimates derived from five years of data was not significantly different from that where ten years of data were used ($D_{0.05} = 0.192$, $D=0.185$). Five years of data were therefore simulated in the fishery simulation runs.

7.3.3 Examination of the simulated locations

Both the Nazareth and BIOT (Chagos Archipelago) fishing regimes were simulated within MIDAS (Section 7.2.1). The aim of this simulation was to assess the outputs from each fishing regime for significant differences; if outputs were not significantly different, runs could concentrate on a single fishing regime.

Based on the most appropriate settings identified in Section 7.3.1 and 7.3.2, length frequency distributions for the two fishing regimes were simulated. Parameter estimates, and management actions based on these estimates, were compared for significant differences. Runs were performed at $F=1.2yr^{-1}$; differences would be most prominent at this level.

The majority of the biological and fishery parameter estimate distributions resulting from the two fishing regimes were not significantly different (Kolmogorov-Smirnov test, $D < D_{0.05}$ where $D_{0.05}=0.192$). However, significant differences were found in the Beverton and Holt's Z and length at first capture distributions (Kolmogorov-Smirnov test, D=0.31 and D=0.25 respectively). For these two parameters at this F level, the mean parameter estimates from BIOT (Chagos Archipelago) were greater than those from Nazareth.

Since the two fishing regimes produced mainly similar parameter distributions, it was decided to concentrate on one location during the fishery simulations. As the continuous fishing regime was simpler to model, Nazareth was selected.

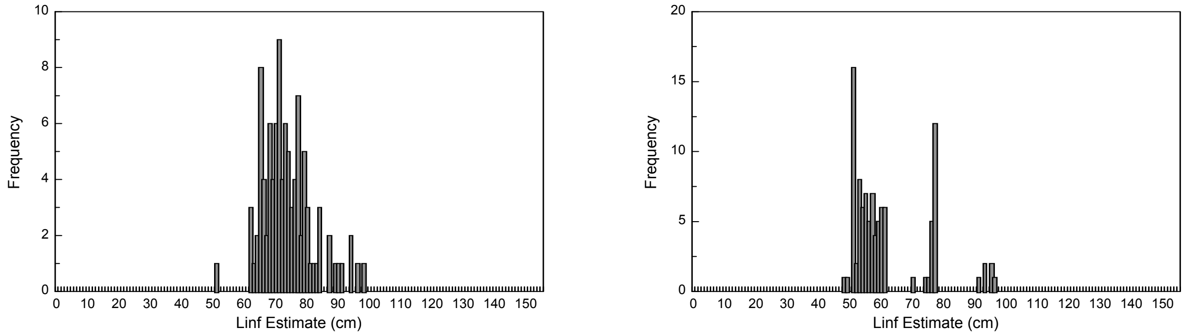
7.3.4 Examination of the growth parameter estimation methods

Growth parameter estimates output from the three estimation methods provided in LFDA (ELEFAN, SLCA, PROJMAT) were compared. This simulation aimed to identify whether specific estimation methods were unsuitable for further use. Growth parameters were estimated based on length frequency distributions simulated at $F=0.25yr^{-1}$, using the appropriate settings identified in Sections 7.3.1 to 7.3.3.

Growth parameter estimates resulting from PROJMAT were inconsistent. While L_∞ estimates were similar to those from ELEFAN (although these were distinct modes, Figure 7.2b), K estimates tended toward zero. Both parameter estimates from SLCA tended towards the boundaries of the search grid (Figure 7.2c). Those from ELEFAN, while biased, were more consistent (Figure 7.2a). All showed a tendency to overestimate L_∞ (true mean $L_\infty = 48.5$).

a) ELEFAN

b) PROJMAT



c. SLCA

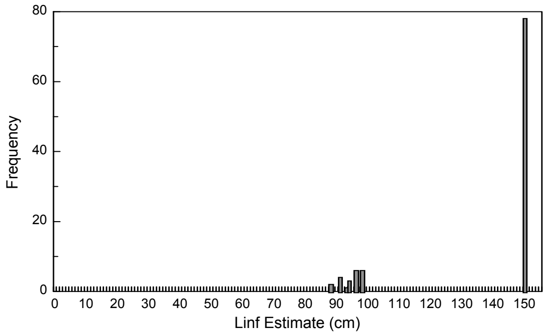


Figure 7.2 L_∞ estimates from the three length-based growth estimation methods. 100 individuals were simulated in each run. F=0.25yr^{-1}.

Based on this preliminary study, the use of SLCA and PROJMAT was discontinued. Only ELEFAN was used in the fishery simulation runs.

7.3.5 Examination of annual variability in recruitment

Due to an error in the program, annual variability in recruitment was not enabled during the simulation process. Once this had been discovered, the potential effect of this variation on the growth and total mortality estimates was examined. Simulations were performed using the Nazareth fishing regime at F=0.25yr^{-1}. Runs were performed both with recruitment based purely on the spawning stock biomass and the level of density dependence in the stock recruitment relationship (recruitment CV=0%), and with additional variability around this recruitment included (recruitment CV=61%, Chapter 4, Table 4.5).

The distributions of both growth and total mortality estimates derived from runs with and without annual variation in recruitment were not significantly different at the 5% level, as identified through the Kolmogorov-Smirnov test (Table 7.1). The total mortality estimate from the length-converted catch curve approached significance (*P*=0.065). Variable recruitment increased the variation of the points in the descending limb of the catch curve, affecting the total mortality estimates. Due to the limited impact of annual variability in recruitment on the parameter estimates for this species, its absence from the fishery simulations was not critical.

Table 7.1 Effect of annual variation in recruitment on the length-based estimates of growth parameters (through ELEFAN) and total mortality. Two distributions were significantly different if $D_{0.05} > D$.

Parameter	Mean estimate with annual recruitment CV		Kolmogorov-Smirnov test statistics	
	CV=0%	CV=61%	$D_{0.05}$	D
L_∞	64.7	64.0	0.192	0.050
K	0.21	0.22		0.120
BH Z	0.97	1.01		0.110
LCCC Z	1.15	1.24		0.185

The limited impact of annual recruitment variation on ELEFAN growth parameter estimates was contrary to views expressed in the literature (Rosenberg and Beddington, 1987). This may have been the result of the different population parameters used in each simulation; unlike the fast growing species simulated by Rosenberg and Beddington (1987), the current study examined slow growing fish species. Slow growth resulted in indistinct modes in the length data, which did not correspond to individual cohorts. This, combined with the level of individual variability in growth and the effects of gear selectivity, appeared to overwhelm the impacts of variation in cohort strength on the length distributions. As expected from Jones (1987b), recruitment variability did affect length converted catch curve estimates of total mortality, although differences in the parameter estimate distribution only approached significance.

7.3.6 Summary

Initial simulation runs investigated the most appropriate settings for the subsequent fishery simulation runs. These simulations indicated that five years of length frequency data, with 400 individuals simulated in each year, were the most appropriate settings within MIDAS. Minor differences in the biological parameter estimates were identified between the two fishing regimes (Nazareth bank and BIOT (Chagos Archipelago)). Hence the constant fishing regime at Nazareth bank was used in further simulations. Only ELEFAN produced consistent estimates for both growth parameters, and hence only this method was used in the fishery simulations. Although annual variation in recruitment was not enabled in the fishery simulations, this appeared to have no significant impact on the results of length-based growth estimation methods.

7.4 FISHERY SIMULATION RUNS

Fishery simulation runs investigated the effects of different levels of fishing mortality, different fishery states, and the action of density dependent growth, on the accuracy and precision of length- and age-based growth estimates (see Section 7.2.3). These growth estimates were used to estimate fishery and biological parameters through length-based methods (see Section 7.2.4).

Four fishery scenarios were simulated. The first two examined the effects of fishing on an ‘established fishery’. This was simulated as a fishery at equilibrium with the level of fishing mortality applied. The second pair of scenarios examined the effects of fishing on a ‘developing fishery’, simulated as an unexploited fishery being exposed to fishing mortality at the beginning of the simulation. In each pair, fishery states were simulated with and without density dependent growth operating. In each of the following sections, a basic description of each simulation is provided. The resultant parameter estimates are then detailed.

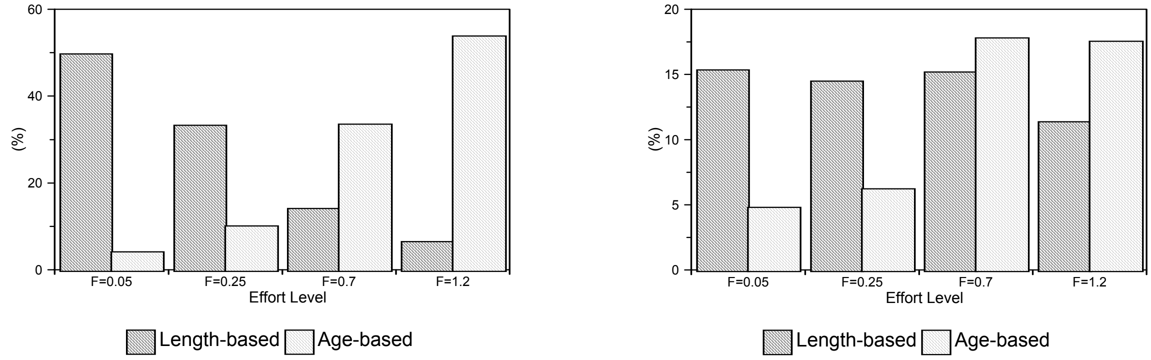
7.4.1 Scenario 1. Established fishery, no density dependent growth

L. mahsena catch length frequencies were simulated from a fishery at equilibrium with the fishing mortality levels applied. Density dependent growth was not operating.

7.4.1.1 von Bertalanffy growth parameters

The von Bertalanffy growth parameters were estimated using ELEFAN (length-based), and from the analysis of age-at-length data (age-based). Statistics for the distributions of 100 L_∞ and K estimates obtained by each method are shown in Figure 7.3.

a. L_∞, bias b. L_∞, CV



c. K, bias d. K, CV

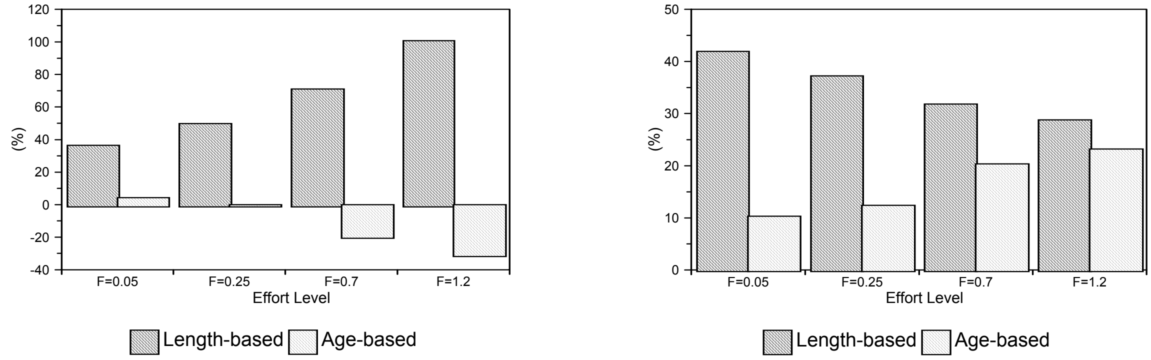


Figure 7.3 Statistics for length-based and age-based von Bertalanffy growth parameter distributions. Bias (%) in mean estimate relative to the true 'seed' value used in the simulation (L_∞ = 48.5, K=0.14) is displayed in graphs a and c. Coefficient of variation (CV%) for the parameter estimate distributions in graphs b and d.

Length-based methods overestimated both L_∞ and K. Bias in L_∞ decreased with fishing pressure, while bias in K estimates correspondingly increased to over 100%. The precision of L_∞ estimates varied little with fishing pressure, while precision of K estimates increased.

The largest individual in the length frequency distribution strongly influenced the length-based L_∞ estimate. Removal of these individuals with increasing fishing pressure led to a reduction in the L_∞ estimate. Although the seed value used to generate the length frequencies was L_∞ = 48.5, individual variability in growth resulted in individuals being present in the catch above 70cm, dependent on the level of fishing mortality. The overestimation of K at all F levels may be a result of the lack of distinct modes in the data. The increase in this overestimation with fishing mortality may relate to the decrease in the L_∞ estimate.

At the lowest fishing mortality level, age-based estimates of L_∞ and K were both accurate and precise (bias was less than 5%, CV was less than 10%). Increasing the level of fishing mortality tended to result in a significant positive bias in the mean L_∞ estimate, and an increasing negative bias in K. Since the selection of individuals for the sample was based on the probability of survival, higher fishing mortality levels decreased the probability of slower growing, older-at-length individuals surviving to the larger length classes. Individuals present in these length classes were therefore younger than average. This lack of old individuals at large lengths reduced the information available on L_∞.

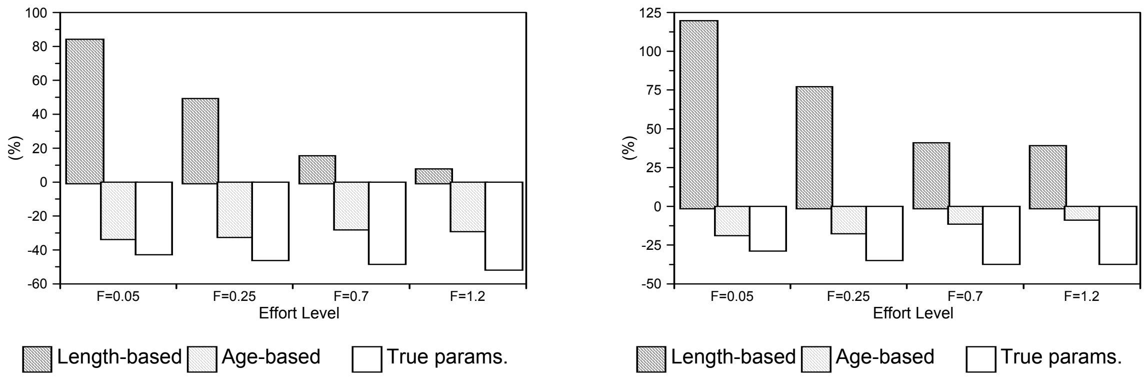
At lower fishing mortalities, growth parameter estimates from age-based methods were less biased, and more precise, than those from length-based methods. At higher fishing mortalities, estimates of L_∞ derived through age-based methods were more biased and less precise than those from length-based methods. Age-based K estimates were more accurate and precise than length-based estimates.

7.4.1.2 Mortality estimates

Total mortality estimates were derived from the catch length frequency distribution simulated for the fifth year. Both the length- and age-based growth parameter estimates were used in these calculations. In addition, the true growth parameters were used, to indicate the accuracy achieved when perfect knowledge on growth is available.

Total mortality estimates

The bias in the estimates from the two total mortality assessment methods is shown in Figure 7.4, by growth parameter estimate.


a. Beverton and Holt's Z

b. Length-converted catch curve Z

Figure 7.4 Bias in mean total mortality estimates by estimation method and growth parameter source. Bias (%) is calculated relative to the true 'seed value' used in the simulation (Z=0.4 + F). Note differences in scale.

Where the length-based growth parameter estimates were used, total mortality was overestimated in both the Beverton and Holt method and the length-converted catch curve; this was seen to a greater degree in the latter method. Accuracy improved with increasing fishing mortality levels. At low mortality levels, the calculation of L_∞ minus mean length ($L_\infty - \bar{L}$) in the Beverton and Holt Z estimator was positively biased by the overestimation of L_∞. This was exacerbated by overestimation of K. While the accuracy of L_∞ estimates improved at high fishing mortality levels, increasing overestimation of K continued to bias the total mortality estimate. In the length-converted catch curve, the time taken to grow through a length class (Δt) was reduced when compared to the true situation. This was a result of positive bias in the L_∞ and K estimates. This steepened the descending limb, increasing the Z estimate.

Where both the age-based and true growth parameters were used, total mortality was consistently underestimated. Length converted catch curve estimates were more accurate. For both methods, bias and precision remained relatively constant with increasing fishing mortality. For the Beverton and Holt equation, L_∞ estimates from age-based methods and the true L_∞ were commonly lower than the largest individual found in the length frequency distribution (L_{max}). $L_\infty - \bar{L}$ was therefore low, which was compounded by the low K estimate.

With increases in fishing mortality, increasing age-based L_∞ estimates were counteracted by decreases in K. For the length-converted catch curve, the slight bias in the age-based growth parameters resulted in a larger Δt, decreasing the gradient of the descending limb of the catch curve. Underestimation of L_∞ also truncated the catch curve at lengths where large numbers of individuals were present.

The most accurate mean total mortality estimates were obtained using age-based growth parameter estimates and the length-converted catch curve. Age-based estimates from Beverton and Holt's method were also more accurate at low fishing mortality levels. At higher effort levels, the use of length-based growth parameters resulted in more accurate estimates from this method. Age-based estimates were also consistently more accurate than the results from the true parameters; age-based L_∞ estimates were closer to the value of L_{max} in the length distributions. As indicated by Wetherall *et al.* (1987), this tended to result in more accurate estimates from Beverton and Holt's method. In the length converted catch curve, the descending limb was not truncated at L_∞. The precision of total mortality estimates derived using age-based growth estimates was also notably higher than those from length-based estimates.

Natural mortality estimates

The bias in natural mortality estimates, using different growth parameters, are shown in Figure 7.5. The true growth parameters resulted in constant natural mortality estimates; Pauly's M=0.4, Ralston's M=0.3. The latter was a 25% negative bias.

a. Pauly's M

b. Ralston's M

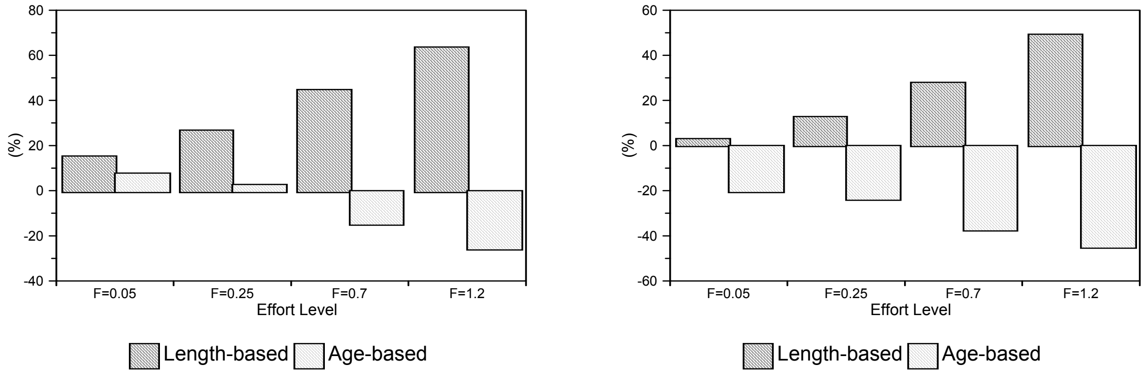


Figure 7.5 Bias in mean natural mortality estimates resulting from length-based and age-based growth parameters. Bias (%) in the mean estimate was calculated relative to the true 'seed value' used in the simulation (M=0.4).

When derived from length-based growth estimates, both Ralston's and Pauly's methods overestimated natural mortality. Since the mean estimate obtained through Ralston's method was consistently less than that from Pauly's method, Ralston's estimates were less biased. Bias in both estimates increased with fishing mortality. Although estimates from Ralston's method were more accurate, they were less precise than those from Pauly's method. In both cases, precision improved with increasing fishing mortality.

Increasing L_∞ had a negative effect on Pauly's M estimate. As length-based L_∞ estimates declined with increasing fishing pressure, this effect was reduced. The positive effect of the increasing K estimates was therefore more pronounced. Since Ralston's M is a positive linear function of K, the estimate increased with fishing pressure.

Derived from age-based estimates, Pauly's M was extremely accurate and precise at low fishing mortality levels. Estimates became negatively biased and less precise with increasing fishing mortality. This was related to the increase in L_∞ and decrease in K estimates with increasing fishing pressure. Since Ralston's M estimates were lower than those from Pauly's equation, they consistently underestimated natural mortality. The decrease in age-based K estimates with fishing pressure had a direct negative effect on Ralston's M estimate.

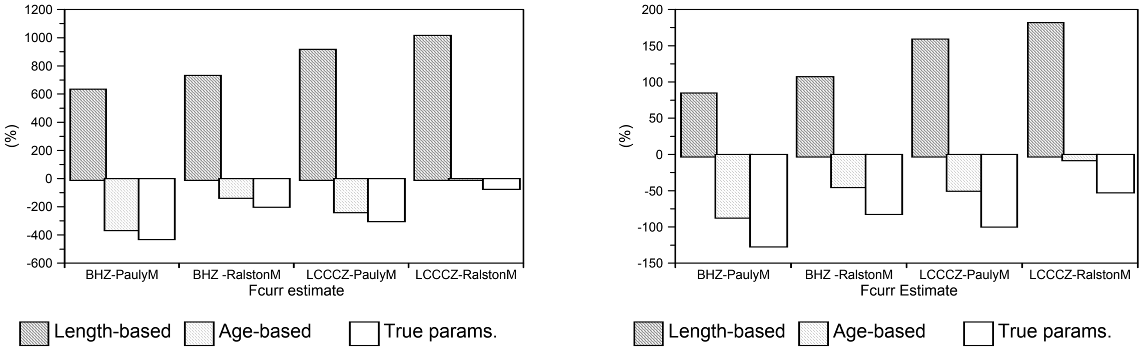
At all fishing mortality levels, the most accurate natural mortality estimate was derived using age-based growth parameters and Pauly's M. For Ralston's M, although age-based estimates were more precise, they were less accurate than those based on length-based growth parameters at the majority of fishing mortality levels. This was a direct result of the low age-based K estimate.

Current fishing mortality (F_{curr})

Estimates of current fishing mortality were derived by subtracting estimates of natural mortality from those of total mortality. Four different estimates of F_{curr} resulted. The bias in these estimates is presented in Figure 7.6.

The accuracy of mean F_{curr} estimates was generally poor. The use of length-based growth parameters tended to overestimate F_{curr}, while both age-based and the true parameters tended to underestimate F_{curr}. These patterns related to bias in the total mortality estimates. At low fishing mortality levels, the use of age-based and true growth parameters resulted in F_{curr} estimates which were less than zero. The accuracy of these F_{curr} estimates improved with increasing fishing mortality.

a. $F=0.05yr^{-1}$ b. $F=0.25yr^{-1}$



c. $F=0.7yr^{-1}$ d. $F=1.2yr^{-1}$

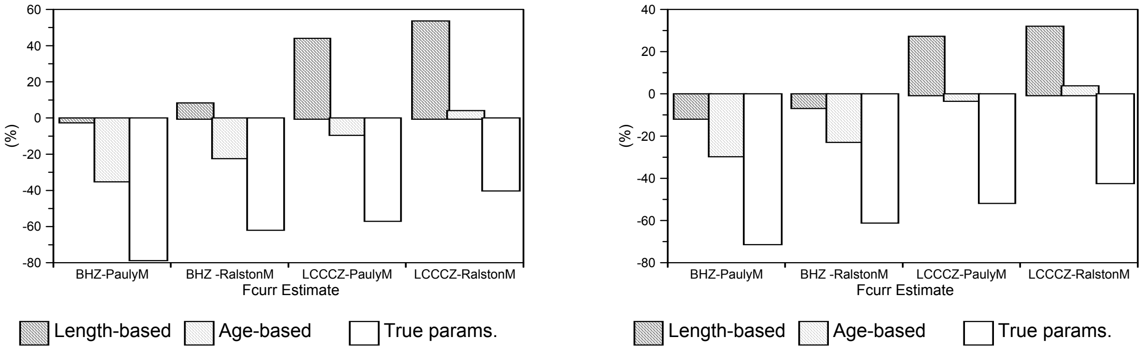


Figure 7.6 Bias in the mean F_{curr} estimate derived from four methods, by true fishing mortality level. BHZ = Beverton and Holt Z, LCCC Z = length-converted catch curve Z. Bias (%) in the mean estimate was calculated relative to the level of simulated fishing mortality.

Trends in F_{curr} were controlled by the total and natural mortality estimates. For length-based methods, total mortality showed a decreasing positive bias with increasing fishing mortality, while natural mortality showed an increasing positive bias. As a result, estimates of F_{curr} improved. While the negative bias in age-based total mortality estimates remained relatively constant, that in natural mortality estimates increased slightly with increasing fishing mortality. This increased the F_{curr} estimate, reducing the negative bias. Where the true growth parameters were used, Pauly's M was correct, while Ralston's M was negatively biased. As total mortality estimates were negatively biased, so were the F_{curr} estimates. For these estimates, the negative bias in Ralston's M, combined with the negatively biased total mortality estimates, resulted in larger, and hence a more accurate, F_{curr} estimates.

At low fishing mortality levels (F=0.05 and F=0.25yr^{-1}), age-based F_{curr} estimates were the most accurate. They remained the most accurate at high fishing mortality levels when F_{curr} was based on the length converted catch curve. However, when based on Beverton and Holt's Z, those derived using length-based growth estimates were more accurate. F_{curr} estimates from true parameters were more biased than age-based estimates, and at F=0.7 and F=1.2yr^{-1}, were less accurate than length-based estimates.

When using length-based growth parameters, F_{curr} derived from Beverton and Holt's Z and Pauly's M was the most accurate at all fishing mortality levels apart from F=1.2yr^{-1}, while that from the length converted catch curve and Ralston's M was the least accurate. Where both age-based and true growth parameters were used, the opposite pattern was found. Age-based growth parameters and the combination of length converted catch curve and Ralston's M led to the most consistently accurate estimate.

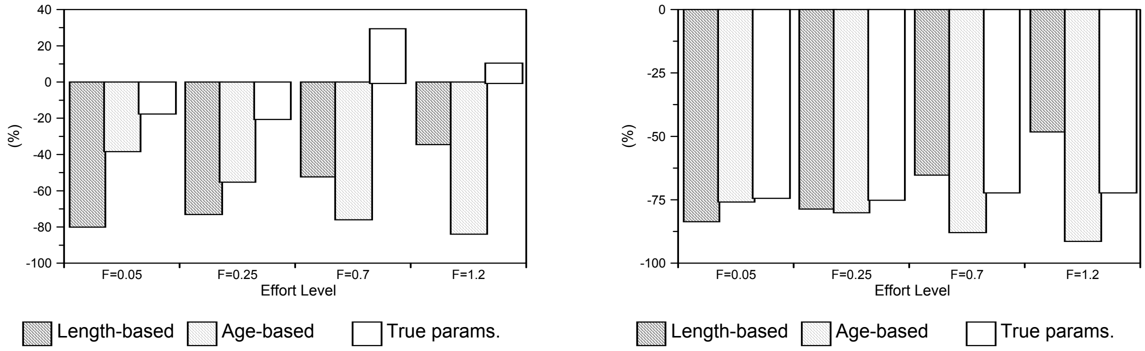
The precision of F_{curr} estimates derived from the three growth parameter estimates remained relatively constant with increasing fishing mortality. Estimates derived using age-based growth parameters, particularly when derived using the length converted catch curve and Ralston's M, were more precise than those from length-based methods.

7.4.1.3 Length at first capture (Lc_{50})

Estimates of length-at-capture calculated from the length-converted catch curve for year one were both accurate and precise when based on either length- or age-based growth estimates. Neither bias nor precision exceeded 10% at any fishing mortality level. Due to the level of accuracy and precision, this parameter will not be discussed in further simulations unless the estimate distributions showed significant differences.

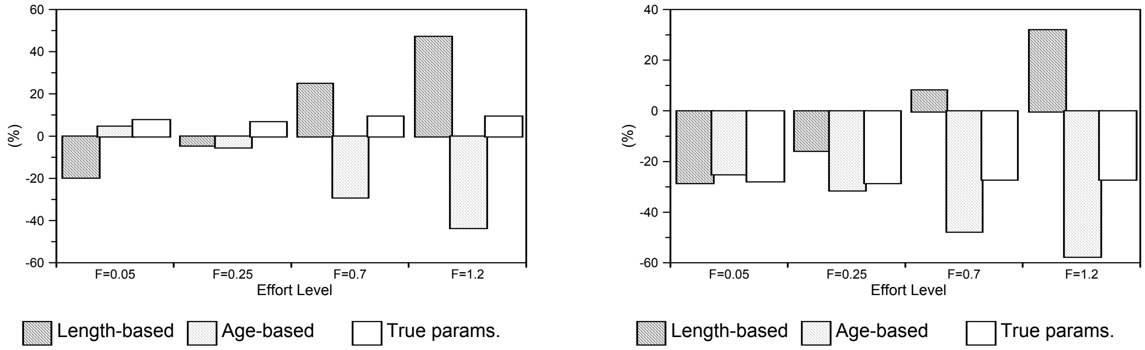
7.4.1.4 Fishing mortality at the maximum yield per recruit (F_{MYPR}) and $F_{0.1}$

Yield effort curves were constructed from the parameters derived using each set of growth parameters. From the curve, both effort at maximum yield per recruit (F_{MYPR}) and the point at which the curve reached 10% of the initial gradient ($F_{0.1}$) were calculated. Bias in these estimates is presented in Figure 7.7.



a. F_{MYPR} based on Pauly's M

b. F_{MYPR} based on Ralston's M



c. $F_{0.1}$ based on Pauly's M

d. $F_{0.1}$ based on Ralston's M

Figure 7.7 Bias in the F_{MYPR} and $F_{0.1}$ estimate distributions. The bias (%) in this mean was calculated relative to the true 'seed value' used in the simulations (F_{MYPR} = 3.1, $F_{0.1}$ = 0.41).

F_{MYPR} was underestimated at all F levels when derived from length- or age-based growth estimates. With increasing fishing mortality, length-based estimates improved, while age-based estimates became more biased. Compared to estimates of F_{MYPR}, $F_{0.1}$ estimates were generally more accurate at all but the highest fishing mortality levels. Estimates showed similar trends to that in F_{MYPR}. As a result, length-based $F_{0.1}$ estimates showed negative bias at low F levels, and positive bias at high F. Age-based estimates were accurate at low F levels, and showed increasing negative bias. The use of the true growth parameters resulted in relatively constant bias in $F_{0.1}$. The trends were related to those seen in M (Figure 7.5). Even though Pauly M estimates were exact when using the true growth parameters, F_{MYPR} and $F_{0.1}$ were still slightly inaccurate, and varied with fishing pressure. Since the growth parameters, and hence natural mortality, were constant between simulation runs, this variation resulted purely from that in the Lc_{50} estimate.

Mean F_{MYPR} and $F_{0.1}$ estimates calculated using Ralston's M were consistently less than those based on Pauly's M. Hence, estimates derived using Ralston's M tended to show increased negative bias. Where Pauly's M resulted in positive bias, however, estimates based on Ralston's M were the most accurate. When derived from length-based growth parameters, F_{MYPR} and $F_{0.1}$ based on Pauly's M tended to be more precise, while estimates using Ralston's M were more precise when age-based estimates were employed. Precision tended to decrease with increasing fishing mortality.

Based on the true parameters used within MIDAS, the yield-effort curve for *L. mahsena* indicated stock collapse at effort levels greater than F=1.7yr^{-1}. The true value of F_{MYPR}, F=3.1yr^{-1}, is therefore at an unsustainable fishing mortality level. This discrepancy is a result of the assumption in the yield-per-recruit analysis that recruitment is constant. This assumption is false at high fishing mortality levels where the spawning stock biomass is heavily affected by fishing. The use of F_{MYPR} as an indicator fishing mortality level for stock assessments is therefore inappropriate for this species.

7.4.1.5 Summary

Age-based methods resulted in the most accurate estimates of K at all fishing mortality levels, and the most accurate estimates of L_∞ at low fishing mortality levels. Age-based estimates of growth were generally more precise than those from length-based methods. The accuracy and precision of growth parameters directly affected the estimates of total and natural mortality, and hence estimates of F_{curr}.

The use of the true growth parameters resulted in poor estimates of total fishing mortality, due to individual growth variability. These growth parameters will not be examined in the remaining fishing simulations. Studies also indicated that the use of two estimates of F_{curr} (confident and cautious) were suitable to describe the trends across the range of estimates. In turn, the use of F_{MYPR} as an indicator effort level for stock assessments was found to be inappropriate for this species.

7.4.2 Scenario 2. Established fishery, with density dependent growth

This scenario examined the effect of density dependent growth in an established fishery on the estimation of growth and other biological and fisheries parameters.

As in Scenario 1, the fishery was simulated at equilibrium with the applied level of fishing mortality. Density dependent growth was operating in the population, acting either on L_∞ at -70%, or in K at -120%. The maximum density dependent growth gradients were used since they resulted in the most prominent changes in the length frequency distributions (Chapter 5). These simulations would therefore offer the clearest indication of the effects of density dependent growth. In that chapter, it was also noted that the impacts of density dependent growth on the length frequency structure were most significant at F=0.7 and 1.2yr^{-1}. Simulations in this chapter were restricted to these levels of fishing mortality. Parameter estimates were compared with the results from Scenario 1 (Section 7.4.1).

While the effects of density dependent growth were simulated automatically within MIDAS, the age-at-length spreadsheet required modification to simulate these effects. Biological and fishery parameters were then estimated. The full set of analyses performed for Scenario 1 were again carried out. For brevity, however, the results have been condensed. The study therefore concentrates on the differences resulting specifically from density dependent growth.

7.4.2.1 von Bertalanffy growth parameters

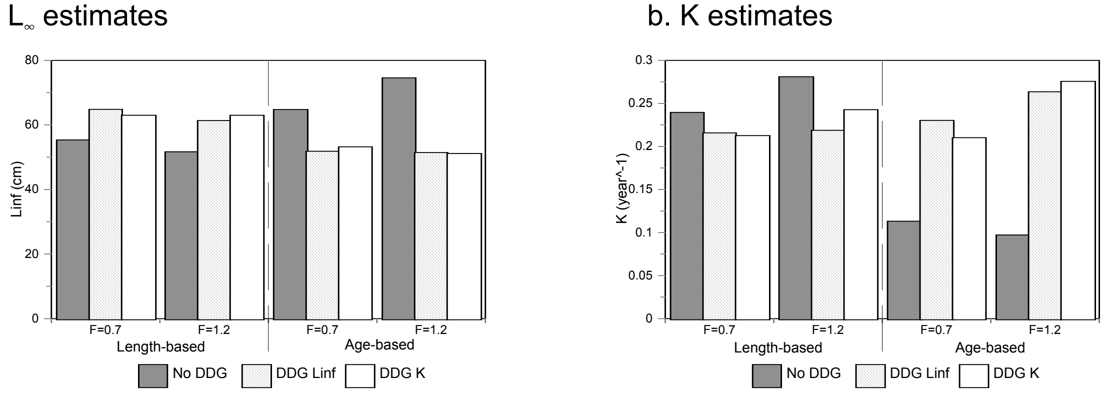
The von Bertalanffy growth parameters were derived through both length-based (ELEFAN) and age-based methods.

The mean population growth parameters used to simulate age-at-length data within the EXCEL^{TM} spreadsheet were adjusted to represent density dependent growth. Population biomass outputs at unexploited equilibrium (B_0) and at each effort level (B) were calculated deterministically from the yield-effort curve using MIDAS. Given the gradient of the density dependent growth relationship, and the assumption that density dependent growth model 1 was operating (Chapters 4 and 5), the population growth parameters were adjusted accordingly (Table 7.2). These mean parameters were then used to simulate the effects of density dependent growth on the age-at-length data. The assumption of density dependent growth model 1 was necessary, since biomass estimates could not be obtained for specific sections of the population, as required by model 2 (Chapter 5). The mean growth parameters used to simulate age-at-length data were therefore slightly over-adjusted.

Table 7.2 Adjustment of the population parameters to simulate age-at-length data under density dependent growth, assuming model 1.

Method	F-level (yr^{-1})	B_0	B	Density dependent growth operating in			
				L_∞ at -70%		K at -120%	
				L_∞ at B_0	L_∞ at B	K at B_0	K at B
Length-based	F=0.7	701	348	48.5	65.6	0.14	0.22
	F=1.2		269		69.4		0.24
Age-based	F=0.7	701	348	43.9	59.4	0.12	0.19
	F=1.2		269		62.8		0.21

Figure 7.8 displays the mean growth parameter estimates obtained from simulated length frequency and age-at-length data, with density dependent growth affecting either L_∞ or K. The bias in these estimates is presented in Table 7.3.


a. L_∞ estimates

b. K estimates

Figure 7.8 Length-based and age-based von Bertalanffy growth parameter estimates (L_∞ and K), indicating the effects of density dependent growth.

Density dependent growth tended to increase the estimate of L_∞ from length-based methods, and correspondingly decrease the estimate of K. In contrast, density dependent growth resulted in increased estimates of K from age-based methods, while L_∞ estimates were correspondingly lower. No notable differences resulted where density dependent growth was operating on either L_∞ or K.

Table 7.3 Bias in length-based and age-based growth parameter estimates, related to the 'true' population growth parameters (as presented in Table 7.2).

DDG in	F level (yr^{-1})	Bias in length-based estimates		Bias in age-based estimates	
		L_∞	K	L_∞	K
None	0.7	14%	71%	33%	-19%
	1.2	6%	101%	54%	-31%
L_∞	0.7	13%	54%	-13%	64%
	1.2	-12%	56%	-18%	88%
K	0.7	30%	3%	10%	11%
	1.2	16%	1%	6%	31%

Increases in L_∞ (length-based) or K (age-based) estimates resulting from density dependence were, to an extent, offset by increases in the 'true' population parameter, where density dependence was operating in L_∞ or K, respectively. Where density dependence affected the opposite parameter, bias generally increased.

As length-based K estimates decreased with increases in L_∞, the accuracy of K estimates was improved, when compared with the situation without density dependence (Table 7.3). A similar pattern was found in the age-based estimates, with L_∞ estimates improving as a result of increased K estimates.

Increases in either L_∞ or K due to density dependent growth resulted in larger individuals appearing in the length frequency distributions. These represented either individuals with increased L_∞ values due to density dependence in L_∞, or,where density dependence was operating in K, individuals with naturally large L_∞ values growing toward this size faster. This influenced L_∞ estimated from length-based methods. Increases in K due to density dependence could potentially improve K estimates; as a result of the increased growth rate, modes in the data might become more distinct. However, no consistent pattern was found to indicate this.

In contrast, age-based methods interpreted increases in length-at-age resulting from density dependent growth as increased growth rates to a lower asymptotic length. This was a result of changes in the underlying age structure. Density dependent growth resulted in increased numbers of larger, younger individuals in the catch; the probability of such individuals reaching larger sizes was relatively high compared to older, slower growing individuals. This increased the K estimate, but reduced the information on asymptotic length. However, a small number of relatively slow growing, older individuals remained in the catch. Their presence combined with the negative correlation between the L_∞ and K estimates to reduce the L_∞ value.

7.4.2.2 Other parameter estimates

Scenario 1 described the knock-on effects of the use of estimated growth parameters on subsequent parameter estimates in detail. In the following sections, therefore, the effects of density dependent growth on the estimates of further biological and fisheries parameters are presented in a summarised form. The majority of changes in the parameter estimates can be related to the discussions provided in Scenario 1. Table 7.4 summarises the bias for particular mean parameter estimates, illustrating the general effects of density dependent growth.

Table 7.4 Bias (%) in the mean estimates of total, natural and current fishing mortality, and in $F_{0.1}$ using length and age-based growth parameter estimates. Selected parameter estimation methods are shown to illustrate trends.

F-level	Method	DDG	Bias in mean parameter estimates (%)			
			B&H Z	Pauly's M	F_{curr} (B&HZ - Pauly's M)	$F_{0.1}$ (Pauly's M)
F=0.7	Length-based	None	16%	45%	-1%	25%
		DDG L_∞	-10%	29%	-33%	-39%
		DDG K	-10%	29%	-32%	-42%
	Age-based	None	-27%	-14%	-34%	-29%
		DDG L_∞	-40%	44%	-88%	-19%
		DDG K	-35%	35%	-75%	-31%
F=1.2	Length-based	None	8%	64%	-11%	47%
		DDG L_∞	-29%	33%	-49%	-33%
		DDG K	-27%	45%	-52%	-28%
	Age-based	None	-28%	-25%	-28%	-43%
		DDG L_∞	-39%	58%	-71%	-12%
		DDG K	-31%	63%	-62%	-16%

These trends were mirrored by the estimates from the alternative methods. Since density dependent growth affects the true value of $F_{0.1}$, deterministic runs were performed within MIDAS to identify these $F_{0.1}$ values (Table 7.5). These were used when calculating bias in $F_{0.1}$.

Table 7.5 True $F_{0.1}$ values (yr^{-1}) from the simulated yield-effort curve of *L. mahsena* with and without density dependent growth operating.

DDG	$F_{0.1}$ (yr^{-1})
None	0.41
DDG L_∞ at -70%	0.65
DDG K at -120%	0.71

Density dependent growth resulted in lower total mortality estimates where either length-based or age-based growth parameters were used. Density dependent growth increased the mean length of the length frequency distribution. In Beverton and Holt's method, this decreased the value of L_∞ - $\bar{L}$. Although affected by changes in the growth parameter estimates, this decreased the total mortality estimate. Density dependent growth also increased the proportion of large individuals in the length frequency distributions (Chapter 5). In the length-converted catch curve, this increase in the frequency of larger size classes combined with changes in the growth parameter estimates (which increased Δt at these sizes) to decrease the gradient of the descending limb, and hence the total mortality estimate.

With density dependent growth, natural mortality estimates using length-based growth parameters decreased, while estimates from age-based estimates increased. This was directly related to the growth parameter estimates. For Pauly's M, the increases in L_∞ and decreases in K resulted in decreases in the M estimate. As age-based growth parameters showed the opposite trend, Pauly's M estimates increased. Ralston's M, being directly related to K, followed the trends seen in the estimates of that parameter (a decrease in length-based K, an increase in age-based K).

As a result of the decrease in the total mortality estimates, where density dependent growth was operating, F_{curr} estimates were lower than those without density dependent growth. This increased the general underestimation of this parameter at high fishing mortality levels. F_{MYPR} and $F_{0.1}$ estimates decreased when length-based growth parameters were used, and increased notably where age-based estimates were applied. These patterns related directly to the trends in natural mortality estimates.

7.4.2.3 Summary

The presence of density dependent growth led length-based methods to produce an increased estimate of L_∞ (leading to a corresponding decrease in K), while age-based methods produced increased estimates of K. As a result of increased growth rates, a greater proportion of larger individuals were present in the length frequency distribution, decreasing the estimates of total mortality. Although estimates of M were affected by the changes in the growth parameters, estimates of F_{curr} generally declined.

7.4.3 Scenario 3. Developing fishery, no density dependent growth

In this scenario, the population was simulated at unexploited equilibrium until 'time zero'. At this time, the population was exposed to the selected constant fishing mortality. Length frequency samples were simulated over the subsequent five years, and growth parameters estimated using ELEFAN. The age-at-length spreadsheet simulation was also modified to improve the simulation of transient fishing mortality. Biological and fishery parameters were then estimated using these growth estimates and the last year of length frequency data.

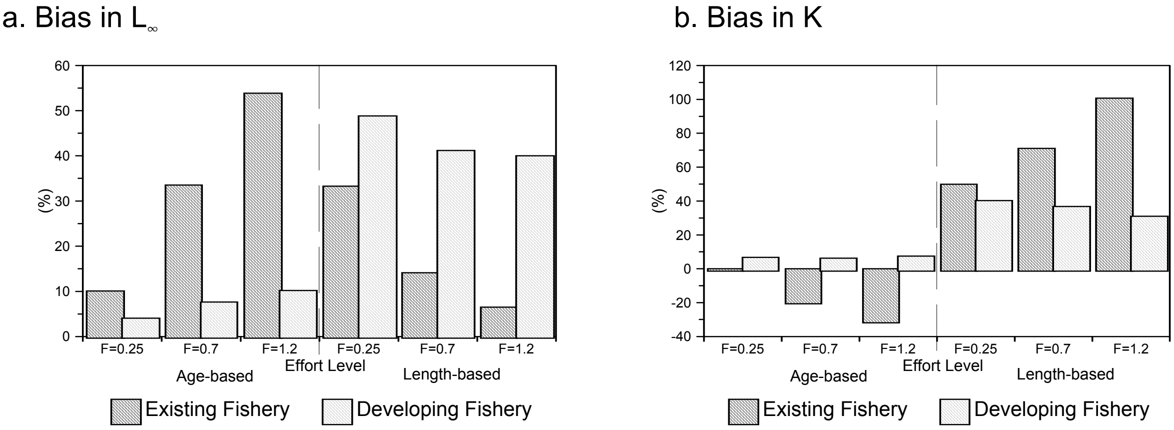
The work described in Chapter 5 indicated that length frequency distributions from a developing fishery were not significantly different to those from a fishery at equilibrium where fishing was initiated at $F=0.05yr^{-1}$. Simulations were therefore only performed at the three higher levels of fishing mortality ($F\geq0.25yr^{-1}$) where the differential between the developing and equilibrium fishery states was greater.

As in Scenario 2, while the full set of analyses were carried out, the results have been condensed for brevity. The section concentrates on the differences resulting specifically from the transient effects of fishing.

7.4.3.1 von Bertalanffy growth parameters

The use of the age-based growth parameters calculated for the equilibrium fishery (Scenario 1) would not accurately represent estimates derived using samples from a developing fishery. The impact on the age-at-length data of five years of transient fishing mortality following unexploited equilibrium would be far less than that in the exploited equilibrium simulation.
To simulate the effects of transient fishing mortality in the simulation of age-at-length, calculation of fishing mortality within the EXCEL^{TM} spreadsheet (Chapter 4, Section 4.3.1.2) was modified. The difference between current age and age at recruitment to the fishery (Ac_{min}, age at 13cm) was assessed for each individual within each size class. Where this difference was greater than 5 years, fishing mortality was applied to each individual for the previous five years only, using the selectivity ogive. Relative to the equilibrium fishery, values of P_{surv} were increased. This method therefore assumed that age data were collected exclusively from the fifth year of the fishery.

The growth parameter estimates derived from length- and age-based estimates are presented in Figure 7.9, and compared with the estimates from the existing fishery simulation (Scenario 1).


a. Bias in L_∞

b. Bias in K

Figure 7.9 Bias in the mean growth parameter estimates derived through length- and age-based methods from both the existing (Scenario 1) and developing (current scenario) fisheries.

Age-based growth estimates from the developing fishery were both more accurate and precise than those from length-based methods. They were also more accurate than both length-based and age-based estimates derived from the existing fishery.

In the developing fishery, L_∞ was overestimated by length-based methods at all fishing mortality levels. Since the impact of fishing on the length structure was reduced compared to the existing fishery, there was a greater proportion of larger individuals present. This positively biased L_∞. While K estimates remained overestimated, their accuracy was improved, and estimates remained stable with changing fishing mortality. However, parameter estimates were less precise than those from the developed fishery.

Due to the reduced impacts of fishing in this scenario, there was increased information on the value of L_∞ in the age-at-length data; fewer large slow growing individuals were removed. This reduced the positive bias resulting from high proportions of young, fast growing individuals in the larger length classes. In turn, this improved the K estimate. The precision of both growth parameter estimates was also improved.

7.4.3.2 Other parameters

As in Scenario 2, the following section presents the effects of the transient fishery situation in a condensed form. Table 7.6 summarises the estimates for particular parameters. These are presented to illustrate the general consequences of collecting data from a developing fishery. These trends were mirrored by the outputs obtained from the alternative parameter assessment methods.

Table 7.6 Bias (%) in the mean estimates of total, natural and current fishing mortality, and of $F_{0.1}$, from length- and age-based growth parameter estimates. Estimates from existing and developing fisheries presented. Only selected parameter estimation methods are shown to illustrate the trends.

F-level (yr^{-1})	Method	Fishery	Bias in mean parameter estimates (%)			
			B&H Z	Pauly's M	F_{curr} (B&HZ - Pauly's M)	$F_{0.1}$ (Pauly's M)
F=0.25	Length	Existing	49.2	26.9	84.7	-3.9
		Developing	41.0	17.3	79.2	-17.5
	Age	Existing	-31.1	2.8	-85.5	-4.7
		Developing	-47.9	9.5	-139.6	7.0
F=0.7	Length	Existing	15.6	44.8	-1.3	25.0
		Developing	0.5	17.9	-9.6	-13.6
	Age	Existing	-27.2	-14.5	-34.4	-28.7
		Developing	-52.6	8.2	-87.4	0.2
F=1.2	Length	Existing	7.8	63.8	-10.9	47.3
		Developing	-12.7	15.0	-21.7	-15.4
	Age	Existing	-27.8	-25.3	-28.6	-43.1
		Developing	-54.5	8.2	-75.4	-2.3

Age-based total mortality estimates were lower than those calculated from the existing fishery, increasing the negative bias. Length-based Beverton-Holt Z estimates were also lower, while length-converted catch curve Z estimates increased. In the developing fishery, length frequency distributions were less affected by fishing mortality compared with the existing fishery. Mean length was therefore greater, reducing the Beverton and Holt total mortality estimate. Length-converted catch curve estimates from the developing fishery were also negatively influenced by the increased number of large individuals in the length frequency distributions. Such decreases were supplemented by the lower age-based L_∞ estimates, which truncated the catch curve descending limb, and hence decreased the gradient. For length-based growth estimates, however, the increase in L_∞ estimates decreased Δt, thereby increasing the gradient of the descending limb, positively biasing the total mortality estimate.

The negative bias in total mortality estimates derived from age-based growth parameters increased with fishing mortality, while positive bias in length-based estimates tended to decrease. As a result, at high F this led to negative bias. Overall, Beverton-Holt estimates derived using length-based growth parameters were most accurate. Of the length-converted catch curve estimates, those derived from age-based growth parameters were most accurate.

Compared with the existing fishery estimates, natural mortality estimates based on length-based growth estimates decreased, while those derived from age-based estimates increased. Estimates for the developing fishery were more accurate than those for the existing fishery. Following the pattern found in the growth parameters, estimates were relatively constant between fishing mortality levels. Overall, Ralston's M estimated using length-based growth parameters (not shown) was the most accurate.

The use of age-based growth parameters underestimated F_{curr}. Confident length-based estimates also underestimated F_{curr} at higher fishing mortality levels, while cautious length-based estimates consistently overestimated F_{curr}. Overall, cautious age-based F_{curr} provided the most accurate estimates of the true level of fishing mortality.

Estimates of F_{MYPR} and $F_{0.1}$ followed the trends in the natural mortality estimates; length-based estimates were lower than those from the existing fishery, while age-based estimates increased. $F_{0.1}$ estimates based on Pauly's M were more accurate than those based on Ralston's M, where either set of growth parameters was used. Overall, $F_{0.1}$ derived using age-based growth estimates was the most accurate.

7.4.3.3 Summary

Since the developing fishery had suffered a lower level of fishing mortality, and hence the length and age structure was less affected by fishing, age-based growth parameter estimates were more accurate than those from the existing fishery. Length-based L_∞ estimates were positively biased by the increased proportion of large individuals present in the length distribution. As a consequence, however, K estimates were improved.

Due to the increased proportion of larger individuals in the length structure, estimates of total mortality were negatively biased. Therefore, F_{curr} estimates were generally underestimated. Trends in F_{curr} were influenced by changes in natural mortality, which were affected by the growth parameter estimates. M estimated using length-based growth parameters declined, while that from age-based growth parameters increased. $F_{0.1}$ and F_{MYPR} showed identical trends to that in M.

7.4.4 Scenario 4. Developing fishery, with density dependent growth

As in Scenario 3, fishing mortality was applied to a previously unfished population, simulating a newly developed fishery. In the current scenario, however, density dependent growth was operating in either L_∞ or K. Simulations were again performed at F=0.7 and $1.2yr^{-1}$.

Due to the complexities of simulating transient fisheries where density dependent growth was operating, age-at-length data could not be simulated using the EXCEL^{TM} spreadsheet model. The results from this scenario therefore concentrate on the effects of transient density dependent growth on length-based growth parameter estimates.

While the full set of analyses were carried out, the results have again been condensed for brevity. The effects of density dependent growth in a developing fishery were concentrated upon.

7.4.4.1 von Bertalanffy growth parameters

The mean von Bertalanffy growth parameters estimated through ELEFAN in the developing fishery, with and without density dependent growth operating, are presented in Table 7.7

The level of bias in the growth parameter estimates could not be calculated. Due to the transient nature of the fishery and the effects of density dependent growth, the 'true' mean population growth parameters were continuously modified with each change in population biomass.

Table 7.7 Mean L_∞ and K estimates from length-based methods, with and without density dependent growth, and the CV (%) of the estimate distribution.

Parameter	F level	No DDG		DDG L_∞ at -70%		DDG K at -120%	
		Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
L_∞	F=0.7	68.5	16.5	70.5	12.1	68.4	12.3
	F=1.2	67.9	14.2	66.7	13.6	65.7	13.5
K	F=0.7	0.19	34.1	0.19	38.1	0.20	35.5
	F=1.2	0.18	33.4	0.20	33.2	0.19	35.6

Density dependent growth had little effect on the length-based L_∞ and K estimates derived from the developing fishery. ELEFAN L_∞ estimates were strongly related to the largest individual present in the length frequency distribution. In this scenario, the largest individuals were present in the length frequency for year one. In this year, fishing (and density dependence) had had little effect on the catch length structure. Differences due to density dependent growth were only apparent two or three years after the initiation of fishing (Chapter 5), by which time, mean length had been notably reduced. Due to the similarity in the length frequencies of year 1 between scenario 3 and the current scenario, L_∞ estimates were comparable. As a result of the relationship between growth parameters, estimates of K were also comparable.

Although age-based growth parameter estimates could not be derived for this scenario, some inferences can be drawn from the results of the previous studies. Age-based growth parameter estimates would be expected to lie somewhere between those identified in Scenario 3, the transient fishery without density dependent growth, and that in the equilibrium fishery with density dependent growth (Scenario 2). As a result, estimates are likely to be more accurate that the length-based growth parameters calculated in the current scenario.

7.4.4.2 Other parameter estimates

This section summarises the effects of density dependent growth in combination with the collection of data from a developing fishery (Table 7.8). The bias in particular parameter estimates are presented to illustrate general trends. These trends were mirrored by the alternative parameter estimation methods.

Density dependent growth had little effect on the length-based growth parameter estimates. Differences in the biological and fisheries parameters were therefore the result of differences in the length frequency distribution in year five. As indicated in Chapter 5, the effects of density dependent growth were significant by that time.

Table 7.8 Bias (%) in the mean estimates of total, natural and fishing mortality, and of $F_{0.1}$ derived using length-based growth parameter estimates. Selected parameter estimates are shown to illustrate trends.

F-level	DDG	Bias in mean parameter estimates (%)			
		B&H Z	Pauly's M	F_{curr} (B&H Z -Pauly's M)	$F_{0.1}$ (Pauly's M)
F=0 → 0.7	None	0.5	17.9	-9.6	-13.6
	DDG L_∞	-14.9	14.2	-31.7	-53.1
	DDG K	-10.4	20.0	-27.7	-45.1
F=0 → 1.2	None	-12.7	15.0	-21.7	-15.3
	DDG L_∞	-33.6	21.6	-52.0	-43.7
	DDG K	-32.5	20.7	-50.2	-47.0

Total mortality estimates, which in the developing fishery (Scenario 3) were generally lower than those from the existing fishery (Scenario 1), were further reduced where density dependent growth was operating. Estimates became increasingly underestimated with increasing fishing mortality. As in scenario 2, density dependent growth increased the mean length in the length frequency distribution, reducing the Beverton and Holt total mortality estimate. The increased number of individuals present in the larger size classes reduced the gradient of the catch curve descending limb, and hence decreased Z, counteracting the positive bias in the estimate identified in Scenario 3.

Natural mortality estimates were unaffected by the presence of density dependent growth. This was a result of the similarities in the length-based growth parameter estimates between Scenario 3 and the current scenario. However, density dependent growth resulted in lower F_{curr} estimates, due to the lower total mortality estimates.

Estimates of F_{MYPR} and $F_{0.1}$ were unaffected by density dependent growth, due to the similarities in natural mortality estimates in the current scenario and Scenario 3. However, the true $F_{0.1}$ and F_{MYPR} levels increased as a result of density dependent growth. $F_{0.1}$ estimates in the current scenario therefore showed increased negative bias.

7.4.4.3 Summary

Due to the limitations of the spreadsheet-based age-at-length simulation, analyses could only be performed for length-based growth estimates. In the transient fishery, density dependent growth had little effect on these growth estimates; the high proportion of large individuals present in the length frequency distributions of the early years was more influential on the growth estimates than changes in later years resulting from density dependent growth.

Total mortality estimates were negatively biased. This was a result of the increased proportion of large individuals in the catch due to density dependent growth. Although natural mortality estimates were unaffected, due to the lack of change in the growth parameters, F_{curr} estimates were underestimated as a result. $F_{0.1}$ and F_{MYPR} estimates were unaffected by density dependent growth. However, since the true values of these parameters increased where density dependent growth was operating, estimates were increasingly negatively biased.

7.5 DISCUSSION

Using Monte-Carlo simulation methods, the study described in this chapter examined the accuracy and precision of length-based and age-based growth parameter assessment methods under four different fishery scenarios, and a range of fishing mortality levels. These growth estimates were then used in length-based methods to calculate further biological and fisheries parameters.

Throughout the study, a summary of each fishery simulation has been provided. This section therefore aims to bring together these results to discuss the extent to which the main aims of the chapter were achieved.

7.5.1 Growth parameter estimation methods

This section discusses the two growth parameter estimation methods used; using length frequencies (length-based) and using age-at-length data (age-based). The accuracy of growth estimates from each method for *L. mahsena* is first discussed. The effects of fishing on these estimates are then detailed.

7.5.1.1 Length-based methods

Of the three length-based methods of growth estimation available in LFDA, only ELEFAN produced relatively accurate growth parameter estimates for *L. mahsena* (Section 7.3.4). Growth parameter estimates derived using PROJMAT and SLCA tended toward the extremes of the search range examined. This was contrary to the results of Isaac (1990), which indicated that SLCA, rather than ELEFAN, produced more accurate K estimates for slow growing species. However, Rosenberg and Beddington (1987) noted that the accuracy of ELEFAN K estimates increased with decreasing simulated K (from K=1.0 to K=0.4). The failure of SLCA and PROJMAT may relate to the methods used to assess growth from the length frequencies, combined with the lack of information on the growth parameters provided by these length frequencies.

ELEFAN estimates of the von Bertalanffy growth parameters showed considerable bias in all scenarios. For example, under equilibrium conditions without density dependent growth, both L_∞ and K were considerably overestimated; at F=0.25yr^{-1} the level of bias was 33% in L_∞, and 50% in K. These were notably higher than levels identified in the literature. Due to the different growth parameters and levels of individual growth variability, no direct comparison could be drawn. However, as an example of the differences, at F=0.3yr^{-1}, the study described in Isaac (1990) indicated bias in ELEFAN estimates of 12% for L_∞, while that in K was -11%.

ELEFAN L_∞ estimates appeared to be strongly influenced by the largest individuals present in the length frequency distributions. In turn, this was influenced by the level of individual growth variability. While the true population mean L_∞ was 48.5cm, at lower fishing mortality levels individuals were present at sizes greater than 70cm. As noted by Hampton and Majkowski (1987) and Isaac (1990), this resulted in positive bias when compared to the mean L_∞ value. Since most of the growth parameters estimated using length-based methods are assumed to describe mean growth, they ignored the influences of individual growth variability (Sainsbury, 1980).

The overestimation of L_∞ followed the patterns found in the simulation studies of Hampton and Majkowski (1987), Rosenberg and Beddington (1987), and Isaac (1990). However, in those studies, ELEFAN tended to underestimate K. In the current study, K was overestimated. This may result from the relative values of mean K used. In the literature, populations were simulated with much faster mean growth rates than those used in the current study (commonly K=0.5; Hampton and Majkowski, 1987) to K=0.7 (Rosenberg and Beddington, 1987), although K=0.1 was studied briefly by Isaac (1990). Under faster growth rates, more distinct (widely spaced) modes should result. These may be interspersed with apparent modes resulting from random sampling artefacts. Growth curves fitted through such modes would result in the underestimation of the growth rate found in the literature. In contrast, modes seen in the simulated *L. mahsena* length frequencies were comprised of a number of age classes, due to slow growth rates and individual growth variability. Growth curves fitted through these modes therefore overestimated K.

The results of this study therefore suggest ELEFAN overestimates both L_∞ and K in long-lived slow-growing species, in contrast to the situation for faster growing species where K tended to be underestimated.

7.5.1.2 Age-based methods

Age-based *L. mahsena* growth estimates were generally both accurate and precise. For example, under equilibrium fishing mortality at $F=0.25yr^{-1}$, L_∞ was overestimated by 10%, while K was underestimated by 0.7%.

Individual growth variability affected age-based growth parameter estimates. Since the effects of natural and fishing mortality depended on the length of a fish, only relatively fast growing individuals survived to reach the larger size classes. Samples from these classes were therefore dominated by the faster growing proportion of the population (*e.g.* Myers, 1989a). Slower growing individuals were subjected to a greater level of both fishing and natural mortality, as they grew through vulnerable size classes at a slower rate. At larger sizes, therefore, faster growing, younger individuals were present, decreasing the information available on L_∞, and hence indirectly affecting the estimate of K. The effects of individual variability were also noted during the adjustment of the underlying population mean growth parameters (so that sample estimates matched those resulting from the actual fishery samples; Chapter 4, Section 4.3.1.2). When population growth parameter values were reduced below a certain point, individuals surviving to larger sizes had growth parameter sets from the extremes of the population parameter distributions. This strongly influenced the resultant growth parameter estimates.

7.5.1.3 Comparison of the two growth estimation methods

Throughout the study, age-based methods tended to result in more accurate growth parameter estimates. For example, in a developing fishery (Scenario 3) where the impacts of fishing were minimal ($F=0.25yr^{-1}$), age-based estimates of L_∞ and K were slightly positively biased (bias in L_∞ = 4%, K=7%), while those from length-based methods were both strongly positively biased (bias in L_∞=49%, K=40%).

The lack of distinct modes and modal progression in the length frequency distributions of this species (due to slow growth and the level of individual growth variability) offers little information on the growth of *L. mahsena*. As a result, length-based growth estimates appear neither accurate nor precise. In contrast, age-based methods, through the direct assessment of age-at-length, resulting in more accurate and precise estimates of *L. mahsena* growth.

The increased precision of age-based growth estimates was particularly notable in the estimates of K. Due to the lack of information in the length frequency distributions, even at low fishing mortality levels, a range of growth parameter estimates may have fitted the data with similar score values, resulting in the imprecision identified.

These basic levels of accuracy and precision were affected by the effects of fishing on the populations.

7.5.1.4 Effects of fishing on the growth parameter estimates

The effects of fishing can be broken down into the direct effects (removal of individuals) and indirect effects (density dependent growth).

As seen in Scenario 1, the removal of large individuals through fishing tended to improve the accuracy and precision of the L_∞ estimate derived through length-based methods. Indeed, at high fishing mortalities under equilibrium conditions, length-based L_∞ estimates were less biased than those from age-based methods. However, decreases in the L_∞ estimate resulted in corresponding increases in the value of K, which became increasingly overestimated with increasing fishing mortality.

At all simulated equilibrium fishing mortalities, age-based estimates of K were more accurate and precise than those from length-based methods (Scenario 1). However, with increasing fishing mortality, the level of positive bias and imprecision in L_∞ estimates increased. This resulted from the effects of individual growth variability mentioned above. As fishing mortality increased, the probability of slow growing individuals surviving to large sizes was low. As a result, increasing proportions of fast growing, younger individuals were caught at larger size classes, correspondingly decreasing the information on L_∞.

While age-based growth estimates were the most accurate and precise in the majority of cases, they were affected by fishing at high fishing mortality levels. In practice, however, fisheries institutions assessing heavily exploited fisheries may have access to historical age-at-length data from a period of lighter exploitation. More accurate growth parameter estimates could then be derived. Where such data are not available, an alternative approach is to use growth assessments from nearby, less heavily exploited locations. While the resultant estimates will be affected by local environmental differences (Chapter 6), they are likely to remain more accurate than those derived through length-based methods. Such suggestions only hold where density dependent growth is not operating, due to its effects on growth at high exploitation levels.

Under equilibrium fishery conditions (Scenario 2), density dependent growth was detected through both growth estimation methods. However, the interpretation of increased growth rates was different. Density dependent growth increased both length-at-age, and the number of large individuals in the length frequency distribution. Age-based methods interpreted the former as an increase in K, and hence a lower estimate of L_∞. The latter was interpreted by length-based methods as an increase in L_∞, and hence a decrease in K. Neither growth estimation method could therefore identify the parameter affected by density dependent growth in the simulation.

Under transient conditions (Scenario 4), length-based methods did not detect the presence of density dependent growth. This was a result of the presence of large individuals in the early years of the developing fishery. Hence, the direct and indirect effects of fishing in the following years did not affect the growth parameter estimates.

Bias in growth parameter estimates was therefore a combination of that inherent in the methods used, and that arising from the impacts of fishing. Since growth parameters are used in a number of other parameter estimation methods, their use in such methods has the potential to result in serious ‘knock-on’ effects.

7.5.2 Effects of bias in growth parameter estimates on other parameters

Growth parameter estimates and the form of the length frequency distribution affected the total mortality estimates. Age-based growth parameters generally resulted in the most accurate total mortality estimates, particularly when derived using the length-converted catch curve under equilibrium conditions (Scenario 1). When using length-based growth parameters, Beverton and Holt Z estimator was the most accurate.

Using length-based growth parameters under equilibrium conditions, total mortality estimates from both methods were positively biased due to the overestimation of both L_∞ and K (see also Wang and Ellis, 1998; Isaac, 1990). Total mortality was consistently underestimated where both age-based and the true growth parameters were used. This was related to individual variability in growth; individuals were present in the length structure at lengths greater than the value of L_∞ used. Length structures were therefore curtailed at L_∞, leading to the underestimation of Z. As noted in the study of Wetherall *et al.* (1987), Beverton-Holt Z estimates, and from this study the length-converted catch curve, can be biased considerably unless L_∞ is known accurately.

Density dependent growth reduced the estimates of total mortality. Increased growth rates resulted in an increased proportion of large individuals in the catch. When derived using length-based growth parameters, this reduced the positive bias seen at equilibrium. When using age-based growth estimates, the negative bias in estimates was increased. Similar effects were noted in the developing fishery simulation (Scenario 3), since an increased proportion of large individuals remained in the length distribution.

The effects of density dependence may be reduced through the estimation of total mortality using age frequency distributions. Although not examined in this study, density dependence will have a minimal effect on the population age structure when compared to the length structure. Increased growth rates due to density dependence may result in an increased proportion of younger individuals resulting in the catch, since they reach exploitable lengths at a younger age. However, since this is likely to affect the ascending limb of the catch curve, rather than the desending limb, the impact on total mortality estimates may be minimal.

Growth parameter estimates had a direct effect on the empirical natural mortality estimates. Increases in L_∞ decreased Pauly's M, while increases in K had an increased positive effect. Ralston's M estimate was directly related to the magnitude of K. Since the value of natural mortality used in the simulations was derived using Pauly's equation, this method resulted in the most accurate estimates where age-based growth parameters were used (Scenario 1), while Ralston's estimates were negatively biased. Since length-based growth parameters were overestimated, Ralston's M proved the most accurate when these parameters were used. Density dependent growth was interpreted as increases in a single growth parameter by each growth estimation method. As a result, estimates of M using length-based growth parameters were decreased, reducing the level of positive bias, while age-based estimates were increased, positively biasing M estimates. The opposite trend was found in the developing fishery (Scenario 3).

As growth parameters were related to the total and natural mortality estimates, they were also related to the estimated F_{curr} level. This parameter could be calculated through four combinations of total and natural mortality. Under equilibrium conditions, the most accurate F_{curr} estimate was derived using age-based growth parameters, subtracting Ralston's M from the length converted catch curve total mortality estimate ('cautious estimate'). When using length-based growth estimates, subtracting Pauly's M from Beverton and Holt's Z estimate ('confident estimate') resulting in the most accurate F_{curr}. The true growth parameters consistently underestimated total mortality, and hence F_{curr}. Under equilibrium conditions, the accuracy of all F_{curr} estimates improved with increasing simulated fishing mortality. Since density dependent growth resulted in a decreased estimate of Z, F_{curr} estimates were also decreased. This tended to increase the negative bias resulting from the use of age-based growth estimates, and decrease the positive bias where length-based estimates were used.

As a result of the nature of the developing fishery, the true level of F_{curr} could not be established. In such cases, it would appear advisable to remain cautious until the fishery had adjusted to the level of fishing mortality applied. More accurate assessments could then be made using age-based growth parameter estimates. However, if the effort level was high, the stock might become seriously depleted before equilibrium was reached. In such cases, assessment of the rate of change in mean length or age may be appropriate.

The yield-effort curve was strongly influenced by the magnitude of the natural mortality estimate. Hence it was strongly, if indirectly, influenced by the growth parameter estimates from which M was derived. However, even where the true growth parameters were used, and therefore natural mortality estimates were constant across F levels (and accurate where Pauly's M was used) small inaccuracies still resulted due to small variations in the Lc_{50} estimate (Scenario 1).

With increasing simulated equilibrium fishing mortality, $F_{0.1}$ estimates derived from length-based growth parameters increased, while those estimated using age-based estimates decreased. This followed the pattern in the natural mortality estimates. Where density dependent growth was operating, the opposite trend was seen. This resulted from the effects on the growth parameter estimates, and hence on the estimate of M.

Fishing effort targets derived through yield-per-recruit analyses are based on long-term stability in the life history parameters (Beverton and Holt, 1957). In a transient population, density dependent growth will continually alter the life history parameters (due to variation in recruitment, adjustment to changes in fishing pressure). Care should therefore be taken that the growth parameters used are suitable. To account for changes due to exploitation level, the von Bertalanffy growth parameters would have to be re-assessed frequently.

As indicated in the results of Scenario 1, F_{MYPR} estimates from the yield-effort curve were at levels of fishing mortality at which the stock would collapse. This was a result of the assumption that the level of recruitment was unaffected by fishing mortality. As a result, F_{MYPR} was an inappropriate limit reference point for this species.

In summary, both fishing and density dependent growth affected the outputs of length-based biological and fishery parameter estimates both directly (*e.g.* total mortality estimates), and indirectly through the effects on growth parameter estimates (*e.g.* natural mortality, $F_{0.1}$). In turn, bias and imprecision in these parameter estimates will affect stock assessments based upon them, and hence management actions. This will be examined in the next chapter.

7.5.3 Summary

By comparison with length-based growth parameter estimates, age-based estimates were both more accurate and precise. Both methods, but in particular length-based estimates, were biased by individual growth variability. Growth parameter estimates were also notably affected by the removal of individuals through fishing, and the effects of density dependent growth. In turn, the accuracy of growth parameter estimates had direct 'knock-on' effects on the estimates of further biological and fishery parameters. The impact of these effects on stock assessments, and hence management actions, will be examined in the following chapter.

Since current estimates of growth and mortality for the study species are derived using length-based methods, the results of this study indicate that these assessments may be flawed. This is particularly true since density dependence has been indicated in the study species (Chapter 6). There are therefore potential advantages in using age-based methods of assessment in these locations. In Chapter 9, both length-based and age-based methods of growth and mortality estimation will be used both to investigate whether the results of this simulation study can be identified using actual fisheries data, and to assess the status of the study fisheries.

8. The suitability of length- and age - based methods for informing management: Management strategy simulation.

8.1 INTRODUCTION

As indicated previously (see Chapter 7), due to the perceived difficulty in ageing tropical fish, the practical problems of funding validation studies, and the subsequent time and expense involved in the use of otoliths for age assessment, length-based methods have been used extensively in the tropics (Venema *et al.*, 1988). Such methods are not ideally suited to long-lived, slow-growing species and thus sometimes inappropriate length based methods have been applied to derive estimates of growth. This leads to inaccurate growth parameter estimates (Chapter 7). Uncertainty in tropical fish stock assessments arises from the use of such potentially biassed growth parameter estimates as inputs for further calculations; for example in the estimation of mortality and yield-per-recruit (Rowling and Reid, 1992; Mees and Rousseau, 1997; see also R 5484, Chapter 7). This 'knock on' effect increases uncertainty in biological reference points on which management actions may be based.

In addition to uncertainty in the estimates of growth parameters, fishing may affect growth parameter estimation and the rate at which fish grow. By harvesting fish of particular sizes, bias may be introduced into the estimation of growth. By changing the density of fish populations, growth rates of individuals in the population may change due to fishing (see Chapter 7). This chapter addresses the question of whether such changes are significant for the management of the resource.

In order to evaluate the management performance of length based assessment methods utilising uncertain growth parameter data, a technique known as 'management strategy simulation' is employed. This technique is used to investigate :

- The effect of uncertainty in growth parameter estimation on management performance;
- The effect of fishing induced changes in growth rate on management performance;
- The differences in management performance between age and length based methods of growth assessment.

Guidelines for management are also developed.

8.2. METHODOLOGY

8.2.1. Management strategy simulation

Management strategy simulation is a technique which uses intensive computer simulation studies to model and analyse the behaviour of complex systems (all the processes that occur in fisheries management) by using a simpler model of the system. Simulations described in previous chapters (see Chapter 7) related to improved assessment of the fisheries, which is just one part of the process of management. An example of a typical simulation model for fisheries management is indicated in Figure 8.1, which outlines the processes that occur and which need to be simulated in the model both under the water, i.e. the fish stock and fishing of that stock; and above the water, i.e. catching the fish, and the management of the fishery (From FMSP project R6437).

Below the water an 'Operating Model' simulates the dynamics of the fish stock and the effect of fishing on it. Above the water, each of the processes from fishing, data collection, annual assessment, management advice and the effects of management actions on the resources need to be modelled in some way. Being in a computer program, the true state of the fish stock is known at all times in a simulation model. This knowledge would not, however, be available to either the scientist doing the assessment, or to the manager.

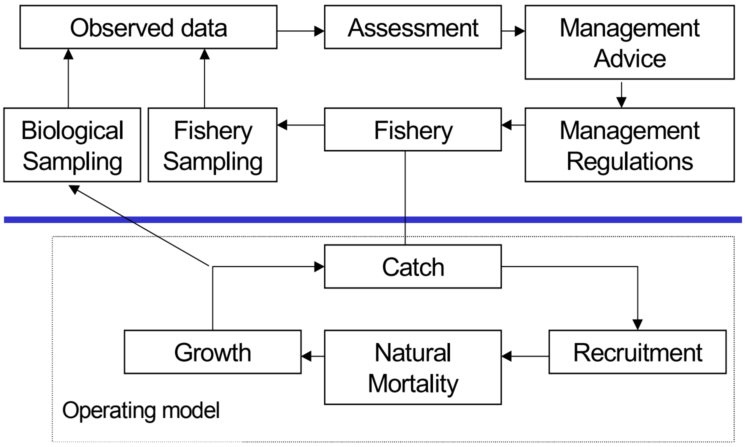


Figure 8.1 The processes that must be modelled in management strategy simulations for fisheries.

The key to understanding the behaviour of this system is that the entire management process has to rely on imperfect information. Further, things can go wrong in every one of the processes simulated. Proper understanding of the system as a whole must take account of possible imperfections in each part of the system. In general, until now, most attention has been paid to improving the methods used in assessment. Management strategy simulation has been devised as a way to analyse the system as a whole. Similarly, up to this point the present study has examined uncertainties in assessment of growth and the effects of that uncertainty on biological reference points used to derive management advice. The present chapter describes the results of a simulation model for the whole system.

8.2.2 The management strategy simulation model developed for the present study

Length based yield-per-recruit analyses have been applied to derive target effort levels, upon which management advice was based in each of the case study countries (R5484 in MRAG, 1996b; Seychelles, Mees and Rousseau, 1997; British Indian Ocean Territory, Mees *et al*, 1999). Effort control determined by $F_{0.1}$ was the management strategy selected for examination in the current study (due to the lack of a stock recruitment relationship for *L. mahsena*, the species selected for this study, it was not possible to determine $F_{MSY,}$ and F_{opt} from the yield-per-recruit analysis was unrealistically high, hence $F_{0.1}$ was selected, see Chapter 7). The management simulation model developed for this purpose is described in Figure 8.2.

MIDAS, the Multi-species Interactive Dynamics Age-structured Simulation model (described in Chapter 4 and Appendix 2) simulates the processes that occur in the fish stock, and fishing on that stock. The remainder of Figure 8.2 represents the processes that occur in managing the resource. A two stage process was adopted for the current management strategy simulations:

(a) Data sets for each scenario (a range of Fstart values, density dependent growth on/off, see below) were simulated prior to the onset of management. Growth parameters and associated $F_{0.1}$ values were estimated for *Lethrinus mahsena*, the species selected for study. *L. mahsena* was selected since estimates of individual variability in growth rate were available for this species (see Chapter 3).

(b) These parameter estimates were used as input for management simulations within the ‘operating model’. Simulations were run with management rules applied over a 20 year period. The output from management simulation was a set of indices of management performance.

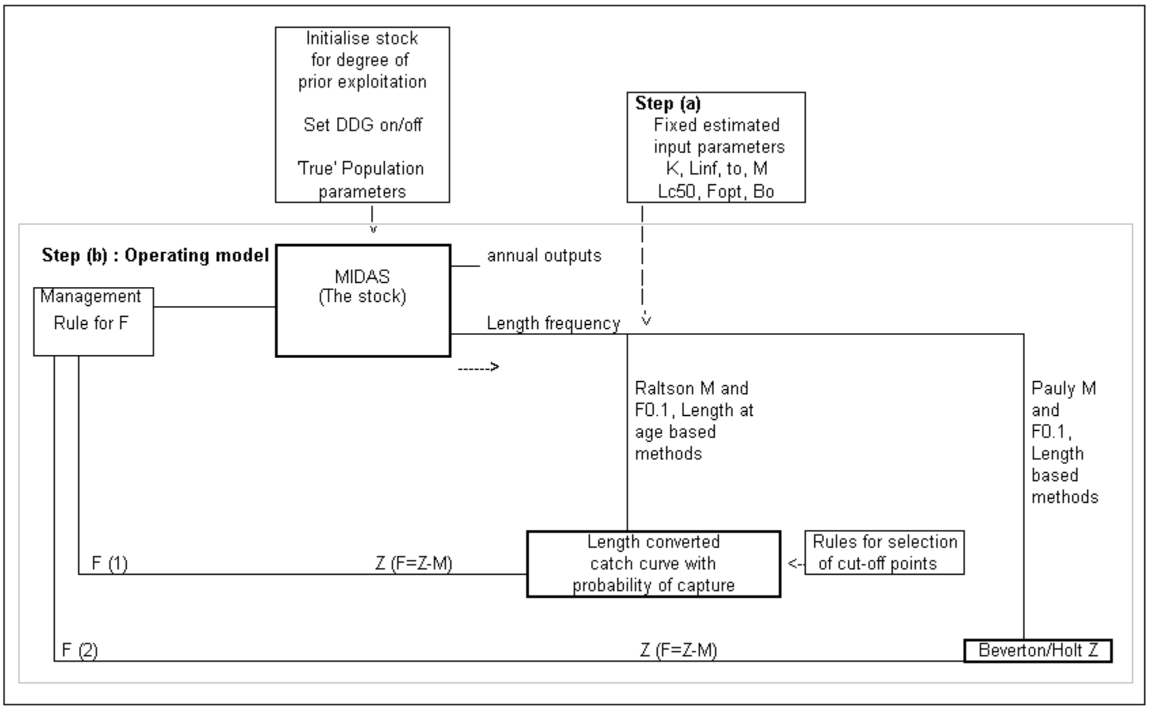


Figure 8.2 Diagrammatic representation of the fisheries management strategy simulation model used to investigate the effect of uncertainties in growth parameter estimation and variation in growth rate due to fishing on management (effort) controls derived from yield per recruit analyses.

Uncertainties in growth parameter estimates derived from length- and age-based[2] methods of assessment were described in Chapter 7. The resulting effects on the assessment of stock status, on which management actions are based, were described. The effects of changes in growth rate due to fishing through the mechanism of density dependant growth (DDG) were also investigated.

In the current study, outputs from the simulations described in Chapter 7 were used as input parameters (Figure 8.2, step a). Length-based methods were subsequently used to estimate total mortality. Using the input estimates of M, annual fishing mortality estimates could be derived. The input parameters therefore represented the estimation of parameters at the start of management, and were unchanged during the period of the simulation.

---

[2] The results of runs employing age-based growth parameter estimates are described as ‘age-based’ in the subsequent text. However, it should be noted that they do not represent the results from a full age-based assessment, since length-based methods are employed to derive further parameters.

Using the outputs from Chapter 7, and the management strategy simulation model, the two principal objectives of how (i) uncertainties in growth parameter estimates; and (ii) changes in growth rate due to fishing, affect our ability to manage the resource were examined. Thus:

- To take account of uncertainty in growth parameter estimation and draw conclusions on its effect on management performance, steps (a) and (b) were repeated 100 times for both age- and length-based data. These inputs encapsulate not only the uncertainty in growth parameter estimation (K, L_∞), and individual variability in growth, but also uncertainty in biological reference points (BRPs, $F_{0.1}$) derived from them.
- To evaluate the effects of growth rate changes due to fishing management simulations were compared with and without DDG operating (the mechanism for assessing growth parameter inputs with DDG derived from ageing techniques is explained in Chapter 7, scenario 2).

The effect of uncertainty in input growth and biological reference points on management is interpreted through examination of management performance. Greater uncertainty and variability is expected to lead to lower management performance, i.e. more optimistic and pessimistic results might be expected. Additionally, as fixed input parameters (with and without DDG) were available from both length frequency and age-at-length data, it was possible to compare the resultant management performance of the two methods of growth estimation.

In more detail, the steps in the management simulation process are as follows (with and without DDG):

(i) MIDAS (the stock) is initialised for a certain degree of prior exploitation until the stock reaches an equilibrium state at that level of exploitation. Simulations were run for a range of starting fishing mortalities, to represent a range of states from lightly fished to over-exploited. Previous analysis indicated that for management of *L. mahsena* based on $F_{0.1}$, the optimum fishing mortality was 0.41 (Chapter 7). Simulations were also run with a range of F_{start} values about 0.4 (0.05, 0.25, 0.7 and 1.2yr^{-1}), chosen to represent the range of estimates of current fishing mortality across the three study fisheries.

(ii) Following initialisation of MIDAS, management simulations were run over a period of 20 years. MIDAS generates a number of annual outputs of the true population parameters (Table 8.1). These are the details that would not be known to the stock assessment specialist or fisheries manager. MIDAS also simulates catch true length frequency distribution. This output is known to the stock assessment specialist through the biological sampling programme. The management strategy simulation model uses the output length frequency data to determine current fishing mortality, as a stock assessment specialist would do, using one of two methods: a length converted catch curve, or the Beverton and Holt Z estimator (these methods are detailed in Chapter 4). In simulations, the length converted catch curve was used with age-based growth parameters, and the Beverton and Holt method for length-based growth parameters, as these methods were shown to give the most reliable results respectively (Chapter 7).

Table 8.1 A list of the relevant outputs from MIDAS used in assessment of the performance of fisheries management. These are the true population parameters, including fishing mortality (unknown to the stock assessment specialist), and the catch per annum.

Before Initialisation: Unexploited equilibrium states
- The unexploited biomass, ExBo;
- The unexploited spawning stock biomass, SSBo;

Time 0-20: Exploited equilibrium state for F_{start} :
- The exploited biomass each year, ExB;
- The spawning stock biomass each year, SSB;

- Total catch per annum
- Fishing mortality, F
- Length frequency distribution

(iii) In order to derive estimates of fishing mortality, and $F_{0.1}$ (i.e. F_{target}) fixed estimate input parameters for each F_{start} value (i.e. at year 0) are required. These were derived in step (a) outside the simulation model. Simulations were run using:

- growth parameters derived from length-based methods of assessment, and their corresponding estimates of mortality, Lc_{50}, and $F_{0.1.}$ The Pauly estimate of M and resulting $F_{0.1}$, were found to be most suitable for length-based data (see Chapter 7), and these values were applied in simulation studies;
- growth parameters derived from aging techniques applied to otoliths, from which, using length based methods, corresponding estimates of mortality, Lc_{50}, and $F_{0.1.}$ were derived. The Ralston estimate of M and resulting $F_{0.1}$, were found to be most suitable for length-at-age data (see Chapter 7), and these values were applied in simulation studies.

In order to take account of uncertainty in the estimation of growth parameters and corresponding biological reference points, each 20 year simulation run employed a different set of fixed input parameters, as derived in Chapter 7. Table 8.2 provides examples of the parameters used for each of the above. In total, 100 runs were performed for each 20 year simulation.

Table 8.2 Example of fixed input parameters for MIDAS derived using length frequency and length at age data (see Chapter 4) for each of the F_{start} values applied.

Assessment method	F_{start} (year 0)	Linf	K	t_0	M (Pauly)	M (Ralston)	Lc_{50}	$F_{0.1}$ (Pauly M)	$F_{0.1}$ (Ralston M)
Length	0.05	67.00	0.11	-0.50	0.33	0.24	21.90	0.26	0.18
Length	0.25	64.00	0.22	0.00	0.52	0.47	21.60	0.39	0.34
Length	0.70	50.00	0.15	-0.60	0.44	0.33	23.30	0.48	0.34
Length	1.20	46.00	0.30	-0.30	0.71	0.64	21.00	0.68	0.60
Age	0.05	49.00	0.16	-0.30	0.46	0.34	21.10	0.45	0.32
Age	0.25	53.00	0.13	-0.40	0.40	0.29	20.80	0.37	0.26
Age	0.70	75.00	0.09	-0.50	0.28	0.20	22.50	0.21	0.15
Age	1.20	72.00	0.10	-0.50	0.30	0.22	22.00	0.23	0.16

(iv) Management is based on estimates of current fishing effort. Fishing mortality was increased or decreased by a preset percentage each year, moving the current effort towards the target effort (i.e. $F_{0.1}$). Management rules are set in the simulation model which determine the new fishing mortality applied to the stock (i.e. to be fed back into MIDAS), *i.e* which adjust the true underlying F within MIDAS by the appropriate amount. Prior to running simulations to examine the specific objectives of this study, two different management rules were investigated :

- Knife edge selection (i.e. increase or decrease F to the target value immediately each year);
- A more realistic rule whereby fishing mortality increased or decreased by a preset percentage each year to meet the target F. Two scenarios were examined:
    - If current F< 0.8 x target F, actual F in MIDAS increased by 20% that year, otherwise actual F increased to target F ; If current F> 1.167 x target F, actual F in MIDAS decreased by 16.7% that year, otherwise actual F decreased to target F (see box 8.1 for explanation).
    - If current F< 0.6 x target F, actual F in MIDAS increased by 40% that year, otherwise actual F increased to target F ; If current F> 1.286 x target F, actual F in MIDAS decreased by 28.6% that year, otherwise actual F decreased to target F.

Box 8.1 Calculation of percentage changes in effort for management rules.

For the fixed percentage change rule, instead of increasing F by Y% if below the target and decreasing by the same Y% if above the target, it was considered to be more appropriate to increase by Y% if below the target, and to decrease by Z% if above the target, where

$$Z = 100 \times \left[\frac{Y}{100 + Y} \right]$$

i.e., if increasing by 20% if below the target, the equivalent would be to decrease by 16.7% if above the target. For example the opposite of doubling effort (Fx2) is halving it (F/2).

In performing the initial runs, it was found that the knife-edge rule was not appropriate. The reason for this was that, when using the length-based input parameters, frequently the Beverton & Holt Z estimator produced an estimate of Z that was less than that of natural mortality (M). This resulted in a negative estimate of current fishing pressure, which was ‘corrected’ by the management rule to a low value of F (0.0001). The knife-edge management rule called for an immediate increase or decrease to the target level. This was implemented by calculating the ratio of target F to current F, to give the appropriate conversion factor to feed back into MIDAS to give the next year’s fishing effort. However, for the extremely low values of current F that resulted where Z<M, the conversion factors were obviously inappropriately high.

Whilst modifications to this management rule could have been devised to handle these particular instances, it was noted that using the fixed percentage change rule with large percentages would be likely to give very similar results, and would be a more appropriate way of modelling this rule. The management rule was therefore applied for different percentage values (Y= 20 and 40).

A number of different simulations were performed for various scenarios (range of starting efforts, density dependent growth either on or off etc). Not all management rules were examined for each scenario, only those that were necessary to investigate the project objectives:

- Effect of uncertainty in growth estimation on management performance

  - Both age- and length-based growth parameter estimates were used. Density dependent growth was not operating. Management performance was examined at a range of Fstart values, using the sets of 100 input parameters which encapsulated the uncertainty in the growth parameters. Conclusions were drawn on the effect of uncertainty in growth parameter estimation on management performance by comparing outputs with those from simulations where perfect information was available. In these runs, the management rule was applied directly to the true underlying F in MIDAS, *i.e.* the value of the current F was taken to be the true F, and the management rule was applied to this value to determine the management action (see Section 8.3).

- Effect of fishing induced changes in growth on management performance
  - Both age- and length-based growth parameter estimates were used. However, within growth parameter estimation methods, results were compared where density dependent growth was either operating, or not operating. This was examined at high Fstart values only, since Chapter 5 indicated that density dependent growth only had a notable effect at such levels of fishing mortality. Conclusions were derived on the effect of DDG.

- Comparison of length vs age based methods
  - The results of the use of age- and length-based growth parameter estimation methods were explicitly compared. In these runs, density dependent growth was not operating. Comparisons were made at a range of Fstart values.

8.2.3 Measurement of management success

The study evaluated management performance by analysing four chosen performance measures: two stock conservation measures and two fleet performance measures (see below). Histograms of these outputs for each performance measure were produced.

Conservation measures:

- Final year ExB/ExB_0: the ratio of final year (in year 20) exploitable biomass to unexploited biomass. This measure gives an indication of the probability of stock collapse. From MIDAS outputs at F_{MSY}, the optimum ratio was 0.422. Values greater than this indicate that the fishery was under exploited, and less than this that it was over exploited.

- The frequency over the entire 20 year period that spawning stock biomass (SSB) dropped below 20% of unexploited SSB[3]. Optimally this would never occur since at $F_{0.1}$ for *L. mahsena* with the population parameters used, the SSB is 21% of initial levels (but see Section 8.4). In the current simulations, high frequencies of high values suggest that the SSB fell below sustainable levels frequently and therefore there was danger of recruitment overfishing. High frequencies of low values suggest that the SSB was within sustainable levels for the majority of the simulated period, and that the probability of recruitment overfishing was low.

Fleet performance

- Final year effort: the frequency with which the simulation model reached the optimum final year F (in year 20) of 0.4 (as the true value of the target F, $F_{0.1,}$ is 0.41). Values greater than 0.4 suggest the final effort applied was too high and that overcapitalisation has occurred leading to likely over exploitation. Below that value, effort is too low and the resource will be under exploited.

---

[3] Mace and Sissenwine (1993) and Mace (1994) suggested that spawning stock biomass should not be allowed to fall below 20% and 30% of the initial biomass for stocks with average resilience to overfishing, and for little known stocks respectively.

- Average catch: in order to compare the success of different scenarios, histograms of the average catch removed each year were plotted. This can be compared to the MSY value of 75 (units).

These measures enable the success of management measures for each scenario examined to be determined independently. Furthermore, to help explain the performance of management measures, histograms of the values of target F. i.e. the $F_{0.1}$ values input into MIDAS for each run of 20 years (100 in total) were plotted where necessary.

8.3. RESULTS

As stated, the objectives of the management strategy simulations were to investigate:

(i) The effect of uncertainty in growth parameter estimation on management performance;
(ii) The effect of fishing induced changes in growth rate on management performance;
(iii) The differences in management performance between age and length based methods of growth assessment.

In each case, conclusions were drawn on management performance based on information derived from stocks fished at a range of fishing intensities. These represented lightly exploited stocks such as those at Chagos, through to heavily fished stocks, such as those at the Mauritian Banks.

For objectives (i) and (iii), conclusions were derived from simulations of the fish stock without density dependent growth (DDG) operating. For objective (ii), conclusions were derived by comparing simulations without DDG against those with DDG.

8.3.1 Effect of uncertainty in growth estimation on management performance

As described, the effect of uncertainty in growth parameter estimates was interpreted through an examination of management performance using sets of input parameters which encapsulated the degree of variability and uncertainty in growth parameter estimation, and thus in subsequent biological reference point estimation. Management performance was evaluated using the four measures described (Section 8.2.3):

(1) the final year exploitable biomass (ExB) as ratio of unexploited (ExB_0);
(2) the number of years that spawning stock biomass (SSB) fell below 20% of unexploited (SSB_0);
(3) final year F; and
(4) average catch over the 20 year simulation period.

As described in Section 8.2.3, each performance measure had an optimum value, and the effect of uncertainty in growth parameter estimates was determined by investigating the performance of each measure relative to this optimum, *i.e.* the frequency of achieving the optimum, and the range of variability in each measure.

In a perfect situation, that is with perfect information and no variability in growth or recruitment, the optimum value for each performance measure would be achieved in every simulation. As a result of recruitment and growth variability, however, even where perfect information on growth was available, variability in management performance around the optimum would result. This was demonstrated by running simulations using the true values of current fishing mortality in each year, and the true value of $F_{0.1}$. These runs only allowed for recruitment variability, not variability in growth, as input parameters and simulated length-frequencies were not used to estimate current fishing mortality. Comparing the results of these simulations with those using estimates of current fishing mortality therefore shows the degree of worsening of management performance that resulted from the effect of uncertainty and variability in the growth parameter estimates on the estimates of current fishing mortality and $F_{0.1}$.

The effect of uncertainty was investigated assuming density dependent growth was not operating. The fixed percentage management rule was applied, where effort was increased by 20% if below the target effort level, and decreased by 16.7% if above, as described in Section 8.2.2.

In the following subsections, each performance measure is considered in turn. For each, histograms of the frequency distributions of that measure were produced, for different values of Fstart. The *x*-axes of the histograms show the midpoint of the frequency distribution, selected to be appropriate for each indicator in order that the optimum value for that indicator is at a midpoint of a bin. For example for the final year F the bin size is *e.g.* 0.35-0.45, with midpoint 0.4; for average catch the bin size is eg 70-80, with midpoint 75.

8.3.1.1 Final year exploitable biomass

As stated, the optimum value of this ratio is the value at equilibrium maximum sustainable yield, 0.4, and ideally there would be a narrow range of outcomes about this value. As can be seen in Figure 8.3, for the length-based inputs, there is a high level of variability about this value for all starting efforts, ranging from 0.3-1.2 for a starting effort of F=0.05, to 0-0.9 for a starting effort of F=1.2. For the lower two starting efforts, histograms show that the stock is under-exploited (for example, for Fstart=0.05 the mode of the frequency distribution is at 0.8, *i.e.* the stock has only been reduced to 80% of unexploited biomass), whereas for the higher two starting efforts, the stock is tending towards over-exploitation (mode = 0.4 but the distribution is skewed to the left for Fstart=1.2).

For the age-based inputs, there is a similarly high level of variability in the outcomes (Figure 8.4), from 0.2-1.1 for Fstart=0.05, to 0.5-1.2 for Fstart=1.2. For the lowest starting effort of F=0.05, the results show slight under-exploitation, as the mode of the distribution of ExB/ExB_0 is at 0.5. As the starting effort increases, the degree of under-exploitation increases, with the mode of the distribution at 0.8 for Fstart=1.2.

The runs performed using the true values of current effort and $F_{0.1}$ (Figure 8.5) still show a degree of variability of outcomes, although a slightly narrower range of values than either the length or age-based inputs. For example, for Fstart = 0.05, these runs give final year ExB/ExB_0s ranging from 0.3-1.0, compared to 0.3-1.2 for length-based and 0.2-1.0 for age-based inputs. However, the modes of the distributions remain closer to the optimum of 0.4 across the range of starting efforts, and the proportion of times that the optimum is achieved is greater than for either length- or age-based inputs, again across the range of starting efforts. For these runs, the optimum of 0.4 is achieved for a minimum of 21% of runs (Fstart = 0.7), and up to 29% of runs for Fstart = 1.2. In comparison, the optimum is achieved for a maximum of 28% of runs for length-based inputs (Fstart = 1.2), but only 3% of runs for Fstart = 0.05. For age-based, the optimum is achieved between 0% of runs (Fstart = 1.2) and 23% of runs (Fstart = 0.05).

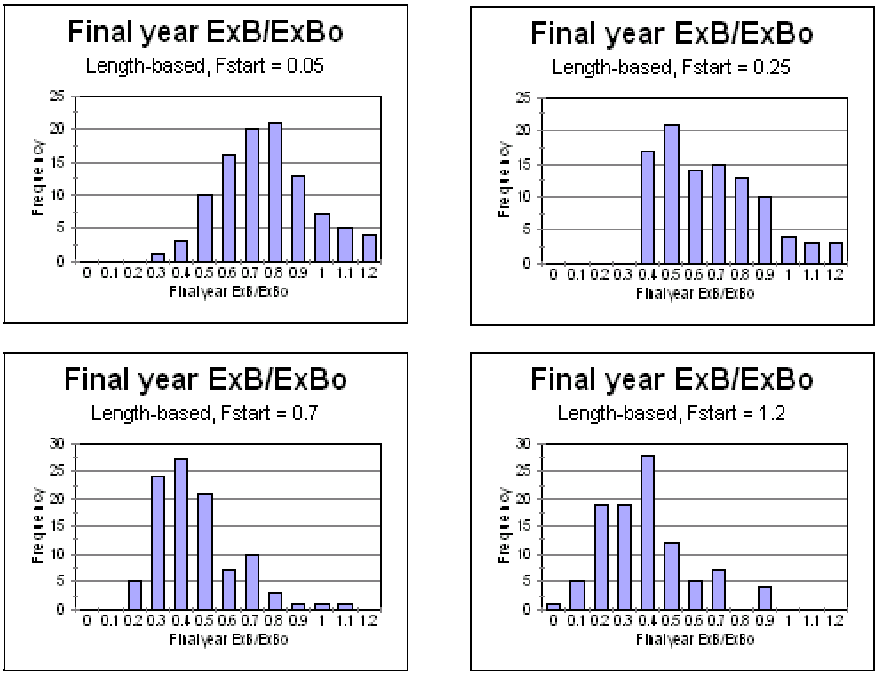


Figure 8.3 Histograms of final year ExB/ExB$_0$ for length-based inputs for all Fstarts, density dependent growth not operating.

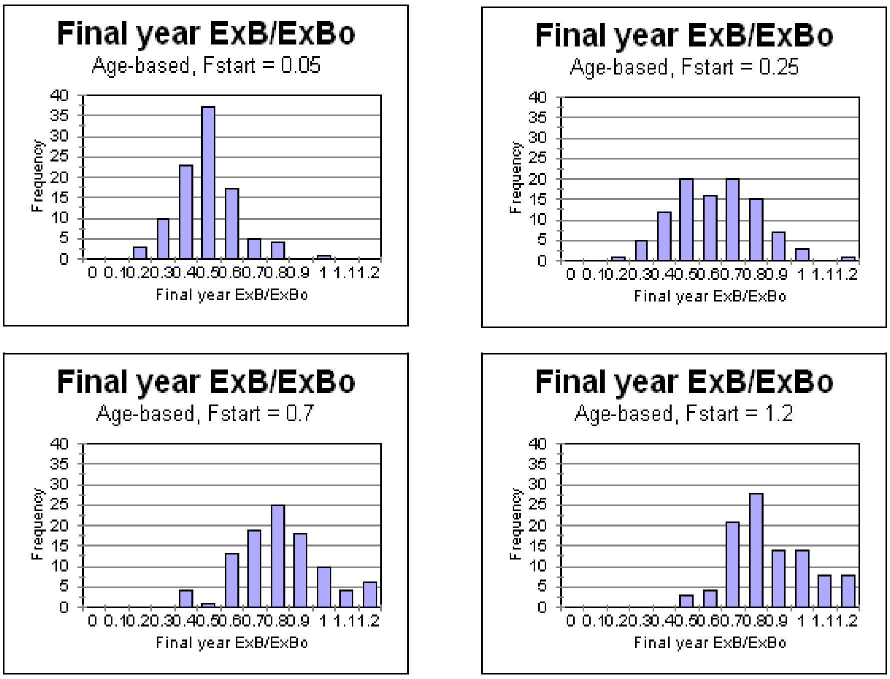


Figure 8.4 Histograms of final year ExB/ExB$_0$ for age-based inputs for all Fstarts, density dependent growth not operating.

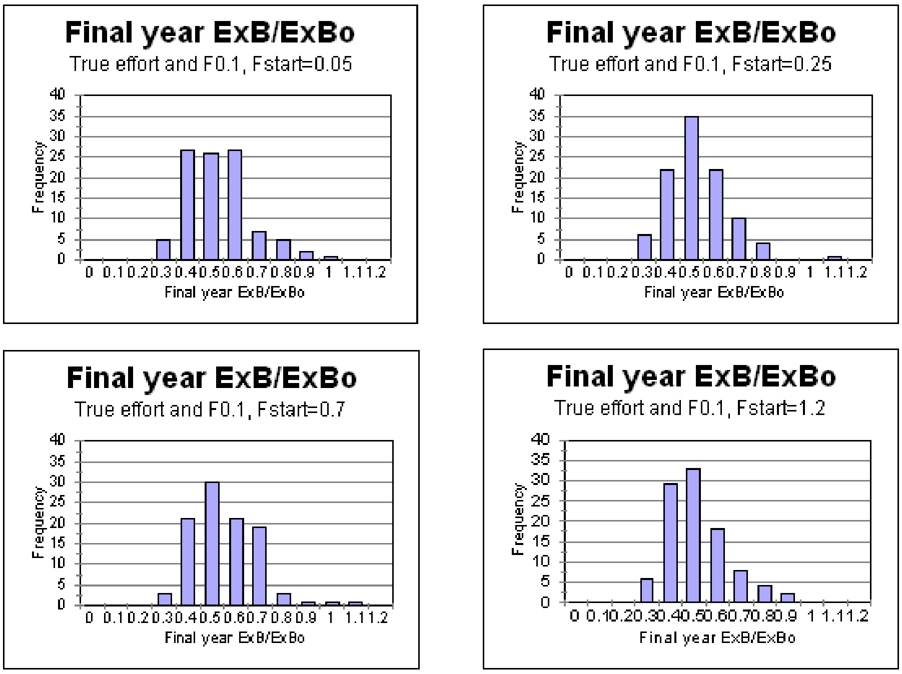


Figure 8.5 Histograms of final year ExB/ExB$_0$ for true current F and F$_{0.1}$, for all Fstarts, density dependent growth not operating.

8.3.1.2 Spawning stock biomass

Optimally, the spawning stock biomass (SSB) would not be reduced to below 20% of the unexploited level for any of the twenty years of the simulation period (but see Section 8.4). For the length-based input parameter simulations (Figure 8.6), good management performance was achieved for the lowest starting effort of 0.05, with SSB remaining above 20% of unexploited in all years in 94% of the runs. However, with increasing starting effort, performance deteriorated substantially, with SSB being reduced to below 20% in all years of the simulation period for 42% of runs for Fstart=0.7, and for 66% of runs for Fstart=1.2.

For the age-based input parameters (Figure 8.7), management was poor at the lowest starting effort of 0.05, with SSB being reduced to below 20% of unexploited for 6 years of the simulation period in 47% of the runs. Increasing starting effort led to a slight deterioration in performance, with 10 years of the simulation period having SSB less than 20% of unexploited for 56% of the runs, for a starting effort of 1.2.

The runs using true effort and F$_{0.1}$ (Figure 8.8) did not perform as well as length-based inputs but better than age-based for the two lower starting efforts. For example, at Fstart = 0.05, the true effort runs had 23% of runs where SSB never fell below the threshold value, compared to 94% for length-based, but only 12% for age-based inputs. At the highest starting efforts, the true effort runs performed better than the length-based inputs, but not as well as the age-based ones.

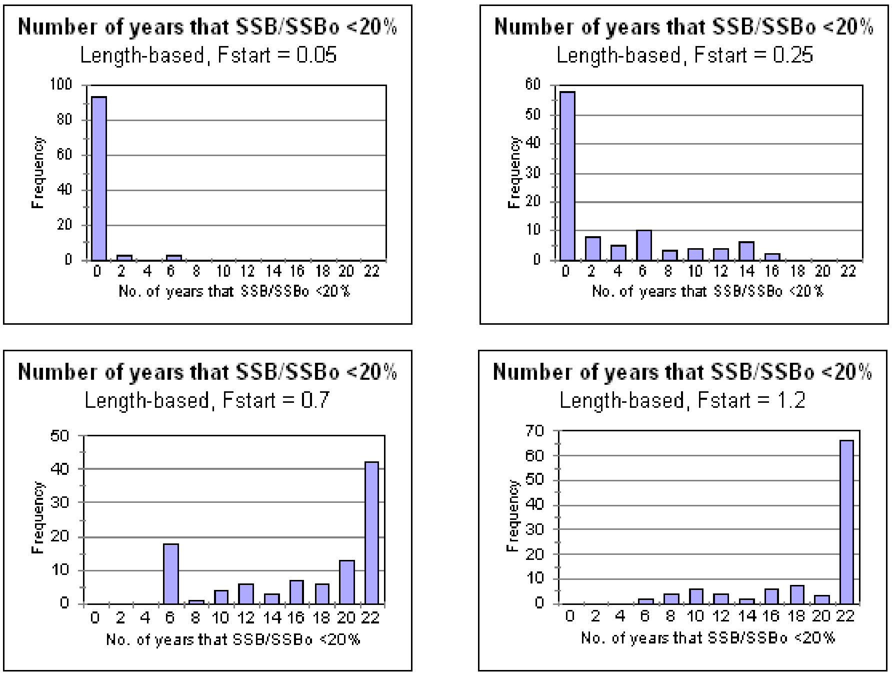


Figure 8.6 Histograms of the number of years that $SSB/SSB_0 < 20\%$, for length-based inputs for all Fstarts. Density dependent growth not operating.

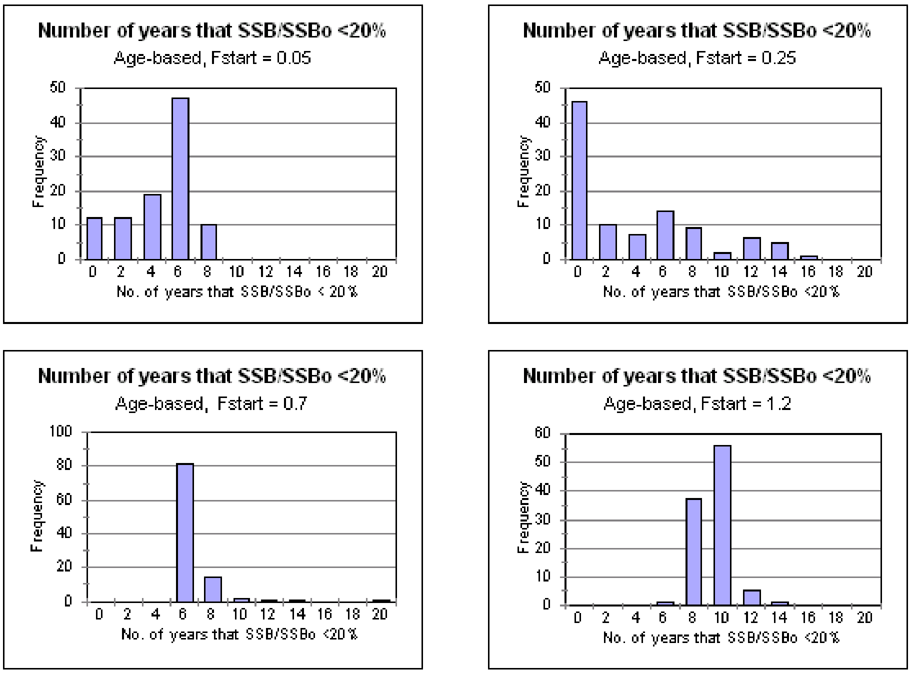
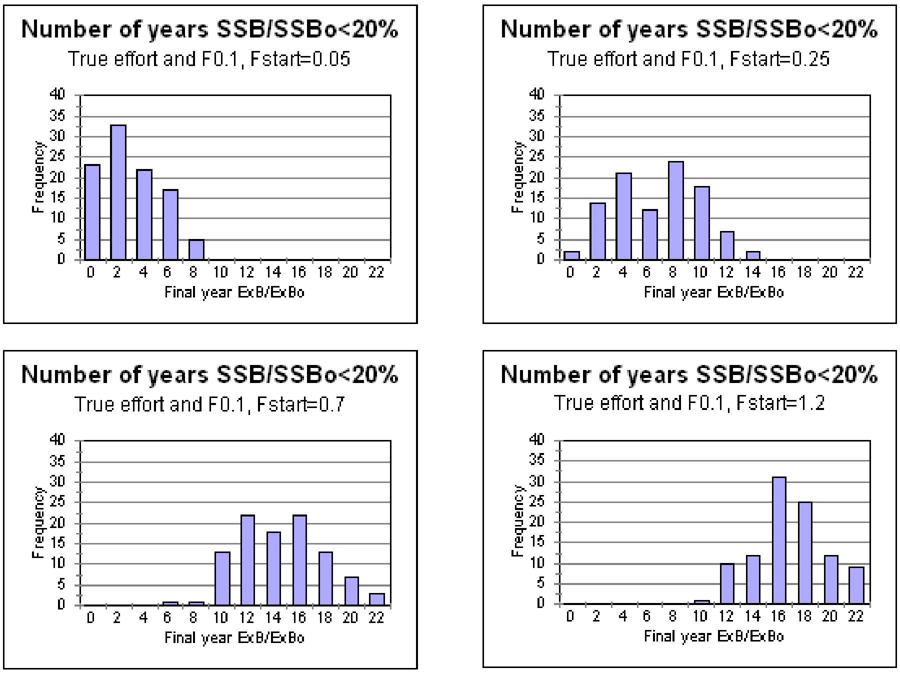


Figure 8.7 Histograms of the number of years that $SSB/SSB_0 < 20\%$, for age-based inputs for all Fstarts. Density dependent growth not operating.



Number of years SSB/SSBo<20%
True effort and F0.1, Fstart=0.05

Number of years SSB/SSBo<20%
True effort and F0.1, Fstart=0.25

Number of years SSB/SSBo<20%
True effort and F0.1, Fstart=0.7

Number of years SSB/SSBo<20%
True effort and F0.1, Fstart=1.2

Figure 8.8 Histograms of the number of years that $SSB/SSB_0 < 20\%$, for true current F and $F_{0.1}$, for all Fstarts. Density dependent growth not operating.

8.3.1.3 Final year effort

The optimum value of the final year fishing effort is the target effort level $F_{0.1}$, for which the true value is 0.4 (0.41). After 20 years of simulated management, it would have been expected that the current fishing effort would be close to this value. Figures 8.9 and 8.10 show the results for the length- and age-based input parameters respectively.

For the length-based input parameters (Figure 8.9), the lowest starting effort of 0.05 shows a narrow range of outcomes, 0.1-0.5, but only achieves the optimum value of 0.4 in 3% of runs, whereas a final year F of 0.1 occurs in 77% of runs, suggesting that the stock will be underexploited. As starting effort increases, the range of values of outcomes increases, and the distributions become more even. For example, for a starting effort of 1.2, final year Fs between 0.1-1.2 are achieved, with modes at 0.6 and 1.2, but the other values fairly equally distributed.

The age-based input parameters (Figure 8.10) show an opposite trend, with the widest spread of outcomes at the lower starting efforts (for example, from 0.1 to 1.0 for Fstart = 0.05). The optimum of 0.4 is achieved for 25% of runs for Fstart =0.05, and for 9% of runs for Fstart = 0.25. For the two higher starting efforts, the range is much smaller, but in both cases the mode of the distribution is at 0.1 (in 79% of runs for Fstart = 0.7, and 97% of runs for Fstart = 1.2), suggesting under-exploitation of the stock.

For the simulation runs using the true values of current effort each year, and the true value of $F_{0.1}$, the target effort level is obviously reached by the final year of simulation in each run, thus these histograms are not shown. In fact, the greatest number of years taken to reach $F_{0.1}$ is 13 years, for a starting effort of 0.05.

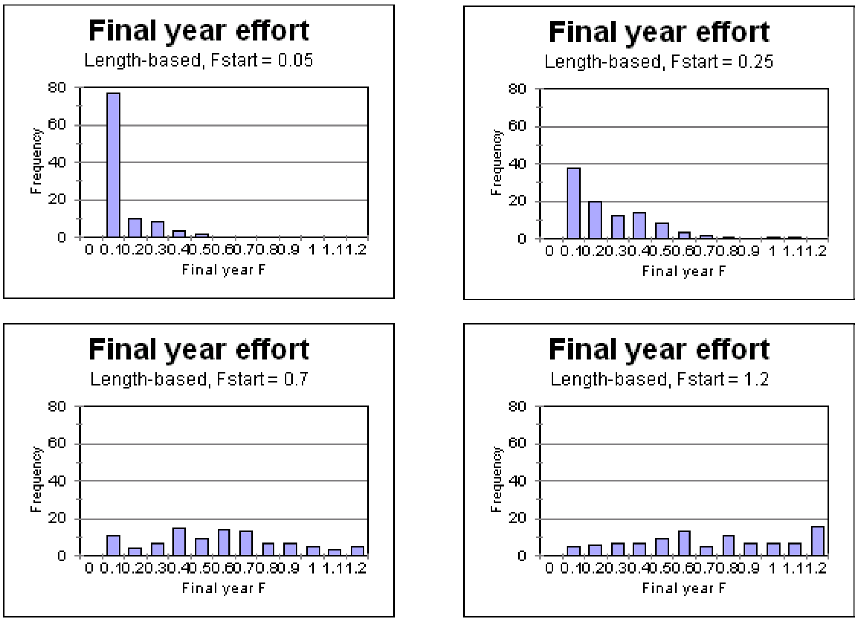


Figure 8.9 Histograms of final year effort for length-based inputs for all Fstarts. Density dependent growth not operating.

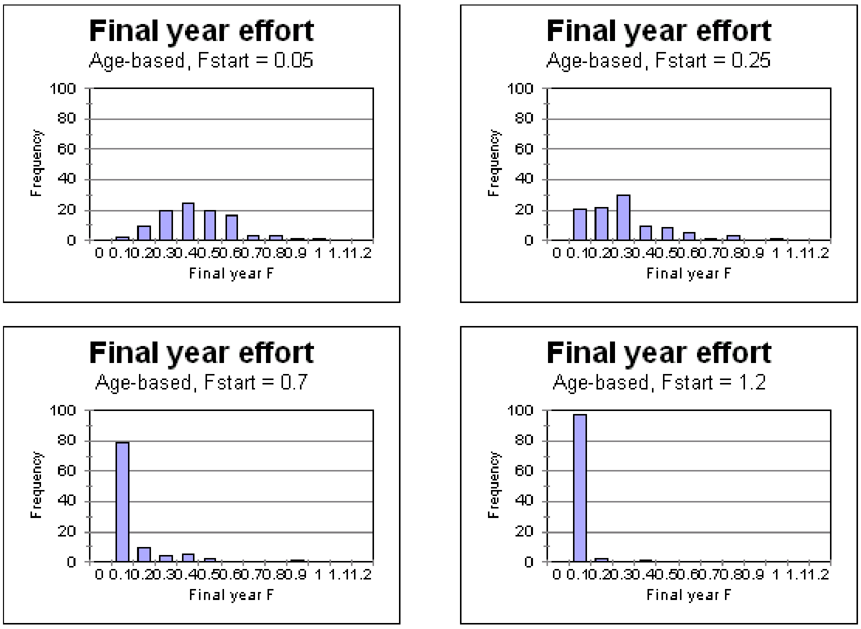


Figure 8.10 Histograms of final year effort for age-based inputs for all Fstarts. Density dependent growth not operating.

8.3.1.4 Average catch

The average catch per year for each simulation can be compared to the optimal value, which by definition is the value of the maximum sustainable yield (MSY; from MIDAS outputs, MSY=75 units). Figures 8.11 and 8.12 show the average catch per year for each starting effort for both length-based and age-based input parameters respectively. It can be seen that in each case, the outcomes are a wide range of values about the optimum, MSY, except in the case of the two higher starting efforts for the age-based input parameters, where the average catch is below 75 in virtually all runs, the mode being at 35 in both cases, and for length-based inputs at Fstart = 0.05, where again the average catch is below 75 (mode at 25). For the length-based inputs, catches tend to increase with increasing starting effort, whereas the opposite is true for age-based.

Figure 8.13 shows the results from runs using true effort. In general, there is a narrower range of outcomes than for length-based inputs, for all starting efforts, but not such an improvement on the range of outcomes when compared to age-based inputs. However, for all starting efforts, the distribution of average catch when using the true effort remains much closer to the optimum value of 75 units (the modes of the distributions are between 55-75 for the different starting efforts).

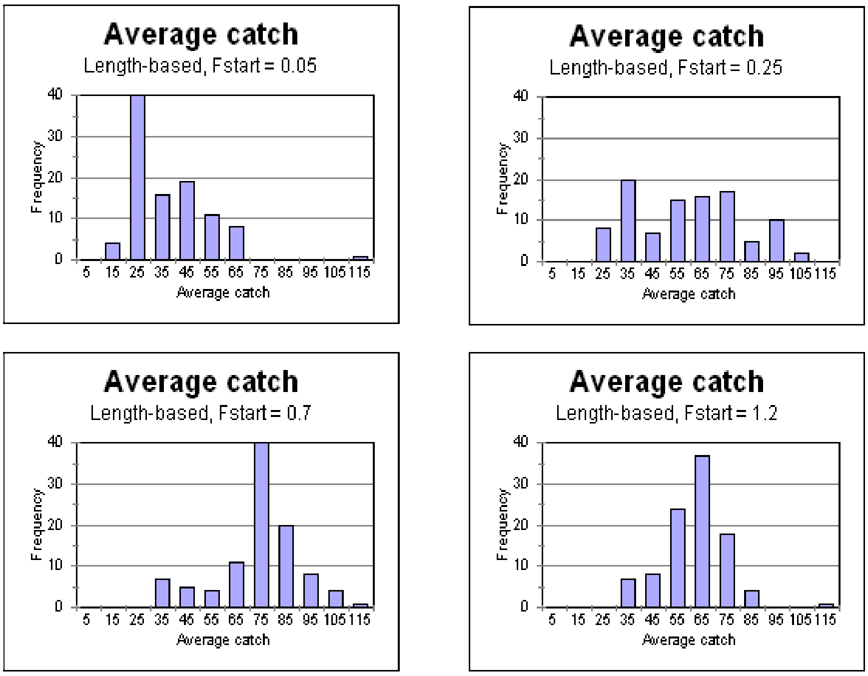


Figure 8.11 Histograms of average catch for length-based inputs for all Fstarts. Density dependent growth not operating.

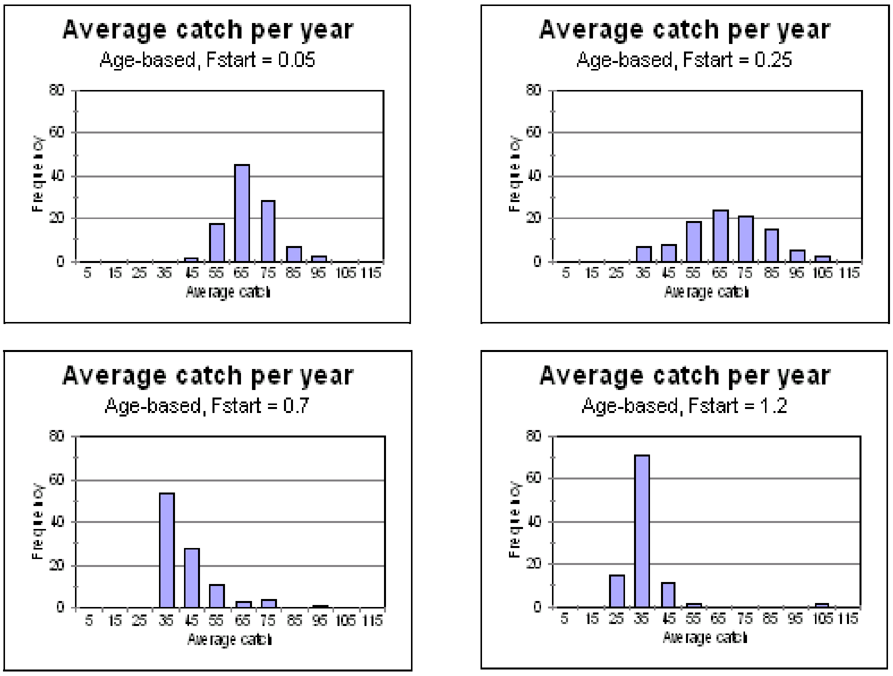


Figure 8.12 Histograms of average catch for age-based inputs for all Fstarts. Density dependent growth not operating.

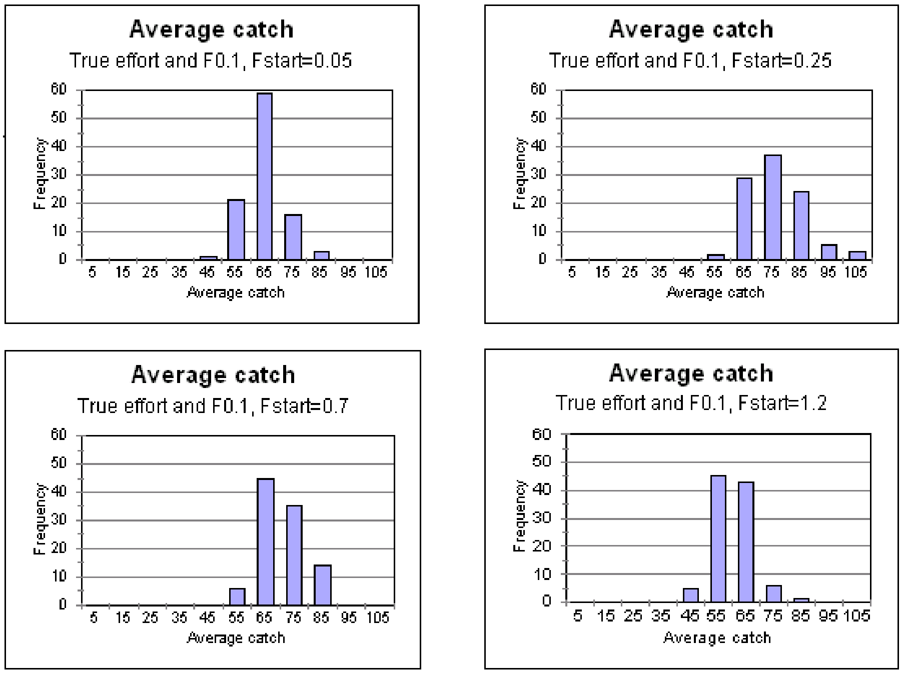


Figure 8.13 Histograms of average catch for true current F and $F_{0.1}$, for all Fstarts. Density dependent growth not operating.

8.3.1.5 Conclusions on effects of uncertainties in growth parameter estimates.

For both the length-based and age-based input parameters, management performance is poor: the different performance measures have in general shown a great degree of variability in outcomes, and the optimum value for each measure is often achieved in only a low proportion of the runs.

When comparing these runs with those using the true effort and true value of $F_{0.1}$, management performance worsens when using either length- or age-based growth parameter estimates to derive estimates of current effort and $F_{0.1}$. This is shown most clearly for the final year effort performance measure, where using the true effort values results in the optimum being achieved by the final year in every run. The poor management performance for the age- and length-based inputs is therefore clearly entirely due to the uncertainties and variability in growth parameter estimates. The final year ExB/ExB_0 and average catch showed worse performance when using length- or age-based inputs, which resulted in a slightly wider spread of outcomes, and lower frequencies of achieving the optimum value in each case. However, spawning stock biomass did not indicate any consistent improvements over age- or length-based inputs, as compared to using the true effort and $F_{0.1}$

Thus it is concluded that uncertainty and variability in growth parameter estimation led to poor management performance for both length-based and age-based inputs.

At this stage it does not appear that either length-based or age-based inputs perform substantially better than the other. However, as has been noted from the final year ExB/ExB_0 performance measure (Section 8.3.1.1), the age-based inputs appeared to result in under-exploitation for all starting efforts, whereas the length-based inputs resulted in under-exploitation at the lower starting efforts, and tended towards over-exploitation at the higher starting efforts. It is therefore not appropriate to compare the performance of length-based and age-based inputs directly without tuning each to perform optimally. This tuning process, and the resultant comparison is described in Section 8.3.3.

8.3.2 Effect of fishing-induced changes in growth rates on management performance

The second objective of the management strategy simulations was to determine to what extent fishing-induced changes in growth rates affect our ability to manage the resource. Such changes in growth rate are controlled in the simulation model through the density dependent growth component. Thus to determine the effect, comparisons are made between the outputs of simulations with and without density dependent growth operating. As described in Chapter 5, density dependent effects only become apparent at higher fishing efforts, and thus the comparisons are only made for the two higher starting efforts of F=0.7 and 1.2. It was noted that results were similar whether density dependence was operating in L_∞ or K. This was expected, since no noticeable differences in growth parameter estimates (Chapter 7) or yield effort curves (Chapter 5) were observed where density dependence was operating in either L_∞ or K. Thus only the results of runs with density dependence operating in L_∞ are presented. Again, each performance measure is considered in turn.

8.3.2.1 Final year exploitable biomass

Figures 8.14 and 8.15 show the distributions of final year exploitable biomass as a proportion of the unexploited level for length-based and age-based inputs respectively, (Fstart = 0.7 and 1.2), with both no density dependence and for density dependence operating in L_∞.

For length-based inputs, where density dependent growth is not operating, distributions of final year ExB/ExB_0 show a tendency towards overexploitation (Section 8.3.1.1). The degree of overexploitation is severely exacerbated when density dependence is operating (Figure 8.14). For example, for a starting effort of 1.2, with no density dependent growth, the mode of the distribution is at 0.4 (and occurs in 28% of the runs), whereas with density dependence, the mode is at 0.2 (occurring in 26% of the runs).

For age-based inputs (Figure 8.15), without density dependence the stocks are underexploited at high starting efforts. However, density dependent growth again causes overexploitation (for example, for Fstart = 1.2, without density dependence the mode is at 0.8, occurring in 28% of runs, with density dependence the mode is at 0.2, occurring in 34% of runs).

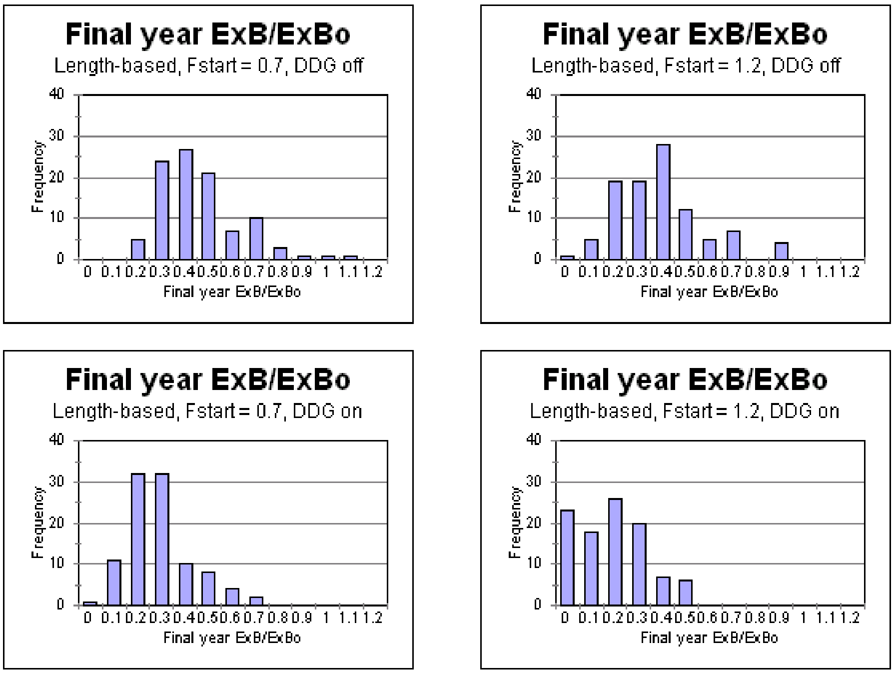


Figure 8.14 Histograms of final year ExB/ExB_0 for length-based inputs for Fstart = 0.7 and 1.2, without and with density dependent growth operating in L_∞.

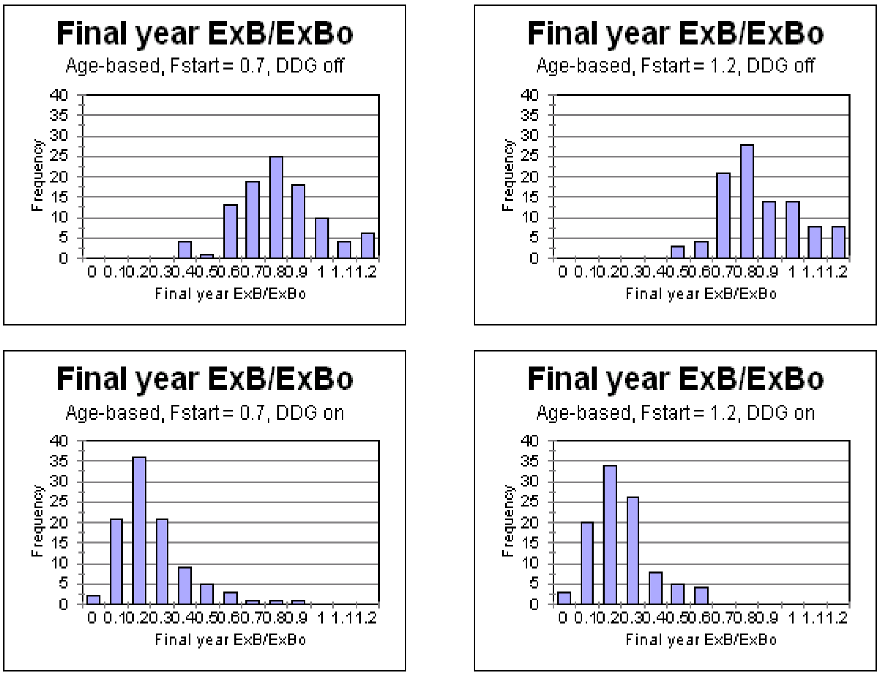


Figure 8.15 Histograms of final year ExB/ExB$_0$ for age-based inputs for Fstart = 0.7 and 1.2, without and with density dependent growth operating in L_∞.

8.3.2.2 Spawning stock biomass

Figures 8.16 and 8.17 show the distributions of the number of years that spawning stock biomass fell below 20% of the unexploited level. This is presented, for length-based and age-based growth inputs respectively (Fstart = 0.7 and 1.2), for both no density dependence, and density dependence operating in L_∞.

As in Section 8.3.1.2, the spawning stock conservation measure performs poorly for the length-based inputs at high starting efforts where density dependence is not operating. For example, 42% of runs have 20 years where spawning stock is reduced to below 20% of unexploited for a starting effort of 0.7. Where density dependent growth is operating, performance is improved, with a reduced number of years where the spawning stock is below 20%. For example, for a starting effort of 0.7, in no runs is the spawning stock reduced below 20% in all 20 years of simulation.

For the age-based inputs, the opposite pattern occurs. Where density dependent growth is operating, management performance is worsened (Figure 8.17). For example, for a starting effort of 0.7, with no density dependence, spawning stock biomass is reduced to below 20% of unexploited levels for 6 years in 81% of runs. With density dependent effects operating, the reduction in spawning stock biomass occurs for 16 years in 44% of the runs.

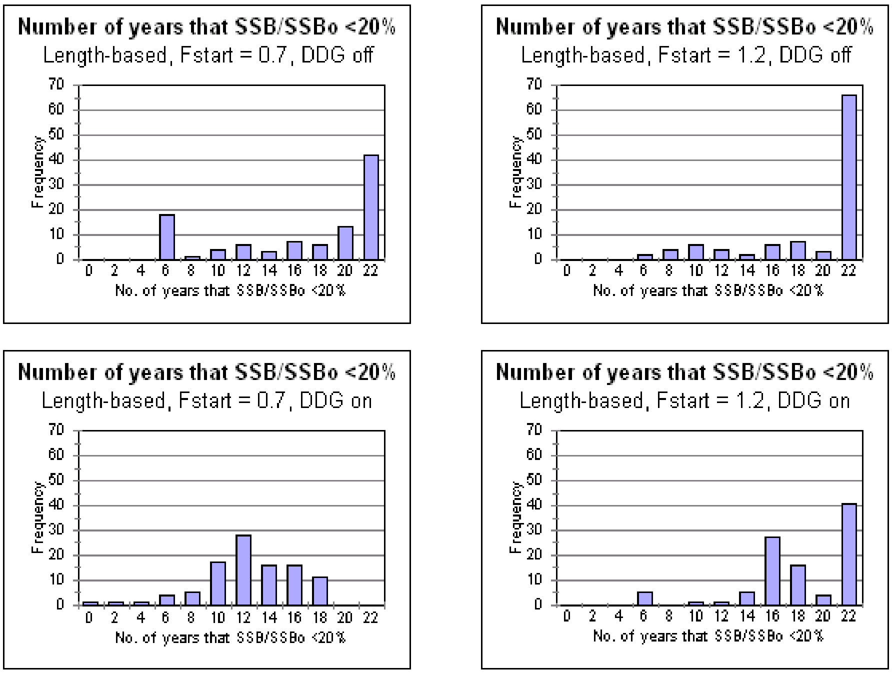


Figure 8.16 Histograms of the number of years that SSB/SSB$_0$ < 20% for length-based inputs for Fstart = 0.7 and 1.2, without and with density dependent growth operating in L$_\infty$.

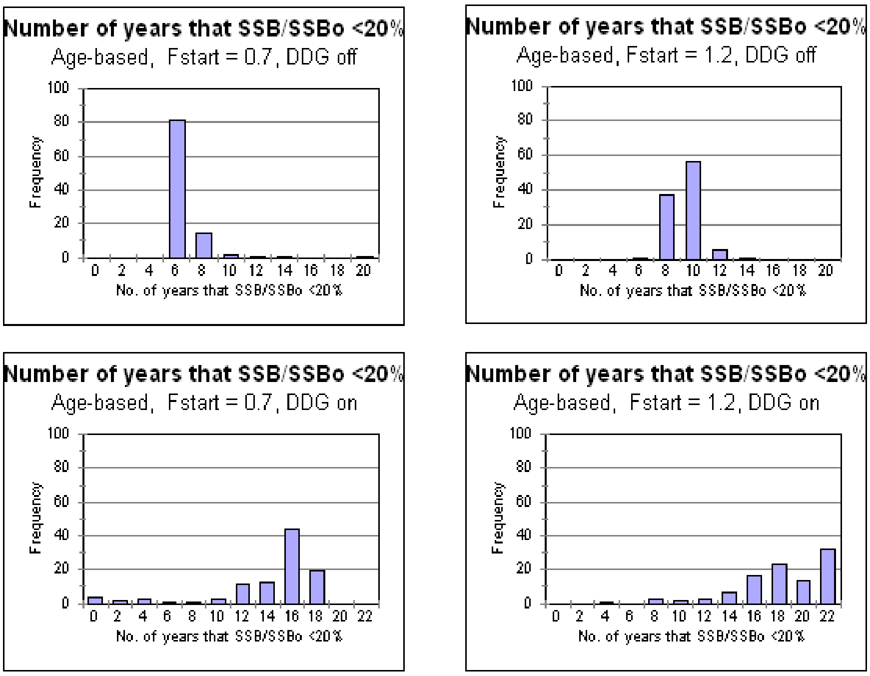


Figure 8.17 Histograms of the number of years that SSB/SSB$_0$ < 20% for age-based inputs for Fstart = 0.7 and 1.2, without and with density dependent growth operating in L$_\infty$.

8.3.2.3 Final year effort

The distributions for final year effort, with and without density dependent growth operating, for the two higher starting efforts, are shown in Figures 8.18 and 8.19 (for both length-based and age-based inputs respectively).

Length-based growth inputs show a dramatic increase in the value of final year effort with density dependent growth operating, as compared to the situation without (Figure 8.18). For a starting effort of 0.7, without density dependent growth operating, the distribution of final year efforts was fairly uniform between the range 0.1-1.2. With density dependence operating, however, final year effort was more normally distributed between 0.5-5.0, with the mode at 2.5. Age-based inputs (Figure 8.19) resulted in a similar increase in final year effort with density dependent growth operating.

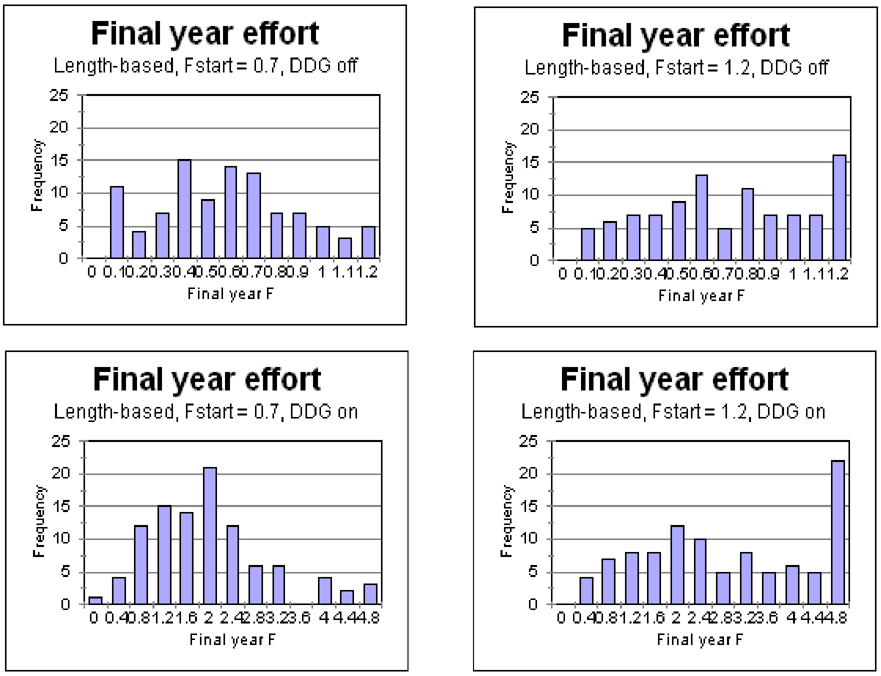


Figure 8.18 Histograms of final year effort for length-based inputs for Fstart = 0.7 and 1.2, without and with density dependent growth operating in L_∞.

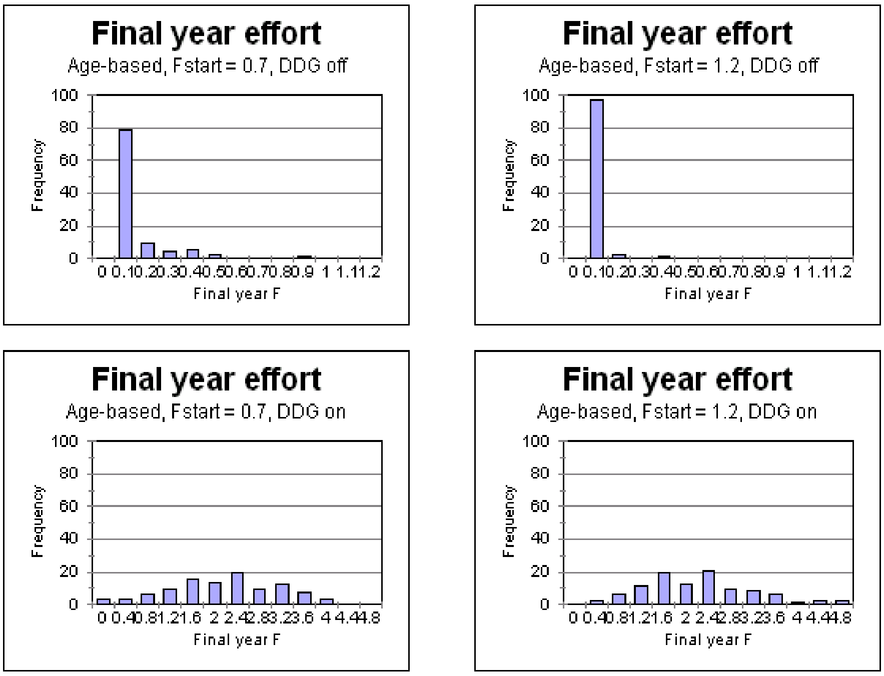


Figure 8.19 Histograms of final year effort for age-based inputs for Fstart = 0.7 and 1.2, without and with density dependent growth operating in L_∞.

8.3.2.4 Average catch

The distribution of average catches, resulting from length- and age-based growth inputs with and without density dependent growth operating are shown in Figures 8.20 and 8.21 respectively (for the two higher starting efforts). In both cases, density dependent growth resulted in substantially higher average catches. For example, using age-based inputs and an Fstart of 0.7, the mode of the distribution of average catch was 165 with density dependence operating, compared to 35 without density dependent growth.

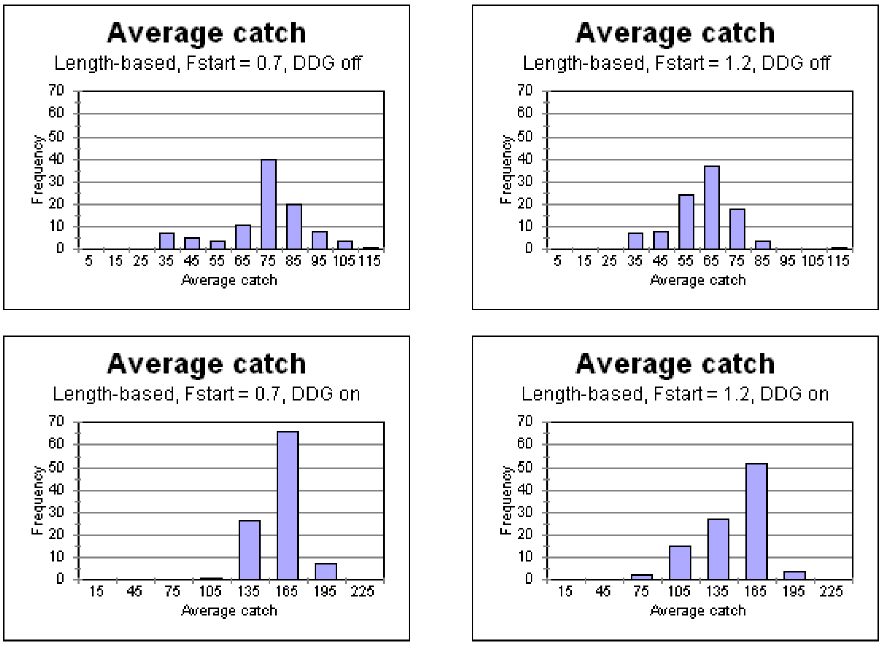


Figure 8.20 Histograms of average catch for length-based inputs for Fstart = 0.7 and 1.2, without and with density dependent growth operating in L_∞.

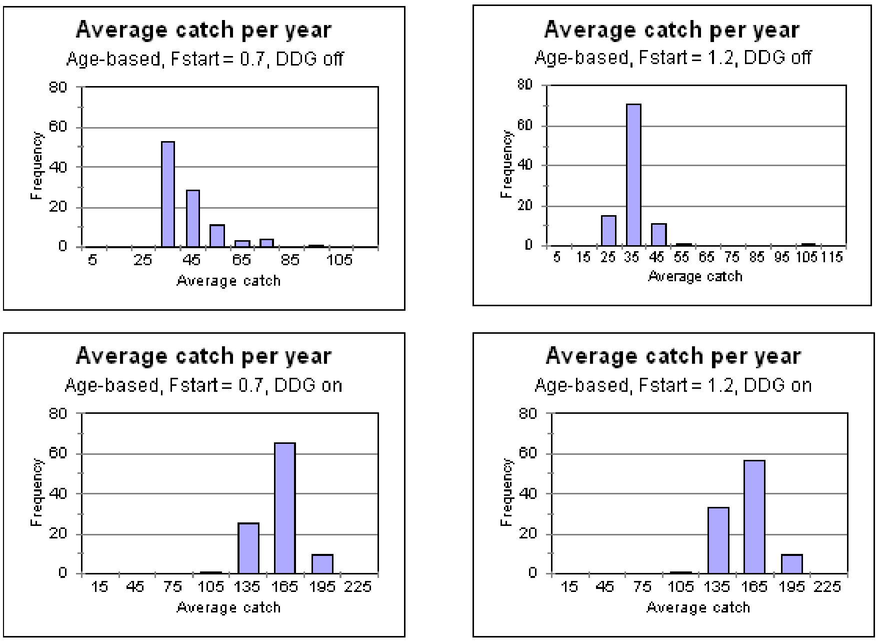


Figure 8.21 Histograms of average catch for age-based inputs for Fstart = 0.7 and 1.2, without and with density dependent growth operating in L_∞.

8.3.2.5 Conclusions on the effects of fishing-induced changes in growth rate on management performance

The results show that management performance is substantially worse where density dependent growth is operating, regardless of the growth parameter estimates used. The only exception to this was that density dependence improved the performance of the spawning stock measure for length-based inputs. This is not surprising, as the managed stock was over-exploited where density dependent growth was not operating; faster growth due to density dependent effects will result in fish reaching maturity earlier. The same effect was not seen for age-based inputs however, most likely due to the stock being under-exploited without density dependent growth occurring, but over-exploited if density dependent effects did operate.

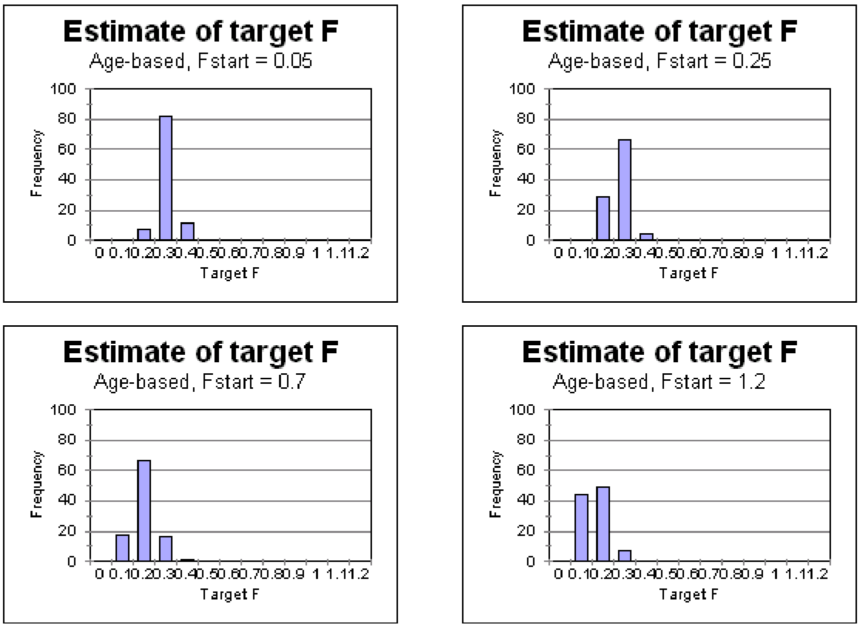
Density dependent growth also increased average catches. However, the distribution of final year effort indicates that these catches are clearly unlikely to be sustainable.

8.3.3 Comparing relative performances of length-based and age-based input parameters

8.3.3.1 Tuning of both age-based and length-based inputs

As already mentioned in Section 8.3.1.5, it was considered that a direct comparison of the relative performance of length-based and age-based input parameters could not be made. Distributions of final year ExB/ExB_o indicated that the use of age-based inputs consistently led to under-exploitation for all starting efforts (Figure 8.4), whereas the length-based inputs led to under-exploitation for the two lower starting efforts, but tended towards overexploitation for the two higher starting efforts (Figure 8.3). Tuning was therefore required to ensure the use of either growth parameter estimate resulted in optimum performance.

Histograms of the target effort levels, that is estimates of $F_{0.1}$ input into the model, were plotted in order to examine this (Figures 8.22 and 8.23 for age- and length-based inputs respectively). It was clear that, for all starting efforts, estimates of target effort were too low for the age-based inputs. In fact, this should have been expected from the results of Chapter 7, where it was found that $F_{0.1}$ was generally underestimated when using both length- and age-based growth parameter estimates. For length-based inputs, it appeared that estimates were closer to being correct, and that there was no consistent pattern of under- or overexploitation across the range of starting efforts.



Estimate of target F
Age-based, Fstart = 0.05

Estimate of target F
Age-based, Fstart = 0.25

Estimate of target F
Age-based, Fstart = 0.7

Estimate of target F
Age-based, Fstart = 1.2

Figure 8.22 Histograms of estimates of target F ($F_{0.1}$) for age-based inputs, for all Fstarts, no density dependent growth operating.

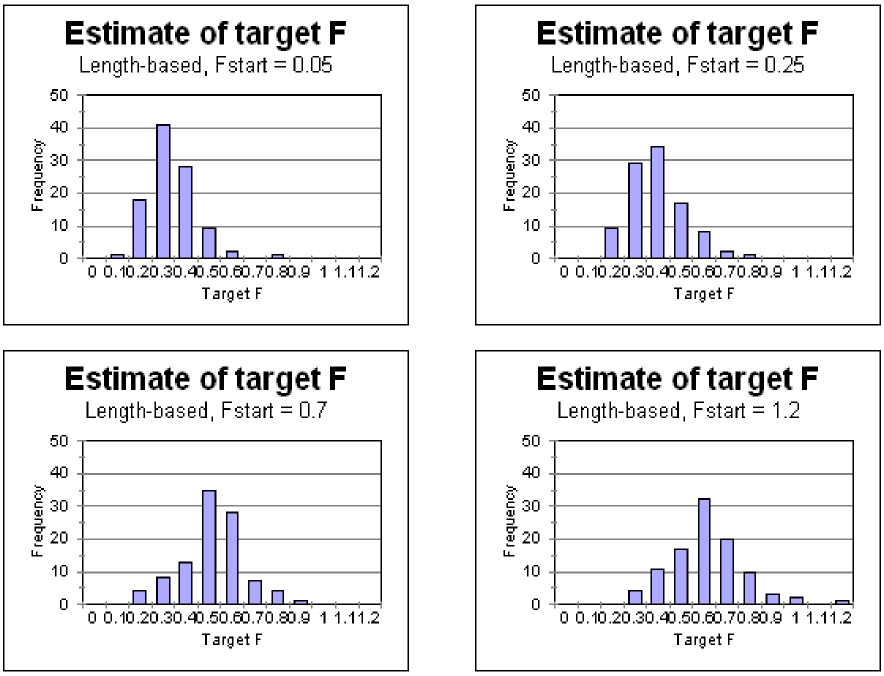


Figure 8.23 Histograms of estimates of target F ($F_{0.1}$) for length-based inputs, for all Fstarts, no density dependent growth.

Thus it was decided to determine a suitable multiplying factor for raising the estimates of target effort such that management resulted in exploitation at a more suitable level. In this study, tuning optimised management for an average final year effort of 0.41 (the optimal value).

A range of values of multiplying factor were investigated (only using a starting effort of 0.4, which is the optimum effort level, to minimise computer simulation time), as given in Table 8.3, together with a summary of the results. Given the non-linear relationship between raising factor and average final year effort (Figure 8.24), a range of likely values was first investigated, and then iterative methods were used to give an average final year effort close to 0.41. It should be noted that different multiplying factors were required for length-based and age-based growth inputs, due to the more substantial underexploitation arising from the age-based inputs. This tuning was also performed without density dependence operating.

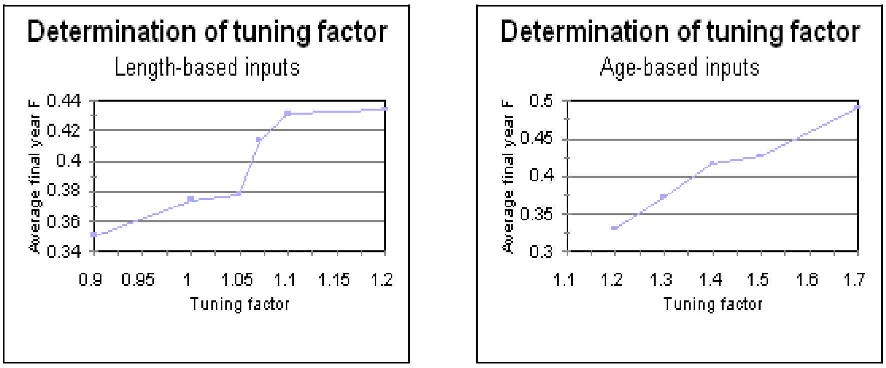


Figure 8.24 Graph of tuning factor against average final year effort, over the range investigated, for both length- and age-based inputs, for Fstart=0.4.

Table 8.3 Summary of the results of using different multiplying factors for estimates of target F ($F_{0.1}$) for a starting effort of 0.4.

Raising factor	Average final F	
	Length-based inputs	Age-based inputs
0.9	0.3507	-
1	0.3743	-
1.05	0.3779	-
1.07	0.4136	-
1.1	0.4312	-
1.2	0.434	0.331
1.3	-	0.3723
1.4	-	0.4171
1.5	-	0.4271
1.7	-	0.491

From the results summarised in Table 8.3 and Figure 8.24, a multiplying factor of 1.4 was chosen for age-based inputs, and a factor of 1.07 for length-based inputs. These multiplying factors were applied to the estimated fixed input Ftarget parameter, i.e. the estimate of $F_{0.1}$, in order to better estimate the true value. These multiplying factors were applied in all subsequent runs.

8.3.3.2 Overall comparison of tuned[4] length-based and age-based inputs

Once the two types of input parameters had been tuned to perform optimally, by applying the appropriate multiplying factors to the $F_{0.1}$ estimates, a direct comparison of the management performance could be made. Figure 8.25 shows, for each performance measure, the mean value of that measure for each of the four starting efforts, for both tuned length- and age-based inputs.

---

[4] Note that 'tuned' and 'tuning' refer here to the process of identifying the appropriate multiplication (or correction) factor. This should not be confused with the usual meaning of 'tuned' in age based assessment, e.g. where VPA is tuned to a series of commercial or survey indices of abundance.

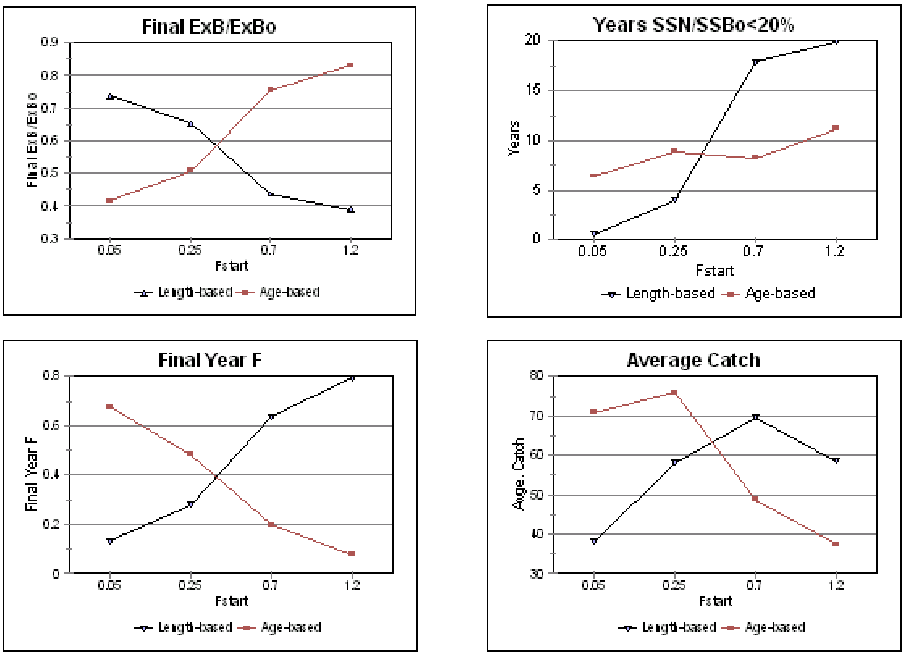


Figure 8.25 Mean values of each performance measure, for tuned age-based and length-based inputs, for all Fstarts.

Length- and age-based inputs appeared to perform comparably at a starting effort of 0.4, the final year effort level used for tuning both types of inputs (Figure 8.25). The actual comparison of length-based and age-based inputs at this effort level used for tuning will be discussed in more detail later (Section 8.3.3.3). However, it is clear that at higher and lower effort levels, management performance generally deteriorates, and in different directions for length-based and age-based inputs:

Final year ExB/ExB$_0$: Mean final year ExB/ExB$_0$ shows opposite trends for length-based and age-based inputs. For length-based, the mean value decreases as starting effort increases, from 0.74 at Fstart = 0.05 to 0.39 at Fstart = 1.2. Age-based growth inputs result in an increase in mean final year ExB/ExB$_0$ as starting effort increases, from 0.42 at starting effort 0.05 to 0.83 at starting effort 1.2. Thus at low starting efforts, age-based inputs perform better, whereas length-based inputs perform better at higher starting efforts. The range of means across the four different starting values is slightly lower for length-based than age-based inputs.

Number of years that SSB/SSB$_0$<20%: In both cases, the number of years that the spawning stock biomass (SSB) is reduced below 20% of unexploited levels increases with starting effort. For low starting efforts, the length-based inputs perform better than the age-based. For example at a starting effort of 0.05, length-based inputs reduce SSB below the threshold for an average of 0.58 years, compared to 6.38 years for age-based. Conversely, at higher starting efforts, age-based inputs result in improved management performance.

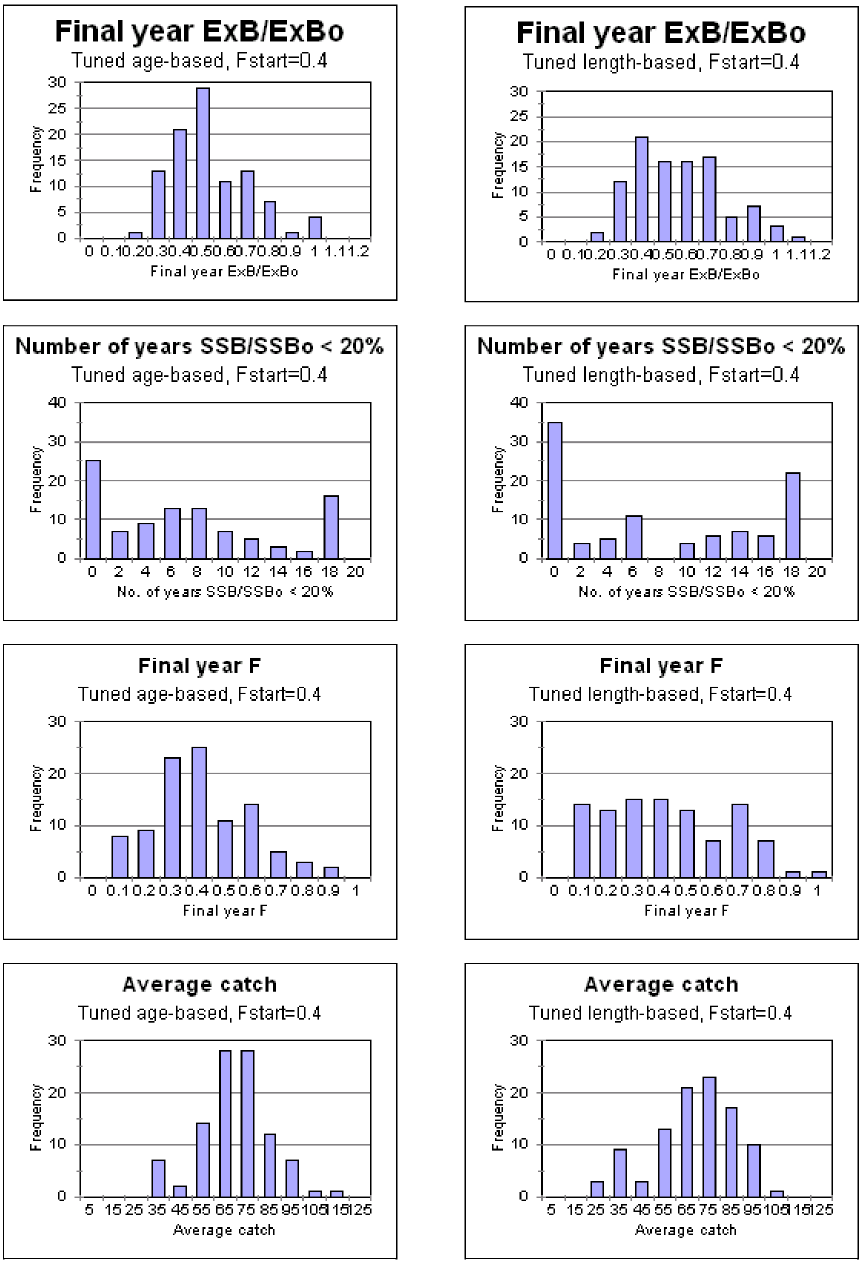
Final year effort: The mean values of final year effort show an opposing trend to those in mean final year ExB/ExB$_0$: means increase with increasing starting effort for length-based inputs, and decrease with increasing effort for age-based. At higher or lower starting efforts than that used to tune the inputs (F=0.4), neither method performs better than the other, one is too low and the other too high in each case. The range of means across the four starting efforts is similar for both age-based and length-based growth inputs.

Average catch: For age-based inputs, means of the average catch per year increase from 70.89 units for a starting effort of 0.05 to 75.97 units for a starting effort of 0.25, then decrease down to 37.51 units for the highest effort level. For the length-based inputs, the means increase from a lower value of 38.01 units for a starting effort of 0.05 up to a maximum of 69.66 units at a starting effort of 0.7, then decrease slightly for the highest effort level.

It is clear that, away from the effort level of 0.4 used for tuning both types of inputs, neither method performs well, and neither is consistently better than the other, due to the opposing trends in means of the performance measures.

8.3.3.3 Comparison of length- and age-based inputs at the effort level used for tuning

The above results were contrary to expectation from the earlier work (Chapter 7), which showed that age-based methods more accurately estimate the growth parameters, and thus subsequent biological reference points. It would therefore be expected that this increased accuracy from age-based inputs would result in better management performance. However, as was shown above, neither method performed well away from the effort level of F=0.4 used for tuning, and thus the relative performance of the length-based and age-based inputs was examined in more detail at this particular effort level. Figure 8.26 shows the distributions of each performance measure for a starting effort of F=0.4 for tuned length-based and age-based inputs. Comparing each performance measure in turn.



Final year ExB/ExBo
Tuned age-based, Fstart=0.4

Final year ExB/ExBo
Tuned length-based, Fstart=0.4

Number of years SSB/SSBo < 20%
Tuned age-based, Fstart=0.4

Number of years SSB/SSBo < 20%
Tuned length-based, Fstart=0.4

Final year F
Tuned age-based, Fstart=0.4

Final year F
Tuned length-based, Fstart=0.4

Average catch
Tuned age-based, Fstart=0.4

Average catch
Tuned length-based, Fstart=0.4

Figure 8.26 Comparison of each performance measure, for tuned age-based and length-based inputs, for Fstart = 0.4.

Final year ExB/ExB$_0$: The range of final year ExB/ExB$_0$ is slightly lower for age-based growth inputs (0.2-1.0) compared to length-based (0.2-1.1). The optimum value of this ratio, 0.4, is achieved in 21% of runs in both cases. However, age-based outputs are more normally distributed.

Number of years that SSB/SSB$_0$<20%: Length-based growth inputs perform better in respect to the proportion of runs in which SSB is never reduced below 20%, (35% of runs for length-based, as compared with 25% of runs for the age-based inputs). However, age-based inputs result in a lower proportion of runs where SSB is reduced below 20% for 18 out of the 20 years of simulations (16% for age-based, 22% for length-based inputs).

Final year effort: Again, the range of final year Fs is slightly lower for the age-based inputs (0.1-0.9) compared to length-based (0.1-1.0), but is substantially more normally distributed, with a mode at 0.4 (25% of runs). Length-based inputs result in a more even distribution of final year effort, particularly over the range 0.1-0.7. The optimum value of F=0.4 is achieved in 15% of runs for length-based.

Average catch: The range of values of average catch is similar for both age- and length-based inputs (35-115 for age-based, 25-105 for length-based). However, the histograms for age-based are much more normally distributed, and the optimum value of 75 is achieved in 28% of runs, as compared to 23% of runs for length-based inputs.

Thus the performance measure used for tuning, the final year effort, indicate that age-based inputs perform considerably better than length-based. As discussed below (Section 8.4.1.2), it is appropriate to give more weight to the performance measure used for tuning when making the direct comparison of tuned age- and length-based growth inputs. Final year ExB/ExB$_0$ and average catch performance measures also showed an improvement when using age-based inputs. The spawning stock biomass performance measure was less conclusive, but did show an improvement in the proportion of runs where SSB was reduced below the threshold level in the majority of years (*i.e.* greater than 12 years). Age-based growth parameters therefore reduced the risk of recruitment overfishing.

The fact that the age-based inputs performed better than length-based at the effort level used for tuning, but that away from this effort level neither method performed well, suggests that it would be necessary to tune at the effort level appropriate for a particular fishery in question, for whichever growth estimation method was used. As an illustration, the tuning process was repeated for starting efforts of F=0.05 and 1.2, the extremes of the range of effort levels used in this management strategy simulation. As before, methods were tuned to achieve an average final year F as close as possible to the optimum of 0.41, and tuning was conducted without density dependent growth operating. The appropriate multiplying factors are shown in Table 8.4, and the resulting histograms for each performance measure shown in Figure 8.27 (Fstart = 0.05) and Figure 8.28 (Fstart = 1.2).

Table 8.4 Multiplying factors derived for both age- and length-based inputs for Fstart = 0.05, 1.2.

	Age-based inputs	Length-based inputs
Fstart = 0.05	0.89	2.22
Fstart = 1.2	3.4	0.4

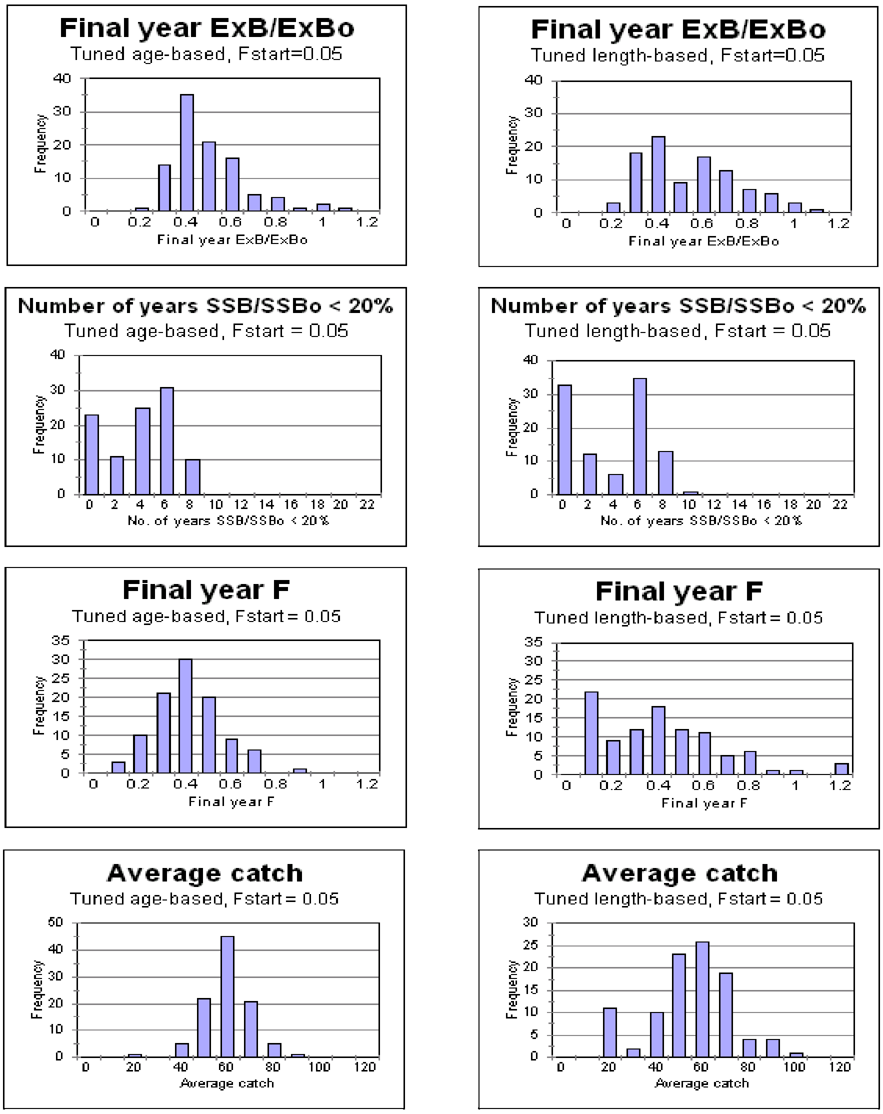


Figure 8.27 Comparison of each performance measure, for tuned age-based and length-based inputs, for Fstart = 0.05.

Figure 8.27 shows a similar result to the histograms for inputs tuned at 0.4 (Figure 8.26) in that age-based inputs are again demonstrating better management performance at the effort level used for tuning, in particular when comparing the relative performance of the two conservation measures, final year ExB/ExB_0, and final year F: the age-based inputs are more normally distributed, and achieve the optimum values in a greater proportion of runs. However, at the higher effort level of 1.2 (Figure 8.28), both methods perform particularly badly, despite tuning, with a wide spread in outcomes for each measure. For the final year effort, although the mean across the 100 runs is close to 0.41 in each case, there is a great deal of spread, from 0.1-1.2 in each case, and the distributions are not remotely normally distributed. In fact, length-based inputs perform marginally better than age-based when looking at this performance measure, in achieving the optimum value of 0.4 in a greater proportion of runs.

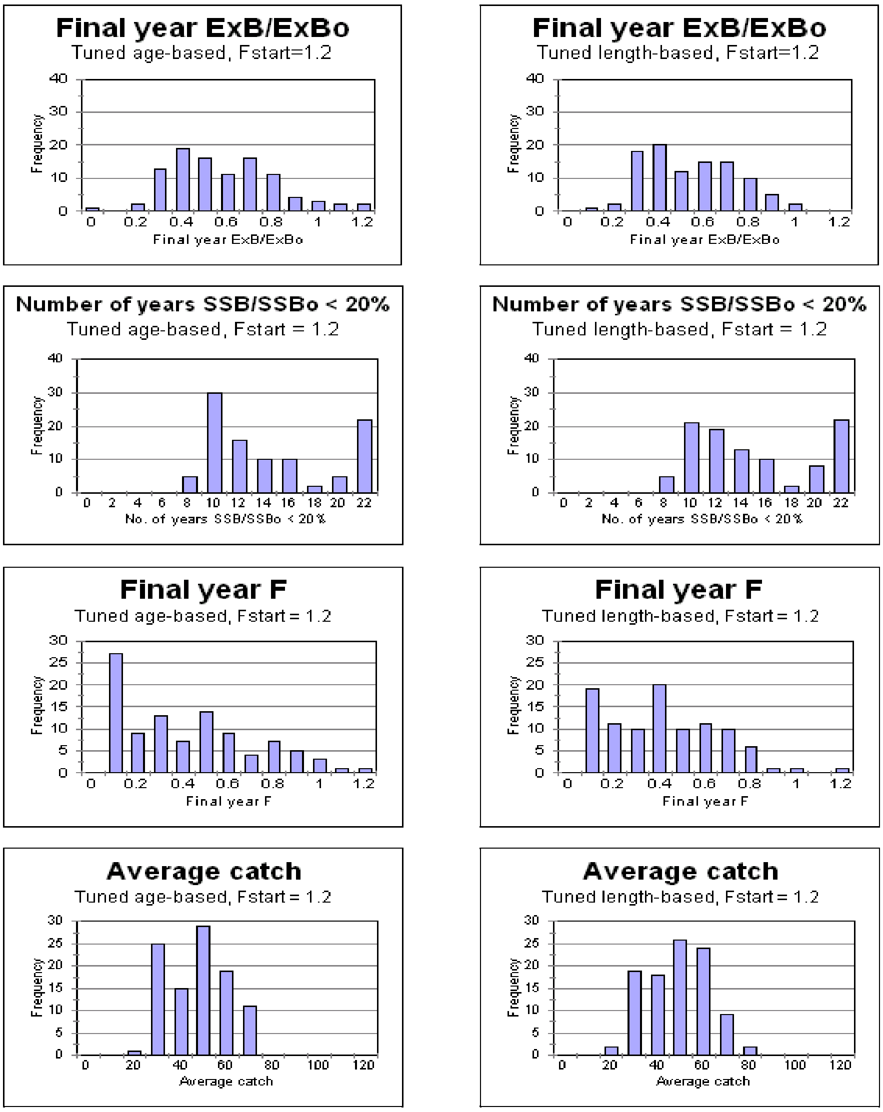


Figure 8.28 Comparison of each performance measure, for tuned age-based and length-based inputs, for Fstart = 1.2.

8.4 OVERALL DISCUSSION AND CONCLUSIONS

8.4.1 Discussion

This study aimed to address certain specific objectives relating to a manager’s ability to accurately manage a fish stock using analytical fishery models, such as yield-per-recruit, where there was uncertainty in growth parameter inputs to those models, or where fishing affected estimation of growth parameters. Age- and length-based methods of growth assessment were also compared.

The aim of this programme was not to establish an optimum management strategy, and thus the comparison of different management strategies was not central to this study. However, although beyond the direct objectives of this study, brief investigations of different management rules were performed. In addition to the fixed percentage management rule using a 20% increase and 16.7% decrease employed for the majority of the management simulations, a brief investigation was made of the use of this management rule with a 40% increase and 28.6% decrease. The results of these simulations are not shown, but indicated that management performance worsened slightly when using the 40% increase (28.6% decrease) rule, as compared to the 20% increase (16.7% decrease). The purpose of mentioning these details here is simply to highlight the fact that alternative management actions may achieve different results in terms of management performance.

8.4.1.1 Management performance measures

In evaluating management performance in order to derive conclusions on each of the objectives, four indicators were employed (final year ExB/ExBo, number of years that SSB fell below a threshold value, final year F and average catch, see Section 8.2.3 above). Certain details relating to these indicators require further discussion.

Final year F: In the simulations, management aimed to achieve (and sustain) the target effort (*i.e.* $F_{0.1}$, F=0.41 for *L. mahsena*) within the 20 year period of management. Final year F indicates whether this target was achieved at the end of the 20 year period. Looking in more detail at the estimates and true values of current effort over the 20 year simulation period for individual runs, it was noted that, for low starting efforts, the true current effort would frequently increase past the target, and thus end up too high at the end of the 20 year period. The converse was frequently found for high starting efforts. Variability in the true final year effort is due to inaccuracies in the estimates of both the current effort and Ftarget, resulting from inaccuracies and variability in the growth parameter estimates. As both estimates of current effort and Ftarget are used each year in the management rule to determine whether to increase or decrease effort in the subsequent year, the inaccuracies and variability in growth parameter estimates result in a failure to achieve the optimum final year F. This results in the patterns of over- or under-exploitation observed in the final year ExB/ExB_0.

Spawning stock biomass: It should be noted that the ratio of spawning stock biomass to unexploited levels at the equilibrium target effort level, $F_{0.1}$ (= 0.41), is 21.3%. Thus the choice of a 20% level for this spawning stock biomass performance measure might be questionable. However, while at starting efforts of 0.4 and higher, spawning stock biomass is already at this level or lower at the start of the simulations, a high number of years in which SSB is below 20% of SSB_0 indicates a failure of management to adjust the F level suitably. For the two lowest starting efforts, 0.05 and 0.25, the value of the ratio at equilibrium is 80% and 36% respectively, and thus a high number of years below 20% for these two starting efforts is indeed indicative of poor management performance.

The value of the SSB/SSB_0 ratio at equilibrium MSY is 10.9%, and thus it might have been more appropriate to use a 10% level for the SSB performance measure. The value of 20% was chosen however in relation to estimates quoted in the literature (Mace and Sissenwine, 1993).

Average catch: For the real study fisheries, neither MSY nor F_{MSY}, can be estimated, due to the lack of information on the stock recruitment relationship (see Chapter 7). However, in simulations it is valid to compare performance against the optimum catch that could have been achieved rather than that at $F_{0.1}$ (which can be calculated for the real fishery), as MSY can be determined within the model.

8.4.1.2 Management simulation objectives

Chapter 7 indicated that length-based von Bertalanffy growth parameter estimates showed considerable variability and bias both with and without density dependent growth operating. Biological reference points calculated using these parameters similarly showed considerable variability and bias. Age-based estimates were generally accurate and precise, and showed less variability and bias both with and without density dependent growth than length-based methods. Biological reference points calculated using these parameters were more accurate than those from length frequency data, but, nevertheless were variable and biased.

The study initially examined management performance with these uncertain inputs and concluded that neither length nor age based inputs performed well. In order to compare the two methods fairly, tuning of the estimates of target effort ($F_{0.1}$) was required for the effort level appropriate to the fishery in question. The method chosen for tuning was to optimise the average final year effort. It should be noted that other methods, for example tuning such that the final year ExB/ExB_0 is not reduced below 40% would have also been valid.

The selection of average final year effort as the basis for tuning implies that the other performance measures are not necessary optimised (the use of other performance measures for tuning may have resulted in different multiplying factors). When comparing the performance of length- and age-based growth inputs directly, therefore, it is most appropriate to give more weight to the comparisons of the average final year effort. For this measure, it was seen that age-based inputs did perform noticeably better than length-based, at low to medium effort levels. At the highest starting effort level, both inputs performed particularly poorly, with length-based inputs actually performing marginally better. However, in the results described in Chapter 7 it was shown that age-based estimates of growth parameters were highly accurate at low to medium effort levels. Thus, in the simulations at the highest starting effort level, where effort is subsequently reduced, it would be appropriate to re-estimate growth parameters using age-based methods. The resulting improved estimates of growth (compared with initial estimates), would then lead to improvements in the estimates of subsequent biological reference points, and hence improved management during the remaining period of the simulation.

Whilst age-based inputs were shown to be in general better than length-based at the effort level used for tuning, management performance was still not as good as might have been expected from the results of Chapter 7. Away from the effort level used for tuning, both methods were particularly poor. The results of the tuned age-based inputs at the tuning effort level still showed considerable variability, which was perhaps surprising. However, it should be recalled that whilst age-based methods were used to determine growth parameters accurately, subsequent parameter estimates utilised length-based methods of assessment. This result suggests that if any part of the stock assessment includes length-based components, then the assessment is inadequate. The improved accuracy and precision gained through the use of age-based growth parameters is diluted. Further simulations using a full age-based stock assessment would be appropriate to identify the impact of length-based methods in the stock assessment, and identify the potential improvements resulting from increased age-based components.

The study also looked at effects of density dependent growth. Management performance was found to deteriorate substantially where density dependent growth was operating, suggesting that the application of the $F_{0.1}$ management strategy without tuning is likely to result in overexploitation in this situation. The deterioration in management performance is a result of the greater inaccuracies in growth parameter and subsequent biological reference point estimates where density dependent growth is operating. From Chapter 7, it was shown that whilst density dependence generally improved the accuracy of $F_{0.1}$ estimates, it decreased the accuracy of current F estimates, which were (increasingly) negatively biased under density dependent growth. This underestimation of current F would therefore lead to true effort levels being increased beyond the target, resulting in overexploitation of the stock.

As seen in Chapter 5, density dependent growth affects the yield/effort curves, and thus the value of $F_{0.1}$. In simulations conducted with density dependent growth operating, it was assumed that $F_{0.1}$ is constant throughout the 20 year simulation period. However, due to the transient effects of density dependence on both growth parameters and length frequency distributions, in reality $F_{0.1}$ would not remain constant under transient fishing pressure. In cases of higher fishing pressure, where effort is being reduced towards the target, the reduction in effort will cause stock biomass to increase, and thus the density dependent effects to be reduced. This would cause a reduction in the true value of $F_{0.1}$. Thus simulations performed with density dependence on, where $F_{0.1}$ is assumed to be constant, will have the target effort level too high. This will contribute to the worsening management performance. In order to address this, the management strategy simulation model would need to re-estimate growth and subsequent parameters periodically during the 20 year simulation period, where density dependent growth is operating and fishing effort is altered.

The tuning process to optimise the performance of both length- and age-based inputs, as described above, was conducted without density dependent growth operating. As noted, it is necessary to tune at the level of effort appropriate to the fishery in question. It has been shown (Section 8.3.2) that, for untuned inputs, density dependent growth results in overexploitation. Where tuning is conducted with density dependence off, in a fishery where density dependent growth is actually operating, severe overexploitation will result if the multiplying factor is greater than 1. Indeed, with density dependence operating, a substantial reduction in effort is required. Therefore, tuning should be conducted with density dependent growth operating, leading to a multiplication factor less than 1.

However, it should be noted that we do not know what the true level of density dependence is, as we cannot determine this from the available data. It would be appropriate to conduct further simulations to determine the effect of different levels of density dependence on the correction factor derived. This was outside the scope of the current project. In the absence of this information, the precautionary approach would be to assume the extreme level of density dependence used for the simulations in this study, as this will result in the greatest reduction to the estimates of target effort.

8.4.1.3 Summary conclusions

This study has used a technique known as management strategy simulation to simulate the whole management process. Conclusions have been derived on the effect of uncertainty in growth parameter inputs and the effects of fishing on management performance . Age- based and length-based methods of assessment were compared. Neither age- nor length-based methods performed well, though age-based methods were better. Uncertainty arising from the use of length-based assessment methods with both length- and age-based inputs led to poor management performance, exacerbated by the indirect effects of fishing investigated through density dependent growth (DDG) of fish.

A summary of the conclusions relating to management performance derived from the management strategy simulation follows:

- Uncertainty and variability in growth parameter estimation led to poor management performance for both length based and age-at length based methods of assessment;

- Where DDG occurs, management performance is worse for both length-based and age-based methods of assessment compared to the case where DDG does not occur;

- To improve management performance, it was necessary to apply a correction factor to the target $F_{0.1}$ value. A different correction factor was required for fisheries at different levels of fishing intensity: with DDG not operating neither age nor length based methods performed well except at the F value used to determine the correction factor. At that value, age-based methods of assessment performed better than length-based methods, except at the highest effort level. At this level, age-based growth inputs showed no advantage over length-based, and neither inputs performed especially well. Although not examined specifically during the study, where DDG was operating, given that this worsened management performance, the appropriate tuning factors would be smaller than those derived where DDG was not operating (and certainly <1);

- At high starting efforts, it would be appropriate to re-estimate the growth parameters, using age-based methods, and the subsequent biological reference points during the 20 year simulation period. In simulations where DDG was not operating, the reduction in effort would then allow more accurate growth parameters to be re-estimated through age-based methods, thereby improving management performance. Where DDG is operating, the assumption of constant $F_{0.1}$ means that the 'manager' is effectively ignoring the transient effects of density dependence. Simulations where growth parameters, and hence $F_{0.1}$, are re-estimated periodically during the simulation period should be conducted in order to determine whether an improvement in management performance results;

- The use of length-based components in stock assessment leads to inadequate management performance, despite the use of accurate age-based growth parameter estimates; full age-based assessments should be evaluated in order to determine if this confers a significant improvement in management performance.

8.5 MANAGEMENT GUIDELINES

The following indicates the management guidelines that have arisen directly from consideration of the management strategy simulation studies. These details have been incorporated into the overall data collection and management guidelines, taking into account details from other studies conducted during the project, and presented at the beginning of this document in the Final Technical Report.

- Assessments must be tuned for the current level of exploitation in a particular fishery. Age-based growth parameter inputs are considered the most appropriate at low to medium effort levels. At the highest effort level, however, there is no obvious advantage of age-based inputs. Note that in order to conduct tuning, management strategy simulations such as those described in this chapter are required with appropriate input parameters relating to the fishery in question.

- For lightly exploited fisheries, the appropriately tuned correction factor should be applied, and tuning may be done assuming that density dependent growth does not apply (whether or not DDG does apply has little effect).

- For heavily exploited fisheries, the precautionary approach would be to assume DDG does apply, in which case a reduction in target F will be required, thus a need to tune with DDG on to give a correction factor < 1.

The appropriate course of action would be different in lightly and heavily fished locations. At a lightly fished location, for example Chagos, growth parameter and $F_{0.1}$ estimates are not strongly affected by density dependent growth (see Chapter 5). It is therefore safe to apply a correction faction derived assuming no density dependence.

In contrast, in an already heavily fished location such as the Mauritian Banks, if density dependent growth does occur (Chapter 6), it will impact estimates of growth, and therefore subsequent estimates of biological reference points for management. In this scenario, applying a correction factor determined assuming no density dependence could exacerbate the effects of over-fishing, if that correction factor is greater than 1. The precautionary approach therefore would be to assume that density dependence does apply, and determine the appropriate correction factor accordingly (which will then be less than 1).

9. Assessment of the status of the case study fisheries

9.1 INTRODUCTION

Most fish stock assessment methods require some estimates of growth parameters. Current von Bertalanffy growth parameter and mortality estimates for the study species in Seychelles, Mauritius and BIOT (Chagos Archipelago) have been calculated from length-based methods (Bertrand *et al.*, 1986; Mees, 1993; MRAG, 1996d). As indicated by the results described in Chapter 7, length-based methods may give rise to significant bias in growth estimates. Management actions based on assessments of current fishing mortality and yield-per-recruit can be affected by errors in the estimated growth parameters. The results presented in Chapter 7 and 8 indicated how age-based estimates resulted in more accurate growth parameter estimates for exploited *L. mahsena* populations, and hence improved management (although tuning is required). These findings suggest that age-based estimators can improve the effectiveness of current management in the study locations.

In the simulations described in Chapter 7, age-based growth estimates were used to derive further biological and fishery parameters through length-based methods. However, where age data are available, total mortality can be assessed directly through the construction of an age frequency distribution (numbers at age).

Age frequency distributions can be calculated by a number of methods. By ageing a relatively large sample of randomly selected individuals, an age frequency distribution can be constructed directly. Alternatively, an age-length key (ALK) may be used (*e.g.* Holden and Raitt, 1974). Here, the proportional age frequency for each length class can be used to transform length frequency distributions into age frequency distributions. The ALK requires a limited number of samples from all classes in the length frequency. This method therefore offers potential savings in time and effort over the direct assessment of catch age frequency. A further methodology used to assess an age frequency distribution is through an otolith weight-age relationship (Boehlert, 1985). As growth is deposited on the otolith each year, its size and weight should increase (Fowler and Doherty, 1992). If such increases can be related to a specific age, a calibration curve can be developed (Ferreira and Russ, 1994). In contrast to the assessment of age through otolith readings, which involve subjective decisions as to the age of a fish, otolith weight offers an objective method of ageing (Worthington *et al.*, 1995a). In turn, the method should also be cheaper than direct ageing, offering considerable benefits to resource-limited developing countries.

The first aim of the work described in this chapter was to compare estimates of biological and fishery parameters for the study species derived through length- and age-based methods. A limited number of studies have compared such outputs for tropical species. An investigation by Mathews (1974) concluded that the study of otoliths in four species of tropical fish resulted in more reliable growth rate estimates than those resulting from modal separation of length frequencies (*e.g.* Bhattacharya's method; Bhattacharya, 1967), although a combination of techniques was helpful. Shepherd *et al.* (1987) examined the length-based assessment of growth parameters for *Otolithes argenteus* in the light of estimates derived through age-at-length data. While the goodness of fit response surfaces of the length-based methods included peaks at or near the combination of growth parameter estimates derived from age-at-length data, these rarely coincided with the global maximum. Length-based methods could not distinguish the correct parameter combination for this species without additional information. This was attributed to the fact that modes were not easily distinguished in the length composition data, a feature common to the study species of the current project. In contrast, Mathews (1987) obtained similar growth and mortality estimates for *O. argenteus* from age-based and length-based analyses. However, for two other species examined in the same study, growth and mortality estimates from length- and age-based methods were very different. Therefore, where hard parts such as otoliths can be read, they appear to result in different, and assuming correct validation and ageing, more accurate assessments of growth than length-based methods.

The second aim of the work performed was to derive the first age-based growth and mortality estimates for the study locations. Based on these, the current status of the stock in each location was assessed.

Historical length frequency data are used to re-assess the length-based growth parameter estimates for the study species in each location. The validation of *L. mahsena* and *A. virescens* otoliths as an ageing tool (Chapter 2) also allows age-based estimates of growth and mortality to be derived. Direct comparisons of the estimates resulting from each method are made, to identify whether trends identified in Chapters 7 and 8 are found in assessments of actual data.

In Chapter 7, 'age-based' total mortality estimates were derived from age-based growth parameters applied to length-based methods. In this chapter, however, total mortality estimates will also be derived using catch curves based on age frequency distributions. These age frequency distributions will be assessed using three methods; directly from otolith assessments, through an age-length key, and via an otolith weight-age relationship. These estimates will be compared to those resulting from the application of length-based methods (Beverton and Holt's Z estimator and the length-converted catch curve).

Ultimately, the parameter estimates derived from the different methods will be used to assess current fishing mortality (F_{curr}) and yield-per-recruit (specifically $F_{0.1}$). Length-based and age-based assessments of the current status of the stock will then be compared. The most appropriate methodologies identified will then be used to provide the best indication of the degree of current exploitation.

9.2 METHODOLOGY

Since otoliths from *P. filamentosus* could not be validated, age-based estimates of growth or mortality could not be derived. This would have confined analyses for this species to a re-assessment of length-based estimates of growth and mortality. Given the variability and inaccuracy of length-based estimates shown in Chapter 7, there was considered to be no merit in this; the study therefore concentrates on data for *L. mahsena* and *A. virescens*.

The following section describes the length- and age-based methods used to estimate von Bertalanffy growth parameters for the two study species. The methods used to estimate total mortality are then described. Two length-based methods of total mortality estimation were used: Beverton and Holt's Z estimator, and the length-converted catch curve. In each of these methods, both length- and age-based growth parameters were used, as in Chapter 7. Age-based total mortality estimation involved the derivation of an age frequency distribution. This was achieved using three methods: individual otolith readings, through conversion of length frequencies using age-length keys, and the use of otolith weight as a measure of age[5]. Using each of the length-based and age-based catch curves, estimates of both the age and length at first capture (Ac_{50} and Lc_{50}) were derived.

---

[5] There were insufficient otolith weight data available to warrant a comparison with the results of the other estimation methods. However, the results obtained from this method proved interesting. In order to maintain the focus of this chapter, the calculation and use of otolith weight-age relationships is described in Appendix 7. The results are discussed briefly in Section 9.4.

To estimate yield-per-recruit, and hence $F_{0.1}$, estimates of the natural mortality rate were also required. Both Pauly's and Ralston's empirical formulae were employed for this purpose. Estimation of $F_{0.1}$ through the yield-per-recruit equation, and the methods used to estimate the current level of fishing mortality (F_{curr}) are then given.

The results described in Chapter 6 indicated significant variability in length and age structures between areas within a location. One of the recommendations that arises from that chapter is for assessments to be carried out by localised area, where possible. Unfortunately, the length and age sampling programmes used in this study had not been designed with such detailed examination in mind. Dis-aggregation of the available data into statistical areas reduced the sample sizes, affecting parameter estimates and masking any differences between statistical areas. Comparisons were therefore limited to those between locations.

9.2.1 Estimation of growth parameters

Growth parameter estimates were derived using both length-based and age-based methods. These were described in Chapter 4 (Section 4.3.2).

9.2.2 Estimation of total mortality and length/age at first capture

Total mortality estimates were derived through both length-based and age-based methods. Using the length- or age-based catch curves, estimates of length and age at first capture were also made.

9.2.2.1 Length-based estimation of mortality and length at first capture

Length-based estimates of total mortality and length at first capture were derived from the 1997 length frequency distribution for each location. This was the only year in which both length and age data were available from all study locations.

As described in Chapter 4, total mortality was estimated using the Beverton and Holt Z estimator (Beverton and Holt, 1956), and the length-converted catch curve procedure contained within the FAO - ICLARM Stock Assessment Tool (FiSAT; Gayanillo *et al.*, 1994). Length-at-first-capture estimates were derived through FiSAT. Ac_{50}, and through the growth parameters Lc_{50}, were interpolated.

Both the length- and age-based growth parameter estimates derived in the current chapter were used in the estimation of total mortality and length/age at first capture.

9.2.2.2 Age-based estimation of mortality and age at first capture

As described in Chapter 4, total mortality was estimated from age frequency distributions derived through either individual otolith assessments, and through the conversion of length frequency data using an age-length key. The resulting age frequency distributions were used to construct an age-based catch curve. Total mortality was then calculated from the descending limb of this catch curve. The age at which 50% of individuals were vulnerable to the gear (Ac_{50}) was then estimated from the ascending limb of the age-based catch curve (see also Chapter 4).

9.2.3 Estimation of natural mortality, F_{curr} and $F_{0.1}$

Natural mortality was estimated using the empirical equations of Pauly (Pauly, 1980) and Ralston (Ralston, 1987). Both length- and age-based growth parameter estimates were used to estimate natural mortality (M) from each equation.

F_{curr} was calculated by subtracting total and natural mortality estimates. The particular combination of total and natural mortality estimates used were based on the results of the simulations reported in Chapter 7. As the study fisheries have been exploited over an extended period, the results of the equilibrium simulations were assessed. In this case, the most accurate length-based estimates of F_{curr} using length-based growth parameters resulted from the subtraction of Pauly's M estimate from the Beverton and Holt estimate of Z. Where age-based growth parameters were used in length-based methods, F_{curr} derived from the subtraction of Ralston's M from the length-converted catch curve were the most appropriate.

In the study described in the current chapter, estimates of total mortality were also derived directly from age-based catch curves. This was not examined in Chapter 7. Therefore, two estimates of F_{curr} were derived, by subtracting the two natural mortality estimates from each age-based total mortality estimate.

Yield-per-recruit was derived using the EXCEL^{TM} spreadsheet described in Chapter 4 (Section 4.4.1). For each location, $F_{0.1}$ estimates were calculated for different combinations of growth, natural mortality and age at first capture estimates. Ac_{50} estimates were derived directly from age-based methods or, in the case of length-based methods, converted from Lc_{50} using the relevant growth parameter estimates. The estimate of M used corresponded to that used in the estimation of F_{curr} to which the $F_{0.1}$ estimate was to be compared. Based on the gear selectivity ogive estimated for each species (Chapter 4, Section 4.2.1.5) Lc_{min} was set at 13cm for *L. mahsena* and 25cm for *A. virescens*.

For each parameter combination, the yield-per-recruit was maximised using the Excel Solver^{TM} routine. $F_{0.1}$ was then assessed as in Chapter 4.

9.2.4 Assessment of stock status

Two methods were used to assess the status of the stocks in each location. The first was through comparison of the estimated $F_{0.1}$ with the estimated level of F_{curr}. The second method compared the F_{curr} estimate to the estimate of M. If F_{curr} was greater than M, concern was warranted where the length at capture estimate was lower than the length at maturity (Lm_{50}; either that assessed in Appendix 6, or 50% of L_∞) (*e.g.* Caddy and Mahon, 1995; Mees *et al.*, 1999). In both cases, the percentage by which each F_{curr} estimate exceeded the reference effort level was assessed. The status of the stocks were examined based on the magnitude of the difference between the reference effort level and estimated level of fishing mortality. To enable the outcomes of the stock assessments to be assessed easily, this difference was used to develop four indications of potential concern for the stock (Table 9.1).

Table 9.1 Level of concern for the stock based on the relative values of $F_{0.1}$ or M and of fishing mortality (F_{curr}).

F_{curr} in relation to F_{ref} ($F_{ref} = F_{0.1}$ or M)	Level of concern
$F_{curr} > 2.0F_{ref}$	Serious concern
$1.5F_{ref} < F_{curr} < 2.0F_{ref}$	Concern
$F_{curr} < 1.5F_{ref}$	No concern

The percentages at which the level of concern changed are essentially arbitrary, and are used for illustration only.

From Chapter 8, management based on $F_{0.1}$ using either length- or age-based growth parameters requires a degree of tuning to compensate for the inaccuracies and trends resulting from the two methodologies. Therefore, the effect on the stock assessments of tuning current $F_{0.1}$ estimates, based on outputs of Chapter 8 and the estimates of F_{curr}, was examined.

9.3 RESULTS

The results are presented in four sections. In the first, growth parameter estimates from length- and age-based methods are described. Secondly, total mortality and length/age at first capture estimates are presented. The third section presents the estimates of natural mortality, F_{curr} and $F_{0.1}$. Finally, these estimates are used to assess the status of the study stocks.

9.3.1 Von Bertalanffy growth parameter estimates

Growth parameter estimates derived through both length- and age-based methods are presented by species.

Although the three length-based assessment algorithms available in LFDA4 (ELEFAN, PROJMAT, SLCA) were used during the study, only ELEFAN provided feasible growth parameter estimates. SLCA estimates tended towards unfeasibly high L_∞ and K values, while PROJMAT estimates tended towards high values of L_∞ and low K values. All length-based growth parameter estimates presented here were therefore derived using ELEFAN.

Patterns in the frequency distributions indicated that it might be appropriate to fit seasonal growth curves to the data. However, the application of seasonal models did not change the estimated values of L_∞, K or t_0, the score function, or improve the fit to the data (assessed visually). All length-based estimates presented here therefore represent non-seasonal growth curves. Age-based growth parameter estimates were derived through non-seasonal growth functions in all cases apart from *A. virescens* from BIOT (Chagos Archipelago), where both non-seasonal and seasonal curves were fitted.

9.3.1.1 *Lethrinus mahsena* growth parameter estimates

The length and age data available to perform age-based estimates of growth are presented by location in Table 9.2.

Table 9.2 Summary of the *L. mahsena* samples aged by bank.

Location	Numbers of individuals			Fork Length Range (cm)	
	Aged	Random Samples	Targeted Samples	Minimum	Maximum
BIOT (Chagos)	644	472	172	18	51.5
Nazareth	962	721	241	20	50
Saya south	1261	690	571	13.5	55
Saya north	758	20	738	14	54
Seychelles	1117	1117	-	16	45

The growth parameters derived for *L. mahsena* from length- and age-based methods are presented in Table 9.3, together with estimates from the literature.

Table 9.3 *L. mahsena* length-based (‘Length’) and age-based (‘Age’) growth parameter estimates, by location. For length-based estimates, data series is also shown.

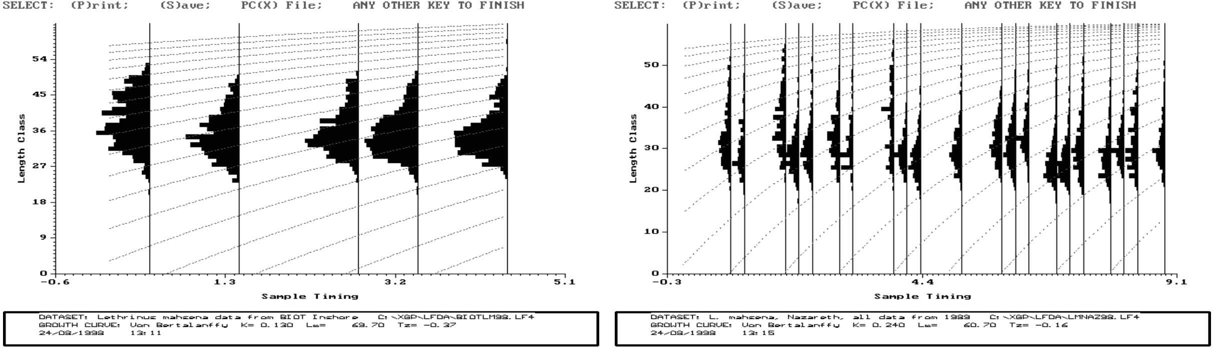
Location	Method	L_∞	K	t_0	Period	
					From	To
BIOT (Chagos)	Length	69.7	0.13	-0.4	May ‘94	Jul ‘98
	Age	66.3	0.1	-1.5	-	-
Nazareth bank	Length	60.7	0.24	-0.2	Q4 ‘89	Q4 ‘97
	Length[1]	61.7	0.1	-0.7	-	-
	Age	72.6	0.1	-2.9	-	-
Saya north	Length	58.7	0.22	-0.2	Nov ‘77	Aug ‘87
	Age	66.4	0.1	-1	-	-
Saya south	Length	59.8	0.22	0	Q1 ‘90	Q1 ‘95
	Age	64.3	0.1	-0.7	-	-
All Saya	Length[2]	59.8	0.1	-1.8		
Seychelles	Length	48.5	0.35	-0.6	Q4 ‘90	Q2 ‘98
	Age	78.2	0.1	-2	-	-
Yemen	Length[3]	58.9	0.32	-	-	-

[1] Bautil and Samboo (1988)

[2] Bertrand *et al.* (1986)

[3] Dalzell *et al.* (1992)

Note that the Seychelles length-based estimate was based on two length frequency distributions only. Given the between-year variability in the length frequencies identified in Chapter 6, these growth parameter estimates are open to error. The fit of the resultant growth curves to the length frequency and age-at-length data are presented in Figures 9.1 and 9.2.

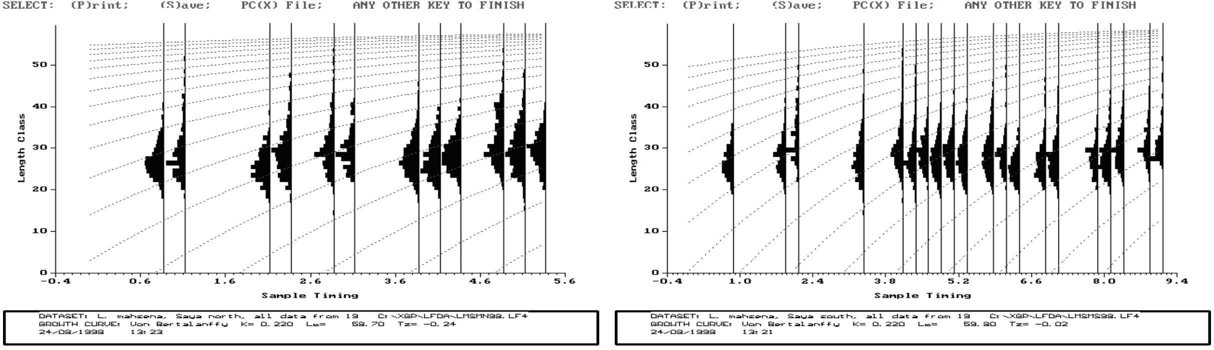


a. BIOT (Chagos Archipelago)

```
SELECT:  (P)rint;   (S)ave;   PC(X) File;   ANY OTHER KEY TO FINISH
DATASET:  Lethrinus mahsena data from BIOT Inshore    C:\XGP\LFDA\BIOTLM98.LF4
GROWTH CURVE:  Von Bertalanffy  K= 0.130  L∞=     69.70  Tz= -0.37
24/08/1998     13:11
```

b. Nazareth

```
SELECT:  (P)rint;   (S)ave;   PC(X) File;   ANY OTHER KEY TO FINISH
DATASET:  L.  mahsena, Nazareth, all data from 1989    C:\XGP\LFDA\LMNAZ98.LF4
GROWTH CURVE:  Von Bertalanffy  K= 0.240  L∞=     60.70  Tz= -0.16
24/08/1998     13:15
```



c. Saya north

```
SELECT:  (P)rint;   (S)ave;   PC(X) File;   ANY OTHER KEY TO FINISH
DATASET:  L.  mahsena, Saya north, all data from 19    C:\XGP\LFDA\LMSMN98.LF4
GROWTH CURVE:  Von Bertalanffy  K= 0.220  L∞=     58.70  Tz= -0.24
24/08/1998     13:23
```

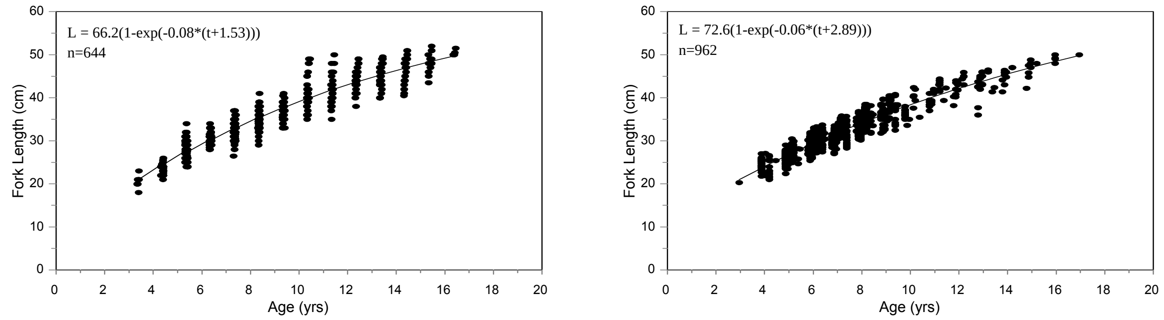
d. Saya south

```
SELECT:  (P)rint;   (S)ave;   PC(X) File;   ANY OTHER KEY TO FINISH
DATASET:  L.  mahsena, Saya south, all data from 19    C:\XGP\LFDA\LMSMS98.LF4
GROWTH CURVE:  Von Bertalanffy  K= 0.220  L∞=     59.80  Tz= -0.02
24/08/1998     13:21
```

Figure 9.1 Screen captures of the best fitting von Bertalanffy growth curves assessed using ELEFAN for *L. mahsena* for locations in the Indian Ocean. Seychelles fit not presented due to limitations in the data.

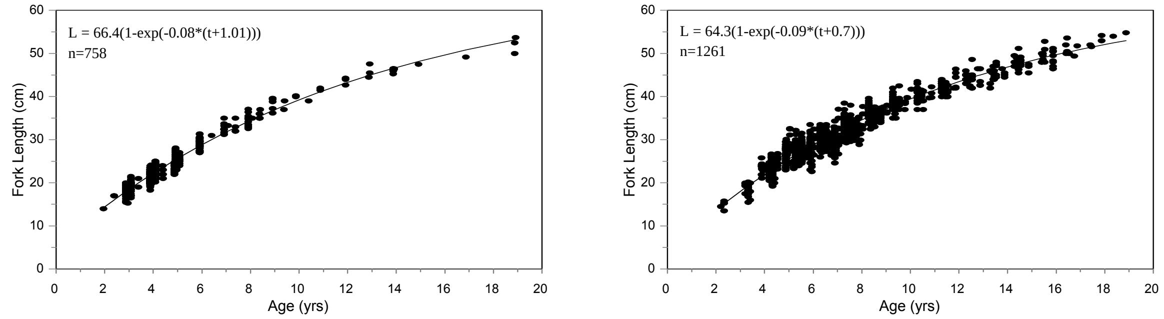
a. BIOT (Chagos Archipelago)

b. Nazareth



c. Saya north

d. Saya south



e. Seychelles

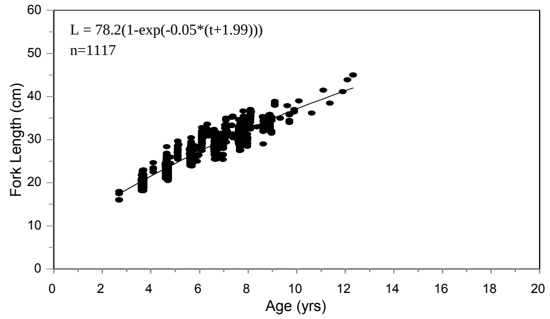


Figure 9.2 Observed lengths-at-age and fitted von Bertalanffy growth curves for *L. mahsena*, by study location.

Length-based L_∞ estimates were generally comparable both across the Mauritian banks, and between assessments in the same location. The L_∞ estimate for BIOT (Chagos Archipelago) was larger than that for the Mauritian banks, while the estimate for Seychelles was lower. K estimates derived during the current study were larger than length-based estimates in the literature. Estimates for the Mauritian banks derived in the current study were relatively consistent (range of K from 0.22 to 0.24). K estimated for BIOT (Chagos Archipelago) (K=0.13) was lower than that for the Mauritian banks, and closer to historical estimates for the latter areas (K = 0.1, Table 9.3). That for Seychelles was high (K=0.35) and closer to the estimate from Yemen (K=0.32, Table 9.3).

Age-based estimates of L_∞ were generally larger than those derived from length-based methods, while estimates of K were lower. Age-based K estimates were closer to that of Bautil and Samboo (1988).

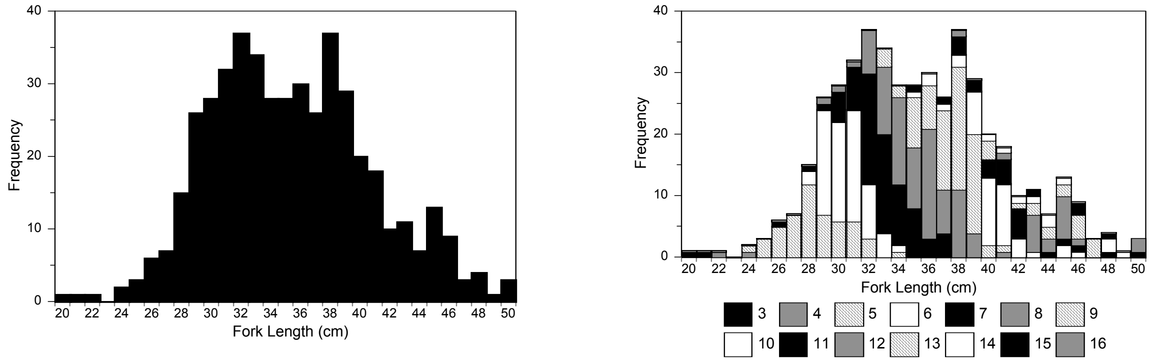
Age-based K estimates were frequently strongly affected by the lack of young individuals in the samples analysed. As a result of a lack of these individuals, the estimate of K was likely to be underestimated. Growth parameters were therefore re-estimated with t_0 constrained to zero

(Table 9.4). If growth follows the von Bertalanffy function, t_0 is generally negative, so that individuals have reached positive lengths at the time of birth. Setting t_0 equal to zero should therefore indicate the likely maximum value for the K estimate.

Table 9.4 Growth parameter estimates for *L. mahsena* by location, where t_0 was constrained to zero.

Location	L_∞ estimate	K estimate
Nazareth	50.4	0.15
Saya south	58.4	0.11
Saya north	54.5	0.13
Seychelles	45.4	0.16
BIOT (Chagos)	55.9	0.12

The underlying age structure of the length frequency distributions was examined (Figure 9.3). Each 'mode' seen in the length frequency data comprised a number of age classes. The length and age structure for BIOT (Chagos Archipelago) is presented as an example.


a. Length frequency

b. Age structure

Figure 9.3 a) Length frequency and b) underlying age structure (years) derived from random otolith samples from BIOT (Chagos Archipelago).

9.3.1.2 *A. virescens* growth parameter estimates

The ranges of length and age data available to perform age-based estimates of growth are presented in Table 9.5, by location.

Table 9.5 Summary of the *A. virescens* samples aged by bank.

Location	Numbers of individuals			Fork Length Range (cm)	
	Aged	Random Samples	Targeted Samples	Minimum	Maximum
BIOT (Chagos)	304	281	23	30	94
Seychelles	1275	1275	0	30	99

The growth parameters derived for *A. virescens* through length- and age-based methods are presented in Table 9.6, together with estimates from the literature. The fits of the resultant growth curves to the data from which they were derived are presented in Figures 9.4 and 9.5.

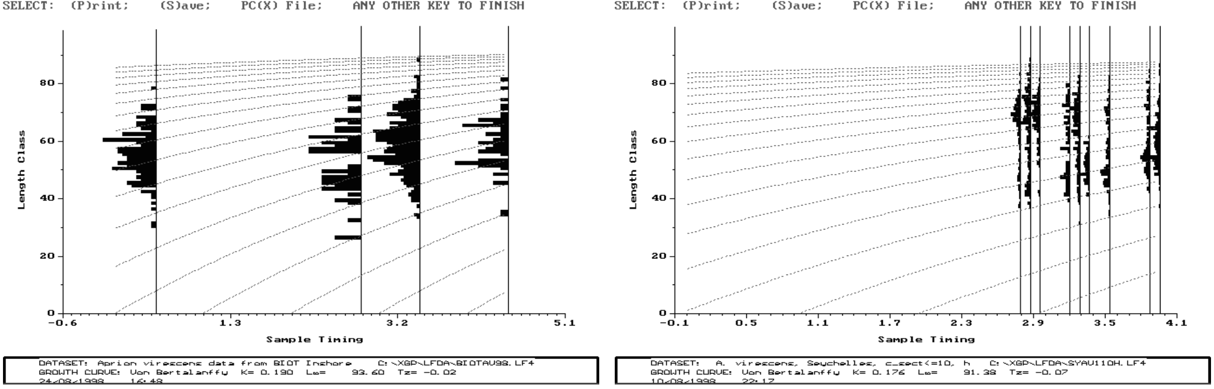
Table 9.6 *A. virescens* length-based ('Length') and age-based ('Age') growth parameter estimates, by location. The time series of data used, and the score function of the resulting length-based fit are shown. All data from handline catches unless otherwise stated.

Location	Method	L_∞	K	t_0	Period	
					From	To
BIOT (Chagos)	Length	93.6	0.2	0	May '94	Jul '98
	Age	104	0	-3.8	-	-
	Age*	98.2	0	-2.6	-	-
Seychelles, all Mahé Plateau	Length	94.7	0.4	-0.9	May '91	Feb '98
		94.6	0.4	-0.8	May '91	Jul '92
		91.4	0.2	0	Oct '93	Dec '94
		82.7	0.4	-0.3	Jan '96	Feb '98
		$99.6^\dagger$	0.2	-0.9	Jan '96	Jul '97
	Length[1]	94.7	0.3	-0.2	Jan '90	Sep '93
	Age	89.9	0.1	-2.3	-	-

[1] MRAG (1996d). NOTE: this estimate was calculated using SLCA.

* derived using a two-phased growth curve (Soriano *et al.*, 1990). h=0.07, t_h=11.1

† length data obtained from droplines



a. BIOT (Chagos Archipelago)

```
SELECT:  (P)rint;    (S)ave;    PC(X) File;    ANY OTHER KEY TO FINISH
```

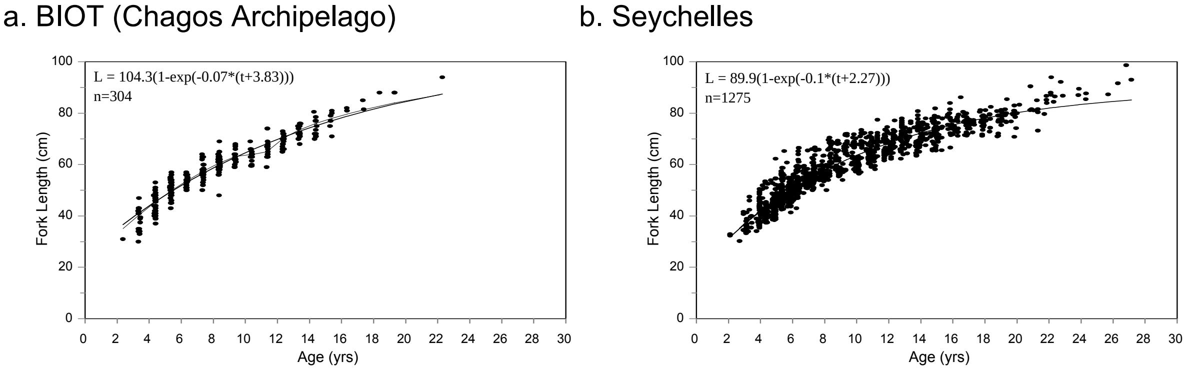
```
DATASET:  Aprion virescens data from BIOT Inshore     C:\XGP\LFDA\BIOTAU98.LF4
GROWTH CURVE:  Von Bertalanffy  K= 0.190  L∞=     93.60  Tz= -0.02
24/08/1998     16:48
```

b. Seychelles, Oct '93 to Dec '94

```
SELECT:  (P)rint;    (S)ave;    PC(X) File;    ANY OTHER KEY TO FINISH
```

```
DATASET:   A.  virescens, Seychelles, c_sect<=10, h    C:\XGP\LFDA\SYAU110H.LF4
GROWTH CURVE:  Von Bertalanffy  K= 0.176  L∞=     91.38  Tz= -0.07
10/08/1998     22:17
```

Figure 9.4 Screen captures of the best fitting von Bertalanffy growth curves assessed using ELEFAN for *A. virescens* for locations in the Indian Ocean. 9.5 b represents an example of the fits obtained for Seychelles.


a. BIOT (Chagos Archipelago)

b. Seychelles

Figure 9.5 Observed lengths-at-age and fitted von Bertalanffy growth curves for *A. virescens* by location. Both non-seasonal and seasonal curves plotted for BIOT (Chagos Archipelago) data. Equation detailed describes the non-seasonal curve.

Length-based estimates of L_∞ from both Seychelles and BIOT (Chagos Archipelago) were relatively consistent. Although estimates ranged from 82.7cm to 99.6cm, six of the seven estimates were larger than 90cm. Estimates of K varied between 0.18 and 0.37, and showed little relationship to the size of the L_∞ estimate.

Age-based L_∞ estimates were generally comparable with those estimated by length-based methods. Estimates of K, however, were consistently lower than length-based estimates. K estimates were again affected by a lack of young individuals in the samples. Age-based growth parameters were therefore re-estimated with t_0 constrained to zero (Table 9.7).

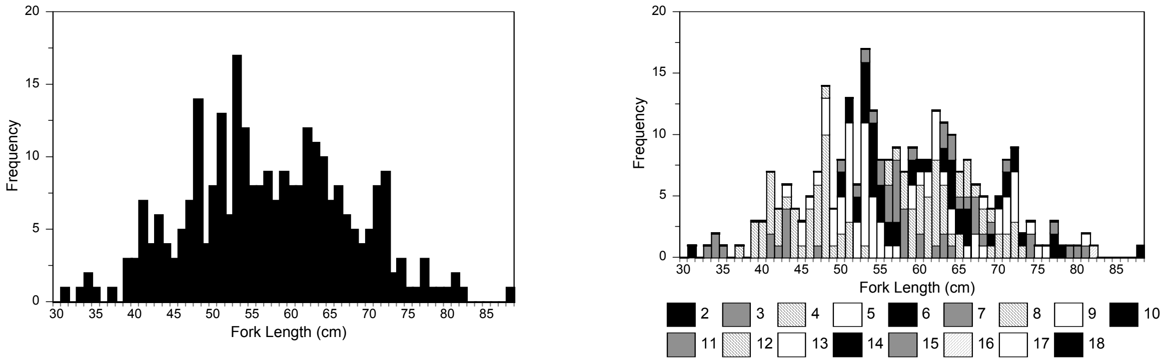
Table 9.7 Age-based growth parameter estimates where t_0 was constrained to zero, by location.

Location	L_∞ estimate	K estimate
Seychelles	80.3	0.17
BIOT (Chagos)	78.4	0.19

Constraining t_0 resulted in similar growth parameter values in each location. K estimates were comparable to that derived through length-based estimates for BIOT (Chagos Archipelago). Age-based estimates still indicated slower growth than the majority of length-based K estimates. For both locations, length-based estimates of L_∞ were larger than those resulting from age-based estimates with constrained t_0 values.

Due to the appearance of the age-at-length distribution for BIOT (Chagos Archipelago), a two-phased growth curve (Soriano *et al.*, 1990) was also fitted to the data. This resulted in an improved fit to the data (Figure 9.5a). However, the two-phased appearance of the growth curve may be a result of the relatively small sample size from this location. Therefore, further estimation methods have used non-seasonal growth parameters. More samples would be required before the nature of the *A. virescens* curve in BIOT (Chagos Archipelago) could be assessed definitively.

The age structure underlying the length frequency distributions was examined. Each apparent mode seen in the length frequency data comprised a number of age classes. The distributions for BIOT (Chagos Archipelago) are presented as an example (Figure 9.6).



a. Length frequency

b. Age structure

Figure 9.6 a) length frequency and b) underlying age structure (years) derived from BIOT (Chagos Archipelago) random otolith samples.

9.3.2 Total mortality and length/age at first capture estimates

This section examines the estimates of total mortality and length at first capture for each species, using the 1997 data sets. As stated earlier, this was the only year in which both length and age data were available from the majority of locations.

Growth parameter estimates are required as input parameters for estimation of total mortality by length-based methods (Beverton and Holt Z estimator, and the length-converted catch curve). Both the length-based and age-based growth parameter estimates derived in Section 9.3.1 were used. Catch curves were also derived directly from age frequency distributions obtained from otolith readings, or the application of an age-length key to the relevant length frequency distribution.

Using the derived catch curves, estimates of the length and age at first capture (Lc_{50} and Ac_{50}) were also calculated. Age-based Ac_{50} estimates were converted into Lc_{50} using the estimated von Bertalanffy growth parameters. Length-based Lc_{50} estimates were converted into Ac_{50} using the inverse of this function.

9.3.2.1 *L. mahsena*

Total mortality estimates derived from length-based methods (using both length-based and age-based growth parameters), and those derived directly through age-based methods, are presented in Table 9.8.

In general, total mortality estimates followed the pattern expected from the level of fishing effort. BIOT (Chagos Archipelago) estimates from each method were consistently the lowest. Saya south and Saya north had the highest estimates of total mortality, while Nazareth and Seychelles estimates were at an intermediate level. However, between this pair, estimated total mortality in Seychelles was greater than that for Nazareth, the opposite expected from the effort levels. The Seychelles estimate from age frequency distributions (‘Afreq’) was also greater than that from the relatively heavily fished banks of Saya de Malha.

Table 9.8 Total mortality estimates derived either from the Beverton and Holt method (B&H Z) or catch curves from length or age frequency distributions (CC Z), for 1997. Lfreq = derived from length frequency; Afreq = derived directly from age frequency, ALK = derived from application of ALK to length frequency. 'Ages used' denotes age classes used in the catch curve regression. Ac_{50} (years) and Lc_{50} (cm) estimates also presented.

Location	Method	B&H Z	CC Z	Ages used	Ac_{50}	Lc_{50}
Nazareth	Lfreq[1]	1.06	1.05	-	1.9	23.9
	Lfreq[2]	0.43	0.4	-	4.1	24.9
	Afreq	-	0.63	7-14yrs	3.5	23.2
Saya south	Lfreq[1]	1.34	1.34	-	2.4	24.3
	Lfreq[2]	0.72	0.66	-	4.7	24.9
	Afreq	-	0.77	6-11yrs	3.4	19.7
	ALK	-	0.92	6-13yrs	2.9	17.7
Saya north	Lfreq[1]	1.36	1.39	-	1.8	21.4
	Lfreq[2]	0.66	0.65	-	4	21.8
	ALK	-	0.72	5-13yrs	2.4	15.9
Seychelles	Lfreq[1]	1.72	1.13	-	1.8	27.2
	Lfreq[2]	0.85	0.49	-	6.9	28
	Afreq	-	0.87	7-12yrs	4.6	22
BIOT (Chagos)	Lfreq[1]	0.93	0.68	-	3.9	29.9
	Lfreq[2]	0.57	0.37	-	6.1	30.4
	Afreq	-	0.4	9-15yrs	5.1	27.3
	ALK*	-	0.48	8-12yrs	4	23.9
	ALK*	-	0.94	13-16yrs	-	-

* age frequency resulting from application of 1997 age-length key to length frequency distribution of that year showed two distinct mortality levels between the ages used in the regressions.

[1] estimate derived using length-based growth parameters (Table 9.3).

[2] estimate derived using age-based growth parameters (Table 9.3).

Both Beverton and Holt's Z estimates and those from the length-converted catch curve were extremely sensitive to the growth parameter estimates used. Total mortality estimates using length-based growth parameters were notably higher than those estimated using age-based growth parameters. The use of age frequencies ('Afreq' or 'ALK') generally resulted in higher total mortality estimates than those from length-based methods where age-based growth parameters were used.

For the Mauritian banks, total mortality estimates from Beverton and Holt's Z and length converted catch curve were comparable where either set of growth parameters were used. For Seychelles and BIOT (Chagos Archipelago), Beverton and Holt estimates were larger than those from the length-converted catch curve.

In BIOT (Chagos Archipelago), the use of the age-length key resulted in two distinct mortality 'phases', with the mortality rate appearing to double from around 12-13 years old. Since such a transition was not found in the age frequency distribution, this may be an artefact resulting from the application of the age-length key to the length frequency distribution. Indeed, it was felt that estimates derived from age frequency distributions estimated directly from otolith assessments were more accurate than that from the age-length key. Given the level of variability in length-at-age for this species, a large sample size was required to cover the range of ages at each length. Sample sizes in the current study were relatively low, particularly at the upper and lower limits of the length frequency distributions.

Lc_{50} estimates from length-based methods were generally consistent between growth parameter estimates. In contrast, Ac_{50} estimates varied notably between age-based methods. Comparisons of the outputs from length- and age-based methods required the conversion of Lc_{50} to Ac_{50}, and *vice versa*. This relied on the growth parameter estimates. Faster growth rates indicated by the length-based growth parameters therefore resulted in a lower Ac_{50} when compared to the age-based estimate. In turn, age-based growth parameters resulted in lower Lc_{50} estimates, due to the relatively slow estimated growth rate.

Between locations, estimates of Lc_{50} and Ac_{50} for Seychelles and BIOT (Chagos Archipelago) were generally larger than those from the Mauritian banks. Across the Mauritian banks, length-based Lc_{50} estimates were relatively consistent.

9.3.2.2 *Aprion virescens*

Total mortality estimates derived through length-based methods (using both length-based and age-based growth parameter estimates), and those derived directly from age frequency distributions, are presented in Table 9.9.

Length-based total mortality estimates derived using age-based growth parameters were notably lower than those using length-based growth parameters. In turn, age-based total mortality estimates (‘Afreq’ or ‘ALK’) were lower than both estimates using length frequency distributions.

Table 9.9 Total mortality estimates (Z) derived either from the Beverton and Holt method (B&H Z) or catch curves from length frequency or age frequency distributions (CCZ), for 1997. Lfreq = derived from length frequency; Afreq = derived directly from age frequency, ALK = derived from application of ALK to length frequency. ‘Ages used’ denotes age classes used in the catch curve regression. Ac_{50} (years) and Lc_{50} (cm) estimates also presented.

Location	Method	B&H Z	CC Z	Ages used	Ac_{50}	Lc_{50}
Seychelles	Lfreq[1]	1.28	1.84	-	2.2	63.4
	Lfreq[2]	1.07	0.39	-	9.8	62.9
	Afreq	-	0.19	5-26yrs	2.7	35.4
BIOT (Chagos)	Lfreq[1]	0.66	0.93	-	3.9	48.9
	Lfreq[2]	0.33	0.47	-	5.3	49.2
	Afreq	-	0.17	5-15yrs	2.8	38.7
	ALK	-	0.17	6-15yrs	3.2	40.5

[1] estimate derived using length-based growth parameters for location (Table 9.6. Seychelles: L_∞=94.7, K=0.36).

[2] estimate derived using age-based parameters for location (Table 9.6).

Beverton and Holt estimates of total mortality were generally lower than those from the length converted catch curve. The exception was the Seychelles estimate employing age-based growth parameters. Both age-based and length-based estimation methods indicated a lower total mortality in BIOT (Chagos Archipelago) compared to Seychelles, although this was marginal where age frequency distributions (‘Afreq’) were used.

Estimates of length- and age-at-first-capture varied between methods. Length-based Lc_{50} and Ac_{50} estimates were generally larger than those estimated using age-based methods. Length-based Lc_{50} estimates were generally consistent between growth parameter estimates, while Ac_{50} estimates varied as a result of the growth parameters used. Length-based Lc_{50} estimates for Seychelles were notably higher than those from BIOT (Chagos Archipelago). Age-based estimates of Lc_{50} and Ac_{50} were comparable between locations.

9.3.3 Estimation of natural mortality, F_{curr} and $F_{0.1}$

The natural mortality rate was estimated through both Pauly's and Ralston's equations, for each set of growth parameters. F_{curr} was then derived through the subtraction of total and natural mortality estimates, using the parameter combinations described in Section 9.2.3.

Estimates of Ac_{50}, growth parameters and the natural mortality rate were used to calculate yield-per-recruit using Beverton and Holt's equation (Beverton and Holt, 1957). $F_{0.1}$ was then estimated.

9.3.3.1 *L. mahsena*

Estimates of natural mortality (M), current fishing mortality (F_{curr}) and $F_{0.1}$ are presented in Table 9.10.

Table 9.10 Estimates of natural mortality (Pauly's M: M_P, Ralston's M: M_R), current fishing mortality (F_{curr}) and $F_{0.1}$, by location for 1997. Estimates of each parameter based on the most appropriate combination of total and natural mortality estimates.

Location	Method	M_P	M_R	F_{curr}	$F_{0.1}$
Nazareth	Lfreq[1]	0.57	0.51	0.49	0.46
	Lfreq[2]	0.22	0.14	0.26	0.11
	Afreq	0.22	0.14	0.41 - 0.49	0.10 - 0.17
Saya south	Lfreq[1]	0.54	0.47	0.8	0.45
	Lfreq[2]	0.29	0.2	0.42	0.17
	Afreq	0.29	0.2	0.48 - 0.57	0.14 - 0.21
	ALK	0.29	0.2	0.63 - 0.72	0.13 - 0.18
Saya north	Lfreq[1]	0.54	0.46	0.82	0.41
	Lfreq[2]	0.27	0.18	0.47	0.13
	ALK	0.27	0.18	0.45 - 0.54	0.11 - 0.16
Seychelles	Lfreq[1]	0.77	0.74	0.95	0.89
	Lfreq[2]	0.19	0.12	0.37	0.1
	Afreq	0.19	0.12	0.68 - 0.75	0.08 - 0.14
BIOT (Chagos)	Lfreq[1]	0.37	0.29	0.56	0.34
	Lfreq[2]	0.27	0.18	0.19	0.18
	Afreq	0.27	0.18	0.13 - 0.22	0.16 - 0.26
	ALK	0.27	0.18	0.21 - 0.30	0.15 - 0.23

[1] estimate derived using length-based growth parameters for location (Table 9.3).
[2] estimate derived using age-based parameters for location (Table 9.3).

The estimates of both M and $F_{0.1}$ derived using length-based methods and length-based growth parameters were consistently larger than those estimates derived from other methods. The large estimate of M was a direct result of the length-based growth parameter estimates. As noted in Chapter 7, M and $F_{0.1}$ were directly related, and hence a correspondingly large $F_{0.1}$

estimate resulted. By comparison, age-based growth parameter estimates resulted in lower M estimates, and hence lower $F_{0.1}$ estimates.

The lowest F_{curr} estimates tended to result from subtraction of Ralston's M from the length converted catch curve total mortality estimate employing age-based growth parameters (Lfreq[2]). The largest estimate resulted from the subtraction of Pauly's M, estimated using length-based growth parameters, from Beverton and Holt's Z (Lfreq[1]).

As a result of the large estimate of total mortality when using length-based growth parameters (Table 9.8), F_{curr} estimates were generally larger than those resulting from the use of age-based growth parameters. However, the overestimation of M through length-based methods reduced the difference between F_{curr} values derived using the two sets of growth parameters (*e.g.* Table 9.10, Nazareth bank). In turn, F_{curr} estimates derived using age-based total mortality estimates ('Afreq', 'ALK') were generally comparable to those derived using length-based total mortality estimation methods and age-based growth parameters (Lfreq[2]).

As a result of the trends in total mortality, F_{curr} estimates followed the expected pattern related to the level of fishing effort applied. BIOT (Chagos Archipelago) F_{curr} estimates were the lowest, while estimates from the banks of Saya de Malha were higher than those for Nazareth bank. All methods indicated that Seychelles had been subjected to a higher level of current fishing mortality than expected.

9.3.3.2 *A. virescens*

Natural mortality (M), current mortality (F_{curr}), and $F_{0.1}$ estimates are presented in Table 9.11.

Table 9.11 Estimates of natural mortality (Pauly's M: M_P, Ralston's M: M_R), current fishing mortality (F_{curr}) and $F_{0.1}$, by location in 1997. Estimates based on the most appropriate combination of total and natural mortality estimates.

Location	Method	M_P	M_R	F_{curr}	$F_{0.1}$
Seychelles	Lfreq[1]	0.65	0.76	0.62	0.89
	Lfreq[2]	0.29	0.22	0.1	0.35
	Afreq	0.29	0.22	<0	0.18 - 0.25
BIOT (Chagos)	Lfreq[1]	0.43	0.4	0.23	0.47
	Lfreq[2]	0.22	0.16	0.31	0.16
	Afreq	0.22	0.16	≤0	0.13 - 0.18
	ALK	0.22	0.16	≤0	0.19

[1] estimate derived using length-based growth parameters for location (Table 9.6, Seychelles: L_∞ = 94.7, K=0.36)

[2] estimate derived using age-based parameters for location (Table 9.6)

Parameters estimated through length-based methods with length-based growth parameters were larger than those from either age-based growth parameters, or age-based methods. Using the total mortality estimate from the age-frequency distributions, and estimates of natural mortality from the age-based growth parameters, F_{curr} estimates resulted which were less than, or equal to, zero. The fact that F_{curr} estimates were less than zero may indicate that the empirical equations for natural mortality had overestimated M for this species, or alternatively that total mortality had been underestimated using age-based catch curves.

9.3.4 Assessment of stock status

Stock status was assessed through two methods. In the first, F_{curr} estimates were compared to that of $F_{0.1}$. In the second, comparisons were made between M and F_{curr}, and Lm_{50} with Lc_{50}.

In the latter comparison if F_{curr} was greater than M, concern was warranted if Lc_{50} was less than Lm_{50}.

The percentage difference between the F_{curr} and reference fishing mortality level estimates was assessed. The results are presented in Table 9.12 for *L. mahsena*, and Table 9.13 for *A. virescens*. As noted in Chapter 8, the use of length- or age-based growth parameter estimates required tuning of the reference effort level ($F_{0.1}$), dependent on the level of exploitation in the fishery. Using the outputs of that chapter, the effect of tuning on the stock assessments was also examined, based on the corresponding estimate of F_{curr}. Due to the uncertainty over the exact values required for tuning at the F_{curr} levels estimated in Tables 9.10 and 9.11, percentages in Table 9.13 have been rounded to the nearest 10%. The level of concern is based on the untuned $F_{0.1}$.

For *L. mahsena*, F_{curr} for the Mauritian banks and Seychelles (estimated for all methods) was greater than the estimate of $F_{0.1}$. For the majority of these locations, F_{curr} was larger than both estimates of natural mortality. In BIOT (Chagos Archipelago), length-based estimates of F_{curr} were generally larger than both $F_{0.1}$ and M. Age-based methods ('Afreq'), however, indicated that F_{curr} was close to, or less than, both reference mortality levels ($F_{0.1}$ and M). The use of age-length keys generally resulted in larger estimates of F_{curr} than those from the direct assessment of age frequency distributions. As a result, the amount by which F_{curr} exceeded $F_{0.1}$ was increased. This was particularly notable at Saya south (SMS).

Age-based methods tended to indicate that concern, or serious concern, was warranted for both the Mauritian banks and Seychelles. In contrast, length-based estimates, in conjunction with length-based growth parameter estimates, indicated no cause for concern. No concern was expressed for BIOT (Chagos Archipelago) through any method.

The pattern was strongly influenced by the estimated $F_{0.1}$ values. Generally, estimates of F_{curr} derived using length- and age-based growth parameters were relatively comparable. For length-based growth parameters, these estimates corresponded with relatively large $F_{0.1}$ values (Table 9.10), while $F_{0.1}$ estimated using age-based growth parameters was notably lower. As a result, where age-based growth parameters were used, the estimate of F_{curr} tended to be larger than that of $F_{0.1}$, resulting in concern for the stock.

In the majority of cases, tuning the reference effort level for the stock assessment based on the corresponding fishing mortality (F_{curr}) level had a minimal impact on the overall level of concern for the fishery. Only at Nazareth bank was the level of concern reduced by tuning in the case of the age-based F_{curr} estimate. However, F_{curr} remained over 100% greater than the estimated $F_{0.1}$ level.

Table 9.12 *L. mahsena* stock status indicated by the comparison of F_{curr} and $F_{0.1}$, and the comparison of Lc_{50} with Lm_{50}, and F_{curr} with M, by study location for 1997. M_P = Pauly's M, M_R = Ralston's M. BIOT = BIOT (Chagos Archipelago).

Location Code	Z Method	$F_{0.1}$ and F_{curr}			F_{curr} and M, Lc_{50} and Lm_{50}	
		% F_{curr} >$F_{0.1}$	% F_{curr} > tuned $F_{0.1}$	Concern	% F_{curr} > M_P or M_R	Concern
NAZ	Lfreq[1]	7%	0%	None	-14% / -4%	None
	Lfreq[2]	136%	70%	None	15% / 86%	None
	Afreq	188%	110%	**Concern**	123% / 193%	**Concern**
SMS	Lfreq[1]	78%	100%	None	67% / 70%	None
	Lfreq[2]	147%	130%	None/ **Concern**	45% / 110%	None
	Afreq	171%	150%	**Concern**	97% / 140%	None
	ALK	300%	200%	**Serious**	148% / 215%	**Concern**/ **Serious**
SMN	Lfreq[1]	100%	150%	None	52% / 78%	None
	Lfreq[2]	262%	240%	**Serious**	74% / 161%	None/ **Concern**
	ALK	238%	190%	**Serious**	100% / 150%	None/ **Concern**
SEY	Lfreq[1]	7%	50%	None*	23% / 28%	None*
	Lfreq[2]	270%	250%	**Serious***	95% / 208%	None/ **Serious***
	Afreq	436%	220%	**Serious***	295% / 467%	**Serious***
BIOT	Lfreq[1]	65%	50%	None	51% / 93%	None
	Lfreq[2]	5%	20%	None	-30% / 5%	None
	Afreq	-15%	-20%	None	-19% / -27%	None
	ALK	30%	10%	None	11% / 17%	None

* Lc_{50} > Lm_{50} in Seychelles

[1] estimate derived using length-based growth parameters for location (Table 9.3)

[2] estimate derived using age-based parameters for location (Table 9.3)

Table 9.13 *A. virescens* stock status indicated by the comparison of F_{curr} and $F_{0.1}$, and the comparison of F_{curr} with M, and Lc_{50} with Lm_{50}, by study location for 1997. M_P = Pauly's M, M_R = Ralston's M. BIOT = BIOT (Chagos Archipelago).

Location Code	Z Method	$F_{0.1}$ and F_{curr}			F_{curr} and M, Lc_{50} and Lm_{50}	
		% F_{curr} >$F_{0.1}$	% F_{curr} > tuned $F_{0.1}$	Concern	% F_{curr} > M_P or M_R	Concern
SEY	Lfreq[1]	-30%	-10%	None	-5% / -18%	None
	Lfreq[2]	-71%	-80%	None	-66% / -55%	None
	Afreq	$F_{curr} < 0$	-	None	$F_{curr} < 0$	None
BIOT	Lfreq[1]	-51%	-70%	None	-47% / -43%	None
	Lfreq[2]	94%	50%	None	61% / 41%	None
	Afreq	$F_{curr} < 0$	-	None	$F_{curr} < 0$	None
	ALK	$F_{curr} < 0$	-	None	$F_{curr} < 0$	None

[1] estimate derived using length-based growth parameters for location (Table 9.6)

[2] estimate derived using age-based parameters for location (Table 9.6)

For *A. virescens* in both locations, in the majority of cases F_{curr} was lower than the reference mortality levels. Only for BIOT (Chagos Archipelago) in the Lfreq[2] assessment was the estimated F_{curr} greater than $F_{0.1}$ or M. This resulted from the relatively high length-converted catch curve estimate of total mortality (defined by the form of the length frequency) when compared to Seychelles. However, the results indicated that there were no concerns over the status of either study population at the current level of fishing effort. As in the case of *L. mahsena*, tuning the $F_{0.1}$ level had little effect on the level of concern for the study fisheries.

9.4 DISCUSSION

This study had two aims. The first was to compare the outputs of length- and age-based methods of growth and mortality estimation, and to examine whether the results of the simulations performed in Chapter 7 were mirrored when using actual fisheries data. The second was to obtain the first age-based growth and mortality estimates for the study locations, and, based on these estimates, to examine the current stock status in each location.

9.4.1 Growth parameters

Von Bertalanffy growth parameters were estimated through two methods; by analysing length frequency data with the ELEFAN computer programme, and by fitting growth curves to length-at-age data from otolith assessments. The results of the two methods were compared using auximetric grids, while age-based growth parameters from different locations were compared using likelihood ratio tests.

Only ELEFAN was selected to be used in this study. Initial studies indicated that both SLCA and PROJMAT estimated growth parameters which tended toward extremely high or low values. A similar pattern was seen in Chapter 7, and found by both MRAG (1996d) and Posada and Appeldorn (1996) for these and related species. Although SLCA and PROJMAT appear appropriate for use on faster growing species (*e.g.* Basson *et al.*, 1988; Isaac, 1990), they appear inappropriate for the slow growing species studied.

As indicated by Mulligan and Leaman (1992), growth parameter estimates resulting from both length-based and age-based methods were affected by the data to which they were applied.

As described in Chapter 7, length-based estimates were influenced by the size range of the assessed length distributions. Similar patterns were identified in the results described in the current chapter. For example, the increased L_∞ estimate derived for BIOT (Chagos Archipelago) compared to the Mauritian banks was related to the greater proportion of large individuals sampled at the former location. Due to the negative relationship between the two growth parameters, this resulted in a relatively low estimate of K for BIOT (Chagos Archipelago).

Age-based methods were also affected by the size range of data assessed. The presence of small individuals in the sample, particularly those of 2 years old or less, was critical to achieving a reasonable estimate of K. Such data 'anchored' the growth curve at t_0 (*e.g.* for *L. mahsena*, Saya south and Saya north). Assessments for Nazareth bank, BIOT (Chagos Archipelago) and Seychelles were affected adversely by the lack of such individuals, resulting in the probable underestimation of K. Samples lacking these individuals are common in fisheries data (*e.g.* Rowling and Reid, 1992; Ferreira and Russ, 1994; Jones and Wells, 1998; Vilizzi and Walker, 1999), as a result of gear selectivity. Due to the underestimation of K, and hence low gradient of the growth curve, L_∞ was overestimated. For *L. mahsena* at Saya south and Saya north, where K estimates were felt to be more accurate, L_∞ estimates from length- and age-based methods were comparable. Both were influenced by the largest size class seen in the samples.

Age-based growth parameter estimates consistently indicated slower growth than that estimated through length-based methods for both species. In part, this may have resulted from the lack of young individuals in the sample (Figures 9.2 and 9.5). To compensate for this, t_0 was constrained to zero, thereby artificially 'anchoring' the growth curve, and age-based growth parameters were re-estimated. The resulting parameters were felt to represent the likely upper limit of the K value, given the data analysed. The resulting K estimates remained lower than those derived from length-based methods.

For *L. mahsena*, the age-based estimates of K derived in this study were comparable to those length-based estimates (derived using Bhattacharya's method) reported in Bautil and Samboo (1988) for Nazareth bank, and in Bertrand (1986) for Saya de Malha bank. On examination of the length frequency data used in these studies, the distributions appeared similar to those assessed in the current study. There were few clear modes present. As such, the apparent accuracy of the K estimate from Bhattacharya's method is somewhat surprising. The length-based estimate reported in Dalzell *et al.* (1992) for the Yemen was comparable to the length-based estimate derived in the current study for Seychelles, and slightly higher than the length-based estimates for all other locations.

For *A. virescens*, age-based estimates of K were notably lower than previous literature estimates. Length-based estimates of K derived in the current study were similar to length-based estimates for Seychelles presented by Mees (1993), and to age-based estimates for this species at New Caledonia (Loubens, 1980). Since otoliths are thought to provide better estimates of growth for *A. virescens*, the latter estimate indicates this species may grow faster in this location.

The results of this study, and comparisons with literature estimates, supports the results of Chapter 7; ELEFAN tends to overestimate K in these long-lived, slow growing species. This contrasts with the findings of Hampton and Majkowski (1987), Rosenberg and Beddington (1987) and Isaac (1990), who found that ELEFAN and SLCA tended to underestimate K in simulations of faster growing species.

Unlike the study of Shepherd *et al.* (1987), age-based growth estimates did not correspond to local peaks in the score function of the length-based methods. The region of the age-based estimates was characterised by a uniformly low goodness of fit score. Therefore, the length frequency distributions appeared to contain little information with which length-based methods could identify the slower growth rate. As indicated by the comparison of length structure and underlying age structure for both species, modes seen in the length distributions did not relate to individual age classes. Hence, where length-based estimation methods attempted to fit growth curves through modes in these distributions, each 'cohort' thus described encompassed a number of age classes, resulting in the overestimation of the growth rate (*e.g.* Figure 9.3).

If the density dependent growth model put forward in Chapter 4 were operating, age-based methods would indicate an increase in the magnitude of the K estimate, while length-based methods would show an increase in L_∞. It appears unlikely, however, that growth parameter estimates from either method are sufficiently accurate to identify density dependent growth. Age-based estimates of K are biased by a lack of young individuals in the sample. For length-based methods, L_∞ estimates are biased by the length range of the sample analysed. To assess density dependent growth, samples would therefore need to be consistent and accurate, an unlikely situation due to the level of between-year variability in the length frequency distributions identified in Chapter 6. In the absence of direct growth rate adjustments (*e.g.* rearing studies), it is suggested that the examination of length-at-age data (Chapter 6) is the most appropriate to identify density dependent growth.

9.4.2 Mortality estimates

Total and natural mortality were estimated through a number of methods, using the estimated length-based or age-based growth parameters. In turn, these mortality estimates were used to estimate the level of current fishing mortality (F_{curr}), in the light of the results from the simulations performed in Chapter 7.

As shown in Chapter 7, total and natural mortality estimates, and hence the resulting F_{curr} estimate, were strongly influenced by the growth parameters used. As indicated by the sensitivity analyses presented in Mees and Rousseau (1997), total mortality estimates are positively correlated with both K and L_∞. High total mortality estimates therefore resulted from length-based methods employing length-based growth parameters (higher K), while low estimates resulted from the use of age-based growth parameters (lower K counteracting increases in L_∞).

Length-based estimates of total mortality suffer from a number of drawbacks. They require growth parameter inputs; inaccuracies in these estimates will contribute to the level of bias in the total mortality assessments. Length-based total mortality estimates are likely to be improved by using age-based growth parameters. However, these growth parameters remain slightly flawed if the age range sampled is truncated. Length-based methods suffer from further problems where density dependent growth is operating; the effect of increased growth rates on the length frequency distribution results in the underestimation of total mortality (Chapter 7).

For these reasons, the use of age-based methods is likely to result in more accurate total mortality estimates. While growth parameter estimates and the length structure are affected by density dependence, the effect on the underlying age structure may be minimal. Some effects may remain, however. Increased growth rates may lead to an increase in the proportion of younger individuals in the catch age structure. Such increases would be likely to affect the ascending limb of the catch curve, minimising the effect on total mortality estimates. However, care is still warranted since, in the extreme case, such increases could positively bias the total mortality estimate.

For *L. mahsena*, age frequency distributions generally indicated a higher level of mortality than estimates from length-based methods using age-based growth parameters, the pattern expected to result from density dependence. For *A. virescens*, however, the opposite trend was found; age-based total mortality estimates in both Seychelles and BIOT (Chagos Archipelago) were lower than length-based estimates of mortality. Evidence for density dependent growth was identified in both species in Chapter 6. However, the effects of density dependence on total mortality estimates may be masked by variation resulting from the methods employed, samples examined, and growth parameters used.

Estimates resulting from the use of age-length keys were generally comparable to those derived directly from age frequency distributions. One problem with the use of the age-length key is the degree of variability in age-at-length, which is high in these slow growing species. To obtain a definitive age-length key, therefore, sufficient otoliths must be assessed in each size class to cover the ages present adequately. Where the variability in age-at-length is high, such as in the study species, this number may be significant (Holden and Raitt, 1974). If an age-length key must be constructed each year, it may prove more beneficial to concentrate on the direct construction of an age frequency distribution.

The simulations performed in Chapter 7 indicated that Beverton and Holt's total mortality estimates tended to be lower than those from the length-converted catch curve. In this study, however, total mortality estimates from the length-converted catch curve were consistently lower. In part, this may be a result of the increased level of control the user had in selecting the points of the catch curve through which to estimate total mortality. Such control was not available in Chapter 7.

The total mortality estimates for a location, and hence F_{curr} estimates, generally related to the level of fishing effort applied. Estimates for *L. mahsena* from BIOT (Chagos Archipelago), for example, were the lowest, while corresponding estimates for the Mauritian banks were larger. Both length- and age-based estimates for Seychelles were larger than that expected from the level of fishing effort experienced from 1991. This may be the result of a comparatively high level of historical fishing before 1991, when compared to BIOT (Chagos Archipelago) (see Chapter 6). In turn, if the level of natural mortality was significantly higher in this location, this might also contribute to the increased total mortality estimate. Alternatively, samples from Seychelles may have been biased, either by the effects of gear selectivity, or the localised population structure from the areas in which samples were taken (Chapter 6).

While estimates of total mortality resulting from age-based methods avoid the problems inherent with the use of growth parameters in the estimation process, problems in the estimation of F_{curr} still arose due to the lack of independent natural mortality estimates. Currently, estimates must be derived from the empirical equations of Pauly and Ralston. These require the use of growth parameter estimates, to which the resultant mortality estimates are directly related (Chapter 7). As a result, natural mortality estimates derived from length-based methods were greater than those from the age-based estimates of growth. If these equations accurately estimated natural mortality, then those values derived using age-based growth parameters are the most appropriate. However, given the potential underestimation of age-based K estimates, M could also be underestimated at most locations.

For *A. virescens*, the age-based total mortality estimate (Z=0.17 to 0.19) was comparable to the natural mortality rate estimated using age-based growth parameters. The collection of additional data for young individuals would improve growth parameter estimates, increasing the K estimate, and decrease that of L_∞. As a result, estimates of M from both Pauly's and Ralston's equation would increase above the current Z estimates. Assuming the empirical formulae accurately represent the natural mortality rate in this species, this suggests that current total mortality estimates are indeed close to the level of natural mortality. This is supported by the catch age structure in these locations (Chapter 6), which contained a number of older individuals, indicating a low level of fishing mortality. The estimates of M are notably lower than previous estimates of natural mortality (M=0.49, van der Knapp *et al.*, 1991; Mees, 1992; M=0.51-0.68, Mees *et al.*, 1999). These were generally derived using length-based growth parameter estimates, which accounts for these differences.

As *L. mahsena* was more heavily exploited, estimates of total and natural mortality could not be related in this way. To obtain independent estimates of natural mortality in these locations, further age-based estimates of total mortality under different levels of fishing effort would be required.

The empirical estimates of *L. mahsena* natural mortality for the Mauritian banks in this study were comparable to those derived by Bertrand *et al.* (1986) and Bautil and Samboo (1988) for Nazareth (M=0.22) and Saya de Malha banks (M=0.2) respectively. In these studies, estimates were derived through iterative use of the length-based cohort analysis (Jones, 1984b), with data fitted using different selected values of M. Despite the fact that the growth parameters used appear suitable, the method relies on the catch length structure, which may show considerable between-year variation, or be affected by density dependent growth (Chapter 6). Despite their similarity to the empirical estimates derived in the current study, the literature estimates are therefore open to some uncertainty.

F_{curr} was estimated through the subtraction of the natural mortality estimates from total mortality. Estimates were consistently high when derived from length-based growth parameters. Given the problems inherent in length-based total mortality estimation methods, age-based F_{curr} estimates are felt the most appropriate for these species. It should be noted that the use of age-based growth parameter estimates in combination with the age-based estimates of total mortality may result in slightly cautious (positively biased) F_{curr} estimates; if the empirical formulae are accurate, M may be underestimated as a result of the underestimation of K.

For *A. virescens*, F_{curr} estimates derived through age-based methods were equal to, or less than, zero. As stated, the estimate of total mortality from the age frequency may be equivalent to natural mortality. Given the greater mobility of this species (Chapter 6), and the fact that it is generally not targeted in these fisheries, the effort level applied in each location as a whole may not have affected the catch length or age structure. Localised fishing effort, however, may be sufficient to affect both the length and age structure and the rate of growth, as indicated in Chapter 6.

9.4.3 *L. mahsena* otolith weight - age relationship

The reading of otoliths can introduce bias through subjective assessments of the ages assigned to individuals. To minimise this bias, the use of otolith weight has been put forward as a non-subjective method of age assessment (Boehlert, 1985; Worthington *et al.*, 1995a; Worthington *et al.*, 1995b). Once the relationship between age and otolith weight has been determined, errors of this type are only introduced during the estimation of otolith weight, which may be easier to quantify and correct (Richards *et al.*, 1992).

A. virescens otoliths could not be used to derive an otolith weight - age relationship, since the structure and fragile nature of the otoliths made them prone to breaking on extraction from the fish. The study described in Appendix 7 therefore concentrated on the otoliths of *L. mahsena*. A relationship was derived for four of the study locations. Each relationship was assessed to examine its suitability for use in routine ageing. Employing the relationships, an age frequency distribution was obtained from measured otolith weights, and an estimate of total mortality derived. These distributions, and the resulting estimates, were then compared to those estimated from the true underlying age structure.

The slow growth rate of *L. mahsena*, combined with the notable variation in otolith weight-at-age, reduced the precision of the relationship between otolith weight and age. This was particularly true at older ages, since growth slowed and the level of overlap in otolith weight between ages increased. Otolith weight could not accurately discriminate between individual age classes, rendering the relationship insufficiently accurate to assess individual age-at-length.

However, the otolith weight-age relationship was capable of deriving accurate age frequency distributions. Such distributions estimated using the relationship at each location were not significantly different from the true underlying age structure. Total mortality estimates derived from these age frequencies were also generally comparable. Estimates obtained from distributions derived using the otolith weight-age relationship were more precise, a result of the smoothing effect of the relationship; irregularities in the age distribution were reduced. However, the accuracy of estimates could be affected by a strong age class; slight errors in the relationship can result in influential age classes being assigned to neighbouring classes, significantly altering the age distribution.

L. mahsena otolith weight represents a rapid and potentially cheap method (relatively to in-depth otolith studies) to routinely assess age structure, and hence total mortality. As noted in Appendix 7, given limited resources, the saving in time and money offered by the method may allow increased numbers of fish to be examined, reducing sampling error. Routine monitoring could provide estimates of spatial and temporal variation in longevity and mortality, and monitor recent levels of recruitment (Worthington *et al.*, 1995a).

9.4.4 Length/Age at first capture

Length at first capture (Lc_{50}) and age at first capture (Ac_{50}) were derived from length frequency or age frequency distributions, respectively. Estimates of each parameter were converted into the opposite form, as required, using the estimated growth parameters.

Both the growth parameters used to convert length into age for the catch curve, or convert one estimate into another, and the suitability of the regression fitted to the descending limb, influenced the estimates. Chapter 7 indicated that length-based estimates of Lc_{50} were accurate. Assuming this held in practical assessments, Lc_{50} estimates resulting from the conversion of the age-based Ac_{50} estimates were inaccurate, since they were consistently lower than length-based estimates. This resulted from the low age-based K estimates, resulting in the underestimation of length-at-age at these relatively young ages.

The most appropriate estimate will be dependent on the parameter required. Given the results of Chapter 7, and the comparison of length-based and age-based assessments, if Lc_{50} estimates are required, the outputs of length-based assessments appear appropriate. Length-based estimates of Lc_{50} were relatively consistent between the growth parameter estimates used.

The direct calculation of Ac_{50} from the age frequency frequently suffered from a lack of points (age classes) in the regression of the ascending limb, contributing to uncertainty in the estimates. For length-based methods, such influences were reduced by the increased number of length classes available. However, Ac_{50} estimates from length-based methods required conversion from Lc_{50}. Length-based growth parameters are unsuitable for such a conversion. However, lengths estimated for Lc_{50} were sampled in the length-at-age data from which age-based growth parameters were derived. Therefore, the most appropriate Ac_{50} estimates are likely to result from the conversion of length-based Lc_{50} estimates using age-based growth parameters.

9.4.5 Stock assessment based on comparisons of F_{curr} with $F_{0.1}$ or M

Based on the derived parameter estimates, the status of the study populations was assessed through two different methods. In the first method, estimates of F_{curr} were compared to those of $F_{0.1}$. In the second, F_{curr} was compared to the estimate of M. If F_{curr} was greater than M, concern was warranted where the Lc_{50} estimate was lower than that of Lm_{50} (either that derived in Appendix 6, or 50% of L_∞).

Where length-based growth parameter estimates were used for *L. mahsena*, management indicated no concern was warranted for any location. In stark contrast, estimates derived using age-based growth parameters frequently indicated concern for the study populations. These results were strongly influenced by trends in the estimate of $F_{0.1}$; while estimates of F_{curr} from both methods were relatively comparable, length-based $F_{0.1}$ estimates tended to be greater than those from age-based methods.

The question arises, which of these assessments is more likely to indicate the true status of the fishery? Are estimates of $F_{0.1}$ derived using length-based growth parameters more likely to be greater than the corresponding F_{curr} estimates, when compared to those using age-based growth parameters, at the fishing mortality levels identified for the study fisheries?

One source of information to help answer such questions is the results of simulations performed in Chapter 7. The stock assessments derived in that chapter were summarised using qualitative management action criteria. In itself, this offers little information to answer these questions. However, individual assessments of $F_{0.1}$ and F_{curr} derived using length- and age-based growth parameters, on which these management actions were based, were available for each simulation. Given that the level of fishing mortality in the actual fisheries has been relatively constant, the results from the equilibrium simulations (Scenario 1) were re-examined. The percentage of simulation runs in which the $F_{0.1}$ estimate was greater than that of the estimated F_{curr} level (using the same parameter combinations as those in the current chapter) for each growth parameter estimation method, is presented in Table 9.14.

Table 9.14 Percentage of simulation runs performed in Chapter 7 in which estimated $F_{0.1}$ was greater than estimated F_{curr} ($F_{0.1} > F_{curr}$), by fishing mortality level and growth parameter estimation method.

	$F=0.05yr^{-1}$	$F=0.25yr^{-1}$	$F=0.7yr^{-1}$	$F=1.2yr^{-1}$
Length-based	56%	42%	33%	11%
Age-based	99%	56%	0%	0%

From Table 9.17 the percentage of age-based simulation runs in which $F_{0.1} > F_{curr}$ decreased rapidly with increasing fishing pressure, while those derived using length-based growth parameter estimates decreased at a slower rate.

The majority of F_{curr} levels estimated in the current chapter for the study *L. mahsena* populations (Table 9.10) corresponded to fishing mortality levels between the levels $F=0.25yr^{-1}$ and $F=0.7yr^{-1}$ simulated in Chapter 7. At such fishing mortality levels, the trends in the simulation results indicate that, when compared to assessments using age-based growth parameters, length-based assessments would result in a higher proportion of situations in which $F_{0.1}$ estimates were greater than those of F_{curr}. The results of the fishery simulations of Chapter 7 therefore agree with the results of the stock assessments performed in the current chapter.

The study fishery stock assessments are therefore examined in the light of both the discussions made earlier in the current chapter, and the results of simulations performed in Chapters 7 and 8.

In those chapters, stock assessments made using age-based growth parameters and the 'cautious' F_{curr} estimate resulted in a greater proportion of 'correct' management actions. In the current chapter, it therefore appears appropriate to concentrate on stock assessments derived using age-based growth parameter estimates. In Chapter 8, assessments required tuning to the level of exploitation in the fishery. Based on the tuning factors calculated in that chapter, $F_{0.1}$ estimates derived in the current study were adjusted as appropriate, and the effect on stock assessments examined.

As discussed earlier in this chapter, the most accurate F_{curr} estimates are likely to result from age-based total mortality estimates, and the use of age-based growth parameter estimates in the empirical formulae for natural mortality. Examination of these particular estimates of current fishery status for *L. mahsena* (Table 9.12) indicate that the fishing mortality level in 1997 was frequently well over 100% greater than the level of $F_{0.1}$ or estimated M at both the Mauritian banks (Nazareth, Saya north and Saya south) and Seychelles. While tuning for age-based methods did tend to reduce the difference between the two estimates, F_{curr} generally remained notably greater than the adjusted reference effort level.

For the Mauritian banks, current fishing effort would need to be decreased considerably before the level of fishing mortality was reduced to the level of $F_{0.1}$. In turn, given the degree to which estimated fishing mortality was greater than $F_{0.1}$, such decreases are urgently required. In Seychelles, however, the fact that the estimated length at first capture was greater than the estimated length at maturity would limit the exploitation of the spawning stock biomass, thus avoiding recruitment overfishing. However, current effort is very high, and may result in growth overfishing. If this level of fishing mortality is maintained, the relationship between the lengths at maturity and capture, and trends in the mean length and age of the catch, should be closely monitored.

No concern was expressed for the *L. mahsena* population in BIOT (Chagos Archipelago), where the 1997 fishing mortality level was approximately equal to $F_{0.1}$ and the natural mortality rate. In this location, it appears that fishing effort should not be increased to ensure that the conservation management objective is maintained.

For *A. virescens*, no concern was warranted from the comparison of F_{curr} with both $F_{0.1}$ and M for either BIOT (Chagos Archipelago) or Seychelles. In both locations, age-based estimates indicated that F_{curr} was equal to, or less than, zero. The Lc_{50} estimate for Seychelles was approximately equal to the estimate of Lm_{50} (Appendix 6). If this length at maturity held for BIOT (Chagos Archipelago), the current length at capture estimate is approximately 20cm below this length, indicating caution is required. However, different patterns in Lm_{50} were found for *L. mahsena* between locations, which may also hold for *A. virescens*. Further investigations of the length at maturity are required for this species in BIOT (Chagos Archipelago), before a more definitive assessment can be made.

The low level of fishing effort applied to *A. virescens* indicates that if effort could be targeted on this species, it could be increased. Such increases require caution, however, since this species is only a small part of the multispecies demersal catches on the banks. Increases in effort might also impact on other species populations, which have been more seriously affected by historical fishing.

From the results of this chapter, and those from Chapter 7 and 8, age-based growth parameters and total mortality estimation methods have a number of advantages over the use of length-based methods for long-lived, slow growing species. However, developing countries may encounter problems associated with the costs of this methodology. In Chapter 10, the costs incurred in both length-based and age-based methods of growth assessment will be compared to the benefits obtained in terms of additional revenue from the fishery resulting through improved management. This aims to answer whether the additional costs of age-based methods are outweighed by the benefits which result.

9.4.6 Summary

Age-based estimates of growth and total mortality appear more accurate than length-based estimates for the study species. Length-based methods cannot accurately assess the true underlying age structure from the length frequencies of these long-lived, slow growing species. Problems were encountered during the age-based estimation of growth parameters due to a lack of smaller individuals in the samples from the majority of locations. However, age-based estimates indicated that *L. mahsena* growth rate was comparable to that identified by Bautil and Samboo (1988) through length-based methods. The growth rate indicated for *A. virescens* was notably lower than that identified in previous assessments using length-based methods (Mees, 1992; MRAG, 1996d). This species is more vulnerable to fishing than previously thought.

Inaccuracies in the growth parameter assessments affect length-based total mortality estimates. Density dependent growth would also result in the underestimation of total mortality derived through length-based methods (Chapter 7). The estimation of total mortality by assessing the age structure was felt to minimise these potential biases.

Natural mortality estimates for these species are currently derived using empirical formulae. These require growth parameter inputs, and hence the resultant estimates are potentially biased. The examination of age structures over time, at different levels of effort, would allow an independent estimate of M to be derived.

Serious concern was warranted for *L. mahsena* stocks on the Mauritian banks and in Seychelles. Fishing levels were notably higher than the estimated level of $F_{0.1}$. Despite the extremely high level of fishing mortality at Seychelles, however, concern was mitigated by the relative sizes of the lengths at capture and maturity. Both *L. mahsena* and *A. virescens* stocks in BIOT (Chagos Archipelago), and for the latter species in Seychelles appear lightly exploited at the level of the location. However, such assessments ignore the potential for localised depletion, which may result from fishing practices and the localised population distribution identified in Chapter 6.

10. The costs and benefits of different growth assessment methods

10.1 INTRODUCTION

As noted throughout this report, one of the potential constraints on the use of age-based methods is the cost associated with this methodology. The requirements in manpower, skill and time involved in preparing and reading an otolith are far greater than those involved in the measurement of an individual fish length. Furthermore, the method requires a number of capital investments, such as microscopes and specialised otolith sectioning equipment. These costs render establishing a routine ageing programme unattractive for relatively cash-poor fisheries institutions.

Majkowski *et al.* (1987) noted that the expense of data collection programmes is sufficiently high to warrant the examination of their effectiveness in relation to those costs. However, few published studies have formally calculated the costs involved in assessments through either age- or length-based methods. In Morgan (1983), costs involved with initiating of an ageing programme for the assessment of local fish species around Kuwait were estimated. It was concluded that age-based analyses were 'substantially more expensive' than length-based analyses. In a further examination of Kuwait fishery assessments, Mathews (1987) presented costings for the use of age-based methods. These included the stages of validation, routine ageing, age-length key construction, and subsequent analyses. It was concluded that length-based methods would have cost only 10% of the total price of age-based methodologies.

Simple examinations of the costs involved in different methodologies for stock assessment do not take into account the potential benefits resulting from their use. In Chapters 7 and 8, age-based growth parameters were shown to result in significantly better management advice for long-lived, slow growing species, when compared to that derived using length-based growth parameter estimates. If the additional costs of age-based methods are outweighed by the potential benefits obtained, this method would then make financial sense. To examine this, a cost-benefit analysis is required.

10.1.1 Cost - benefit analysis

Cost-benefit analysis can be described as a group of methods used to analyse project worth (Parker, 1990a). The analysis generally involves three steps:

i) identification of the costs and benefits of the project (including external effects on other parts of the economy, even when these are not obviously apparent, or quantifiable)
ii) evaluation of costs and benefits
iii) comparison of costs and benefits, discounting, and calculation of project worth

Costs are generally easier to identify than benefits, since they are generally directly quantifiable. However, both costs, and in particular benefits, can be intangible. Examples of intangible benefits include improved nutrition. Although such benefits and costs are real, they do not lend themselves to valuation. They should still be recognised, even if no actual value can be assigned, since they may make an important contribution to the project objectives.

Projects generally aim to achieve a long term goal. Once costs and benefits have been quantified, therefore, analyses must compare different projects, lasting several years, with different cost and benefit streams. Therefore, methods involving 'discounted measures' are required. In such measures, costs and benefits are discounted; future benefits and costs are 'reduced' to their 'present worth'. From a number of potential methods (*e.g.* internal rate of return, net present worth), the net benefit-investment ratio (N/K ratio) was selected as a convenient criterion for ranking projects (Gittinger, 1982).

10.1.1.1 Net benefit-investment ratio (N/K ratio)

In essence, the net benefit-investment ratio is calculated by dividing the present worth of net benefits by the present worth of the investment. Benefit is taken as the net present worth of the incremental net benefit stream in all years after that stream has first turned positive. This includes later years in which costs are greater than benefits (*i.e.* years in which 'benefit' was negative); such years act to reduce the value of the benefit stream (*e.g.* year 7 in Figure 10.1). Cost is taken as the present worth of the incremental net benefit stream while that stream was initially negative. Generally, an incremental net benefit stream is negative in the early years of the project, turning positive as the initial investments are 'paid off'.

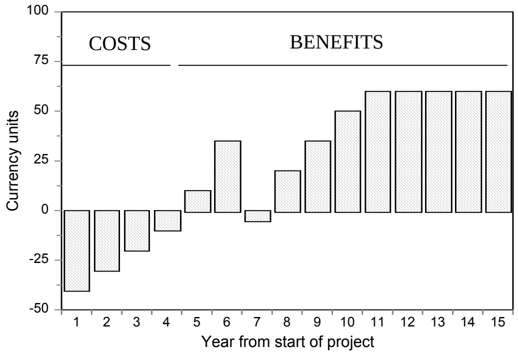


Figure 10.1 Costs and benefits for a project over 15 years, as defined by the N/K ratio.

In the example presented in Figure 10.1, the N/K ratio would be the sum of the 'benefits' in years five to fifteen, divided by the sum of the 'costs' in years one to four.

The work described in this chapter will examine the costs involved in length-based and age-based growth assessments. The assessment and management of *L. mahsena* populations will be used as an example. Using the results of simulations performed in Chapters 7 and 8, costs of each method will be compared with benefits, in terms of the potential revenue gained from the fishery over a fixed time period. The cost-benefit analysis aims to answer the question of whether the advantages identified in the use of age-based over length-based growth assessment methods for snappers and emperors are outweighed by the costs involved in the methodology.

10.2 METHODOLOGY

To calculate the net benefit-investment ratio (N/K ratio), time streams of costs and benefits involved in each methodology are required. In the following two sections, the methods used to calculate these costs and benefits are described.

Two growth parameter estimation methods were examined; that using length frequencies, and that based on age data (otoliths). For the latter, two alternatives were examined; otolith preparation occurring in-house, or being sub-contracted to another institution.

The costs involved in each method were calculated based on the actual costs incurred in the current project while employing each growth assessment scheme in Mauritius (Nazareth Bank) and Seychelles.

Benefits were quantified as the revenue from a fishery managed using growth parameters estimated through each method, at a range of fishing mortality levels. Since actual data were not available to quantify this benefit, yields (and hence revenue) were estimated through simulation. This utilised the results of simulations described in Chapters 7 and 8. Cost and benefit time streams were derived over 25 years. This was the approximate projected lifespan of the otolithometry equipment used in the age-based assessment method. From these time streams, the N/K ratio was calculated for each growth parameter estimation method, at each initial fishing mortality level.

10.2.1 Estimation of costs

Costs were estimated for the two growth assessment methods; the use of length-based methods such as ELEFAN, and the assessment of age using otoliths. For a detailed description of these methods, refer to Chapter 4. Further costs in the time stream were incurred through annual fishing mortality assessments. These were assumed to be derived through length-based methods, using growth parameter estimates from each assessment method (Chapter 4).

Costs involved in validation were not included in the overall costs of age-based assessment. It is possible to combine the collection of otoliths for growth assessment with the requirements for validation through marginal increment analysis and edge analysis (Chapter 2); the collection of individuals for growth assessment can be spread throughout the year, providing the monthly samples required. Additional costs of validation are therefore minimised.

10.2.1.1 Number of individuals required for assessments

Total costs were dependent on the number of individuals sampled. Therefore, the number of sampled individuals required for each estimation method was considered first.

Although statistical methods are available to calculate the optimum number of individuals required for particular methodologies (*e.g.* Gulland, 1966; Holden and Raitt, 1974; Pauly, 1984), in practice sampling is generally limited by the time and resources available.

The simulation studies performed in Chapter 7 indicated that for length-based growth assessment methods, a minimum of 400 individuals were required annually to ensure a satisfactory degree of precision. However, this ignores the practical aspects of the fisheries studied; a number of different vessels/vessel types operate in the fisheries, which are currently sampled in a stratified manner. The aim of this study was to mimic as closely as possible the actual investments made in sampling methodologies. Therefore, the actual number of *L. mahsena* length samples taken in each year, at each study location, was assessed.

Between 1995 and 1997, over 2,000 fish per year were sampled for length from Nazareth Bank (Appendix 4). Previous to this, however, numbers were generally below 1,500 individuals each year. Based on this information, it was assumed that 2,000 fish were sampled each year from Nazareth Bank (Mauritius). No data were available for this species from Seychelles. An identical number were therefore assumed to be collected. It was assumed that five years of length frequency data were required to assess growth parameters (Chapter 7), and hence, 10,000 individuals were required in total. To assess fishing mortality on an annual basis through length-based methods, using either length-based or age-based growth parameter estimates, 2,000 individuals were again assumed to be required.

To calculate the number of otoliths sampled for growth assessments, the structured sampling programme simulated in Chapter 4 was used. This assumed 10 individuals were sampled per 2cm length class (12-46cm). The exception was the last routinely sampled size class (46-48cm), in which only 5 individuals were taken. Based on this sampling protocol, 180 individuals were required to estimate growth parameters through age-based methods. While reading otoliths, a proportion of the sample from each study location were found to be unreadable (*pers.*

obs.). To compensate for this, additional otoliths would be required. Therefore, the number of otolith samples required was increased, based on the proportion of unreadable otoliths found (Table 10.1).

Table 10.1 Number of individual otoliths assessed from each location during the current study, and the corresponding number of unreadable otoliths.

Location	Otoliths sampled	Unreadable otoliths	Percentage	Multiplier	Total number required
Mauritius	774	51	6.6%	1.066	192
Seychelles	1217	99	8.1%	1.081	195

10.2.1.2 Cost classes

This section provides a basic description of cost 'classes' incurred when employing each growth assessment methodology. A general description of the costs covered by each class is provided.

• Startup costs	Purchase of various pieces of equipment required to undertake growth assessments.
• Travel costs	Costs involved in travel to and from port to measure or obtain samples.
• Processing	Cost of data collection (costs incurred undertaking collection, not including travel time), data entry, basic data verification.
• Fish purchase	Costs of fish purchase, applied to otolith studies only.
• Preparation	Preparation of otoliths before reading (mounting in resin, sectioning and staining, embedding on slides, paperwork); preparation can be performed 'in-house' by the institution (incurring startup costs and staff costs), or sub-contracted to other institutions (avoiding both startup and staff costs, but incurring others). Applied to otolith studies only.
• Reading	Reading of annual increments in prepared otoliths; assumed to be performed in-house. Applied to otolith studies only.
• Data analysis	Analysis of collected data to estimate growth.

Table 10.2 indicates the costs which apply to each methodology.

Table 10.2 Cost classes incurred using each methodology.

Cost class	Methodology	
	Length-based	Age-based
Startup	✔	✔
Travel	✔	✔
Processing	✔	✔
Fish purchase		✔
Preparation		✔
Reading		✔
Analysis	✔	✔

10.2.1.3 Calculation of actual costs

The following sections describe in detail the evalulation of the actual costs incurred within each of these classes. All costs were calculated in local currency (Mauritian rupee, Seychelles rupee), or converted from pounds sterling (GB£) to local currency using a conversion rate obtained on the 14/10/98; GB£1 to Rs 41.66 Mauritian, GB£1 to Rs 8.91 Seychelles (source: *Financial Times*).

Timesheets

A timesheet system was introduced at both AFRC (Mauritius) and SFA (Seychelles) to collect data on the length of time staff spent performing tasks for each assessment method (in person hours). Two timesheets were devised; one covered time spent collecting length frequency data, and the other otolithometry studies (Appendix 8). A timesheet was completed by each staff member involved in the project. The corresponding staff grade was also noted, so that wage costs incurred could be calculated. Both AFRC and SFA kindly provided appropriate wage scales for different staff grades.

Startup costs

This analysis assumed institutions had none of the specialised equipment required to perform each assessment (*e.g.* measuring boards, microscopes). The costs incurred in purchasing this equipment were termed 'startup costs'. Costs of equipment such as vehicles and computers (and the time of IT staff to construct databases *etc.*) were ignored in this analysis. Such items are available for general use in the collaborating institutions. Startup costs were based on UK prices, obtained from CEFAS (otolith equipment) or directly from costs incurred during the current project.

This assessment is based on the costs and benefits incurred through the use of each method for one species, *L. mahsena*. However, startup costs will not apply to one species alone. A measuring board, for example, would be used to collect length measurements from a number of species. Similarly, it is unlikely that once otolithometry equipment had been invested in, it would be employed for a single species. To reflect this, a startup cost *per species* was calculated; startup costs were divided by the number of species likely to be examined using each method.

In Seychelles, length frequency and biometric data are routinely collected for nine species (MRAG, 1996d). Amongst these are *P. filamentosus*, for which otoliths cannot be used for ageing (Chapter 2). While nine species could therefore be examined using length-based methods, otoliths could be used for only eight (assuming validation is successful for all species). These eight are; *Aprion virescens*, *Lethrinus nebulosus*, *Lethrinus variegatus*, *Lethrinus mahsena*, *Lutjanus bohar*, *Aphareus rutilans*, *Lutjanus sebae* and *Epinephelus chlorostigma*.

In Mauritius, species from both the banks fishery and local lagoon fishery could be assessed using each method. Species from the banks fishery were included where they comprised over 5% of the catch (data from Samboo, 1989; MRAG, 1997a). For the lagoon fishery, length data are routinely collected from 6 species. Overall, growth in nine species can be assessed; *Lethrinus mahsena*, *Lethrinus variegatus*, *Lethrinus nebulosus*, *Lethrinus croccineus*, *Lethrinus rubrioperculatus*, *Epinephelus fasciatus*, *Mugil cephalus*, *Naso unicornis*, and *Siganus sutor*.

Travel costs (Port trips)

Costs involved in travelling to and from port were assessed on a per trip basis. Therefore, the number of individuals sampled per trip to port, and hence the number of trips required to complete the sampling programme was assessed. This information was obtained from timesheet data. The total number of fish collected over the period of the timesheet data was divided by the number of trips undertaken during that time. From this, an average number of fish sampled during each port visit was calculated. The number of port trips required to achieve the defined sample size was then calculated by dividing that sample number by the average number of fish sampled per trip. This was then rounded to the next higher integer (*e.g.* if 4.01 trips were required, 5 trips would be necessary to complete the sampling programme).

The total time spent travelling to and from port, by grade, was assessed from timesheet data. This figure was divided by the number of trips made to calculate an average time (hours) spent travelling to port by grade.

The overall wage costs of travel to and from port to achieve the specified sampling regime was calculated using the number of trips required, the average time spent travelling per port trip by each grade, and the wage rate per hour.

Petrol costs were also included in the calculation of travel costs. The distance from the research centre to sampling point (port/market) was estimated (Mauritius and Seychelles assumed to be a 20 mile round trip), and a nominal fuel consumption figure of 35mpg applied. The number of litres of fuel used per trip was then calculated, (4.546 litres in a gallon, 0.571 gallons used per trip) and multiplied both by the price of fuel (Mauritius: Rs 7.65/litre (S. Rathacharen, *pers. com.*), Seychelles: Rs 5.70/litre (D. Boullé, *pers. com.*)) and number of trips required to complete the sampling programme. In Seychelles, length frequency sampling occurred close to the main offices. Travel was therefore on foot, and incurred no petrol costs.

Processing costs

Processing time was assessed as that taken to collect length/biometric data, enter data into a database, and verify entered data. For otolithometry, additional costs included time spent selling fish after otolith extraction and administration of these funds.

Using timesheet data, the total time spent processing fish for each method was calculated by grade. An average time per sampled individual was calculated by dividing these values by the number of fish processed for each methodology within the timesheet period. Time required to process a specified number of individuals for each method was then calculated for each grade scale, and overall wage costs calculated.

Fish purchase costs

Where otoliths were required, fish had to be purchased from fishing companies or fishermen. The reason for this was twofold; damage to fish resulting from otolith extraction reduced their market value, while the time required to perform these operations meant extraction could not be performed at the sampling site. Hence they were purchased, and analysed at the fishery institutions.

A purchase cost per fish was calculated. The cost per kilogramme for *L. mahsena* was obtained from the purchase price of this, or related species, in Mauritius and Seychelles. An average weight per individual was calculated from the otolith database constructed for this project. Cost per fish was then calculated by multiplying these two values. The total cost of fish purchase was then estimated using the cost per fish and the number of otoliths specified for the sampling programme (while two otoliths were extracted, only one was used for ageing purposes).

A proportion of the purchase cost was subsequently recouped by re-selling the fish after otolith extraction. In Mauritius, re-sale price was set at 88% of initial outlay (S. Rathacharen, *pers. com.*). In Seychelles, approximately 60% of the purchase price was recouped by resale (R. Azemia, *pers. com.*). Recouped cost per individual was calculated by multiplying total purchase cost by 0.88, or 0.60, respectively. Actual expenditure through fish purchase was therefore the initial outlay minus that recouped through re-sale.

Further costs of otolith collection included the purchase of otolith envelopes to store the otoliths (approximately GB£ 0.01 per otolith (*pers. obs.*)).

Preparation costs

Otolith preparation costs were derived for two potential routes; preparation could occur either in-house, or be sub-contracted to an outside institution. For the latter, costs were calculated based on those indicated by CEFAS, who prepared otoliths during the current study. In-house preparation occurred significant start-up costs (*e.g.* purchase of microtome for otolith sectioning). Sub-contracting incurred no startup costs, but included the costs of sending otoliths to and from the contracted party, along with the costs of preparation charged by the contractor.

In-house preparation costs were calculated based on preparation time for an individual otolith. This was set at six hours per 100 otoliths (R. Millner, *pers. com.*). An assumption was therefore made that technicians performing the work were as experienced as those at CEFAS. This therefore ignored costs incurred in training staff in preparation techniques. These may represent a significant cost for age-based methods. However, the evaluation of these costs was not straightforward. The potential effects of these unquantified costs will be discussed in Section 10.4.3.

In-house preparation costs were calculated from the preparation time per otolith, the wage rate of the grade performing this assessment (assumed to be grade 2) and the number of sampled otoliths. In addition, recurrent costs of resin and dye were included at GB£ 0.03 per otolith (R. Millner, *pers. com.*).

The preparation costs incurred through sub-contracting were set at GB£ 0.80 per otolith, based on advice from CEFAS. This included costs of both personnel and materials. Costs of sending otoliths to the contracted institution were assumed to be a single payment (all otoliths were sent at one time to the institution). Cost was estimated at GB£ 60 per 200 otoliths (*pers. obs.*).

Reading costs

The time taken to age an individual using its otolith was estimated at five minutes (0.08 hours, *pers. obs.*). Reading costs were calculated as the product of the required number of otoliths, reading time per otolith, and the appropriate wage rate. This work was assumed to be performed by personnel of grade 2.

The costs incurred during the initial training of personnel in otolith reading were ignored in these costs. The potential effects of this will be discussed in Section 10.4.3.

Data analysis costs

The time required to analyse the data and obtain a growth assessment through either method was estimated at five days. An eight hour working day was assumed. Total analysis cost was calculated as the product of time (in hours) and the wage of grade 1 personnel assumed to perform this assessment. Data analysis costs were therefore identical between growth assessment methods.

10.2.1.4 Estimation of annual fishing mortality

The costs described above were solely for the estimation of growth parameters. In this study, however, benefit was assessed based on annual stock assessments (and hence management) arising from the use of these growth parameters to estimate the level of fishing mortality (F). The costs involved in the annual assessment of this parameter had to be accounted for in the cost time stream.

Annual fishing mortality was assumed to be estimated through length-based methods, as described in Chapter 4, and simulated in Chapter 7. Therefore a length frequency distribution was required annually. It was assumed that an identical number of length samples to that collected annually for length-based growth estimation were required (2,000 individuals). As a result, the annual cost of collecting this distribution, and its use to assess annual fishing mortality, were assumed to be identical to the annual costs involved in collecting length frequency data for the length-based assessment of growth parameters.

10.2.1.5 Calculation of cost time stream

Costs involved with growth parameter estimation (including startup costs) were assumed to occur in year zero, along with costs involved in the estimation of fishing mortality for that year.

Based on the simulations described in Chapter 7, five years of length frequency data were assumed to be required to estimate growth parameters through length-based methods. Year zero costs for length-based growth parameter estimation therefore consisted of startup costs, plus costs incurred in the collection and assessment of length frequency data during the five years previous to year zero. For four of these five years, data analysis costs were not incurred, since the assessment of growth occurred at the end of the fifth year. It was assumed that the final year of length frequency data was also used to estimate annual fishing mortality for year zero, and so no additional costs were incurred.

For age-based growth parameter estimation methods, year zero costs consisted of three elements. These were: startup costs (which depended on the otolith preparation method), costs involved in the collection of one year of otolith data (through which growth parameters could be estimated), and costs incurred through the collection of one year of length frequency data (for annual fishing mortality estimation).

In both cases, costs in subsequent years were incurred through the collection of length frequency data only; annual fishing mortality estimates were then derived using these length distributions and the growth parameters estimated in year zero throughout the remaining 25 years. Management action was then taken based on the comparison of the estimated fishing mortality and value of $F_{0.1}$ (Section 10.2.2).

10.2.2 Estimation of benefits

Benefits were quantified as the revenue generated from the fishery under management based on each growth assessment method.

Initially, it was intended to use the outputs from the management strategy simulation to assess the benefits resulting from the use of different growth parameter estimation methods (Chapter 8). However, due to delays in the management strategy simulation, arising from the need for tuning, simpler simulations were performed to assess benefits. These simulations used the outputs of analyses performed in Chapter 7.

In that chapter, both length-based and age-based growth parameter estimates were simulated at four different levels of equilibrium fishing mortality, without density dependent growth operating (Scenario 1). These growth estimates were used to estimate biological and fishery parameters from simulated length frequency data. Simple management actions were then taken, based on stock assessments derived using the relative sizes of estimates of $F_{0.1}$ and the current fishing mortality rate (F). The resultant distribution of management actions indicated the probability that a certain action would be taken at a simulated fishing effort level, when using the specified growth estimation method.

In the current study, simple management simulations were performed to assess the benefits arising from each growth assessment method. The management simulation is described in detail in the following section. Management actions were selected based on probability distributions derived from the F_{curr} and corresponding $F_{0.1}$ estimates of Chapter 7, using the criteria detailed in Chapter 9 (Table 9.1). As noted in Chapter 8, tuning was required for length- and age-based methods, to achieve the management aim ($F_{0.1}$) within the desired time period. Tuning was therefore required to remove the influence of the reference effort level selected from the cost-benefit analysis. The methods used to select this management reference level, and the resulting management action probability distributions are first presented. The management simulation is then described. In this simulation, the effects of each management action on the effort level was represented through the use of an 'F-multiplier' (F_{mult}), which formed a numerical equivalent to the qualitative management action. The methods used to set these F_{mult} values are presented. Finally, the methods used to calculate the financial benefits (fishery revenue) are described.

Assessment of management reference effort levels

Using the criteria detailed in Chapter 9 (Table 9.1), each of the 100 output F_{curr} and $F_{0.1}$ estimates were used to derive management action probability distributions. This indicated the probability of one of the four management actions being taken at each effort level.

Age-based growth parameters resulted in suitable management actions based on the reference level $F_{0.1}$. Stock assessments called for drastic action or decreases in fishing mortality at high F levels, and increases in F at low levels (see Table 10.4). Over the period of the management simulation, effort tended to $F_{0.1}$ from both high and low initial F levels. Unlike the simulations performed in Chapter 9, the reference effort level did not require tuning where age-based growth parameters were used.

In contrast, the use of length-based growth parameters resulted in a high proportion of cautious actions (*e.g.* decreases in effort or drastic action) which were inappropriate at most fishing mortality levels. From the results of the simulations performed in Chapter 7, the probability of a management action being taken at each fishing mortality level was assessed. These are presented as cumulative probability distributions in Table 10.3.

Table 10.3 Management action cumulative probability distributions resulting from the use of length-based growth parameter estimates, at four simulated levels of fishing mortality (yr^{-1}).

Simulated F:	0.1	0.25	0.7	1.2
Drastic Action	0.15	0.16	0.15	0.33
Decrease	0.25	0.28	0.29	0.63
No change	0.92	0.94	1	0.99
Increase	1	1	-	1

The effect of cautious management was seen in initial simulations of annual yield over 25 years, using these management action probability distributions. Fishing mortality, and hence yield, decreased to low levels by the end of the 25 year period, regardless of the initial level of fishing mortality (Figure 10.2). As a result, length-based methods would be undervalued in the cost-benefit analysis.

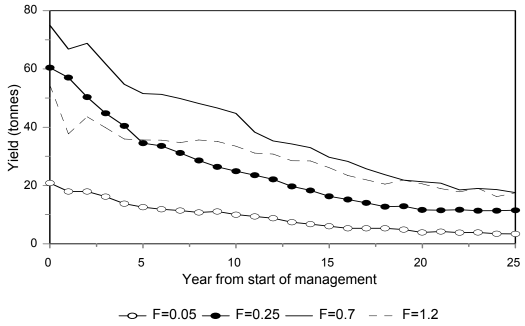


Figure 10.2 Simulated yield over 25 years resulting from management based on $F_{0.1}$, when using length-based growth parameter estimates.

This implied that the management reference level would need to be higher, to reduce this tendency. Using the $F_{0.1}$ and fishing mortality estimates from the simulations performed in Chapter 7, new management action probability distributions were derived, where management was based on multiples of the $F_{0.1}$ estimate. Using the resultant probability distributions, simulations generating a 25 year time series of annual fishing mortality values for each initial F level were performed. The aim of these simulations was to identify the management reference level (multiple of $F_{0.1}$) that resulted in fishing mortalities in the final year close to the true $F_{0.1}$ ($F_{0.1}$ ~ $0.4yr^{-1}$), similar to the tuning described in Chapter 8.

Based on this criteria, a management reference mortality level of $1.65*F_{0.1}$ was selected for length-based methods. The resulting pattern in mean annual fishing mortality at $F=0.05yr^{-1}$ and $F=1.2yr^{-1}$ is presented in Figure 10.3.

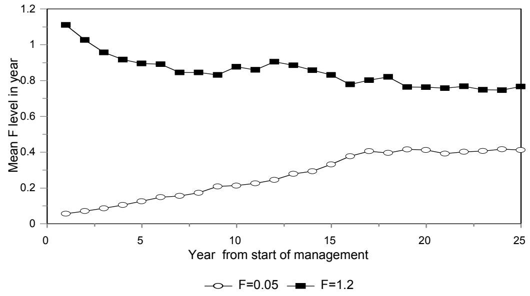


Figure 10.3 Mean fishing mortality level in year following the initiation of management based on $1.65*F_{0.1}$, using length-based growth parameter estimates. Mean F-in-year for initial fishing mortality levels $F=0.05yr^{-1}$ and $F=1.2yr^{-1}$ presented.

For the main simulation, cumulative probability distributions of the management actions were therefore derived for length-based methods based on the reference effort level $1.65*F_{0.1}$.

Management simulation

In Chapter 7, management actions were derived at four equilibrium fishing mortality levels (F=0.05, 0.25, 0.7 and 1.2 yr^{-1}). For each fishing mortality level, the frequency with which each of the four possible management actions were taken was converted into a cumulative probability distribution. This defined the probability of a particular management action being selected at random at each fishing mortality level (Table 10.4).

As stated, the management action probability distributions for length-based methods were based on the use of 1.65*$F_{0.1}$ for length-based growth parameters, while that for age-based growth parameters was based on $F_{0.1}$. In the remainder of this chapter, these reference effort levels will be collectively referred to as 'F_{ref}'.

Table 10.4 Management action cumulative probability distributions resulting from the use of length-based (L) or age-based (A) growth parameter estimates based on F_{ref}, at four simulated levels of fishing mortality (yr^{-1}). The range of fishing mortality levels for which each distribution applied is shown.

Simulated F:	0.05		0.25		0.7		1.2	
F range:	0 - 0.15		0.15 - 0.50		0.50 - 0.90		>0.90	
Method:	L	A	L	A	L	A	L	A
Drastic Action	0.1	0	0	0	0.1	0.44	0.1	1
Decrease	0.1	0	0.11	0	0.13	0.98	0.2	-
No change	0.66	0	0.72	0.85	0.89	1	0.96	-
Increase	1	1	1	1	1	-	1	-

Annual fishing mortality levels for an *L. mahsena* fishery were simulated over a 25 year period. A flow diagram to describe the process used is presented in Figure 10.4.

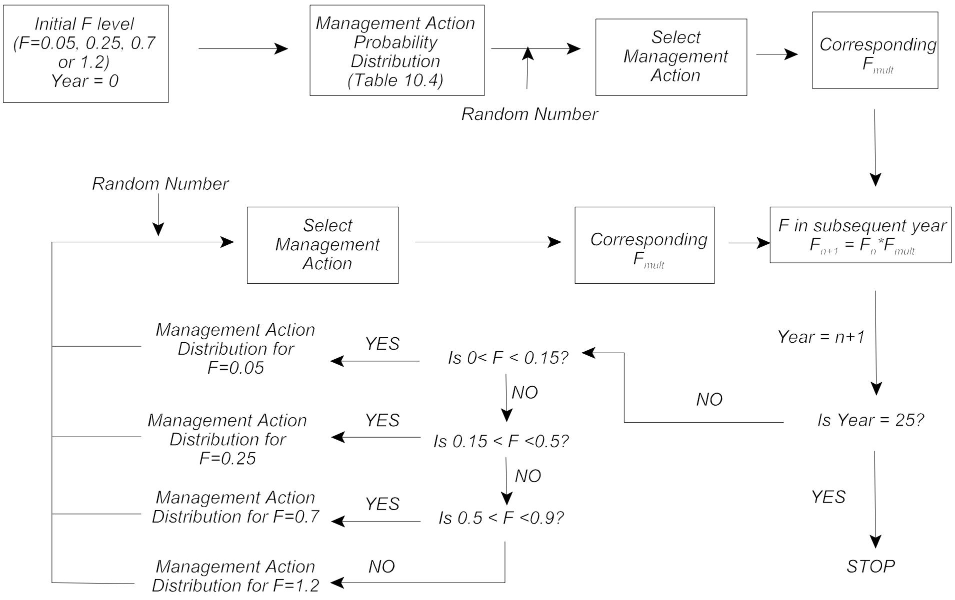


Figure 10.4 Flow diagram of the management simulation of a 25 years time series of annual fishing mortality level.

Simulations were initiated (at year zero) at one of the four fishing mortalities used in Chapter 6. In year zero, a management action was selected from the management action probability distribution corresponding to the initial F level (Table 10.4) using a random number (between

0 and 1). The F level in the following year (n+1) was then modified, based on that management action. The impact of the management action in year n on the effort level in the subsequent year was simulated using the corresponding F-multiplier (F_{mult}), the numerical representation of the effect of that qualitative management action on the fishing mortality level; F_{n+1} =(F_n) * (F_{mult}). The F_{mult} values selected to represent the impacts of each management action are detailed in the section below.

Based on the new F level, a further management action was randomly selected for year n+1. As a result of the management action in the previous year, F_{n+1} was often different from the four initial fishing mortality levels. It was therefore assumed that the management action distributions derived for each initial F level applied to a range of related F levels (Table 10.4, Figure 10.4).

Following this sequence in each subsequent year, a 25 year time series of F values was simulated within an EXCEL^{TM} spreadsheet. Due to the stochastic nature of the simulation (management actions in each year were selected at random from the probability distributions) this was repeated 100 times. This was performed for each initial fishing mortality level, and growth parameter estimation method.

Assessment of F_{mult} values

To simulate the effect of management actions on the fishery, the level of fishing mortality in year n (F_n) was adjusted by a multiplier (F_{mult}) to give the fishing mortality level in the following year (F_{n+1}). The value of F_{mult} was therefore defined to represent the application of each management action. The following describes the methods through which these 'F-multiplier' values were estimated.

In Chapter 7, the management action taken was based on the relative estimated values of F_{ref} and fishing mortality (F). F_{mult} therefore represents the amount by which F would need to be changed to attain the estimated F_{ref}:

$$F_{mult} = \frac{F_{ref}}{F}$$

The definitions of the management actions, in terms of F_{ref} and F, were used to determine the boundaries of the F_{mult} values for each action (Table 10.5).

Table 10.5 Fishery manager's action based on the relative estimates of the reference effort level (F_{ref}) and fishing mortality (F).

F in relation to F_{ref}	Managers Action	F_{mult} boundaries
$F > 2.0\ F_{ref}$	Drastic action	$F_{mult}<0.5$
$1.5\ F_{ref} < F < 2.0\ F_{ref}$	Decrease effort	$0.5 < F_{mult} < 0.67$
$0.5\ F_{ref} <F <1.5\ F_{ref}$	No action	$0.67 < F_{mult} < 2$
$F < 0.5\ F_{ref}$	Increase effort	$F_{mult} > 2$

Using estimates of F_{ref} and F output from the simulation runs performed in Chapter 7 (Scenario 1), distributions of F_{mult} values were calculated for each of the four initial fishing mortality levels.

In that chapter, it was noted that, under equilibrium conditions, the 'confident' fishing mortality estimate (Beverton and Holt's Z minus Pauly's M) resulted in the most appropriate management actions when derived using *length-based* growth parameters. In contrast, the 'cautious' fishing mortality estimate (length-converted catch curve Z minus Ralston's M) resulted in the most appropriate management when derived using *age-based* growth parameters. In this study, these specific fishing mortality estimates were used when calculating F_{mult}, along with the corresponding estimates of $F_{0.1}$ (based on Pauly's and Ralston's M, respectively).

For each F_{mult} distribution derived from the outputs of Chapter 7, an average F_{mult} value was calculated within the boundaries defined for each management action, for each effort level (Tables 10.6 and 10.7).

Table 10.6 Average F_{mult} estimates derived using *length-based* growth parameters in Scenario 1 simulations performed for Chapter 7. Actions based on $1.65*F_{0.1}$ (F_{ref}). Average estimates presented by management action.

Management	$F=0.05\ yr^{-1}$	$F=0.25\ yr^{-1}$	$F=0.7\ yr^{-1}$	$F=1.2\ yr^{-1}$
Drastic Action	0.45	0.44	0.34	0.4
Decrease	0.52	0.62	0.58	0.58
No Change	1.36	1.31	1.4	1.12
Increase	3.28	2.93	2.39	2.49

Table 10.7 Average F_{mult} estimates derived using *age-based* growth parameters in Scenario 1 simulations performed for Chapter 7. Actions based on $F_{0.1}$ (F_{ref}). Average estimates presented by management action.

Management	$F=0.05\ yr^{-1}$	$F=0.25\ yr^{-1}$	$F=0.7\ yr^{-1}$	$F=1.2\ yr^{-1}$
Drastic Action	-	-	0.28	0.14
Decrease	-	0.61	0.55	-
No Change	1.48	1.15	0.77	-
Increase	7.99	2.76	-	-

The F_{mult} values used to define the impact of the management actions (Table 10.8) were based on these mean values, the F_{mult} ranges defined by each management action (Table 10.5), and practical considerations.

Table 10.8 F_{mult} values corresponding to each management action (based on either length- or age-based growth parameters) used in the current management simulation study.

Management	F_{mult}
Drastic Action	0.4
Decrease	0.6
No change	1
Increase	1.7

The value used for 'no change' was assumed to be 1, based on the definition of the management action. F_{mult} values from both growth parameter sources were comparable to this value (Tables 10.6 and 10.7).

The F_{mult} value for the 'decrease' action was set at 0.6. This was comparable to the mean estimates from both growth parameter sources, and was close to the middle of the F_{mult} range defined by that management action.

The F_{mult} value for 'drastic action' was approximated from the length-based mean F_{mult} estimate (Table 10.6). The 70-80% decline in effort defined by the other 'drastic action' estimates were unrealistic for an actual fishery, and in preliminary simulations resulted in large annual fluctuations in effort.

The selection of F_{mult} values for 'increase' was also somewhat arbitrary. All mean estimates implied at least a 200% annual increase in effort for this action, as per the definition (Table 10.5). An increase of this scale was somewhat unrealistic. As a more realistic value, the inverse of the F_{mult} value corresponding to the 'decrease' action was taken (*i.e.* $F_{mult} = 1/0.6$). This was felt appropriate given the precautionary approach taken in the study locations.

Length-based F_{mult} estimates were reasonably comparable between simulated effort levels. In the light of this, and to maintain simplicity, the F_{mult} values defined in Table 10.8 were used at each effort level.

Calculation of fishery revenue

MIDAS was used to simulate annual yield from a *L. mahsena* fishery, based on the fishing regime defined by each 25 year time series of annual fishing mortality levels. This simulation was based on the settings for the *L. mahsena* fishery on Nazareth bank, as defined in Chapter 4. The first management action was taken at year zero. Previous to this time, the fishery was simulated at equilibrium with the selected initial fishing mortality level.

One hundred 25 year series of annual yield values (tonnes) were output from MIDAS, and imported into an EXCEL™ spreadsheet. The average annual yield was calculated, and multiplied by the value of fish in both Mauritius and Seychelles to estimate the average annual revenue. It was therefore assumed that the price of fish remained stable over the 25 year period.

The yield resulting from each management simulation was compared to the situation where 'perfect knowledge' of two biological reference points was available. At time zero, effort was set to either the true $F_{0.1}$ ($F=0.41yr^{-1}$) or F_{MSY} ($F=0.63yr^{-1}$), and held constant in subsequent years. These runs were performed for each of the four initial fishing mortality levels.

Benefits based upon the outputs of Chapter 8

The simulations described above represent a simplified version of the management strategy simulations described in Chapter 8. As a result, the results of the cost-benefit analysis may be different where the outputs from the more complex simulations described in Chapter 8 were used. To examine this, the cost-benefit analysis was performed using the output yields from the management strategy simulation where the reference effort level had been tuned for a starting effort level of $F=0.4yr^{-1}$ (Section 8.3.3).

10.2.3 Net benefit-investment ratio (N/K ratio)

The gross cost and benefit time streams derived through the methods described were used to calculate the N/K ratio for each method (length-based, age-based with in-house preparation, age-based with sub-contracted preparation) and location. The calculations required were performed within a Quattro Pro™ spreadsheet for each simulated initial fishing mortality level.

Year zero costs included the startup costs, and costs of obtaining both the growth parameter estimates, and the first fishing mortality assessment. Benefits were realised from year one, being the revenue from the fishery in each year. For each year, incremental net benefits were calculated as the annual fishery revenue minus the costs incurred in that year through the fishing mortality assessment. This incremental net benefit was then discounted, using the appropriate discount factor for that year, to provide the ‘present worth’ of the project.

To perform the age-based assessments described in this study, the majority of developing countries would require some form of grant or loan. The interest rate on such loans provided a suitable source for the discount rate. Due to a lack of information on the lending rates of international organisations (*e.g.* World Bank, Asian Development Bank), those of the local institutions were examined. For both the Bank of Mauritius and Development Bank of Seychelles, the interest rate was approximately 10%. A lending rate from a larger organisation was assumed to be slightly lower than this. Examining the levels commonly used in other studies (Gittinger, 1982), a discount rate of 8% was selected.

The net benefit-investment ratio was then calculated from the present worth net benefit stream, as the sum of the years in which the present worth was positive, divided by the years in which the present worth was negative (this corresponded to the costs in year zero only). Due to the large profit from the fishery versus the costs involved in the methodology, the positive present worth stream was the sum of years one to twenty five, inclusive.

Net benefit-investment ratios from each growth assessment method were compared to identify which resulted in the greatest return for investment (largest N/K ratio), at each initial fishing mortality level.

10.2.3.1 Sensitivity analyses

Assumptions were made when deriving the costs involved in each growth assessment methodology. The effect of these assumptions on the N/K ratios was examined.

Startup costs

Startup costs were a significant component of the overall investment in age-based growth assessment. As previously stated, these costs did not refer to a single species, and so were defined as a startup cost-per-species. The effect on the N/K ratio of the number of species over which startup costs were divided was examined.

The number of species over which startup costs were divided was varied, and the resulting N/K ratios for length-based and both age-based methods were compared. Using the Quattro Pro^{TM} ‘Optimiser’ routine, at a given initial F level, the difference between the two N/K ratios was minimised by varying the number of species examined by age-based methods. Where N/K ratios were identical, there was no obvious financial advantage in selecting either assessment method. The number of species at which age-based methods gained a financial advantage over length-based methods was then noted.

Individuals sampled for growth estimation

Since the costs involved in obtaining growth assessments through each method were assessed per individual fish, the total number of individuals sampled affected the N/K ratio. The effect of the number of fish examined in each assessment method on the N/K ratio was therefore assessed.

Startup costs and analysis costs were unaffected by the number of fish examined. For all other cost classes, the total cost per year, per individual, was calculated. This variable cost was then incorporated into the N/K ratio assessment. For a selected methodology, the number of fish sampled was varied in the N/K ratio calculation. The number of fish sampled for the opposing methodology, and for the annual fishing mortality assessment, was unaffected by these changes. Using the Quattro Pro^{TM} ‘Optimiser’ routine, the difference between the N/K ratios was minimised by varying the number of fish sampled for the selected methodology. The number of individuals at which each method gained a financial advantage over the other was then noted

10.3 RESULTS

The costs and benefits are first calculated. These are then used in the assessment of the net benefit-investment ratio. The assessments of additional benefits are then presented.

10.3.1 Costs

The annual costs involved in each methodology are described by cost class. All costs were rounded to the nearest Rupee. In each table, length-based growth assessment method has been shortened to ‘length’, age-based methods has been shortened to ‘age’. For age-based methodologies, the costs are broken down into the two preparation methods (in-house, or sub-contracted to an outside institution). Costs involved in the estimation of growth are detailed first, followed by those involved in the annual assessment of fishing mortality. Finally, the cost time stream is derived.

10.3.1.1 Timesheet data

Timesheet data were recorded over varying periods of time, dependent on the location and data collected. The number of fish sampled for length or age data during this period are presented in Table 10.9, along with the number of port sampling trips undertaken to collect this number of fish.

Table 10.9 Period of timesheet data collection, number of individuals sampled for length frequency and otoliths, and corresponding number of trips to port.

Location	Method	Period of collection		Number of fish sampled	No. trips to port
		From	To		
Mauritius	Length	35439	35642	5272	18
	Age	35430	35773	1164	23
Seychelles	Length	01/02/97	16/02/98	4935	73
	Age			1631	69

10.3.1.2 Startup costs

Estimated costs (GB£) of essential equipment for each growth assessment methodology are shown in Table 10.10, by method.

Table 10.10 Start up costs for each growth assessment methodology.

Item	Methodology		
	Length	Age[1]	Age[2]
Measuring board	£ 50	£ 50	£ 50
Precision saw (Struers Accutom 5)	-	£ 5,930	-
Camera & mounting boxes, X-Y table	-	£ 1,116	-
Resin Mould	-	£ 58	-
Binocular microscope (Leica MZ6)	-	£ 2,445	£ 2,445
Light source (Leica Nicholas Illuminator)	-	£ 162	£ 162
TOTAL			
Pounds Sterling (GB£)	50	9760	2656
Mauritian Rupees (Rs)	2083	406608	110655
Seychelle Rupees (Rs)	446	86963	23666

[1] otolith preparation performed in-house
[2] otolith preparation sub-contracted to outside institution

Startup costs were divided by the potential number of species to be examined using each method, to obtain a startup cost-per-species (Table 10.11).

Table 10.11 Startup costs (Rs) per species for each methodology and location.

	Mauritius (Rs)			Seychelles (Rs)		
Method	Length	Age[1]	Age[2]	Length	Age[1]	Age[2]
Startup cost	2083	406608	110655	446	86963	23666
No. species	9	9	9	9	8	8
Cost/species	231	45179	12295	49.5	10870	2958

[1] otolith preparation performed in-house
[2] otolith preparation sub-contracted to outside institution

10.3.1.3 Travel costs (port trips)

The average number of fish collected per trip to port, and the average time spent by each staff grade travelling to and from port was calculated from timesheet data. Using this information and the wage costs for each grade, the cost (wages) per trip to port was calculated (Table 10.12).

Table 10.12 Estimated number of fish collected per trip to port, average time (hours) spent by staff grade during a single trip, and overall cost per trip.

a) Mauritius

Method	Fish sampled	No. trips	Fish / trip	Staff grade	Total time (hrs)	Hours / trip	Cost / trip (Rs)	Total cost (Rs/Trip)
Length	5272	18	293	1	15	0.81	101.25	252.55
				2	32	1.78	97.9	
				3	32	1.78	53.4	
Age	1164	23	51	1	27	1.17	143.25	224.9
				2	14	0.59	32.45	
				3	36	1.54	46.2	

b) Seychelles

Method	Fish sampled	No. trips	Fish / trip	Staff grade	Total time (hrs)	Hours / trip	Cost / trip (Rs)	Total cost (Rs/Trip)
Length	4935	73	44	2	-	0.1*	1.69	1.69
Age	1631	69	24	1	84	0.59	11.68	23.85
				2	102	0.72	12.17	

* Seychelles length frequency data collection is carried out close to the main offices. Travel is on foot. Value of 6 minutes was an estimate based on distance.

Note that differences in the costs between methods for the same grades are due to different periods of time being spent by these grades during each trip. Given the number of fish required for sampling, and hence the number of trips to port, the cost of travel, was calculated (Table 10.13).

Table 10.13 Travel costs (Rs) required to fulfill length frequency or otolith sampling programmes, by location.

Method	Location	Fish required	Fish/trip	Trips required	Cost per trip	Fuel costs	Total cost
Length	Mauritius	2000	293	7	253	139	1907
	Seychelles		44	46	2	-	78
Age	Mauritius	192	51	4	225	79	979
	Seychelles	195	24	8	24	36	227

10.3.1.4 Processing costs

From timesheet data, the time required by each staff grade to process an individual fish for each assessment method was calculated. Using the wage rates for each staff grade, the cost per sampled fish was then calculated for each assessment method (Table 10.14).

Table 10.14 Time spent by each staff grade to collect and process an individual fish for each methodology in Seychelles (Sey.) and Mauritius (Maur.).

Method	Fish processed		Staff grade	Time spent (hrs)		Time/fish		Cost/fish (Rs)	
	Sey.	Maur.		Sey.	Maur.	Sey.	Maur.	Sey.	Maur.
Length	4935	5272	1	115	82	0	0	0.4	2.5
			2	353	383	0.1	0.1	1.18	3.85
Age	1631	1164	1	163	467	0.1	0.4	1.98	50
			2	432	210	0.26	0.18	4.39	9.9

The time required by each staff grade to process the specified number of individuals for growth assessment through length frequency analysis or otolithometry, and hence wage cost, was calculated (Table 10.15).

Table 10.15 Annual processing cost for length-based or age-based growth assessments.

Method	Location	Number required	Cost per fish	Total Cost (Rs)
Length	Mauritius	2000	6.35	12700
	Seychelles		1.58	3158
Age	Mauritius	192	59.9	11501
	Seychelles	195	6.37	1243

10.3.1.5 Fish purchase (otoliths only)

The price per fish was calculated using the price per kilogramme in Seychelles and Mauritius and the average weight (kg.) of individual fish from the otolith database (Table 10.16).

Table 10.16 Prices of fish per kg., average weight, and approximate price per individual.

Location	Species	Price per kg. (Rs)	Average weight (kg.)	Price per individual (Rs)
Mauritius	*L. mahsena*	40.0*	0.568	22.72
Seychelles	*A. virescens*	12.5†	1.499	18.74
	L. mahsena	12.5†	0.403	5.04

* source: S. Rathacharen (*pers. com.*)
† source: Seychelles Catch Assessment Survey

Given the number of individuals required for otolith sampling, the cost of fish purchase was calculated (Table 10.17). A proportion of the costs were recouped by re-selling the fish following otolith extraction. Costs also included those of otolith envelope purchase.

Table 10.17 Cost of fish purchase for otolithometry, and amount recouped from re-sale.

Location	Number required	Purchase cost (Rs)	Amount recouped (Rs)	Otolith envelopes (Rs)	Overall cost (Rs)
Mauritius	192	4362	3817	80	625
Seychelles	195	3654	2192	17	1479

10.3.1.6 Preparation costs (otoliths only)

Based on the number of individuals from which otolith samples were required, costs of processing, both in-house and by sub-contracting an outside institution, were calculated (Table 10.18). Costs included the wage of staff performing the preparation, plus materials (in-house), or the cost of preparation per otolith, and postage (sub-contracted).

Table 10.18 Otolith preparation costs, a) in-house, or b) sub-contracted.

a) In-house preparation

Location	Number required	Time required (hrs)	Material costs (Rs)	Cost (Rs)
Mauritius	192	11.5	240	874
Seychelles	195	11.7	52	250

b) Sub-contracted preparation

Location	Number required	Cost/otolith (Rs)	Postag e (Rs)	Cost (Rs)
Mauritius	192	33	2500	8899
Seychelles	195	7	535	1925

10.3.1.7 Reading costs (otoliths only)

Based on the number of otoliths required, otolith reading costs were assessed (Table 10.19). Costs incurred were the wages of staff performing this task (grade 2), at a rate of 5 minutes per otolith.

Table 10.19 Cost of reading the required number of otoliths.

Location	Number required	Time required (hrs)	Cost (Rs)
Mauritius	192	16	880
Seychelles	195	16.25	275

10.3.1.8 Data analysis costs

For both growth assessment methods, it was assumed that five days per year were required for data analysis by grade 1 staff. Wage costs were calculated accordingly (Table 10.20).

Table 10.20 Cost of data analysis.

Location	Cost (Rs)
Mauritius	5000
Seychelles	792

10.3.1.9 Annual total cost of sampling

Based on the number of fish sampled each year, and the costs incurred in each of the classes calculated above, the total annual cost of each growth assessment method was calculated (Table 10.21). Since this was the annual cost only, it did not include startup costs. In addition, these costs do not include those of annual fishing mortality assessment. These are detailed in the following section.

Table 10.21 Annual cost of assessing growth through length- or age-based methods. All costs in local currency (Rs).

Location	Mauritius		Seychelles	
Method	Length	Age	Length	Age
Number required	2000	192	2000	195
Travel	1907	979	78	227
Processing	12700	11501	3158	1243
Fish purchase	-	625	-	1479
Preparation:				
In-house	-	874	-	250
Sub-contracted		8899		1925
Otolith reading	-	880	-	275
Data analysis	5000	5000	792	792
TOTAL				
Length-based	19607		4028	
Otoliths: *In-house*		19859		4265
Otoliths: *Sub-contracted*		27884		5940

The reader may note that the annual costs involved in the estimation of growth through each method are comparable. This is due to the increased number of individuals required for length-based growth estimation. As a result, more port trips were required to achieve the length-based sampling programme. In addition, the greater number of samples required resulted in processing costs being notably higher for length-based methods, despite the lower cost-per-individual incurred by this method (Table 10.14).

Annual costs for age-based methods were greater than those for length-based methods where preparation was sub-contracted. This was a result of the higher preparation costs incurred. Since startup costs were not included, the method was more expensive than in-house preparation.

10.3.1.10 Estimation of annual F level

For both growth estimation methods, annual estimates of fishing mortality were assumed to be derived using length-based methods. These annual costs were assumed to be identical to those incurred through the annual collection of length frequency data for length-based growth assessments (Table 10.21). Therefore, for Mauritius, annual costs for both growth estimation methods totalled Rs 19,607, while annual costs in Seychelles totalled Rs 4,028 (see Table 10.22).

10.3.1.11 Cost time stream

The costs calculated above represent the annual cost of performing growth assessment through length-based or age-based methods, and of estimating annual fishing mortality. These were used to calculate the cost time stream.

Costs in year zero comprised:

- startup costs incurred due to equipment purchase,
- the costs of growth assessment through each method (length-based methods required five years of data, age-based methods required one year of data),
- the cost incurred through the collection of a single length frequency distribution to assess fishing mortality for year zero.

For length-based methods, cost of fishing mortality assessment was included in that of the fifth year of length frequency data collection. For age-based growth parameter assessment, additional costs of collecting one year of length frequency data to estimate fishing mortality were added (Table 10.21, Mauritius: Rs 19,607, Seychelles Rs 4,028).

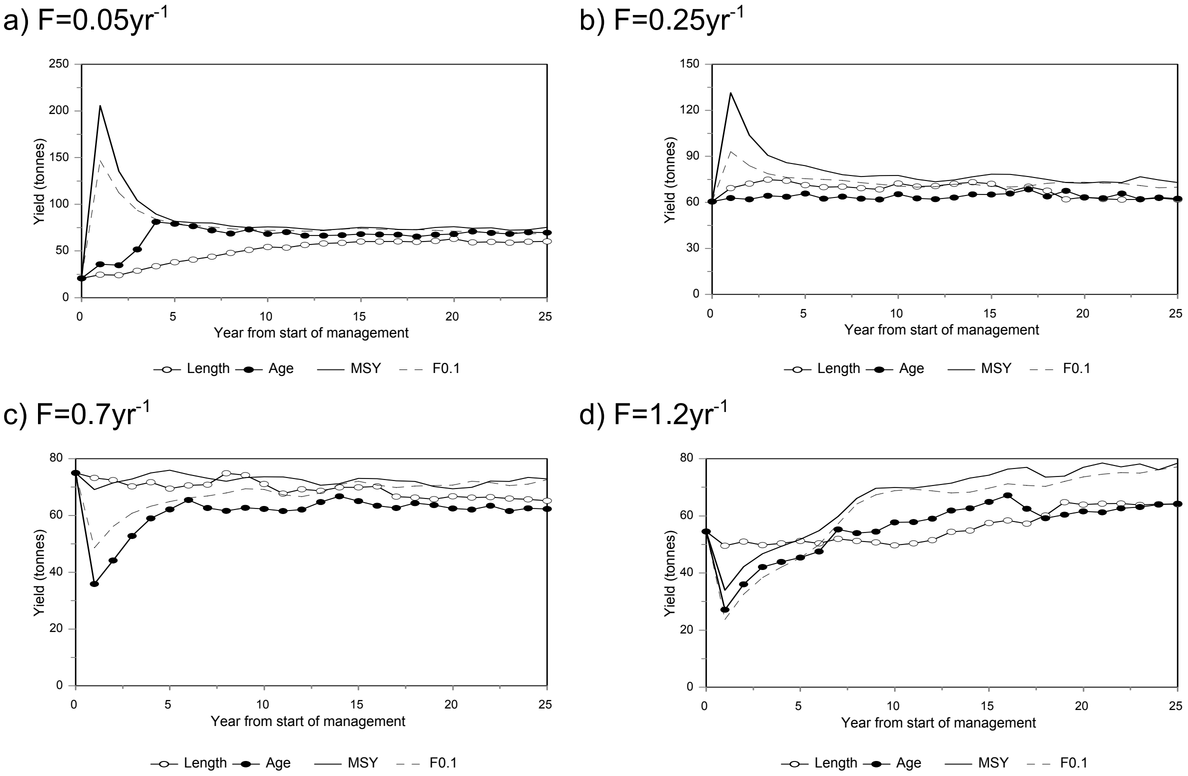
Following year zero, costs for both methods were confined to the routine collection and analysis of length frequency data for estimating fishing mortality. As a result, costs are identical for each assessment method. Costs were discounted at 8% (Table 10.22).

Table 10.22 Discounted cost time stream (at 8%) for Mauritius and Seychelles, by growth parameter estimation method.

Location	Mauritius (MRs)			Seychelles (SRs)		
Method	Length	Age (in house)	Age (sub-contracted)	Length	Age (in house)	Age (sub-contracted)
Year 0	78266	84644	59786	17020	19372	13135
Year 1	18155	18155	18155	3729	3729	3729
Year 2	16810	16810	16810	3453	3453	3453
Year 3	15565	15565	15565	3197	3197	3197
Year *n*	$19{,}607 * \frac{1}{1.08}^{n}$			$4{,}028 * \frac{1}{1.08}^{n}$		

10.3.2 Benefits

The average annual yield derived from the management simulation is presented for each method and initial effort level in Figure 10.5. Yields where effort was set at the true $F_{0.1}$ or F_{MSY} at year zero are also presented for comparison.


a) $F=0.05yr^{-1}$

b) $F=0.25yr^{-1}$

c) $F=0.7yr^{-1}$

d) $F=1.2yr^{-1}$

Figure 10.5 Average yield (tonnes) in each year after initiation of annual management, derived using length- or age-based growth parameter estimates. Average yield resulting from setting effort at true $F_{0.1}$ or F_{MSY} (MSY) is also presented.

10.3.2.1 Benefit time stream

Based on the average annual yields, annual revenue from each fishery was assessed using the prices per kilogramme indicated in Table 10.16. The benefit time stream was then constructed, beginning in year 1. Revenue was discounted, as in the cost time stream, to assess the current worth of annual benefits. Outputs from tuned management strategy simulations initiated at $F=0.4yr^{-1}$ (Chapter 8) were also used in the cost-benefit analysis to examine whether the results from the more complex simulations described in that chapter affected the cost-benefit analysis.

10.3.3 Net benefit-investment ratio (N/K ratio)

The N/K ratios resulting from each method of growth parameter estimation are presented in Table 10.23, for the four simulated initial F levels. An example N/K ratio computation is presented in Table 10.24, for length-based methods in Mauritius (Nazareth bank), initial $F=0.05yr^{-1}$.

Table 10.23 Net benefit-investment (N/K) ratios for the growth parameter assessment methodologies, at the four initial fishing mortality levels, by location.

a) Mauritius

F level (yr^{-1})	Length	Age (in-house)	Age (sub-contracted)
0.05	230	320	454
0.25	376	319	452
0.7	383	291	412
1.2	288	254	360

b) Seychelles

F level (yr^{-1})	Length	Age (in-house)	Age (sub-contracted)
0.05	331	439	647
0.25	541	437	644
0.7	553	399	588
1.2	415	348	514

Where preparation was sub-contracted, age-based methods had a consistently higher N/K ratio than length-based methods. In contrast, however, length-based generally had a financial advantage over age-based methods where preparation was in-house, due to the greater startup costs of the latter method.

Table 10.24 Net benefit-investment (N/K) ratio computation for Mauritius (Nazareth Bank), length-based growth assessment methodology with fishery initially at F=0.05yr^{-1}.

Year	Gross Costs	Gross benefits	Incremental net benefit	Discount factor (at 8%)	Present worth
0	78266	-	-78266	1	-78266
1	19607	834560	814953	0.93	754586
2	19607	982804	963197	0.86	825786
3	19607	970857	951250	0.79	755133
4	19607	1153250	1133644	0.74	833262
5	19607	1347060	1327453	0.68	903442
6	19607	1516059	1496452	0.63	943019
7	19607	1634225	1614619	0.58	942114
8	19607	1757910	1738303	0.54	939151
9	19607	1921533	1901926	0.5	951436
10	19607	2053765	2034158	0.46	942209
11	19607	2277801	2158194	0.43	925613
12	19607	2144238	2124631	0.4	843720
13	19607	2264286	2244679	0.37	825364
14	19607	2325853	2306246	0.34	785187
15	19607	2357248	2337641	0.32	736922
16	19607	2411633	2392026	0.29	698210
17	19607	2406640	2387033	0.27	645141
18	19607	2415910	2396303	0.25	599673
19	19607	2394390	2374783	0.23	550266
20	19607	2432108	2412501	0.21	517598
21	19607	2522314	2502707	0.2	497177
22	19607	2373091	2353484	0.18	432901
23	19607	2393071	2373464	0.17	404237
24	19607	2363053	2343446	0.16	369560
25	19607	2403055	2383448	0.15	348026
			N/K ratio at 8%: $\frac{\sum years\ \ 1-25}{\lvert year\ \ 0\rvert}$		229.6

10.3.3.1 Computations using the results of the management strategy simulations

The N/K ratios calculated using the costs assessed in the current chapter, and the benefits (revenue) assessed using the outputs from the tuned management strategy simulations initiated at F=0.4yr^{-1} (Chapter 8) are presented in Table 10.25.

Table 10.25 Net benefit-investment (N/K) ratios for the growth parameter assessment methodologies calculated using the benefits derived from the outputs of the management strategy simulations, initiated at F=0.4yr^{-1}

Location	Length	Age (in-house)	Age (sub-contracted)
Mauritius	338	311	441
Seychelles	487	426	629

The pattern in N/K ratios is identical to that found when using outputs from the simulations undertaken in the current chapter.

10.3.3.2 Sensitivity analyses

From the N/K ratio tests, age-based methods (with sub-contracted preparation) had a financial advantage over length-based methods. However, this assumed that 9 species could be aged (Section 10.2.1, startup costs). In practice, this number may not be feasible, due to failures in validation. If only a smaller number of species are aged, startup costs (assessed as startup costs-per-species) are greater. The effects of this were examined through sensitivity analyses.

The minimum number of species which could be examined before the N/K ratio for age-based methods equalled that for length-based methods is presented in (Table 10.26). Since length-based methods had higher N/K ratios than age-based methods with in-house preparation (Table 10.23), a higher number of species than that used previously was generally required to give the latter age-based method an advantage.

Table 10.26 Minimum number of species examined using age-based methods before N/K ratio equalled the corresponding N/K ratio for length-based methods, by location.

a) Mauritius

F level (yr^{-1})	Length vs.	
	Age (in-house)	Age (sub-contracted)
0.05	5	2
0.25	13	5
0.7	16	6
1.2	12	4

b) Seychelles

F level (yr^{-1})	Length vs.	
	Age (in-house)	Age (sub-contracted)
0.05	5	2
0.25	11	4
0.7	14	5
1.2	10	3

The number of individuals required to assess growth through each method was also influential on the resulting N/K ratios. The effect of this was also examined through sensitivity analyses. The level to which the number of age samples could be increased without losing the financial advantage over length-based growth assessment methods (*n* for length assumed to remain at 2,000 individuals/year) is presented in Table 10.27, by location. In turn, the number by which length samples would have to be decreased before a financial advantage over the age-based methods (with 192 or 195 individuals sampled, dependent on the location) was gained is presented in Table 10.28.

Since age-based involving in-house preparation resulted in lower N/K ratios than length-based methods, the numbers of otoliths prepared in-house would need to be decreased to gain a financial advantage over length-based methods. In certain cases, this required decreases in the sampled number to a theoretical level below zero. Such cases are noted in the table. Correspondingly, the number of samples examined using length-based methods could be increased before the advantage over age-based method with in-house preparation was reduced.

Table 10.27 Number of otoliths which could be examined while maintaining a financial advantage over length-based methods.

a) Mauritius (for original N/K ratio, age-based *n* = 192)

F-level (yr^{-1})	Age (in-house)	Age (sub-contracted)
0.05	625	742
0.25	27	306
0.7	<0	234
1.2	63	332

b) Seychelles (for original N/K ratio, age-based *n* = 195)

F-level (yr^{-1})	Age (in-house)	Age (sub-contracted)
0.05	548	724
0.25	<0	300
0.7	<0	230
1.2	19	326

Table 10.28 Number of length measurements for length-based growth estimation which could be assessed while gaining a financial advantage over age-based methods.

a) Mauritius (for original N/K ratio, length-based *n* = 2,000)

F-level (yr^{-1})	Length vs.	
	Age (in-house)	Age (sub-contracted)
0.05	1392	941
0.25	2382	1640
0.7	2681	1852
1.2	2286	1572

b) Seychelles (for original N/K ratio, length-based *n* = 2000)

F-level (yr^{-1})	Length vs. Age (in-house)	Length vs. Age (sub-contracted)
0.05	1485	973
0.25	2504	1664
0.7	2813	1874
1.2	2405	1597

10.4 DISCUSSION

The aim of this chapter was to assess length-based and age-based growth parameter estimation methods, in terms of the costs incurred and benefits obtained from their use to derive management.

10.4.1 Costs

Otolithometry, particularly where preparation occurred ‘in-house’, incurred large startup costs when compared to the startup costs incurred during the collection of length frequency data. This difference was reduced when a more realistic measure of startup cost-per-species was estimated.

When the annual expenses involved with each methodology were compared (*i.e.* not including startup costs), length-based methods incurred similar costs to otoliths prepared in-house. This resulted from the larger number of samples required by length-based methods to estimate growth parameters. The annual cost of age-based methods where otolith preparation was performed by a sub-contracted institution was higher, since it incurred an increased cost per otolith. Annual costs resulting from this method could be reduced by using cheaper institutions; costs employed in this study were based on information from CEFAS. It is expected that institutions in other countries, with lower overheads and cheaper labour, would be less expensive.

While growth could be estimated through age-based methods using a single year of data, length-based estimates were assumed to be derived from five years of data. As a result, the overall cost of estimating growth parameters (including startup costs) through length-based methods was comparable to that incurred through in-house otolith preparation; length-based costs were around 90% of age-based costs. In contrast to the annual costs, sub-contracted age-based preparation was cheaper than in-house preparation. This was a result of the lower startup costs incurred by this method. As a result, length-based growth assessment was more expensive than the sub-contracted age-based method (around 130% of sub-contracted costs).

The initial large capital investment (startup cost) involved in the purchase of equipment for age-based assessment was related to the assumed number of species to which the method was likely to be applied. The sensitivity of the N/K ratio to variations in this number of species will be discussed later. However, investment in such equipment offers a further potential income stream, not examined in this analysis. The equipment could be used to prepare otoliths from other international institutions, as performed by CEFAS in the current project. This would increase the number of species examined, and reduce the startup cost-per-species (note that, in this analysis, even if the same species was examined for two locations, they would count as two separate ‘species’). A further advantage of purchasing the equipment would arise where the use of otoliths in local studies was expanded; for example to include annual age-based mortality assessments of species for which growth had been assessed. As noted previously, where startup costs were excluded, the cost-per-otolith for in-house preparation is cheaper than sub-contracted methods.

The cost study reported in Mathews (1987) for Kuwait assessments indicated that length-based method costs were only 10% of those for age-based methods. These costs referred to the process from validation, growth assessment, estimation of mortality via age-length keys, and the derivation of management advice for a number of species. Costs estimated in the current study were based on the estimation of growth parameters and length-based assessment of mortality for one species only. In contrast to Mathews (1987), the current study indicates that the costs of age-based growth assessment are similar to those of length-based methods. In the Kuwait study, validation costs were included. As described previously, these costs were not explicitly incorporated in the current assessment. Any sampling requirements for validation were assumed to be included in the sampling programme for growth estimation, and hence such additional costs were minimised.

Due to the different assessment methods costed, it is difficult to compare the results of this study with that reported in Mathews (1987). However, the results of the current study do contradict the opinion that age-based methods of assessment (in this case growth assessment) are more expensive than length-based methods.

10.4.2 Benefits

The assessment of benefit in terms of yield (and hence revenue) from the fishery were strongly influenced by the management reference level used for each growth estimation method (see also Chapter 8). The use of $F_{0.1}$ for length-based methods frequently resulted in action to decrease fishing effort, or drastic action, at all simulated effort levels (Table 10.3). Since the aim was to compare the growth parameter estimation methods, rather than the management reference level, where length-based growth estimates were used, management was derived relative to the reference level $F=1.65*F_{0.1}$. Management using age-based methods was derived based on $F_{0.1}$. As a result of the use of more appropriate management reference points for each growth assessment method, the overall trends in yields were generally comparable, following those achieved by setting effort to the true value of $F_{0.1}$ or F_{MSY} at year zero.

It should be noted that, as a result of the way in which benefit was calculated (as revenue from the fishery), while outlays (costs) will be incurred by the organisation performing the ageing assessments (*e.g.* SFA, AFRC), benefit does not accrue to that organisation. Instead, benefit accrues directly to the country as a whole. For the organisations performing that work, therefore, justification for the funds required (*e.g.* for startup costs) must be requested in the light of these global benefits to the national economy (including additional employment, increased availability of cheap protein, increased exports and hence foreign exchange).

For a lightly exploited fishery ($F=0.05yr^{-1}$), the use of age-based estimates resulted in greater yields than length-based estimates in all years following the initial management assessment. On average, fishing effort, and hence yield, was increased at a faster rate than that resulting from the use of length-based growth estimation methods. At higher initial fishing effort levels, however, the use of length-based growth parameters generally resulted in marginally higher yields. This was particularly notable at $F=0.7yr^{-1}$ and $F=1.2yr^{-1}$. At these levels, when age-based growth parameters were used, yield initially declined in the first year. This was a result of the high proportion of ‘drastic action’ in the age-based management action distributions at these mortality levels (Table 10.4). Overall however, yields were comparable.

These were the benefits quantified through the simulations described by the current chapter. In addition, a number of unquantified benefits resulted from the use of the different growth parameter estimation methods. These were identified in the outputs of the simulations described in Chapter 8 (Section 8.3.3.3). These included improved management precision, and reduced risk of stock overexploitation. The impacts of these unquantified benefits on the cost-benefit analyses are discussed in the following section.

10.4.3 Net benefit-investment ratio

The cost-benefit analyses were based on the net benefit-investment ratio. Other cost-benefit analysis methods, such as net present worth, would not have affected the results of this analysis; calculation of net present worth involves the summation of the present worth of the benefit stream (in this case, years 1-20), and subtraction of the present worth of the cost stream (year 0). Since the benefits resulting from each growth assessment method are relatively similar, due to the adjustment of the management reference effort level ($F_{0.1}$), differences between the methods would rely on the costs, as in the N/K ratio. However, the results of the net present worth calculations would not have been as clear as those from the N/K ratio. For the net present worth calculation, a small cost would be subtracted from a relatively large benefit in each case. While the pattern found in the results of the N/K analysis would remain, similar overall values would result from the net present worth assessment. Hence the net benefit-investment ratio offered the clearest interpretation of the results.

At all simulated initial fishing mortality levels, age-based methods (where preparation was sub-contracted) had higher N/K ratios than those from length-based methods. Therefore, the advantages of using age-based methods to estimate growth were not outweighed by the costs of their use only where preparation was sub-contracted.

In contrast, when compared with age-based methods where preparation was performed in-house, length-based methods had a higher N/K ratio. This was a result of the additional startup costs involved in the in-house preparation of otoliths when compared to sub-contracted otolith preparation.

As indicated by the N/K ratio, the advantage of sub-contracted age-based methods was greatest at low initial fishing mortality levels. Due to discounting, benefits obtained in the early years had a greater impact on the N/K ratio than yields in later years. At higher effort levels, initial yield from age-based assessments were below those resulting from length-based growth estimates (see Section 10.4.2). These initial years therefore had a disproportionate influence on the N/K ratio.

The outcomes of the cost-benefit analysis were not affected by the relative simplicity of the simulations performed in the current chapter. The use of the available outputs from the management strategy simulations performed in Chapter 8 resulted in an identical pattern of N/K ratios, with those resulting from age-based methods with sub-contracted preparation proving the most financially appropriate. The similarity from both simulations is likely to result from the tuning process undertaken in both studies. As a result, benefits resulting from different growth estimation methods are relatively comparable, regardless of the initial effort level. Hence, differences in the N/K ratios are largely driven by the differences in the costs involved in each method.

Sensitivity analysis examined the effects of varying the number of species over which the startup costs were divided. In both locations, age-based methods (with sub-contracted preparation) maintained their advantage over length-based methods if the number of species studied was reduced to six. The examination of this number of species appears feasible for both fishery institutions.

Sensitivity analyses also examined the number of individuals which could be examined through each method, while maintaining (age-based, sub-contracted), or obtaining (length-based), an advantage over the alternative method. For age-based methods, the increase in the number of individuals examined was generally over 100 individuals. Such increases would cater for any additional sampling required for validation. Length-based methods would require decreases of between 15 and 50% to gain an advantage over age-based methods. However, based on the results of the initial simulations described in Chapter 7, the reduction to such levels would still allow growth parameter estimates to be obtained for these species.

In theory, therefore, length-based methods could prove financially more attractive by reducing the number of individuals sampled annually. In this study, a large number of individuals (and years of data) were required to obtain length-based growth parameter estimates, when compared to that for age-based methods. The numbers for length-based analyses were based on those routinely sampled in the study location, and therefore represent the likely current costs involved in this method. In turn, the relatively low numbers required for age-based methods represent a suitable sampling strategy to estimate growth for these species in the study locations. However, it may be considered that growth parameter estimates could be obtained using a smaller sample size. Length-based methods do indeed gain an advantage over age-based methods if the number of individuals collected on an annual basis is reduced to levels identified in the sensitivity analyses.

The advantage of age-based methods would also be reduced by costs not included in the current analysis: the cost of training staff in otolithometry preparation and reading. The method to quantify such costs was not straightforward; questions arose as to where staff would be trained (at CEFAS, at a more local institution, or would experts travel to the fisheries institutions?), how long training would take, how many people required training? Such costs, particularly those involved in the training of staff in otolith preparation, could prove substantial.

However, the training of staff in otolith preparation and reading represents a one-off cost (*i.e.* a startup cost), the former only being incurred by institutions undertaking in-house preparation. Such additional costs could be offset by additional advantages. Training would allow the establishment of a regional centre for otolith preparation. Startup costs, including such training, are assessed on a per-species basis. The additional number of species examined as a result of forming such a centre would therefore reduce the impacts of these additional startup costs on the cost-benefit analysis considerably. The additional costs of training would therefore have a minimal impact on the results. In turn, the formation of a regional otolith preparation centre would provide additional benefits in terms of revenue, further offsetting the costs of training.

An alternative to establishing a regional otolithometry centre in a government organisation, where costs arise from training and then keeping skilled staff, is to set up such organisation in non-governmental organisations such as Universities. The benefits of this arrangement would depend on the cost charged for preparing the otoliths.

The arguments for length-based methods ignore the additional, but unquantified, advantages of age-based methods which were identified in Chapter 8 (Section 8.3.3.3). The level of precision in the resulting values of fishing mortality were improved; age-based growth estimates were more likely to result in the optimum fishing mortality level. In turn, the use of these growth estimates reduced the probability of over-exploitation (recruitment overfishing). The increased precision of management, combined with the reduced risk of over-exploiting the stock resulting from the use of age-based methods are strong benefits.

Overall, therefore, the use of age-based methods, with otolith preparation performed in-house, appears the most appropriate method from both financial and practical points of view.

10.4.4 Summary

The overall costs of growth parameter estimation for length- and age-based methods were comparable. While age-based methods incurred greater startup costs, length-based methods required a greater quantity of data to obtain growth parameter estimates, increasing the costs of preparation and the number of trips to port required. This result is in contrast to the general perception that age-based methods are more expensive than length-based methods.

Where management was based on suitable reference levels ($F_{0.1}$ for age-based growth parameters, $1.65*F_{0.1}$ for length-based growth parameters, or tuned as in Chapter 8), fishery yields, revenue, and hence benefits resulting from the use of each set of growth parameter estimates, were comparable. However, age-based growth parameters also resulted in a number of additional benefits (Chapter 8).

Based on the cost-benefit analysis, the greatest financial benefit was gained through age-based methods where otolith preparation was sub-contracted. Length-based methods had an advantage over age-based methods (where otolith preparation was performed in-house). However, that assessment ignored potential benefits arising from the establishment of a regional centre for otolith preparation, and the additional, unquantified, benefits of increased precision and improved conservation resulting from age-based methods.

From these analyses, benefits obtained through age-based growth parameter estimation methods outweigh the costs involved in the methodology. Where funding can be obtained and validation achieved, age-based growth parameter estimates offer a financially viable method on which to base fisheries stock assessment for long-lived, slow growing species. Cost-benefit studies such as these may provide the justification required to gain funding for otolith studies from outside funding bodies.

In Chapter 8 it was noted that age-based methods resulted in the most appropriate management decisions. However, the use of length-based methods at any stage of the assessment process had a negative influence on the outcome. Undertaking a fully age-based stock assessment would eliminate these influences, improving management performance further. This might also reduce costs, since length frequency distributions would no longer be required, while the use of otolith weight-age relationships would offer a relatively cheap and rapid method through which age frequency distributions could be derived. This is currently feasible for *L. mahsena* (see Chapter 9, Appendix 7).

Guidelines arising from this project suggest investigating whether improved management does indeed result from a full age-based stock assessment approach. Cost-benefit analyses on the outputs of these simulations are likely to indicate financial advantages over the assessment methods examined in the current study. Such results would provide further incentives for institutions to undertake the recommended shift from length- to age-based methods of assessment.

APPENDICES

Appendix 1. Successful validations of increments in otoliths of Lutjanidae and Lethrinidae

The following tables present studies which have used otoliths from Lutjanidae and Lethrinidae for ageing, and the extent to which the otolith increments were validated. Tables detail studies which examined a) annual rings (annuli) and b) daily rings.

Table A.1.1 Studies examining annual rings in lutjanid and lethrinid species, and extent of validation.

		Annual Rings		
Species	Author	Location	Validated	Extent
Lutjanus adetii	Newman *et al.*, 1996	E Australia	Y	Using tetracycline
Lutjanus anelis	Mason and Manooch, 1985	Florida	Y	Cited in Manooch, 1987. Included back-calculation
Lutjanus campechanus	Manooch, 1982	Florida	Y	Using marginal increment analysis, focus to ring distances, comparison with scales
Lutjanus coccineus	Samuel and Mathews, 1985	Kuwait	Y	Method not specified
Lutjanus eyrthropterus	Milton *et al.*, 1995	Australia	Y	Annuli in *whole* otoliths validated by radioactivity dis-equilibria
Lutjanus griseus	Manooch, 1982	Florida	Y	Using marginal increment analysis, focus to ring distances, comparison with scales
Lutjanus kasmira	Morales-Nin and Ralston, 1990	Hawaii	Y	Annual rings validated by counts of daily rings using SEM
Lutjanus malabaricus	Milton *et al.*, 1995	Australia	Y	Annuli in whole otoliths validated by radioactivity dis-equilibria
Lethrinus nebulosus	Morales-Nin, 1988	New Caledonia	Y	Using otolith microstructure, regularity of ring formation, correlation between mean length-at-age, and back-calculation
Lutjanus peru	Rocha-Olivares and Gomez-Munoz, 1993	La Paz Bay, Mexico	Y	Marginal Increment Analysis
Lutjanus sebae	Milton *et al.*, 1995	Australia	Y	Annuli in WHOLE otoliths validated by radioactivity dis-equilibria
Lutjanus snyagris	Manooch and Mason, 1984	Florida	Y	Cited in Manooch, 1987
Lutjanus quinquelineatus	Newman *et al.*, 1996	E Australia	Y	Using tetracycline

Table A.1.1 Studies examining annual rings in lutjanid and lethrinid species, and extent of validation, continued.

		Annual Rings		
Species	Author	Location	Validated	Extent
Ocyurus chrysurus	Manooch and Drennon, 1987	US Virgin Is., Puerto Rico	Y	Marginal increment analysis
Aprion virescens	Loubens, 1980	New Caledonia	UNK	Cited in Manooch, 1987
Lutjanus bohar	Loubens, 1980	New Caledonia	UNK	Cited in Manooch, 1987
Lutjanus buccanella	Espinosa and Pozo, 1982	SE Cuban Shelf	Y/N	'Growth validity tests' performed but not specified
Pristipomoides filamentosus	Hardman-Mountford *et al.*, 1996	Seychelles	Y/N	Assumed annuli matched approximate 12.4 x assumed monthly rings. Reasonable compatibility with L_∞ from Mees, 1993 (length-based), but differences in K and t_0.
Lutjanus malabaricus		GBR, Australia	N	
Lutjanus erythropterus	McPherson and Squire, 1992	GBR, Australia	N	Validation of age estimates stated to be incomplete
Lutjanus sebae		GBR, Australia	N	

Table A.1.2 Studies examining daily rings in lutjanid and lethrinid species, and extent of validation.

		Daily Rings		
Species	Author	Location	Validated	Extent
Lethrinus choeroryn chus	Morales-Nin, 1989	NW Australia	Y/N	SEM on Daily Rings
Lutjanus coccineus	Brothers and Mathews, 1987	Kuwait	Y/N	SEM on Daily Rings
Lutjanus kasmira	Morales-Nin, 1989	NW Australia	Y/N	SEM on Daily Rings
Pristipomoides filamentosus	Ralston and Miyamoto, 1981	Hawaii	Y/N	Validated in Ralston, 1981
Pristipomoides filamentosus	Radtke, 1987	Hawaii	Y/N	Partial Validation using SEM
Lutjanus sebae	Bach and Chauvelon, 1994	Seychelles	UNK	Not mentioned in paper
Etelis carbunculus	Smith and Kostlan, 1991	Hawaii, NMI, French Polynesia & Vanuatu	N	Based on validation of *P. filamentosus* by Ralston, 1981 Hawaii
Etelis carbunculus	Brouard *et al.*, 1984	Vanuatu	N	Hypothesise rings are daily - authors state this must be checked
Etelis corruscans		Vanuatu	N	
Lethrinus miniatus	Caillart *et al.*, 1986	French Polynesia	N	Assume one ring laid down each day
Lutjanus fulvus		French Polynesia	N	
Pristipomoides flavipinnis	Brouard *et al.*, 1984	Vanuatu	N	Hypothesise rings are daily - authors state this must be checked
Pristipomoides multidens		Vanuatu	N	

Appendix 2. MIDAS model algorithms

This appendix describes the algorithms through which MIDAS operates.

A.2.1 BASIC DYNAMICS

For each stock, the number of fish of age *a* at time *t* is given by

$$N_{a,t} = (N_{a-\delta,t-\delta}\, e^{\frac{-M(a-\delta,B(t-\delta)).\delta}{2}} - C_{a,t})\, e^{\frac{-M(a-\delta,B(t-\delta)).\delta}{2}}$$

where

$M(a,B)$ = adult natural mortality (function of age, various stock biomasses)

$C_{a,t}$ = catch of fish aged $a-\delta$ during the delt ending at time t

$B(t)$ = deviation of current adult biomass from unexploited equilibrium

δ = simulation time step

For each stock and gear combination, the catch of fish aged *a* - *δ* to *a*, taken during the period *t* - *δ* to *t*, is

$$C_{a,t} = \frac{F(a-\delta,t-\delta)}{F(a-\delta,t-\delta)+M(a-\delta,B(t-\delta))} \cdot N_{a-\delta,t-\delta}(1-e^{-[F(a-\delta,t-\delta)+M(a-\delta,B(t-\delta))].\delta})$$

where

$F(a,t)$ = fishing mortality

= $E(t).S(a).q(t)$ where

$E(t)$ = effort by time

$q(t)$ = catchability by time

$S(a)$ = selectivity by age

= $1/[1+e^{(C_1-C_2L_a)}]$ where

L_a = length at age

$C_1 = \frac{\ln(3)\,Lc_{50}}{Lc_{75}-Lc_{50}}, \quad C_2 = -\frac{C_1}{Lc_{50}}$

Lc_x = length at which x% of fish are caught

The catch for a gear is zero if the time falls within the closed season for that gear.

The length and weight of an individual at age *a* (and time *t*) are given by

$$L_a = L_{a-\delta} + (L_\infty - L_{a-\delta}).(1 - e^{-K(t-\delta,B(t)).\delta})$$

$$W_a = A\, L_a{}^{\alpha}$$

where

$K(t,B(t))$ = time (season) and/or density dependent growth rate

L_∞ = asymptotic length

A, α = parameters relating length to weight

A number of parameters can vary with time, or time-related variables. Mortality can be a function of age, catchability and effort are functions of time and growth can be a function of season. These relationships are all specified by means of lookup tables. Function values can be linearly interpolated from the given points, or the points can be used to define a step function.

The lookup tables are implemented the same way for all of the abovementioned cases. Consider mortality (*M*) as a function of age (*a*). Given a table of *n* pairs (a_i, $M(a_i)$), *i*=1...*n*, the step function is defined as

$$M(a) = M(a_i), \text{ for } a_i \le a < a_{i+1}$$

while the interpolated function is given by

$$M(a) = M(a_i) + (a - a_i)\frac{M(a_{i+1}) - M(a_i)}{(a_{i+1} - a_i)}, \text{ for } a_i \le a < a_{i+1}$$

For both functions,

$$M(a) = M(a_1), \text{ for } a < a_1$$

$$M(a) = M(a_n), \text{ for } a \ge a_n$$

A.2.2 BIOMASS INDICATORS

The following biomass indicators are defined:

Given that

A = age group (integer)

$A_{\max}$ = maximum age group

A_{Cmin} = minimum age at capture (all gears)

O_M = maturity ogive (selection function)

S_S, S_E = start, end of spawning season

The spawning stock biomass for a year *y* is defined as

$$\mathrm{SSB}_{\mathrm{y}} = \frac{1}{(S_E - S_S)} . \sum_{A=0}^{A_{\max}} \int_{t=S_S}^{S_E} N_{A+t,y+t} . W_{A+t,y+t} . O_{M_{A+t}} \, \mathrm{d}t$$

The yield over a year *y* is

$$\mathrm{Yield}_{\mathrm{y}} = \sum_{A=0}^{A_{\max}} \int_{t=0}^{1} \sum_{\mathrm{Gears}} C_{A+t,y+t} \, \mathrm{d}t$$

The average exploitable biomass in year *y* is defined as

$$\mathrm{EXB}_{\mathrm{y}} = \int_{t=\mathrm{frac}(A_{Cmin})}^{1} N_{A+t,y+t} . W_{A+t,y+t} \, \mathrm{d}t + \sum_{A=\mathrm{ceil}(A_{Cmin})}^{A_{\max}} \int_{t=0}^{1} N_{A+t,y+t} . W_{A+t,y+t} \, \mathrm{d}t$$

The total biomass in year y is calculated above using the age at recruitment, A_R, instead of the minimum age at capture A_{Cmin}.

A.2.3 RECRUITMENT

The following forms of stock recruitment relationship are available:

i Constant recruitment

$$R = R_{const}$$

ii Beverton-Holt

$$R = \frac{\mathrm{SSB}}{1 - \theta \, (1 - \frac{\mathrm{SSB}}{\gamma})}$$

iii Ricker

$$R = a . SSB . e^{-b . SSB}$$

iv Shepherd

$$R = \frac{p . \mathrm{SSB}}{1 + (\frac{q}{\mathrm{SSB}})^{\beta}}$$

The parameters *p*,*q* and *β*, *a* and *b*, or *θ* and *γ* are specific to the fish stock. The Shepherd SRR may be specified directly by providing the parameters *p*,*q* and *β*, or indirectly by specifying the unexploited equilibrium point and the shape of the SRR relative to that point. This means that the shape of the SRR is fixed, but not the absolute position or size. Given an equilibrium point at (R_0,S_0) (note that once R_0 is specified, S_0 can be calculated), the alternatives are:

a) Where β=1 (Beverton-Holt shape), specify the unexploited equilibrium recruitment (the corresponding spawning biomass is calculated by the program) and a parameter d ($0 < d < 1$) which indicates the degree of curvature (density dependence) of the SRR between the origin and the equilibrium point. The conversion equations are

$$\beta = 1$$

$$p = \left(\frac{1+d}{1-d}\right)^2 . \frac{R_0}{S_0}$$

$$q = \frac{R_0 . S_0}{pS_0 - R_0}$$

b) For a Ricker function shape, specify the unexploited equilibrium recruitment R_0, the ratio of the maximum to the unexploited recruitments R_m/R_0, and the ratio between the spawning biomass at which maximum recruitment occurs and the equilibrium spawning biomass S_m/S_0. Then,

$$0 = \beta\left(\frac{R_m}{R_0} - \frac{S_m}{S_0}\right) + \frac{S_m}{S_0}\left(1 - \frac{1}{(S_m/S_0)^\beta}\right) \qquad \text{(Solve for } \beta\text{)}$$

$$K = \frac{(S_m/S_0).S_0}{\left(\frac{1}{\beta - 1}\right)^{1/\beta}}$$

$$a = \frac{(R_m/R_0).R_0}{K} \, \frac{\left(1 + \frac{1}{\beta - 1}\right)}{\left(\frac{1}{\beta - 1}\right)^{1/\beta}}$$

c) Specify β, the unexploited equilibrium recruitment and the slope G of the function at the equilibrium point given as a fraction of the slope R_0/S_0. The conversion is given by

$$q = S_0 \sqrt[\beta]{\frac{-R_0\beta - (GS_0 - R_0)}{GS_0 - R_0}}$$

$$p = \frac{R_0}{S_0}\left[1 + \left(\frac{S_0}{q}\right)^\beta\right]$$

A.2.4 DENSITY DEPENDENT GROWTH

The model of density dependent growth used in this study related changes in the biomass of either the whole, or part, of the population to changes in either L_∞ or K, dependent on which parameter was specified by the user.

The relationship for L_∞ took the form:

$$L_\infty(B) = L_{\infty 0}[1 - \frac{g(L)}{100}.\frac{B_0(L)-B(L)}{B_0(L)}]$$

The relationship for K took the form:

$$K(B) = K_0[1 - \frac{g(L)}{100}.\frac{B_0(L)-B(L)}{B_0(L)}]$$

where:

B	total biomass, averaged over the previous year
B_o	total biomass at unexploited equilibrium
$L_\infty(B)$	asymptotic length (cm) at biomass B
$L_{\infty 0}$	asymptotic length (cm) at unexploited equilibrium (*i.e.* before any changes due to density dependent growth)
$K(B)$	von Bertalanffy growth rate at biomass B
K_0	von Bertalanffy growth parameter at unexploited equilibrium (*i.e.* before any changes due to density dependent growth)
g	gradient of the density dependent growth relationship, as set by the user. g can be a step or piecewise linear function of l.
$B(L)$	sum of the biomass from all sizes greater than or equal to the length specified (L). Where this length is specified as 0 cm, the total biomass of the population affects the growth.

The value of the growth parameter was therefore directly proportional to the specified biomass, the user having set the gradient of the relationship.

The percentage entered for the gradient (*g*) is always negative, as a reduction in the specified biomass leads to an increase in L_∞ or K. The magnitude of *g* can be viewed as the limit to the change in the growth parameter, since as ***B*** tends to zero, L_∞ tends to L_∞*(1 + *g*/100), and K tends to K*(1+*g*/100). This is the basic density dependent growth relationship used in the three models.

Any number of length groups can be defined, with g for each group relating the growth of group members to the biomass of fish in or larger than that length group. The exception is the very smallest group which is modelled as spatially isolated and whose growth is therefore only influenced by the biomass of its own members. For more information on the three models used during the simulations, see the main text.

A.2.5 INTERACTIONS BETWEEN STOCKS

This feature of MIDAS was not used in the current study. It is included here for completeness.

Let the vector $\mathbf{B}(t) = \mathbf{B}_C(t) - \mathbf{B}_0$ denote the difference between the current adult biomass, $\mathbf{B}_C$(t), and unexploited equilibrium biomass, $\mathbf{B}_0$, for each stock. **B** has dimension N_s by 1, where N_s is the number of stocks. If, when all stocks are unexploited, the age dependent adult mortality for each stock is given by $\mathbf{M}_0(a)$, the juvenile mortality by $\mathbf{JuvM}_0$ and the seasonally variable growth rate by $\mathbf{K}_0$(frac(*t*)), then the influence of the various stock biomasses can be modelled as

$$\begin{aligned} M(a,t) &= M_0(a) + G_M.B(t) \\ JuvM(t) &= JuvM_0 + G_J.B(t) \\ K(t) &= K_0(\mathrm{frac}(t)) - G_K.B(t) \end{aligned}$$

where $\mathbf{G}_M$, $\mathbf{G}_J$ and $\mathbf{G}_K$ are N_s by N_s arrays of constants. These constants are inputs to the model and will usually be positive. The biomass dependent mortalities and growth rate are subsequently limited so that they cannot vary by more than a given percentage around their biomass independent values. This percentage is currently set to 20%.

A.2.6 INITIALISATION

If the user specifies unexploited biomass ratios for all stocks rather than initial recruitment levels, the initial recruitment must be found by iteration. The total recruitment is set to 1000 times the number of stocks, and this total recruitment is initially divided amongst the stocks in the same ratio as the biomasses required. The biomass ratios resulting from the simulation of a cohort of each species' lifespan are compared with the required ones and the initial recruitment ratios are adjusted iteratively until the required result is reached.

At this point, any stock recruitment relationship parameters that are dependent on the position of the unexploited equilibrium can be calculated. If all the stock recruitment relationships are of this form or constant, the situation derived above will be the unexploited equilibrium. If not, the equilibrium and thus the biomass ratios may change once more.

An important parameter that must be set at this stage is the maximum age to which the simulation is run. Since all the stocks are being simulated simultaneously, this age must be appropriate for all stocks. For each individual stock, if M and JuvM are constant, then the age by which a cohort has declined in numbers to 0.1% of its original size is given by

$$A_{\max}[\text{stock}] = \mathrm{round}(-\frac{\ln(0.001) + JuvM.A_r}{M} + A_r)$$

The maximum age $A_{\max}$ is set initially to the largest of these values. However, time, age and biomass dependence may result in all stocks being depleted faster than otherwise; in the event that all stocks have been reduced to less than 0.1% of their biomass before $A_{\max}$ has been reached, $A_{\max}$ will be redefined. This adjustment is only made once.

A.2.7 EQUILIBRIUM CONDITIONS

When a population is in equilibrium, the number of fish of age *x* at a particular time is equal to the number of fish remaining in a cohort *x* years after recruitment. This means that the equilibrium age structure can be found by simply simulating the time history of one cohort at equilibrium. The condition for equilibrium is that the adult biomass each year should be constant, i.e. SSB(*t*+1) = SSB(*t*). This relationship must apply for all stocks simultaneously.

Equilibria are currently calculated by means of a simple iteration : $\mathbf{R}=f(\mathbf{ssb}_1)$, $\mathbf{ssb}_2 = g(\mathbf{R})$ and are calculated repeatedly until $\|\mathbf{ssb}_1 - \mathbf{ssb}_2\| < \varepsilon$, where $\mathbf{ssb}_1$ and $\mathbf{ssb}_2$ are vectors of spawning biomass and **R** is a vector of recruitment for each stock.

Appendix 3. Maximum and minimum L_∞ and K estimates from a number of lutjanid and lethrinid species

Table A.3.1 Maximum and minimum L_∞ and K estimates from a number of lutjanid and lethrinid species.

Species	L∞ (cm)				K			
	Value	Author	Location	Method	Value	Author	Location	Method
Aprion virescens	65.8	Loubens, 1980	New Caledonia	Otoliths	0.26	Mees, 1992	Seychelles	ELEFAN
	104	Mees, 1992	Seychelles	ELEFAN	0.31	Loubens, 1980	New Caledonia	Otoliths
Pristipomoides filamentosus	58	Ralston and Williams, 1988b	N. Marianas	Otoliths	0.15	Uchida, 1986	Hawaii	Otoliths
	97.1	Uchida, 1986	Hawaii	Otoliths	0.31	Ralston, 1980	NW Hawaii	Otoliths
Lutjanus bohar	52	Loubens, 1980	New Caledonia	Otoliths	0.11	Loubens, 1980	New Caledonia	Otoliths
	81.7	Wright *et al.*, 1986	PNG	ELEFAN I	0.33	Munro, 1983	Seychelles	Petersen Method
Lutjanus sebae	72	McPherson and Squire, 1992	NW Australia GBR	vertebrae	0.13	Yeh *et al.*, 1986	NW Australia GBR	vertebrae
	102.5	McPherson and Squire, 1992	Australian GBR	otoliths -validation incomplete	0.31	Mees, 1992	Seychelles	ELEFAN
Etelis carbunculus	54	Smith and Kostlan, 1991	N. Marianas	otoliths	0.13	Smith and Kostlan, 1991	Fr Polynesia	Otoliths
	127	Smith and Kostlan, 1991	Vanuatu	otoliths	0.36	Uchida, 1986	Hawaii	Otoliths
Lutjanus miniatus	45.7	Loubens, 1990	New Caledonia	Otoliths	0.1	Church, 1989	Norfolk Is	Otoliths?
	83	Church, 1989	Norfolk Is	Otoliths?	0.27	Loubens, 1990	New Caledonia	Otoliths

Table A.3.1 Maximum and minimum L_∞ and K estimates from a number of lutjanid and lethrinid species, continued.

Species	L_∞ (cm) Value	Author	Location	Method	K Value	Author	Location	Method
Etelis corruscans	82	Brouard and Grandperrin, 1984	Vanuatu	Otoliths, non-linear regression	0.12	Ralston and Williams, 1988	N Marianas	Non-linear regression
	116	Latu and Tulua, 1991	Tonga	Wetherall	0.13	Langi and Langi, 1987	Tonga	Wetherall
Lutjanus kasmira	21.1	Loubens, 1990	New Caledonia	Otoliths	0.21	Ralston and Williams, 1980	Amer. Samoa	Otoliths
	40	Ralston and Williams, 1980	N Marianas	Non-linear regression	0.38	Loubens, 1990	New Caledonia	Otoliths
Lutjanus synagris	42.2	Pauly, 1978	Cuba	Non-linear regression	0.2	Manooch, 1987	USA	Otoliths
	71	Manickchand-Dass, 1987	Trinidad and Tobago	Otoliths	0.27	Pauly, 1978	Cuba	Non-linear regression
Lutjanus vitta	24	Loubens, 1990	New Caledonia	Otoliths	0.26	Ambak *et al.*, 1985	Malaysia	ELEFAN?
	42.5	Ambak *et al.*, 1985	Malaysia	ELEFAN?	0.37	Davis and West, 1992	Australia	Non-linear regression
Lethrinus mahsena	58.9	Dalzell *et al.*, 1992	Yemen Dem.		0.1	Bautil and Samboo, 1988	Nazareth Bank, Mauritius	ELEFAN
	61.7	Bautil and Samboo, 1988	Nazareth Bank, Mauritius	ELEFAN	0.32	Dalzell *et al.*, 1992	Yemen Dem.	
Lethrinus nebulosus	48	McPherson and Squire, 1992	Australia	Non-linear regression	0.1	Aldonov and Druzhinin, 1979	Yemen Dem.	Ford/Walford Plot
	99.9	Carpenter and Allen, 1989	Yemen Dem		0.34	McPherson and Squire, 1992	Australia	Non-linear regression

Appendix 4. Length frequency data available for the study species, by location

A.4.1 MAURITIUS

Table A.4.1 Summary of *L. mahsena* length frequency data available by year and bank.

Bank	1989	1990	1991	1992	1993	1994	1995	1996	1997
Albatross (ALB)	0	0	0	0	432	0	0	0	0
Chagos (BIOT)	0	0	0	0	185	664	0	84	0
Nazareth (NAZ)	561	363	871	373	1518	1173	2795	2875	2045
North Saya (SMN)	700	0	152	1605	1135	1687	1462	525	766
South Saya (SMS)	558*	692	79*	754	3340	3924	1150	1932	4042
St Brandon (STB)	0	0	0	0	906	587	0	0	0
Total	1819	1055	1102	2732	7516	8035	5407	5416	6853

* Data for Saya South (SMS) for the years 1989 and 1991 were corrupted. Only part of the data could be extracted.

A.4.2 SEYCHELLES

Table A.4.2 Summary of length frequency data available for *A. virescens* by year and sector. All gears amalgamated.

Sector	1991	1992	1993	1994	1996	1997	1998
1	0	0	0	0	3	69	14
2	351	19	120	0	400	642	211
3	18	415	63	0	851	55	43
4	48	178	9	21	241	166	18
5	141	28	57	27	83	238	66
6	279	355	256	797	973	963	211
7	471	198	220	155	766	199	150
8	60	0	0	625	0	0	0
9	1139	850	226	183	331	438	326
10	247	96	232	608	125	143	185
11	23	9	39	29	518	251	181
12	51	15	0	0	0	0	0
13	738	83	26	262	0	0	0
14	157	0	0	0	0	64	0
Unknown	4596	2763	1430	4380	824	0	0
Total	8319	8009	2667	7087	5115	3228	1405

A.4.3 BIOT (CHAGOS ARCHIPELAGO)

Table A.4.3 Number of *L. mahsena* and *A. virescens* individuals sampled by species, year and area within BIOT (Chagos Archipelago).

Area Code	*L. mahsena*					*A. virescens*				
	1994	1995	1996	1997	1998	1994	1995	1996	1997	1998
CAU	0	0	0	0	68	0	0	0	35	13
CH1	52	36	0	80	0	0	0	0	55	0
CH2	0	0	0	0	12	0	0	0	33	0
ECH	168	110	0	177	46	0	12	0	116	17
GAN	0	0	0	0	0	0	0	0	36	0
NCH	30	91	90	139	9	102	20	13	48	0
NEL	113	78	226	88	94	0	13	10	40	4
PIT	215	0	90	230	0	42	0	4	93	9
SCH	0	92	27	196	277	0	6	4	10	14
SEC	0	100	0	292	229	0	6	0	317	12
SPK	0	0	46	0	0	0	0	5	0	2
WCH	34	41	74	137	40	0	4	16	110	3
Total	612	548	553	1339	725	144	61	52	893	74

Appendix 5. Forms tracking the collection of otoliths from the target species

Appendix 6. Examination of sex and maturity data for *L. mahsena* and *A. virescens*

A.6.1 INTRODUCTION

Population sex characteristics can be affected by fishing. Snappers are gonochoristic, *i.e.* sex change does not occur during the lives of individuals (Grimes, 1987). However, selective effects of fishing have particularly significant impacts where species change sex during their lives. *L. mahsena* is a protogynous hermaphrodite; during their life history, individuals change sex from female to male (Bertrand, 1986). Intensive fishing with selective gears may therefore have a significant effect on the sex ratio of this species (Bannerot *et al.*, 1987), and therefore the reproductive potential of the population (*e.g.* Thompson and Munro, 1983). The factor controlling the point at which a species changes sex have not been identified, although several have been implicated. These include sex ration or relative size (Sadovy, 1996). The controlling factor may modify the extent to which fishing affects the sex ratio of the population (Munro and Williams, 1985). Where sex change is controlled by the sex ratio of the population (social control), effects of fishing on that sex ratio and reproductive potential may be minimised. Where the controlling factor is endogenous, the effects of fishing may be pronounced (Russ, 1991; Jennings and Lock, 1996).

This argument may also apply to the age and/or length at maturity. Individuals in exploited populations may mature earlier, in response to increased adult mortality, or through increased growth rates (*e.g.* Stearns and Crandall, 1984; Rochet, 1998).

Biological data collected for both *A. virescens* and *L. mahsena* during otolith sampling will be examined to identify patterns in the sex ratio and maturity data which relate to fishing pressure. This appendix will also derive the first maturity assessments for *L. mahsena* from the Mauritian banks and Seychelles, and improve on the *A. virescens* assessment made by MRAG (1996d) for Seychelles.

A.6.2 METHODOLOGY

Both sex ratio and maturity data were examined for trends related to fishing. Data were examined between geographic locations. Refer to Chapter 4 (Section 4.2.2.2) for details of data collection.

Sex ratio

The overall sex ratio of males to females was calculated for each location from specimens sampled at random. Sex ratio at length was also assessed where there were more than five individuals of each sex present in a length class.

Maturity and Gonadosomatic Index (GSI)

A gonadosomatic index (GSI) was calculated for both sexes;

$$GSI = \frac{gonad\ weight\ (g)}{total\ fish\ weight\ (kg)}$$

Mean GSI values were calculated by sex for each length class. These were assessed to identify a relatively large increase in the average GSI in the small length classes. Such an increase was inferred as the onset of gonadal development (*i.e.* the length at which reproductive potential is first seen; Lm_{min}).

The proportion of individuals mature at length was assessed for females only. On the five point scale used in Seychelles, fish at stages 3+, 4 and 5 were considered mature (MRAG, 1996d). For the eight point scale used in the other locations, individuals of stages 4 or greater were considered mature. The resultant plots were assessed for the length at which 50% of females were mature (Lm_{50}). Lm_{50} was assessed both visually, and by fitting a logistic equation to the percentage of mature individuals (*P(x)*) in each size class (*FL*);

$$P_x = \frac{100}{1+e^{(a.FL\ +\ b)}}$$

where *a* and *b* are fitted parameters, and Lc_{50} = -b/a.

A.6.3 RESULTS

The results are presented by species.

L. mahsena

Data for sex ratio was available from all locations. Maturity data was available from all study locations bar BIOT (Chagos Archipelago).

Sex ratio

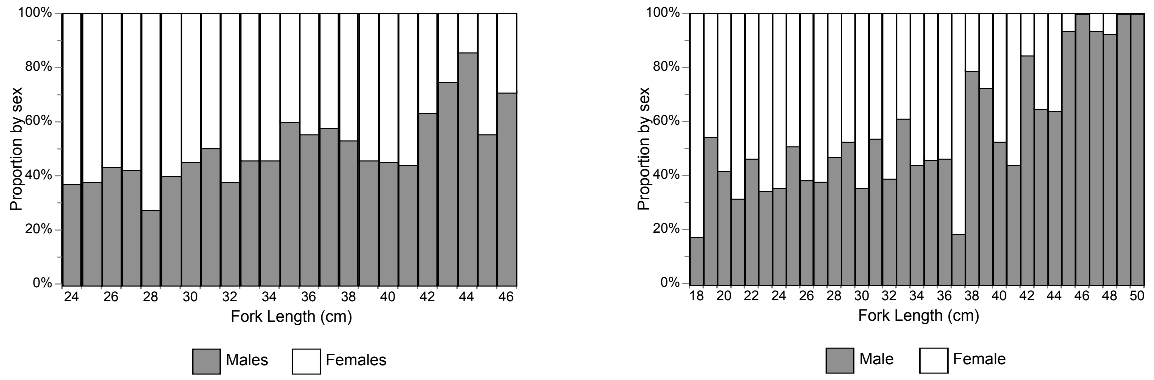
Sex ratios (male : female) for each location are shown in Table A.6.1. Due to the lack of randomly sampled individuals from Saya north, a sex ratio was not calculated for this location. Since the quantity of data collected in each year of the BIOT (Chagos Archipelago) observer programme was limited, all years of data were combined (1995-1998).

Table A.6.1 *L. mahsena* sex ratio by location, and cumulative effort from 1991.

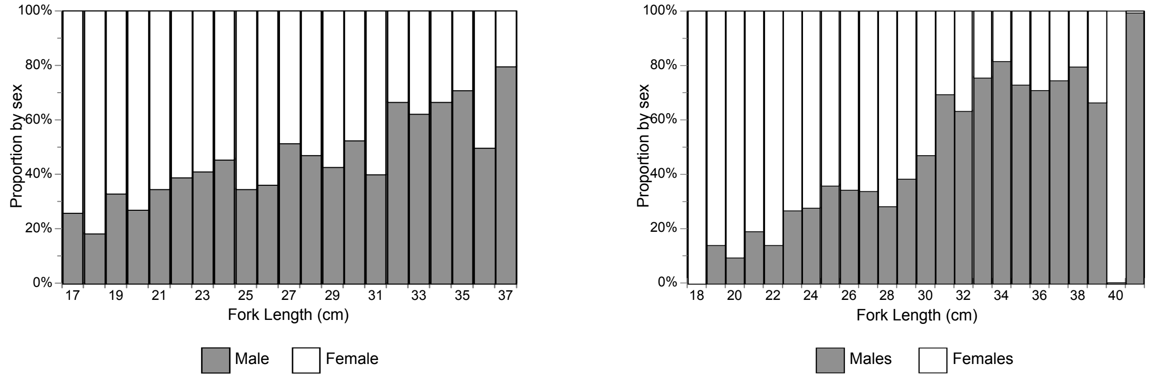
Location	*n*	Sex ratio (M:F)	Cumulative Effort (man days km^{-2})
Nazareth	801	0.92	14.7
Saya South	421	0.96	17.7
BIOT (Chagos)	169	0.35	3.9
Seychelles	1219	0.63	4.2

In all cases, the sex ratio was skewed toward females. On both Mauritian banks, the ratio was only slightly skewed. In Seychelles there were over three females to every two males, while in BIOT (Chagos Archipelago) the ratio was over two females to every male. A significant relationship was identified between the sex ratio and the level of cumulative effort applied in each location (r^2=0.845, *t*-test, *P*=0.040).

Sufficient samples were available from Nazareth, Saya south, Saya north and Seychelles to examine the sex ratio by length (Figure A.6.1). Only lengths with more than five sampled individuals were used.


a. Nazareth bank

b. Saya south


c. Saya north

d. Seychelles

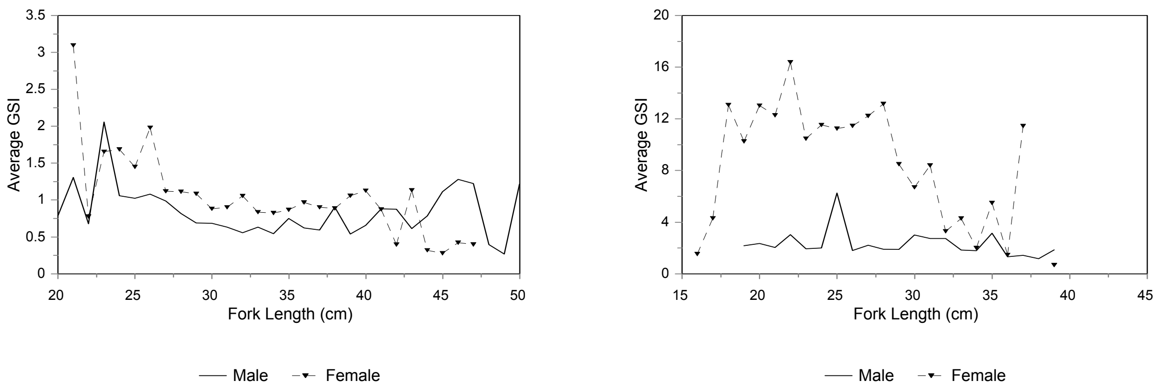
Figure A.6.1 Sex ratio at length by location for *L. mahsena*.

In all locations, there was an increase in the proportion of males at length with increasing size. This was particularly obvious in data from the Seychelles. In contrast, the trend over the limited size range in Nazareth was weak. No individuals in the transitional phase between male and female were found in any location.

Maturity and Gonadosomatic Index (GSI)

Maturity data and GSI were used to identify the lengths at maturity (Lm_{min} and Lm_{50}). Length classes were discarded where there were fewer than five individuals present. Figure A.6.2 displays the GSI for each sex by length for Nazareth and Seychelles. The pattern for Nazareth was typical for the Mauritian banks. There were insufficient samples from BIOT (Chagos Archipelago) to warrant analysis.

GSI was initially high in the Mauritian banks, and in all locations tended to decline with length. Gonads therefore comprised a higher proportion of total body weight at smaller sizes than at larger sizes. At Seychelles, where the range of sizes available included smaller lengths than those at Nazareth, a rapid increase in female GSI was found in the lower size classes. No overall pattern was found for males.


a. Nazareth

b. Seychelles

Figure A.6.2 Average GSI for each sex by length for *L. mahsena*.

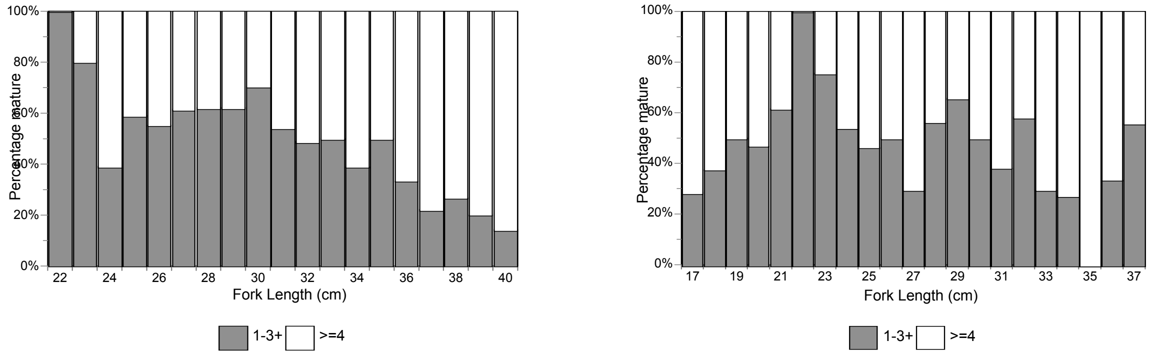
The data implied that the minimum length at maturity for each of the Mauritian banks was less than that of the smallest individuals in the sample (<20cm). For Seychelles, the minimum length at maturity for females appeared to be 17cm. The data for males was less conclusive; although there were large proportional increases in GSI at 22 and 25cm, data were truncated in the lower size ranges. Due to limited sampling at the lengths at which the onset of maturity appeared to occur, results were inconclusive.

GSI for female *L. mahsena* individuals from Seychelles was notably higher than that from any of the Mauritian banks. That for males in Seychelles was comparable. For females in Seychelles, gonads comprise a greater proportion of the total body weight. As a result, females may be more fecund than those on the Mauritian banks.

Percentage of females mature by length and age class were also examined (Figure A.6.3).

a. Nazareth

b. Saya south



c. Saya north

d. Seychelles

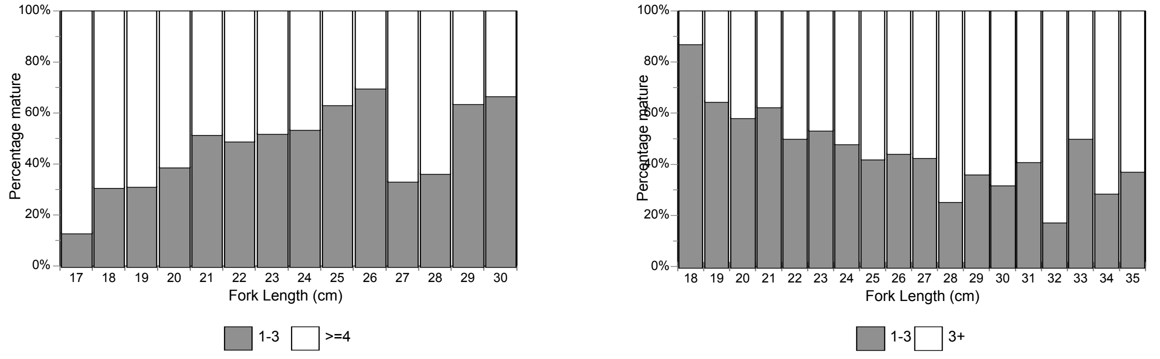


Figure A.6.3 Percentage of mature female *L. mahsena* individuals by length and location.

While GSI data for Nazareth suggested that individuals began to mature at lengths below

20cm, maturity at length data from this location indicated that 50% of individuals did not mature until either 24 or 32cm (Figure A.6.3a). When a maturity ogive was fitted to the data, Lm_{50} was estimated at 31cm. However, an Lm_{50} of 24cm would appear more consistent with the data from the other locations (Table A.6.2). When maturity was analysed by age, 50% of individuals at Nazareth were mature between 7 and 8 years old (7.6 years from the ogive).

The pattern for the other Mauritian banks was confused, with the proportion of individuals mature at Saya south first decreasing with increasing length at smaller sizes. The pattern at Saya north indicated a general decreasing proportion of mature individuals with increasing length. As indicated by the GSI data, this implied that Lm_{50} may occur at, or below, 17cm. Due to the problems with sampling small individuals from the fishery, data for these lengths was sparse. A maturity ogive could not be fitted due to the irregularities in the relationships.

In Seychelles, the length at which 50% of individuals were mature was between 22 and 24cm, corresponding to between 4 and 5 years of age (Table A.6.2). This was considerably younger than the age identified for the majority of the Mauritian banks.

Table A.6.2 Estimated Lm_{50} and Am_{50} for *L. mahsena*, by location.

Location	Lm_{50} estimate (cm)	Lm_{50} estimate from ogive (cm)	Am_{50} estimate (yrs)	Am_{50} estimate from ogive (yrs)
Nazareth	24 or 32	31	36378	7.6
Saya South	<17 or 25	-	36378	6
Saya North	<17 or 27	-	2 or 7-8	5.5
Seychelles	22 - 24	26	36283	4.8

A. virescens

Data for *A. virescens* was available from Seychelles and BIOT (Chagos Archipelago).

Sex ratios

Sex ratios (male : female) for each location are presented in Table A.6.3. Since the quantity of data collected during each BIOT (Chagos Archipelago) observer programme was minimal, all years of data were combined for this location (1995-1998).

Table A.6.3 *A. virescens* sex ratio (M:F) by location, and cumulative effort from 1991.

Location	*n*	Sex ratio (M:F)	Cumulative effort (man days km^{-2})
BIOT (Chagos)	119	1.33	3.9
Seychelles	1865	1.59	4.2

In both locations, sex ratios were skewed toward males, most prominently in the Seychelles sample. Since cumulative effort was relatively comparable between the two locations, fishing did not appear to influence the sex ratio in this species.

Sex ratio was examined by length for Seychelles only (Figure A.6.4). There were insufficient samples across length classes in BIOT (Chagos Archipelago). Sex ratio in Seychelles remained relatively stable with length, being slightly skewed towards males across the sampled size range. The proportion of females at length increased slightly in the larger size classes.

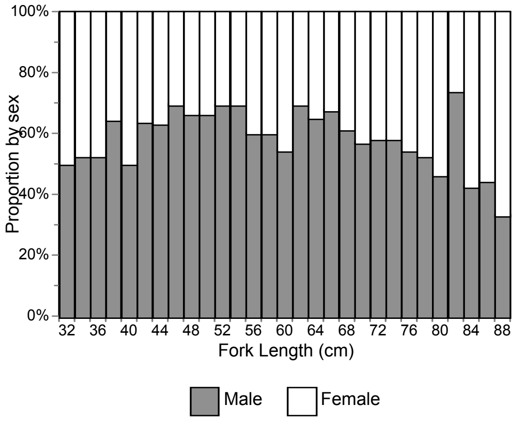


Figure A.6.4 Sex ratio at length for *A. virescens* from Seychelles.

Maturity and Gonadosomatic Index (GSI)

The limited maturity data available from BIOT (Chagos Archipelago) was insufficient to warrant intensive investigation of maturity characteristics. Examinations of maturity and GSI concentrated on Seychelles data.

To smooth erratic jumps in the GSI data, a two point moving average was employed (Figure A.6.5).

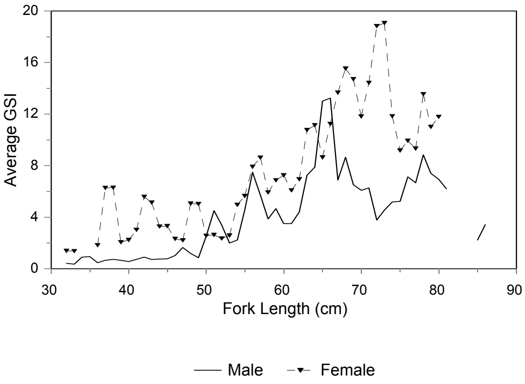


Figure A.6.5 Average GSI by fork length for *A. virescens* from Seychelles.

Proportional increases in GSI at smaller lengths indicated that females first matured around 37cm. Males showed a slight increase in GSI at 33cm, although a notable increase did not occur until 50cm.

For the study of maturity by length and estimation of the Lm_{50}, only data from females were examined (Figure A.6.6). Length classes with fewer than five individuals were discarded.

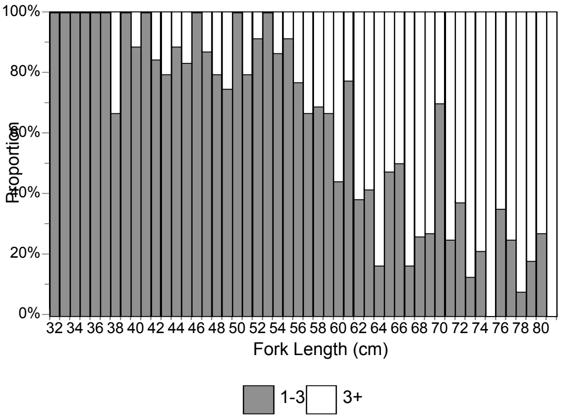


Figure A.6.6 Proportion of *A. virescens* individuals mature at length from Seychelles.

From Figure A.6.6, Lm_{50} for *A. virescens* in Seychelles appeared to be around 60cm. On fitting of a maturity ogive to the data, an estimate of Lm_{50} = 65cm resulted.

The proportion of individuals mature was related to the assessed individual integer age derived from otoliths. From Figure A.6.7, the resulting Am_{50} was between 8 and 9 years, while that estimated using the maturity ogive was 9.3 years (Table A.6.4).

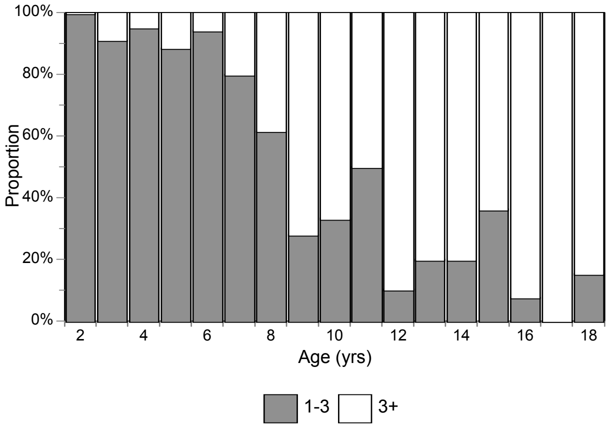


Figure A.6.7 Proportion of *A. virescens* individuals mature at age from Seychelles.

Table A.6.4 Estimated maturity parameters for female *A. virescens*, for Seychelles.

Location	Lm_{50} estimate (cm)	Lm_{50} from maturity ogive (cm)	Ac_{50} estimate from ogive(yrs)
Seychelles	60-62cm	65	9.3yrs

A.6.4 DISCUSSION

Fishing has the potential to impact on the reproductive capability of stocks. For snappers, which are thought to be gonochoristic, the impact on the sex ratio may be minimal, although larger and more aggressive males may be removed first. For protogynous species such as *L. mahsena*, which change sex during their life, selective effects of fishing may result in shifts in the sex ratio. If fishing had seriously impacted on the spawning stock, compensatory changes in the maturity pattern, for example decreases in age or length at maturity (Lm_{50}), may result.

The examination of *L. mahsena* sex ratio by length showed an increasing proportion of males with increasing size, implying protogyny. This followed the general findings of Bertrand (1986) in Saya de Malha. Unlike Bertrand (1986), however, in the current study, males were present in numbers at less than 20cm, and females at sizes greater than 35cm.

Sex ratio for *L. mahsena* showed a consistent skew toward females. This skew decreased with increasing fishing mortality, indicating an increase in the proportion of males in the catch. Males comprised a greater proportion of the larger individuals. Therefore, if the length or age at which sex change occurred remained constant, gear selectivity should result in an increase in the proportion of *females* in the catch (Thompson and Munro, 1983a). Since the opposite trend was found, sex reversal may be under exogenous/social control, resulting in a shift in the length or age at which sex change occurred (Russ *et al.*, 1995). Such a shift would result in an increased number of males in smaller size classes, as seen in the Mauritian banks distributions, compared to that from Seychelles. This would also account for differences in the proportions of sex at length found in this study, compared with the results of Bertrand (1986). Alternatively, sex ratios may represent changes in male and female catchability, since males may be more aggressive.

Such discussion assumes that protogyny is occurring in *L. mahsena*. During the studies, no individuals were found in the process of undergoing sex change. The fact that identification of this state was not a principle aim while sex was being determined may have influenced the lack of sightings. Alternatively, sex change may occur over a short time period, or occur in an un-sampled season or area, reducing the likelihood of encountering individuals in the transitional state.

L. mahsena length at maturity by location was confused by the pattern found in the Mauritian banks. From Saya south and north, the proportion of individuals mature decreased from the smallest sample size (17cm), before increasing again. This pattern implied that Lm_{50} was less than 17cm. The study of Bertrand (1986), as reported in Bautil and Samboo (1988), indicated that the earliest onset of maturity was around age 3 years, approximately 19cm (based on growth parameters used in that study). Further sampling from the smaller size classes would be required to provide more precise estimates of Lm_{50}. Estimates will also be confused by the protogynous nature of this species; as only females were assessed, the point at which sex reversal occurred will influence the estimate of Lm_{50}. Estimates for Nazareth and Seychelles were approximately 50% of the L_∞ estimate of Bautil and Samboo (1988), following the pattern put forward by Grimes (1987) for lutjanids.

The GSI for *L. mahsena* in Seychelles was notably higher than that in the Mauritian banks. A potential cause may relate to the lower fishing mortality in the latter location; lower fishing pressure may allow more energy to be diverted to reproduction. If density dependent growth increased the growth rate on the Mauritian banks (Chapter 6), this may result in the diversion of energy from reproduction to growth, reducing gonad size.

The sex ratio for *A. virescens* was relatively comparable in BIOT (Chagos Archipelago) and Seychelles. In Seychelles, the ratio also remained relatively constant with increasing length, being skewed towards males in the majority of size classes. *A. virescens* therefore appeared to follow the expected gonochoristic pattern of the Lutjanidae.

Assessments for *A. virescens* were performed for Seychelles only. Lm_{50} for females was estimated at 65cm. This estimate lay between the two possibilities put forward by MRAG (1996d) (42cm or 69cm) for Seychelles. The Lm_{50} estimate was considerably higher than estimates derived for this species in other areas of the world, however (Table A.6.5). This estimate is 63% of the L_∞ estimate from MRAG (1996d), larger than the 50% suggested for lutjanids by Grimes (1987).

Table A.6.5 Estimates of Lm_{50} for *A. virescens* from locations around the world (FL: fork length, SL: standard length).

Location	Lm_{50} estimate (cm)	Length measured	Reference
Hawaii	45	FL	Everson *et al.* (1989)
East Africa	41-47	SL	Talbot (1960)
Vanuatu	44	FL	Brouard and Grandperrin (1985)

Appendix 7. The use of otolith weight-age relationships to estimate individual age, and total mortality

A.7.1 INTRODUCTION

As noted in Chapter 9, when compared to direct age assessments, otolith weight-age relationships offer an objective and economic method of ageing fish. Such methods have obvious advantages in financially constrained tropical fisheries institutions.

This appendix describes the studies performed to examine the feasibility of using otolith weight to age the study species. The accuracy of the resulting relationships, and the use of these to construct age frequency distributions, and hence to calculate total mortality, is described. The estimation and use of otolith weight-age relationships for the study species were limited by the relatively small sample sizes available for otolith weight. As a result, comparison with total mortality estimates derived through other methods, as performed in Chapter 9, was not feasible.

A.7.2 METHODOLOGY

The otoliths of *A. virescens* were unsuitable for age assessment using otolith weight, since they were small, delicate, and prone to breaking. Only otoliths from *L. mahsena* were suitable for routine age assessment by weighing, since they were relatively robust.

Sub-samples of *L. mahsena* otoliths were made from the collections at Nazareth bank, south Saya de Malha bank, Seychelles and BIOT (Chagos Archipelago). Samples were taken from a number of months. Where possible, these months were consecutive. Relatively large and small individuals were targeted to improve the accuracy of the derived otolith weight-age relationship. Clean *L. mahsena* otoliths were weighed on a Sartorius electronic scale, to the nearest 0.001g. Initially, pairs of otoliths from 50 fish were weighed in each location to assess the similarity in weights of individual otoliths from the same fish. 85% of the otolith pairs weighed within 0.002g of each other, and the weight of otolith pairs were not significantly different (*t*-test comparison of total data set, P=0.462). Only one otolith from subsequent pairs was therefore weighed.

As growth is added to the edge of the otolith over time (Chapter 2), otolith weight-at-age should increase through the growth year. To account for this, otolith weight was related to the ‘partial age’, as calculated for the estimation of growth parameters (Chapter 4, Section 4.3.2.2).

For each study location, otolith weight was plotted against both estimated age and fork length, and against fork length for each age class separately. Two stepwise multiple linear regression models were fitted to predict age from otolith weight and fork length, and otolith weight from age and fork length. The inclusion level for the independent variables in both models was set at P=0.05. The residuals from the regression model were examined to test the assumption of normality.

The relationship between otolith weight and age was assessed using linear regression with natural log of otolith weight as the dependent variable, and natural log of age as the independent. The relationship between otolith weight and length was similarly assessed.

A relationship between otolith weight and age was derived for each location. This was applied to a random sub-sample of otoliths to estimate age, as a continuous variable, from the otolith weight. Decimal ages were then rounded to the nearest integer, and an age frequency derived.

The percentage of integer ages estimated through otolith weight that agreed with the true integer age was assessed. The CV (%) was calculated as the standard deviation of estimated ages in each age class divided by the corresponding mean estimated age for that age class. Bias was assessed as the true age minus the estimated mean age.

To test for similarities between the otolith weight-age regression relationships, those derived for each location were compared using the GT-2 test.

As stated, age frequency distributions were not compared to those derived directly from age-at-length data or through age-length keys, as assessed in Chapter 9. Comparisons were affected by relatively low sample sizes in distributions derived from otolith weight. Instead, the age frequency distribution resulting from the otolith weight-age relationship was compared to the true underlying age structure for that sample using the Kolmogorov-Smirnov test. Total mortality estimates were derived from both the true underlying age frequency distribution, and the age distribution derived from otolith weight. The amount of randomly sampled data was insufficient to allow sub-division into length classes; total mortality estimates for these samples could not be obtained through length-based methods.

A.7.3 RESULTS

Samples from Nazareth were initially grouped by month, and subsequently amalgamated into two, two-month data sets (Table A.7.1). In the other locations, months of data were initially examined separately, and then amalgamated to increase the sample size.

Table A.7.1 Sample sizes for otolith weight assessment.

Location	Months	Sample Size
Nazareth	Feb/Mar	160
	Oct/Nov	80
Saya south	Apr - Jul	163
Seychelles	Sep - Dec	225
BIOT (Chagos)	Apr - Jun	262

Otolith weight was directly related to both the assessed partial age, and fork length (Table A.7.2).

Table A.7.2 Relationship between otolith weight (grammes) and assessed partial age (yrs); and otolith weight and fork length (cm) for *L. mahsena* by location.

Location	Months	Otolith weight = a*age +b		Otolith weight = (fork length^a) * b	
		a	b	a	b
Nazareth Bank	Feb/Mar	0.026	0.017	1.841	0
	Oct/Nov	0.017	0.059	1.597	0.001
Saya south	Apr/Jul	0.03	-0.007	1.475	0.0011
Seychelles	Sep-Dec	0.03	-0.046	2.272	0
BIOT (Chagos)	Apr-Jun	0.035	-0.048	2.212	0

Within each age class, otolith weight was positively correlated with fork length, indicating a tendency for larger fish to have heavier otoliths than smaller fish of the same age. Otolith average weight increased with age over the range of ages sampled. There was considerable variation in the otolith weight within each age-class. This variability, and therefore the overlap in otolith weights among age-classes, increased with age.

Otolith weight accounted for between 64% and 88% of the variation in age at the study locations (Table A.7.3). The results of the multiple regression indicated that otolith weight was a function of both age and fork length, with the interaction between age and fork length alone accounting for over 74% of the variability in otolith weight.

Table A.7.3 Results of the regressions of *L. mahsena* otolith weight and age, and age and fork length vs. otolith weight, by location.

Location	Otolith weight vs. age regression		Age and fork length vs. otolith weight	
	r^2	*P*	r^2	*P*
Nazareth (Feb/Mar)	0.683	<0.01	0.851	<0.01
Nazareth (Oct/Nov)	0.644	<0.01	0.832	<0.01
Saya south	0.798	<0.01	0.739	<0.01
Seychelles	0.79	<0.01	0.818	<0.01
BIOT (Chagos)	0.877	<0.01	0.909	<0.01

The overall fit of the otolith weight - age relationship was poor. The percentage of individuals estimated to be the same age as that determined by annuli varied between locations (Table A.7.4), but was frequently less than 50%. Estimated ages in all locations were generally more reliable and least biased in the young age classes (Tables A.7.5a to e).

Table A.7.4 Accuracy of the otolith weight-age relationship for *L. mahsena* by location.

Location	Percentage of estimates:	
	identical to true age	greater than 1 year different
Nazareth (Feb/Mar)	46%	21%
Nazareth (Oct/Nov)	34%	45%
Saya south	63%	34%
Seychelles	49%	18%
BIOT (Chagos)	40%	30%

Table A.7.5 Comparison of age determinations from annuli and otolith weight for *L. mahsena*, by location.

a) Nazareth, February/March sample

True Age (yrs)	Count	Range of estimates	Percent Agreement	CV (%)	Bias (years)
3	1	4	0	0	-0.88
4	13	35917	53.8	13.1	-0.23
5	32	36041	59.4	12.7	0.11
6	57	36071	45.6	12.8	0.18
7	31	36165	41.9	12.9	-0.29
8	20	35930	25	16.2	-0.22
9	4	36044	50	10	0.67
10	2	36076	50	5.5	0.57
Overall percentage agreement:			45.6		

b) Nazareth, October/November sample

True Age (yrs)	Count	Range of estimates	Percent Agreement	CV (%)	Bias (years)
3	1	3	100	0	0.06
4	1	4	100	0	0.04
5	6	35916	66.7	24.5	0.79
6	19	36071	36.8	23.4	-0.05
7	16	36072	50	15.3	-0.05
8	18	36165	11.1	24.1	-0.7
9	5	36044	20	6.8	1.22
10	1	7	0	0	2.92
11	6	36169	16.7	9.5	0.08
12	4	36052	50	16.6	0
13	2	36053	0	25.4	0.45
14	1	15	0	0	-0.95
Overall percentage agreement:			36.3		

c) Saya south

True Age (yrs)	Count	Range of estimates	Percent Agreement	CV (%)	Bias (years)
4	9	35918	33.3	6.1	-0.55
5	28	35950	57.1	7.8	-0.48
6	20	35980	80	8.5	-0.24
7	30	36012	86.7	8.5	0.1
8	10	36042	50	13.9	0.12
9	6	36074	33.3	13.4	-0.1
10	3	36135	33.3	18.9	0.41
11	2	36108	50	6.9	0.43
12	1	11	0	0	0.54
13	2	14-18	0	12	-2.81
14	2	14	100	1	0.08
15	2	19-20	0	1.8	-4.2
Overall percentage agreement:			62.6		

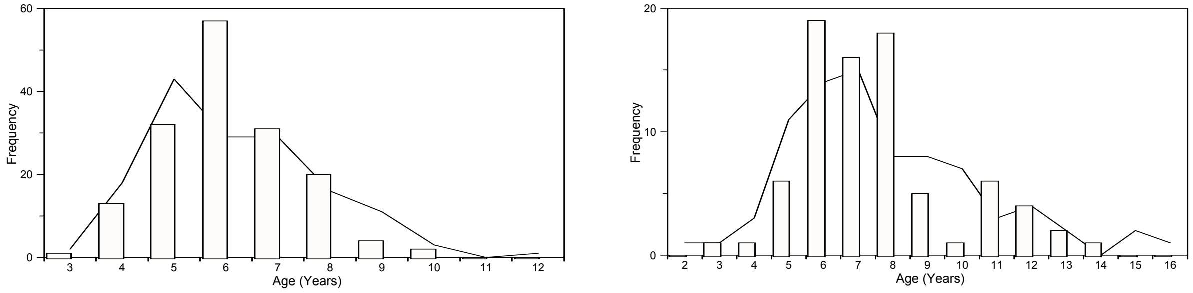
d) Seychelles

True Age (yrs)	Count	Range of estimates	Percent Agreement	CV (%)	Bias (years)
2	4	3	0	4.5	-1.71
3	33	36282	27.3	7	-1.19
4	33	36313	78.8	7.8	-0.77
5	45	36375	46.7	12.8	-0.79
6	46	36376	56.5	9.7	-0.76
7	44	36438	47.7	10.7	-0.52
8	17	36439	41.1	10.1	-0.25
9	2	36378	0	8	1.2
10	0	-	-	-	-
11	1	9	0	0	1.95
Overall percentage agreement:			48.9		

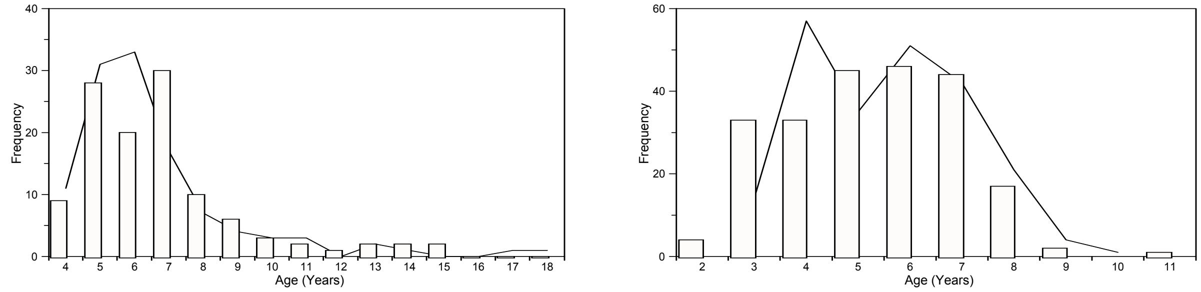
e) BIOT (Chagos Archipelago)

True Age (yrs)	Count	Range of estimates	Percent Agreement	CV (%)	Bias (years)
3	4	35886	0	21.7	-0.6
4	26	35917	88.5	9.1	-0.03
5	32	35978	37.5	16	-0.06
6	34	36011	52.9	10.2	0.04
7	28	36072	42.9	15.8	0.16
8	27	36134	37	16.7	-0.15
9	27	36104	33.3	12	0.4
10	16	36020	25	17	-0.26
11	18	36051	38.9	11.4	-0.13
12	17	36082	29.4	10.8	-0.21
13	21	36083	19	12.2	0.41
14	7	36146	28.6	11.8	-0.47
15	3	14-17	0	9.6	-0.77
16	2	15-17	0	7.3	-0.18
Overall percentage agreement:			40.5		

Age structures for each sample were estimated using the appropriate otolith weight - age relationship (Figure A.7.1). The use of otolith weight tended to smooth the actual age structure. The most abundant age-classes tended to be underestimated by otolith weight, while the strength of the weak age-classes was overestimated. There was no significant difference between the true and estimated age structures for any location (Kolmogorov-Smirnov tests, $P<0.05$). The differences in age structure between locations were maintained when otolith weight was used to estimate age.


a) Nazareth, Feb/Mar

b) Nazareth, Oct/Nov


c) Saya south

d) Seychelles

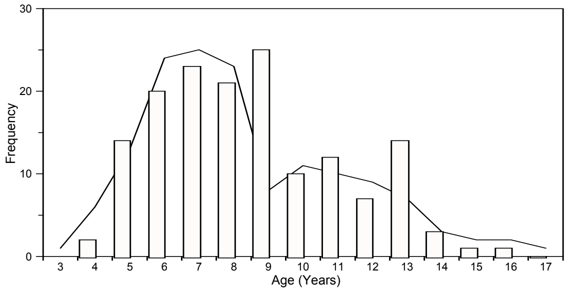

e) BIOT (Chagos Archipelago)

Figure A.7.1 Sample age frequency (bars) and corresponding age frequency derived from otolith weight-age relationship (line).

Total mortality estimates were obtained through catch curves derived from both the true age frequency distributions, and distributions estimated using the otolith weight - age relationship (Table A.7.6).

Table A.7.6 Total mortality estimates by location, and corresponding 95% confidence intervals. Catch curve estimated from age frequency distributions derived from age-at-length data, and the otolith weight-age relationship.

Location	Source	Total Mortality (Z)	95% confidence interval	Ages used in regression
Nazareth, Oct/Nov	length-at-age	0.35	± 0.29	36354
	otolith weight	0.3	± 0.12	36531
Nazareth, Feb/Mar	length-at-age	0.55	± 0.40	36438
	otolith weight	0.87	± 0.34	36438
South Saya	length-at-age	0.64	± 0.13	36135
	otolith weight	0.62	± 0.20	36073
Seychelles	length-at-age	1.04	± 1.43	36408
	otolith weight	1.02	± 0.55	36438
BIOT (Chagos)	length-at-age	0.27	± 0.13	36356
	otolith weight	0.32	± 0.07	36387

At the majority of locations, the use of otolith weight resulted in estimates of total mortality similar to those from the actual age frequency distributions. The exception was the Nazareth February/March sample, although the 95% confidence intervals of each estimate overlapped. The true distribution was dominated by the 6 year old age class, the majority of which was mis-assigned to the 5 year old age class by the otolith weight-age relationship. The precision of the total mortality estimate was generally improved where the estimate was based on the otolith weight age frequency, as seen by the 95% confidence intervals.

The otolith weight - age relationships calculated for each location were compared through the slopes of the regression lines using the GT-2 test (Figure A.7.2).

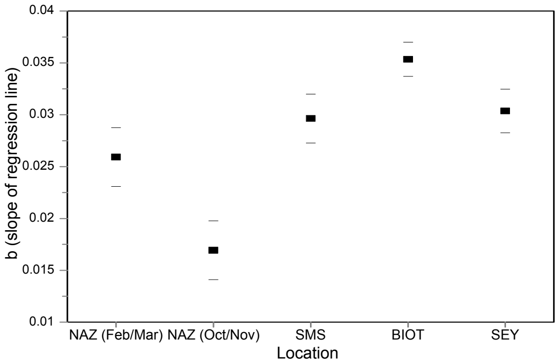


Figure A.7.2 Gabriel's plot of the 95% comparison intervals by the GT-2 method for the regression coefficients of the otolith weight-age relationship.

The slope of the otolith weight - age relationship was significantly steeper in BIOT (Chagos Archipelago) than in the other locations, implying that for a given age, otolith weight was greater. The slope of the otolith weight-age relationship derived from the Nazareth October/November sample was significantly lower than found at all other locations, including the February/March sample for the same location.

A.7.4 DISCUSSION

A. virescens otoliths could not be used to derive an otolith weight - age relationship, since the structure and fragile nature of the otoliths made them prone to breaking on extraction from the fish. The study therefore concentrated on the otoliths of *L. mahsena*. A relationship was derived for four of the study locations. Each relationship was assessed to examine its suitability for use in routine ageing. Using the relationships, an age frequency distribution was obtained from measured otolith weights, and an estimate of total mortality derived. These distributions and the resulting estimates were then compared to those estimated from the true underlying age structure.

The average weight of *L. mahsena* otoliths increased with age, across the age range sampled in each study location. This indicated the potential for otolith weight to provide a rapid and economic method of ageing. Other studies have indicated that the average weight of otoliths in old fish continue to increase, in contrast to variables such as length, weight or otolith length (*e.g.* Secor and Dean, 1989). Otolith growth may be decoupled from other somatic growth rates, making it more closely related to time and age (Reznik *et al.*, 1989). In such cases, otolith weight could provide a more reliable estimate of age than counts of annuli from otoliths where the interpretation of marks is ambiguous, if the inital relationship can be derived accurately.

The derivation of otolith weight - age relationships for other species have resulted in relationships of varying accuracy. Otolith weight explained 95% of the variation in age in the splitnose rockfish (*Sebastes diploproa*; Boehlert, 1985), but only 51% of the variation in age of Pacific Hake (*Merluccius productus*; Beamish, 1979). In the study of damselfish (*Pomacentrus moluccensis* and *P. wardi*) by Worthington *et al.* (1995a), otolith weight explained 84-96% of the variation in age of these species, a range the authors stated as being common for otolith weight - age relationships.

The accuracies of the relationships derived for *L. mahsena* in this study varied between locations. The most accurate relationship was that derived for BIOT (Chagos Archipelago), with 88% of the variation in age explained by otolith weight. At Saya south and Seychelles, the relationship explained approximately 80% of the variation in age. The lowest was for the Nazareth Bank samples, with between 64% and 68% of the variation explained. While the differences in the strength of the relationship cannot be attributed to a single factor, a number of suggestions can be made. Differences do not appear to be a result of otolith increment clarity, since that identified for Nazareth was similar to that in otoliths from BIOT (Chagos Archipelago). However, the relationships will be influenced by the age ranges covered in the data sets for each location. The strength of the relationship for BIOT (Chagos Archipelago), for example, may result from the wide range of ages for which data were available (Table A.7.5e). Differences may also result from local environmental conditions, such as limitations in specific minerals or temperature differences, which may affect otolith deposition rate.

However, the coefficient of determination is not the best method of assessing the utility of otolith weight to assess age, since it does not indicate the precision of the age assessments resulting from the relationship. Where the slope of the relationship is steep, and there is little overlap in the otolith weight range between age-classes, a more reliable estimate of age is possible. The slow growth rate of *L. mahsena* resulted in notable variation in otolith weight at each age, and hence overlap in the weights-at-age. The precision of age assessments through the otolith weight-at-age relationship was reduced as fish became older, and the level of overlap between age classes increased. Otolith weight could not accurately discriminate between individual age classes. As a result, the relationship could not accurately assess individual lengths-at-age.

The otolith weight-age relationship was, however, capable of deriving reasonably accurate age frequency distributions; those derived using the relationship for each location were not significantly different from the true underlying age structure. Total mortality estimates obtained through catch curves derived from the estimated and true age frequencies were generally very similar, while estimates derived from the otolith weight distributions were generally more precise. The latter resulted from the smoothing effect of the otolith weight relationship; irregularities in the actual age frequency distribution were reduced. It was noted that the accuracy of the age frequency distribution derived from the otolith weight relationship could be affected by the presence of a strong age class in the distribution. Slight errors in the relationship could result in such an influential age class being assigned to neighbouring age classes, significantly altering the distribution.

The comparison of otolith weight - age relationships between locations indicated significant differences. This implied that a relationship derived for one location could not automatically be applied in another location. The slope of the relationship in BIOT (Chagos Archipelago) was significantly greater than that found in all other locations. This matched the pattern seen in the length-weight relationship for each location identified in Chapter 6. The two samples from Nazareth bank also showed significant differences in the slope of the relationship. In theory, the use of partial age should have compensated for any differences in the otolith weights due to additional growth in the intervening period between these two samples. While otolith weight potentially offers a rapid method for ageing fish from this location, further studies are required to ensure that there are no specific within-location relationships which could result in such differences.

Although the relationship between otolith weight and age would require confirmation between years, *L. mahsena* otolith weight represents a rapid and potentially cheap method (relative to in-depth otolith studies) to routinely assess age structure, and hence mortality. The saving in time and money that this method offers may allow an increased number of fish to be examined, thereby reducing the sampling error. Routine monitoring could also provide estimates of spatial and temporal variation in longevity and mortality (Worthington *et al.*, 1995a).

Appendix 8. Cost-benefit timesheets for length frequency and biometric (otolith) data collection

Timesheet for the growth project - Cost/Benefit analysis for Length Frequency Data Collection

Name:

Grade:

For each day on which work is performed on the growth project involved with the collection and analysis of length frequency distributions, enter the time spent performing each task on that day in the relevant column.

Date	Number of hours spent on:			
	Travel to and from port	Collecting length frequency data	Entering length frequency data onto computer	Analysis of data and report writing

Timesheet for the growth project - Cost/Benefit analysis for Biometric Data Collection

Name:

Grade:

For each day on which work is performed on the growth project involved with the collection of otoliths and analysis of biometric data, enter the time spent performing each task on that day in the relevant column.

Date	Number of hours spent on:					
	Travel to and from port	Collecting biometric data	Entering biometric data onto computer	Analysis of data and report writing	Sale of fish	Administration of funds

Appendix 9. Papers presented by Albion Fisheries Research Centre at the growth project workshop in Mauritius

The following papers were presented by staff at Albion Fisheries Research Centre during the growth project workshop at AFRC (21-22/9/99).

THE BANKS FISHERY
Data analysis and management

by

C. R. Samboo

SUMMARY

Statistical data on the banks fishery have been collected since 1977. From January 1977 to September 1988 information about each fishing trip was submitted by the skipper and this included : the length of each fishing trip, the number of days on which fishing was done, the number of fishermen, the total catch, and the number of days of inactivity. Since October 1988, the data collected are on a daily basis as per the proforma shown in Appendix 1. In addition samples of the catches were examined for species and size compositions.

Using catch per fisherman day as index of performance, there was no evidence of overfishing on the banks up to 1983, but in some areas the quantities caught were close to the limits established in previous studies and the average weight and length of the fish had been declining substantially. It was strongly advised then that further expansion of the fishery be checked.

The catch per fisherman day up to 1994 indicated overfishing in most areas, and on the Saya de Malha bank the size of the fish has decreased considerably and annual catches have almost regularly exceeded the estimated of potential yield established by joint studies by the Ifremer (Reunion) and the Albion Fisheries Research Centre (Mauritius)

Introduction

The fresh fish supply to the local market in Mauritius comes from our lagoon and offlagoon fishing grounds. Since 1987 chilled fish has been supplied mainly for an export market to Reunion and comes from the offlagoon fishing grounds only. The distant-water fishing grounds (banks) provide frozen fish.

The near-water fishing grounds supply mostly demersal fish which are well appreciated and find immediate local and export markets. The distant-water fishing grounds provide demersal fish, mostly Lethrinidae, and can probably supply pelagic fish, a limited quantity of parrot fish and considerable quantities of small pelagic. This last stock has not yet been tapped and is estimated to have an annual potential yield of 20 000 tons on the Saya de Malha bank (IOFC/DEV/79/45)

Historical review

The fish stocks in these areas were first localised in the eighteenth century by vessels engaged in the inter-island trade. In the early period of this fishery fish were caught mainly for self consumption and salting. Salted fish was exported to Mauritius on a commercial basis from St. Brandon as from 1927 by the Raphael Fishing Co., named after one of the many small islands of the St. Brandon group. Trawling on the banks was attempted by the company in 1931 with the "Fume" but this pioneering operation was unsuccessful and was not pursued (IOFC/DEV/79/45). The company, however, continued the exploitation of the fish resources by handling. The first vessel to have been used for the exploitation of fish stocks on the banks was La Perle1 (ex Thelma). It was operated during the war (in 1939) around the St Brandon group of islands and later for the transfer of frozen fish stored at -5^{o}C to Mauritius (Couacaud 1967).

After the survey of the fishery resources of the Mauritius-Seychelles ridge by Wheeler and Ommanney (Wheeler and Ommanney 1953), systematic exploitation of the banks started. The "Silver Lord" (a warship converted into fishing vessel) owned by the Indian Ocean Trading Company was the first vessel to start exploiting the fish stocks of the Nazareth bank and bringing the frozen product to Mauritius to be retailed at Re 1.00 per Kg. The vessel made a single cruise in 1950 and 3 cruises in 1952 landing each time about 100t of fish. The venture was, however, commercially unsuccessful due to the absence of the necessary infrastructure for the distribution of frozen fish and the relative abundance of fresh fish on the local market.

The Limuria Fishing Co. chartered and eventually purchased the Stella Maru 1 (ex Kaise Maru No. 5) in 1966. The vessel carried 4 pirogues on its first trip and later 5 and 6, equipped with oars and sail, and 16 to 24 fishermen, i.e., 4 fishermen per dory. It visited the Nazareth bank 4 times and landed 20t, 35t,79t and 50t respectively. The catch per fisherman/day was not less than 350 kg (Mr. Robert Talbot, personal communication). The company started the commercialisation of frozen fish on a nation-wide basis. The vessel La Perle 11 of the Raphael Fishing Company then started to the supply of frozen fish to the local market after having previously been used for the transfer of salted fish from St. Brandon. Gutting of fish caught was done on board the mother vessel. Later there was a gradual increase in the number of vessels. The year 1977 when 8 vessels out of which 2 were chartered can be considered as a turning point in the history of the banks fishery and gave an impetus to its progression. The number of vessels declined, however, and in 1980 and 1981 only five motherships were still active.

Fishing vessels and fishermen

Various types (warship, cargo ship, trawler, longliner, etc) and sizes (20 to 60m) of vessels have been used to exploit the banks fishery. Second-hand longliners purchased mainly from Taiwan or Japan have proved to be the best suited vessels. Refitting of such vessels includes accommodation for fishermen, the purchase of dories and outboard motors and tanks for the storing of fuel for daily distribution to fishermen.

Along with the number of mother vessels, the number of fishermen has increased considerably from 336 in 1977 to 629 in 1988. Of the latter some 75 are employed in the St. Brandon fishery. But "good" banks fishermen are scarce and regular and excellent fishermen are even scarcer. Quite often "fishermen" have to be given on-the-job training which logically brings about a considerable loss of precious time during the trip. Fishermen are the only group employed on a performance basis and are presently being paid between Rs2.40 and Rs3.00 per kg of fish caught. The pay could be higher for particular species which are found in greater depths and have a better market value.

Intensity of exploitation

The banks handline vessels operate mostly on the Saya de Malha and the Nazareth banks. The St. Brandon waters are exploited by contractual fishermen from the main island St. Raphael. The Chagos bank has been exploited seventeen times only since 1977. The reasons are that the bank con only be exploited during the winter period which time is used by most fishing companies for maintenance and refitting of their vessels. Also the region is quite remote from Mauritius and almost 10 to 12 days are lost in travel. The productivity of the fishing grounds are in addition much lower than those of Nazareth and Saya de Malha and the most important reason of all is that more often than not the fish caught is a species which is considered as toxic. The Soudan and the Hawkins banks are not exploited at all by Mauritian vessels due to rough grounds, low productivity and abundance of sharks. It has been unofficially reported, however, that these areas are visited regularly by vessels from Reunion.

The Nazareth bank is nearer to Mauritius but the fishing season here is shorter due to bad weather and fishable areas are smaller. These factors explain why it is being less exploited than the Saya de Malha bank and consequently the size of the fish there is still reasonably large.

It should also be noted that the increase in the landings from the Saya de Malha bank coincide with the increase in the number of vessels whereas the number of vessels operating on the Nazareth bank is almost stable together with landings and does not necessarily grow with the increase in the total number of vessels except in 1987 which consequently brought down slightly the catch per fisherman day.

The catch data from each of the banks show the percentage contribution of the Saya de Malha bank in the total catch was declining with a proportional increase from the Nazareth bank. As from 1982 the situation was just the opposite. The catch landed as frozen fish from St. Brandon has been increasing steadily since 1977 with a significant increase in 1988 equivalent to more than 7 times that of 1977. A part of the catch there is salted and exported to Mauritius. Moreover, Saya de Malha is exploited by fishing vessels of Reunion whose annual landings amounted to about 800t up to 1987 and presently they are estimated to be not more than 300t annually. The modest share of the Albatross bank in the total landings rose quite significantly during the last fishing season. Almost all vessels on their way to and back from the main banks have since October 1988 been stopping there for 2 or 3 days. The fishing grounds around Agalega had also been fished but productivity there is extremely poor.

The catch per fisherman day and the size distribution of the fish of Nazareth bank suggest that the stocks of the bank have not reached a stage of overexploitation and appears to have not suffered much with the increase in the number of vessels. A natural limitation to the application of effort in the area of the Nazareth fishing grounds is due to the smallness of the bank and the shorter period during which it can be exploited. As regards the Saya de Malha bank it has been reported and noted that many a time after 1985 the catch consisted of fish of size comparable to that of Nazareth bank. This could probably be explained by the discovery of some virgin stocks being exploited for the first time.

Fishing effort

The Mauritian vessels used to spend on each cruise between 15 and 22 days in fishing and the Koreans 34 to 55 days. During each year the vessels also lost about 60 unproductive days (30 days in travel 30 days in bad weather). The average number of days in port for Mauritian vessels was about 220,whereas for Korean vessels it was about less than 1/2 as much. During the past 3 or 4 years these data have been modified almost completely and all vessels have to spend more days looking for the fish stocks to be exploited. The reason for that could well be the relatively less space for each fishing vessel on the banks.

There was no drastic decrease in the catch per fisherman day up to 1983 which could have been an indication of moderate exploitation of the stocks. The justification given for the low average productivity of the fishermen on he three largest vessels (La Perle II, La Perle III and Nazareth) was attributed to operational problems. With the new method of data collection it has been possible to ascertain the average catch per fisherman day for the period October 1988-July1989 for each of the fishing grounds. It is noted when referring to figure 11 hereunder and table 9 on the following page that there has been a significant decrease in the productivity in all areas. The mean catch per fisherman day in kg has decreased from 100 to 65 kg on the Nazareth and the Saya de Malha banks respectively.

It will be noted by referring to Appendix 1 that as from October 1988 data are being collected on every fishing stocks located at 5° square on each of the banks which henceforth include St. Brandon, Albatross, Nazareth, Saya de Malha South, Saya de Malha North and Chagos.

Discussion

Since 1977 the catch and effort data from the, banks fishery have been compiled systematically and as from 1988 more data are being elicited from the skippers. The proper interpretation of these information could help in setting the trend for the future development of this handling fishery. Moreover, the stocks of fish of each fishing grounds could in future be assessed separately which will give more exposure of the fishery.

The banks fishery has progressed significantly during the past 7-8 years. The conditions that prevailed during the period 1980 to 1983 are no longer valid: the frozen dame berri has now become a premium product for the consumers and more so for the wholesalers and the assumptions made by Wijskstrom and Kroepelien (1979) and Samboo (1983) on the size of the appropriate vessel of the banks fishery are presently not accurate.

The exploitation of the fishery has been on a competition basis by the local fishing companies to the benefit of the consumers through the price control mechanism. But unfortunately stocks of fish are limited and the right to engage in uncontrolled fishing could lead in the not very far future to regular trips to these fishing grounds being a feature of the past.

The length of a trip to the banks has increased since 1983 by at least 10 days consequent to lower catch rates. The rise in the investment for a fishing campaign is therefore on the increase, the fining of price at consumers' level and the annual slight increase in inflation bring along a profit squeeze of these companies. In spite of low profitability the main fishing companies persevere in their operation. Their plausible explanation to this is their "up-to-the-neck" involvement. And it is being noted that all companies have been investing in side activities to diversify their businesses by operating at least 2 vessels or 1 vessel and another business so that if any one of them goes wrong the losses can partly be absorbed by the other. The administration of a second vessel or another related business does not necessitate a considerable increase in all the components of fixed costs.

There is still no evidence that the stocks of fish on the Nazareth bank are being over-exploited when the size of the fish is considered. However, when the effort is increased which happened in 1987 and1988, this brings about a decrease in catch per day for each fisherman. The stocks of Saya de Malha appear to be overfished when the size of its fish is compared to that of the Nazareth bank but sometimes the erratic responses of this bank to increase in effort give the impression that the landings may still be on the left side of the point of the maximum sustainable yield.

With the rise in demand of the frozen banks fish and the profit squeeze it should be expected that a black marketing of he harvest will eventually develop. This may be hard to combat as restaurants of big hotels may possibly be prepared to offer slightly higher prices just to have a regular supply throughout the year.

Another side effect of profit squeeze was the development of dishonest malpractice of marketing of thawed ungutted fish as a fresh product.

Some results of the study on sexual maturity of *L. mahsena* from Saya de Malha bank.

S. Soondron, A. Venkatasami and A. Sheik Mamode

1 Introduction

L. mahsena commonly known as the berri fish is the most important species caught from the waters of Saya de Malha and contributes to some 85% of the total catch.
This paper presents some results of a study undertaken from October 1996 to Jan 1998. It deals with the reproduction of the species, particularly the length at maturity, sex ratio, spawning and some growth parameters.
The paper attempts to evolve some guidelines for management using the relationship between length at first capture and length at first maturity.

2 Materials and methods

Arrangements were made with a bank fishing company to bring ungutted specimens caught on Saya de Malha (South) bank during the fishing trips of its vessel for the period October 1996 to January 1998. Each month, about 200 samples were thus collected for analysis. The length composition of males and females of *L. mahsena*, sex ratio, gonad stages and length at first maturity were assessed based on data of biological analyses for the whole period of investigations (2 288 specimens).

Using the length frequency data collected at the Port during the period of the study , estimation ofgrowth parameters were attempted using FISAT and LENA softwares. The asymptotic length, L was estimated by the Wetherall plot. The growth coefficient, K was obtained using the ELEFAN, while natural mortality, M was estimated using Pauly's formula. Length converted catch curve analysis was used to determine the total mortality, Z.(Annex 3)

Description of maturity of females

Stage 1
The sex glands are thin, transparent and thread like. Sex cells cannot be differentiated with the naked eye. The ovaries are colourless and they do not increase considerably in size and weight.
Stage II
The ovaries occupy a considerable part of the abdominal cavity. The eggs at this stage becomes pale yellowish in colour.
Stage III
Mature oocytes present in fish ovaries. The diameter of the eggs is quite large. The colour of the eggs changes from yellowish to orange and are easily seen with the naked eye.
Stage IV (spawning)
The gonads are similar to those at the third stage of maturity, but they appear slightly inflamed and have a yellowish-reddish colour. The eggs are granular.
Stage V (spent)
The cavity inside the ovary is red and flabby. This stage characterises the post-spawning state of the ovaries. Accumulation of fat around the sex organs is a regular feature at this stage.

3. Results

3.1 Length composition

The length of fish sampled for analysis varied from 16.5 to 53.7 cm. Length of female varied from 17 to 46.5cm. and that of male from 16.5 to 53.7cm. Fig 1 shows the length frequency of the samples.

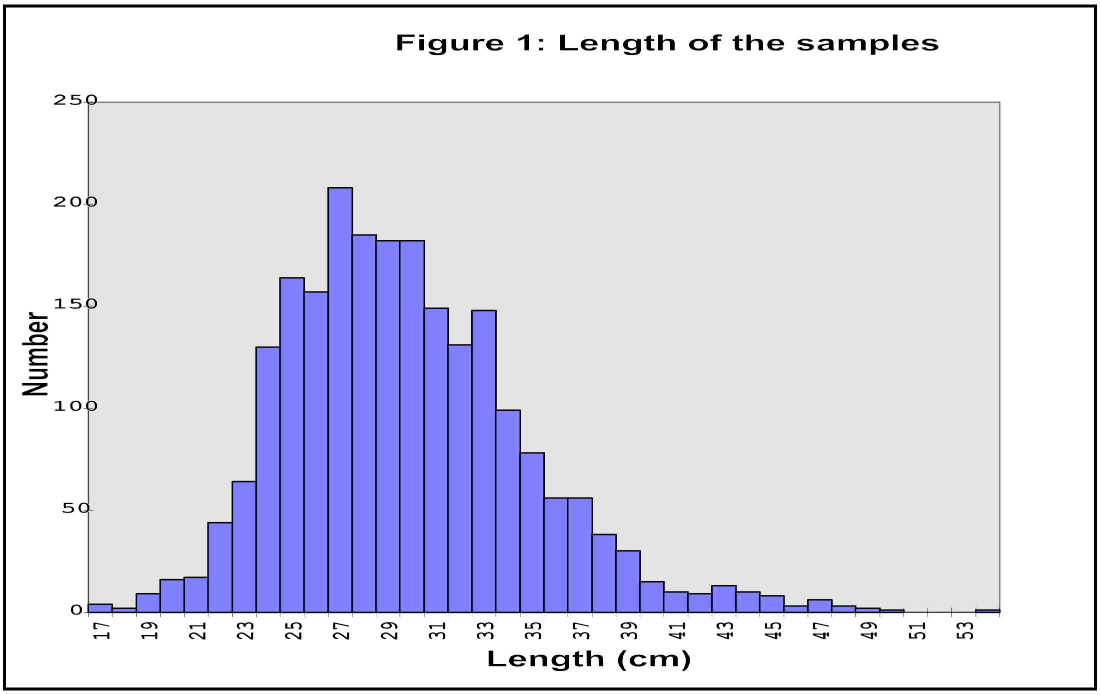
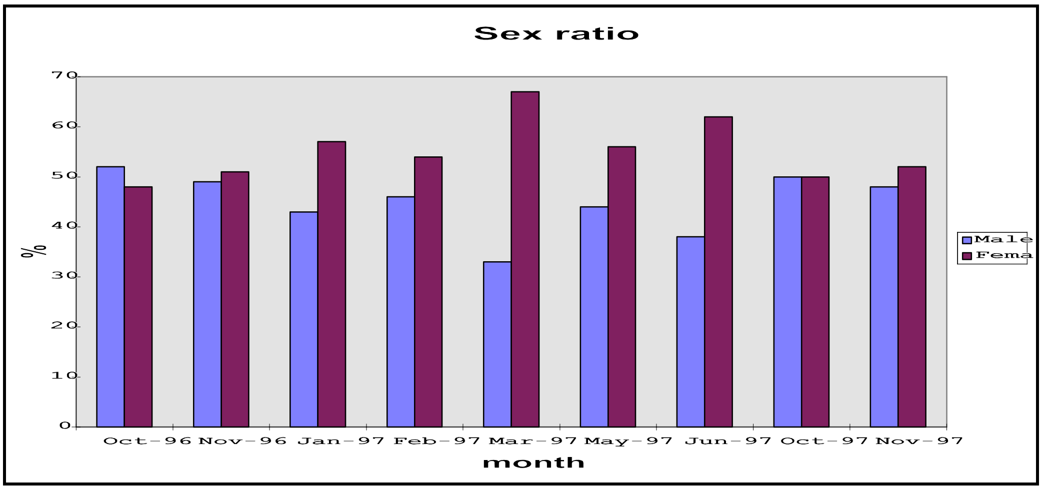


Figure 1: Length of the samples

3.2 Sex ratio

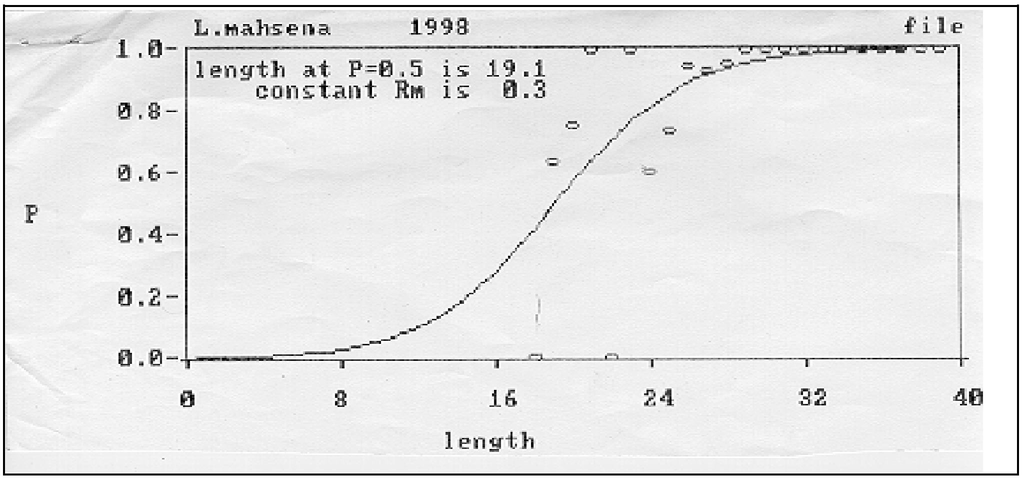
Sex ratio for the 2 288 fish sampled was 1:1 with some predominance of female during certain periods of the year. Fig 2 shows the sex ratio by month.


Sex ratio

As fish grow and become older, the number of females is reduced. In our analysis, the phenomenon was noted when *L. mahsena* reaches a length of about 40 cm. However sex reversal was not observed as stated by Bertrand et al (1989).

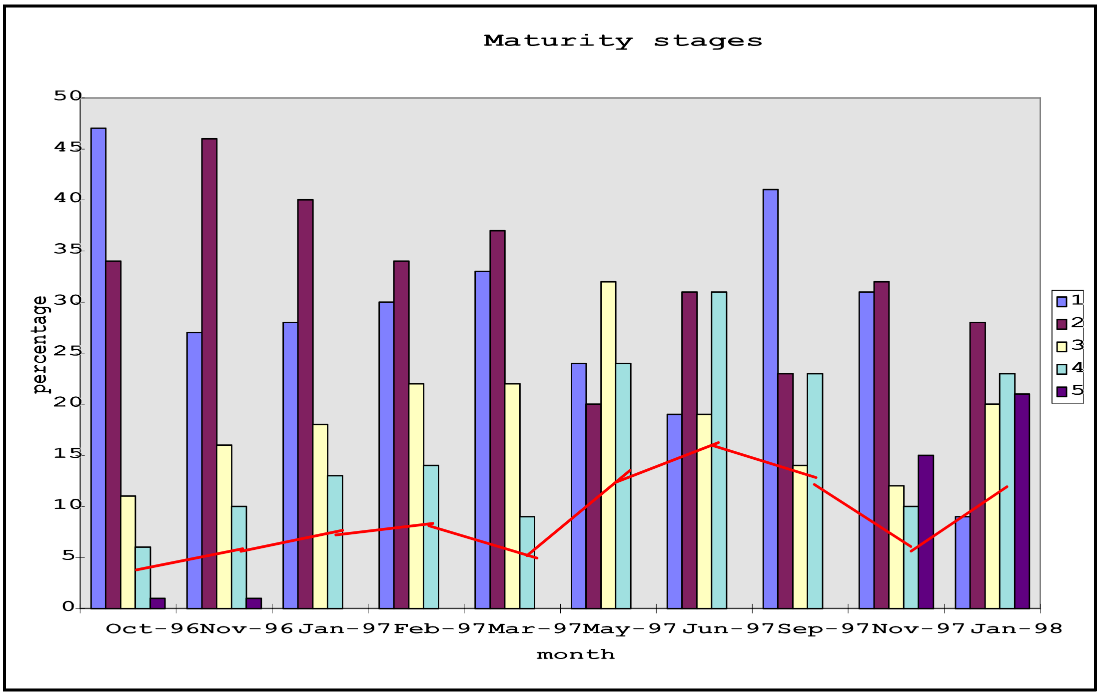
3.3 Length at first maturity (Lm50)

Length at first maturity, (Lm50**)** i.e length at which 50% of all fish at that length are matured, was found to be 19.1 cm, when the fish is approximately three and a half years old.(Annex 2). Fig 3 showing the selectivity curve of % mature females as a function of size. It is to be noted that the only females at stage II and above were considered matured. However, female *L. mahsena* was observed to spawn for the first time when they are 14 cm long (Ratacharen, pers.comm.)



3.4 Spawning period

An attempt was made to establish the spawning period of *L. mahsena* on Saya de Malha bank based on occurrence of spawning individuals. Mature females and males were found throughout the year but individuals at maturity IV were predominant in December and January and during the period May - June.. This indicates that there may be 2 peaks of spawning activity.



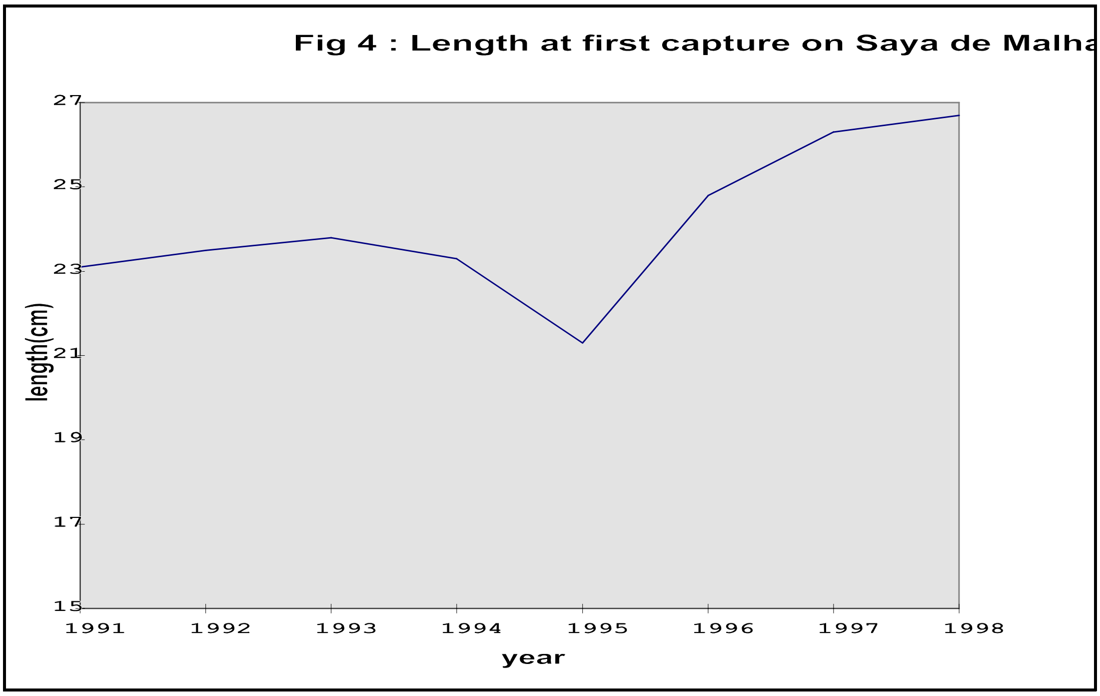
3.5 Growth parameters

Morphometric data were collected at the fishing port during the period of the study. These data includes species composition and fork length distributions of *L. mahsena*. The length frequency distributions were analysed for length at infinity, L , growth coefficient, K, , total mortality, Z and length at first capture, Lc50. Table shows the parameters estimated from the data collected in 1998.

Bank	**L (cm)**	**Z**	**M**	**F**	**K**	**t_0**
Saya de Malha	60.5	0.62	0.3	0.32	0.12	-0.6

3.5 Length at first capture (Lc50)

In 1998, The length at first capture of fish caught on Saya de Malha (South) was 26.7cm. Fig 4 shows the trend in length at first capture of L.mahsena on Saya de Malha bank from 1991 to 1998



4.Conclusion

Two peaks of spawning period occur in May/June and Dec/Jan on the Saya de Malha bank. As the fish grow older the percentage of female individuals is reduced. However, no sex reversal was observed. Length at first maturity is 19.1cm (age=3.5 years). The length at first capture is 26.7cm and is equal to 0.44 L . Lc50 is therefore slightly higher than Lm50. It should, however, be noted that even if Lc50 were equal to Lm50, the small sized fish would face marketing problem and it would not be economically sound to fish at that level. Management of the resource by using Lc50 rather than the mean length would be more appropriate in the shallow water banks fishery. However, care should be taken in the sampling procedure, as very often the catch is segregated according to the size of the fish. Moreover, if fishing is carried out in lightly exploited areas of the banks, bigger size fish would be caught.
At the current fishing mortality and length at capture, the fishery is believed to be exploited at sustainable level.

Results of the Recent Management Measures in the Shallow Water Banks Fishery

A.Venkatasami, S.Soondron, O.Sunassee

1. Introduction

By far the most important supply of fish to the Mauritian market from local production comes from the shallow water banks fishery. These banks are located at distances of over 500 kms from the mainland and consist mainly of the Saya de Malha and Nazareth banks.

In the late eighties and early nineties, concern was expressed over the over-exploitation of these banks, demonstrated by dwindling catch rates (table 2) and the decreasing size of the fish being captured (table 3). Moreover, the fish being small, the industry found it difficult to find buyers, as consumers preferred fish of a better size. Management measures had, therefore, to be applied urgently.

Sustainable exploitation while protecting the resource also safeguards the interests of the fishing fleet and the employment of fishermen. Moreover, it assures a constant supply of fish to the market.

This paper presents the management measures that were introduced and discusses the results that have been achieved so far.

2. Management Measures

2.1. Limited Entry

Limited entry in the shallow water banks fishery was achieved by limiting the number of vessels involved in the fishery through a licensing system that was introduced in 1992. The mechanism for allocating the initial number of licences should normally have been based on the potential yield of the stock. However, in order to avoid laying off of fishing vessels and to safeguard employment, licences were issued to all the seventeen vessels in the fleet. The only merit of the measure was that it did not allow new entrants into the fishery.

2.2. Internally Transferable Quota (ITQ)

As from 1994, in addition to the limitation of entry into the fishery, an internally transferable quota system was set up, to reinforce management measures. The Total Allowable Catch (TAC) was determined as the average of catches for the previous two years and amounted to 5258 tonnes (table 1). The TAC was not based on scientific evidence, but rather accommodated the average performance to again avoid the laying off of vessels and putting into peril the investment of existing companies, which would have led to loss of employment by fishermen and decrease of supply of frozen fish to the market. However, a gradual decrease of 10% was to be applied to the TAC each year, till tangible results in terms of stock recuperation occurred.

Based on the TAC a quota was allocated to each vessel according to its production during the same period of the previous two years. Moreover, since the vessels operated on several banks at a time, the individual quota was further subdivided into sub quota for each of these banks.

The system of allocation of quota to each vessel and sub quota for specific fishing banks, presented several inconveniences – mainly for monitoring and enforcement. It was obvious, the measure relating to allocation of sub quota by bank would, in the absence of adequate enforcement, tempt vessel operators to provide false fishing log returns, thus defeating the purpose for which the measure was intended. Moreover, since quota was allocated to each vessel, companies operating several vessels could not on their own shift quota from temporarily laid up vessels; they instead had to appeal to the fisheries administration to do so, which obviously was time consuming. Subject to the blessing of the fisheries administration, companies could also swap quotas, but this provision failed to satisfy the operators, as at least one operator who was facing difficulties in running its fleet of vessels, placed a high price tag on its share.

2.3. Simplified Quota System

Taking into consideration the various inconveniences of the previous measures and based on the experience gained from the first ever management measures put into practice for the shallow water banks fishery, a simplified approach was adopted in 1995.

The licensing system was maintained and no new entrants were allowed. Instead of a quota to each vessel, the allocation was made to the company, so that the company could decide which vessel to run and when. The company was also thus free to reduce its fleet if that could provide better efficiency.

Moreover, to curb down possible flaw in fishing log returns, the quota was no longer subdivided for each fishing bank. It was believed that since vessels would continue their usual fishing patterns on several banks during the same leg despite the restrictions, the limitation of the fleet and the gradual decrease of the TAC would eventually achieve the expectations of improving fish stock size.

The TAC for the season 95-96 was set at 4752 tonnes after accommodating the demand of the operators and bringing certain corrections to previous estimates. The TAC was now to be reduced by 5% each year.

As from the season 1997-1998, it was also decided that the fisheries administration would itself redistribute any unallocated or underutilised quota to better performing companies to suppress exaggerated or abusive trade offs.

3. Results

3.1. Utilisation of Quota

The TAC which was set since 1994 has never been fully utilised by vessel operators. The amount for each season, the quota used and the rates are shown in table 1.

Table 1: TAC and utilisation of quota

Season	TAC allocated (t)	Quota used (t)	% Quota used	Balance (t)
1994/95	5258	5009	95	249
1995/96	4752	3999	84	753
1996/97	4514	4106	90	408
1997/98	4288	3443	80	845
1998/99	4073	3342	82	731

There are several reasons why the amount allocated remained partially unutilised. The operators, having a bigger number of vessels, had a bigger share of the quota; however, with a large fleet the frequency of breakdowns was higher; it should be reminded that the vessels in the fishery are reconverted old long liners having almost reached the edge of their active life. Moreover, these same bigger operators found it more difficult to find a reliable work force that would not force vessels to shorten their fishing trips through complaints of a sickness and other reasons. These coupled with other business management issues inherent to a big company, are factors that may have directly influenced the quota use.

Therefore, the underutilisation of quota is largely attributed to the efficiency level at which business is managed at the level of fishing companies.

3.2. Evolution of Fishing Effort

Table 2 gives the catch, effort in number of active fishermen days and the catch per fishermen day (CPFD), also used as the unit effort, for the Nazareth and Saya de Malha banks.

Table 2: Catch, Effort and CPFD

(not available)

As seen from the table, the effort applied increased from 53833 fishermen days in 1992 to 69612 in 1994, and later on decreased quite substantially. The increase from 1992 to 1994 had to be expected as fishing effort is not time invariant in a licensing system (Beddington, 1983); the operators would invariably increase their fishing effort in terms of the number of fishermen, number of fishing days and trips. Subsequently, the improved management measures contributed to decreasing the fishing effort.

3.3. Evolution of Catch Rates (CPFD)

One of the main objectives aimed by the management measures was to improve catch rates, which not only contributed to better efficiency in running of vessels, and better economic return to operators, but also to provide fishermen with better revenues.

As can be seen from table 2 and figure 1, the CPFD which was on the decline up to 1996, started recuperating very substantially onwards, for both the Nazareth and Saya de Malha banks.

The fact that the CPFD improved on both major fishing areas and since roughly the same time also demonstrates that the integration of the previous sub areas quota into an overall quota did not have negative impacts on the individual stocks of each area. Ideally, as pointed out by Mees (Mees, 1996) every stock should be managed separately, but as on any trip, most vessels fish on several banks, it is difficult to distinguish between catches from different banks.

3.4. Evolution of Size of Fish Caught

Table 3 shows how the size of fish caught has evolved during the recent years.

Table 3:

(not available)

The length at first capture of the fish has gradually improved during the past three to four years. Detailed results of a study on the length at first capture are discussed by Soondron et al (this workshop).

3.5. Evolution of Landings

Table 4 gives the landings of fish from the banks from 1992 - 1998.

Table 4: Fish Landings

Year	Catch (t)
1992	3.777453e+27
1993	
1994	
1995	
1996	
1997	
1998	

The decreasing catches are due to reasons stated earlier, but has also to be attributed to the fact that the TAC is compulsorily decreased each year as from 1994.

4. Discussion

Sanders (Sanders, 1986) proposed a potential yield of 2887 and 1280 tonnes for Saya de Malha and Nazareth banks respectively, or a total of 4167 tonnes, and subsequently Mees came forward with 2100 and 1680 tonnes (Mees, 1996) or 3780 tonnes in all. The amount of fish landed from the banks after 1996 when the catch rates and the size of fish started to improve has been between 3140 and 3518 tonnes.

These figures along with results of other studies (this workshop) should establish the limits of exploitation of the banks for sustainable development of all compartments of the fishery.

The size of fish having improved, directly influencing a positive response in catch rates, there was no marketing problems for the fish. Hence, the harvesting agent as well as the consumer are satisfied, which indicates that the size at which the fish is caught is an important factor determining the success of the fishery.

Hence, though Potential yield estimates will be used to protect the resource, Economic yield will protect the industry on the whole. Therefore, management measures should not be restricted at solely improving fish stock.

Over the years, the different improvements in the management measures have led to a more simplified mechanism of control, which makes monitoring easier and more reliable, while practically not involving any forms of ever costly surveillance at sea.

5. Conclusion

Recent management measures in the shallow water banks fishery have yielded expected results by decreasing fishing effort and improving catch rates and size at which fish is caught.

Over the years, the different improvements in the management measures applied have resulted into a more simplified mechanism of control, which makes monitoring easier and more reliable, while practically not involving any form of costly surveillance at sea.

Food and Feeding Habits of *Lethrinus mahsena* in the Mauritian Banks

Rathacharen, S. and Degambur, D.

Introduction

The fishery on the Mauritian Banks is multi-species, but on most banks *Lethrinus mahsena* accounts for about 90 per cent of the catches. The fishing grounds are the banks of the Mascarene Ridge, particularly the Saya de Malha and Nazareth Banks. The landings by Mauritius from the Banks Fishery, in 1996 totalled 4,424 tonnes. Most of this was from Saya de Malha Bank (2,283 tonnes) and the Nazareth Bank (1,253 tonnes). The other contributions were from St. Brandon (432 tonnes), Chagos (321 tonnes) and the Albatross Bank (135 tonnes). The food habits study of *Lethrinus mahsena* was undertaken to elucidate its place in the food web of this economically significant fish inhabiting marine waters of the Mauritian Banks. The complex problem of intra-specific dynamics as a result of selective harvesting has not been studied. Economically desirable carnivores have been the objects of most food web studies since their obvious worth invokes greater interest and support (Pinkas, 1971, Brock, 1943; Hart, 1942; Iverson 1962; Baxtail, 1960). The current food habits study was initiated in order to find out about the effects of selective prey and its competitors. This investigation was undertaken from October 1998 to April 1999. Some limitations as concerns continuing digestion between time of capture and preservation, usually a variable period to be considered a limiting factor. Ingested food was a mixture of past and recent feedings. *Lethrinus mahsena* usually inhabits shallow waters up to a depth of 50m and favors a demersal environment. To sample this fish was to sample thousands of kilometres of feeding area, and to learn of its feeding preference and also about the banks marine environment.

Material and methods

Commercial catches from the different banks were the main source of fish specimens. Samples of stomach were taken from fish and placed individually in plastic bottles with coded identification numbers and put in 4% formaldehyde solution. Catch location and date, total length and total weight of each fish were recorded and the sample coded for identification. At the laboratory, the contents of the guts were separated into major forage categories, and excess moisture was removed by draining and the blotting with paper towels. Standard procedures included enumeration of food items and measure of frequency of occurrence (Pinkas, Oliphant and Iverson, 1971). Identification of the majority of forage organisms to the specific level was done through usual taxonomic methods for whole animals. Fish specimens found in the stomachs were identified to the generic and specific level and were measured to the nearest millimeter. Food item is not intended to refer to a species, it may be a taxonomically heterogeneous group classed together by some other common attribute (Laevastu, FAO, 1965). It should be noted that the method of catch has an influence on the stomach content. Food items were identified to the lowest possible taxon. Each food category paused different identification problems. Whole or slightly digested fish or crustacean or Echinodermata presented little difficulty. Identification of partially digested animals, seaweeds and seagrasses was accomplished through exoskeleton, vertebrae of fish, scales of fish and fragments of seaweeds, seagrasses, sea urchins, sea stars and brittle stars. Specific identification of crustaceans normally required appendages be attached and intact. It was possible to establish the specific identity of some well-known crustaceans, bivalves, echinoderms, molluscs and gastropods. Other crustaceans could be designated to order, class, family, or sometimes genus. The occurrence method (Laevastu, 1965) gives the number of fish in which each food item occurs as a percentage of the total number of fish examined. Laevastu, FAO, 1965, suggests that the total number of occurrence of all items be summed, scaled down to give percentage composition of diet. However, for the occurrence method, the importance of small numbers and small food items is magnified which is the same as for the number method. But both volume method and weight method have one setback, that is, large items cause an incorrect picture of their real importance.

Results and Discussion

Of the 398 emperor stomachs taken during the summer season 1998, 21 specimens were from Saya de Malha South, 291 individuals from Saya de Malha North, 26 samples from Nazareth Bank and 60 fish specimens from Saya de Malha Bank. Fish were collected from handline catches on the banks (Latitude 9^{0}18¢S to 16^{0}15¢S and longitude 60^{0}20¢S to 62^{0}14¢E). (Table 1)

Table 1:Number of Samples per Location Bankwise

Bank	Location	Number of Samples Analysed	Total
SMS	10^{0}47¢S 62^{0}03¢E	11	**21**
SMS	10^{0}16¢S 62^{0}13¢E	10	
SMN	10^{0}00¢S 62^{0}10¢E	58	**291**
SMN	09^{0}53¢S 61^{0}25¢E	102	
SMN	09^{0}58¢S 61^{0}48¢E	131	
NAZ	16^{0}15¢S 59^{0}40¢E	15	**26**
NAZ	13^{0}57¢S 61^{0}06¢E	11	
SDM	09^{0}18¢S 60^{0}21¢E	30	**60**
SDM	09^{0}18¢S 60^{0}20¢E	17	
SDM	10^{0}39¢S 62^{0}14¢E	13	
TOTAL			**398**

The present report deals with the food and feeding habits of emperor in relation to months, sizes and sexual maturity stages (Table 2)

Table 2:Biological Parameters of *Lethrinus mahsena* bankwise

Bank	Month	Total length range (mm)	Weight range (g)	Maturity Stage Range	Sex Ratio M:F
SMS	Nov 98	440 - 584	1150 - 2860	2 - 8	1:0.3
NAZ	Nov 98	425 - 525	1300 - 2240	2 - 5	All males
	Dec 98	450 - 563	1520 - 2600	2 - 8	1:1.2
SMN	Nov 98	167 - 270	80 - 330	2 - 8	1:3.8
	Nov 98	485 - 572	1720 - 2600	-	1:0.67
	Dec 98	154 - 290	60 - 290	2 - 8	1:0.93
SDM	Oct 98	240 - 547	210 - 2490	1 - 8	1:0.81

The variation of food items in relation to period (months) and size of the fish, and feeding intensity with respect to months and maturity stages of *Lethrinus mahsena* were made. Among various food components recorded during different months food items classified as Echinodermata (star fish, sea urchins, brittle stars) formed the main part of the diet.(Table 3).

Analysis of frequency of occurrence revealed that species of Phylum Echinodermata were the dominant forage in the size groups of fish 400mm - 580 mm TL, whereas the family Littorinidae constituted the main diet in the size groups of fish 150 mm - 290 mm TL. Among the specimens analysed, 16 had empty stomachs. Echinodermata and Crustacea constituted 55% of food preferred by fish among animal components and *Thalassodendron* sp. among plant materials for size groups of fish greater than 400 mm. *Echinothrix diadema* and *Echinometra mathaei* alone formed 35.75% of the food. Crustaceans, other semi-digested matter and unidentified fragments ranked second and third in total food percentage respectively.

In Saya de Malha North Bank, analysis of frequency of occurrence revealed that for size groups of fish (150 - 290 mm TL), *Littorinidae* (Periwinkles) and *Echinasteridae* (star fish) were the dominant forage. In November 1998, 45 percent of the stomachs contained *Littoraria* sp. followed by star fish, cowries (*Cypraecidae*) and barnacles, amphipods, horn shells, brittle stars, juvenile sea urchins, chitons, crustaceans and *strombidae* (conch shells) but in lesser quantities. Food composition in relation to size groups shows that smaller sized fish preferred mainly small benthic animals and is carnivorous and is mainly hunting macrofauna (predator). The major food items enumerated are mostly found on rocks in lower eulittoral and shallow sublittoral regions. As the stomachs of smaller emperors chiefly consisted of benthic organisms with very few quantities of pelagic ones, it appears that the smaller individuals frequent the bottom for feeding as the larger ones. As for size groups of fish (440 mm - 540 mm TL), *Echinothrix* sp. and *Asteropsis* sp. comprised by volume 25.0% and 20.0% of the stomach contents respectively. Analysis of frequency of occurrence for that size group of fish indicated that Echinodermata (50%) and *Asteropsis* sp. (40%) were the preferred food items. The individual species of sea urchins occurring most often were 25 percent *Echinothrix diadema*, 5 percent *Echinometra mathaei*, 20 percent *Asteropsis* sp., 5 percent *phyllacanthus* sp. and 15 percent barnacles. Several undetermined species of Pisces and Crustacea occurred in a significant portion (22%) of the stomachs. Barnacles of sizes 15 mm - 20 mm were frequent in the guts of these fish. *Thalassodendron* sp. was the least common group by percentage volume (0.2%) but was found in 40% of the stomachs.

In Saya de Malha South samples, four species of sea urchins comprised 81 percent of the stomach contents by volume. Frequencies of occurrence were impressive for these species, 40 percent *Echinothrix diadema*, 80 percent *Echinometra* sp., 40 percent *Echinometra mathaei* and 25 percent *Salmacis bicolor*. Family Strombidae, Crustacea, *Thalassodendron* sp. and *Prionocidaris* sp. contributed little by volume (6.0 percent), but they still occurred in 30.0 percent of the stomachs examined. Unidentified material and fish vertebrae were quite important in species from Saya de Malha South and there frequency of occurrence rated 40 percent and 30 percent respectively and by volume, percentage of these two items comprised only 5 percent each.

The volume of *Echinothrix* sp. *Echinometra* sp. and *Tripneustes* sp. from Nazareth bank was quite substantial (65.0 percent) for fish sizes 450 mm - 570 mm. The contribution of sea urchins, 16 percent, was considerably less than Saya de Malha South.In this region *Ranina ranina* and family Cipraeidae (cowries) replaced Strombidae (conch shells) as the second most important group of food organisms as compared to Saya de malha south region. Despite their medium size (approximately 50 mm long), *Monachester sanderi* contributed a significant fraction of the total food ingested in the area, volumetrically 5.0 percent and by frequency of occurrence 10.0 percent. Pheasant shells, *Phasianella* sp. was, despite a low volume of 3.0 percent, of some significance contributing 16,0 percent by frequency of occurrence. Fragments of crustaceans together with semidigested matter comprised 15.0 percent by volume and 60.0 percent by frequency of occurrence. In this region species of infraorder Brachyura and family Raninidae appear to be common inhabitants of Nazareth waters. Common to Saya de Malha south, sea urchins are quite abundant in Nazareth waters.

In the waters of Saya de Malha, cowries are quite substantial both volumetrically and frequency of occurrence representing 80.0 percent respectively for fish sizes 240 mm to 290 mm. Larger individuals of group size 400 mm - 550 mm preferred Echinodermata and was quite substantial, 55.0 percent by volume and 80.0 percent by frequency of occurrence. Starfish occurred in 40.0 percent of the stomachs examined and crabs were in 55.0 percent while fish bait (75.40 g) occurred in 30.0 percent of the stomachs. Other food comprised < 5.0 percent by volume and occurred by 5.0 percent in the stomachs of *L. mahsena*, sea worms, shrimps, *Anguilla bicolor* (210 mm long) and Mollusca comprised 9.0 percent and Moillusca comprised 9.0 percent volumetrically and contributed 27.0 percent by frequency of occurrence.

Lethrinus mahsena feeds primarily on benthic organisms and secondarily on some pelagic organisms and seagrass (Thalassodrendron sp.) depending on the region.

Despite the lack of specifics, it appears that the sky emperor feeding patterns are nearly the same whether they are occupying the Northern or Southern part of Saya de Malha Bank and Nazareth Bank, the dominant feature being sea urchins, star fish, bivalves gastropods and crabs. This benthic fauna consumed by emperors indicates that on the Mascarene Ridge a large variety of organisms are present in the lower eulittoral, in the shallow lagoons, on rocks, in the coral reefs, the upper eulittoral rocks and also in sheltered areas.

References

1. Abbott, T.R. Coquillages, 1990. Editions Soline, Spain 160pp.

2. Allen, G.R. and Steene R. Indo-Pacific Coral Reef. Field Guide 1994. Tropical Reef

Research, Singapore, 378pp.

3. Carpenter, K.E. and Allen, G.R. FAO species Catalogue. Vol.9. Emperor fishes and large-eye breams of the World (Family lethrinidae). An annotated and illustrated catalogue of Lethrinid species known to date, 1989. FAO species synopsis No 125 (a); 118pp.

4. Cousteau J.Y. L'encyclopedie Cousteau. Vol II La quete de la nourriture, 1980. Graficas Estella S.A., 280pp.

5. Drivas, J. & Jay, M. Coquillages de la Reunion et de L'Ile Maurice, 1988. Les Editions du Pacifique, 159pp.

6. Fischer, W. & Bianchi G. FAO species identification sheets for fishery purposes WIO (Fishing area 51) Vol II. FAO/UN.

7. Frimodt C. Multilingual illustrated guide to the World's Commercial warm water fish, 1995. Fishing News Books, Osney Mead, Oxford, England, 215pp.

8. Iclarm, Fish Base, 1996.

9. Laevastu, T. Manual of methods in fisheries biology, 1965. FAO/UN.

10. Michel, C. Marine molluscs of Mauritius, 1988. Editions Ocean Indien, Mauritius, 83pp.

11. Mohsin, A.K.M., Azmi Ambak, M. Marine Fishes and Fisheries of Malaysia and neighbouring countries, Edi…..

12. Moorjani, S. & Simpson, B. Seaweeds of the Kenya Coast, 1988. Oxford University Press, Nairobi, Kenya, 134pp.

13. Oliver A.P.H. & Richard G. Le Multiguide nature des coquillages marines du monde en couleurs, 1989. Mandarin Offset, Hong Kong, 320pp.

14. Pinkas, L., Oliphant, S., Ingrid L.K. Iverson. Food habits of albacore, blue fin tuna and bonito in California waters, 1971. State of California, 105pp.

15. Richmond, M.D. A Guide to the Seashores of Eastern Africa, 1997, Italgraf A.B., 448pp.

16. SWIOP/MAFNR, 1989. Proceedings of the seminar on the management of the banks handline fishery. FAO/UNDP: RAF/87/008/WP/52/89/E 71p - 85p.

References

Abidi, H., J. Borms, W. Duquet and J. Pontier. (1996). Bayesian estimation of the parameters of a nonlinear model. An application to human height. *Growth development and ageing.* **60**(3-4): 113-129.

Aldonov, V.K. and A.D. Druzhinin. (1979). Some data on scavengers (family Lethrinidae) from the Gulf of Aden region. *J. Ichthyol.* **18**: 527-535.

Allen, G.R. (1985). *FAO species catalogue, Vol. 6. Snappers of the world; an annotated and illustrated catalogue of lutjanid species known to date.* FAO Fish Synop. 6(125), 208pp.

Allen, K.R. (1966). A method of fitting growth curves of the von Bertalanffy type to observed data. *J. Fish. Res. Bd. Canada.* **23**(2): 163-179.

Ambak, M.A., A.K.M. Mohsin and M.Z.M. Said. (1985). Growth characteristics of Lutjanidae off the east coast of Peninsular Malaysia. *In* A.K.M. Mohsin, M.I.H. Mohamed and M.A. Ambak (Eds.), *Ekspedisi Matahari '85: a study on the offshore waters of the Malaysian EEZ*. Vol. 3. Occas. Publ. Fac. Fish. Mar. Sci. Univ., Pertanian, Malaysia, p165-174.

Anon. (1989). Chapter 11, Fisheries. *National Development Plan, 1990-1994*. p23-46.

Anon. (1996). Report on the workshop on ageing of *Sebastes spp. ICES CM1996/G:1*, 32pp.

Anthony, V.C. (1971). The density dependence of growth in the Atlantic herring in Maine. *Rapp. P. V. Reun. Cons. Int. Explor. Mer.* **160**: 197-205.

Ardil, J.D. (1979).Current status of fisheries in Mauritius. FAO/SWIOP Document OISO *RAF/79/065/WP/37/87/E*, 28pp.

Ardil, J.D. (1986). Current status of the fishery in Mauritius. *FAO/SWIOP Document. OISO RAF/79/065/WP/37/87/E*, 30pp.

Bach, P. (1989). Introduction a l'otolithometrie. *Technical Report, SFA/ORSTOM, Victoria, Seychelles.* Aug. 1989, 17pp.

Bach, P. and P. Chauvelon. (1994). Daily growth increments (DGI) density - otolith radius relationship according to the von Bertalanffy's growth model: application to *Lutjanus sebae*. *Technical Report of the Seychelles Fishing Authority, Victoria, Seychelles.* SFA/RD/027, 26pp.

Backiel, T. and E.D. Le Cren. (1978). Some density relationships for fish populations parameters. *In* S.D. Gerking (Ed.), *The Biological Basis of Freshwater Fish Production*. Blackwell Scientific Publications, Oxford, p279-302.

Bannerot, S.P., W.W. Fox and J.E. Powers. (1987). Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico. *In* J.J. Polovina and S. Ralston (Eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management.* Westview, Boulder, Colorado, p561-603.

Barlow, J. (1992). Nonlinear and logistic growth in experimental populations of guppies. *Ecology.* **73**(3): 941-950.

Basson, M., A.A. Rosenberg and J.R. Beddington. (1988). The accuracy and reliability of two new methods for estimating growth parameters from length frequency data. *J. Cons. Int. Explor. Mer.* **44**: 277-285.

Bautil, B. and C.R. Samboo. (1988). Preliminary stock assessment for the Mahsena emperor (*Lethrinus mahsena*) on the Nazareth Bank of Mauritius. *In* M.J. Sanders, P. Sparre and S.C. Venema (Eds.)*, Proceedings of the workshop on the Assessment of the Fishery Resources in the Southwest Indian Ocean*. FAO/UNDP-RAF/79/065/WP/41/88/E, p260-267.

Beamish, R.J. and G. McFarlane. (1983). The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* **112**: 735-743.

Beamish, R.J. and G.A. McFarlane. (1987). Current trends in age determination methodology. *In* R.C. Summerfelt and G.E. Hall (Eds.)*, Age and Growth in Fish*. Iowa State University Press, Ames, p15-42.

Beckman, D.W. and C.A. Wilson. (1995). Seasonal timing of opaque zone formation in fish otoliths. *In* D.H. Secor, J.M. Dean and S.E. Campana (Eds.)*, Recent Developments in Fish Otolith Research*. Vol. No. 19. The Bella W Baruch Library in Marine Science, p27-43.

Bedford, B.C. (1983). A method for preparing sections of large numbers of otoliths embedded in black polyester resin. *J. Cons. Int. Explor. Mer.* **41**: 4-12.

Bertram, D.F., T.J. Miller and W.C. Leggett. (1997). Individual variation in growth and development during the early life stages of winter flounder, *Pleuronectes americanus*. *Fish. Bull.* **95**(1): 1-10.

Bertrand, J. (1986). Data about the reproduction of *Lethrinus mahsena* (Forsskal 1775) on the Saya de Malha banks (Ocean Indien). *Cybium.* **10**(1): 15-29.

Bertrand, J. *et al.* (1986). Pour une evaluation des resources en capitaine /dame berri (*Lethrinus mahsena*) des bancs de Saya de Malha. Report IFREMER/Albion Fisheries Research Centre, Albion Mauritius, 23-25 Juillet, 1985.

Bertrand, J. (1988). Selectivity of hooks in the handline fishery of the Saya de Malha banks (Indian Ocean). *Fish. Res.* **6**: 249-255.

Beverton, R.J.H. and S.J. Holt. (1956). A review of methods for estimating mortality rates in fish populations, with special reference to sources of bias in catch sampling. *Rapp. P.V. Reun. Cons. Int. Explor. Mer.* **140**: 67-83.

Beverton, R.J.H. and S.J. Holt. (1957). On the dynamics of exploited fish populations. *Fish. Invest. Minist. Agric. Fish. Food G.B. (2 Sea Fish.).* **19**: 533pp.

Bhattacharya, C.C. (1967a). A simple method of resolution of a distribution into Gaussian components. *Biometrics.* **23**: 115-135.

Blacker, R.W. (1974). Recent advances in otolith studies. *In* R. Harden-Jones (Ed.), *Sea Fish. Res*. Elek Science, London, p67-90.

Boehlert, G.W. (1985). Using objective criteria and multiple regression models for age determination in fishes. *Fish. Bull.* **83**(2): 103-117.

Bohnsack, J.A. (1982). Effects of piscivorous predator removal on coral reef fish community structure. *In* G.M. Caillet and C.A. Simenstad (Eds.)*, Gutshop '81. Fish food habit studies.* Washington Seagrant Publication, University of Washington, Seattle, p258-267.

Booth, D.J. (1995). Juvenile groups in a coral-reef damselfish: density dependent effects on individual fitness and population demography. *Ecology.* **76**(1): 91-106.

Bowen, S.H., D.J.D. D'Angelo, S.H. Arnold, M.J. Keniry and R.J. Albrecht. (1990). Density-dependent maturation, growth and female dominance in Lake Superior lake herring (*Coregonus artedii*). *Can. J. Fish. Aquat. Sci.,* **48**: 569-576.

Brey, T., S. Soriani and D. Pauly. (1988). Electronic length frequency analysis. A revised and expanded user's guide. *In Berichte aus dem Institut fur Meereskunde an der Christian-Albrechts-Universitat Kiel No 177.*

Brothers, E.B. (1982). Ageing reef fishes. *In* G.R. Huntsman, W.R. Nicholson and W.W. Fox(Eds.)*, The Biological Bases for Reef Fishery Management. Proceedings of a workshop held October 7-10, 1980 at St. Thomas, Virgin Islands of the United States.* US Department of Commerce, National Oceanic and Atmospheric Administration, Beaufort, North Carolina 28516, p3-23.

Brothers, E.B. and C.P. Mathews. (1987). Application of otolith microstructural studies to age determination of some commercially valuable fish of the Arabian Gulf. *Kuwait Bull. Mar. Sci. 1987.* **9**: 127-157.

Brothers, E.B., C.P. Mathews and R. Lasker. (1976). Daily growth increments in otoliths from larval and adult fishes. *US Natl. Mar. Fish. Serv. Bull.* **74**: 1-8.

Brothers, E.B. and W.N. McFarland. (1981). Correlations between otolith microstructure, growth and life-history transitions in newly recruited French grunts (*Haemulon flavolineatum* (Desmarest), Haemulidae). *Rapp. P. V. Reun. Cons. Int. Explor. Mer.* **178**: 369-374.

Brouard, F. and R. Grandperrin. (1984). Les poissons profonds de la pente recifale externe a Vanuatu. *Notes Doc. Oceanogr. Mission ORSTOM Port Vila, Vanuatu.* **11**: 131pp.

Brouard, F. and R. Grandperrin. (1985). Deep-bottom fishes of the outer reef slope in Vanuatu. South Pacific Commission, Seventeenth Regional Technical Meeting on Fisheries, 5-9 August 1985, Noumea, New Caledonia. SPC/Fisheries 17/WP/12, 126p.

Caddy, J.F. and R. Mahon. (1995). *Reference points for fishery management.* FAO Fish. Tech. Pap, **347**. FAO, Rome, 83pp.

Caillart, B. and E. Morize. (1989). Study of the frequency of increment formation on the otoliths of a tropical Serranidae, *Epinephelus microdon*, using a fluorescent marker: Oxytetracycline. *Aquat. Living Resour.* **2** (4): 255-261.

Carlander, K.D. (1987). A history of scale age and growth studies of North American freshwater fish. *In* R.C. Summerfelt and G.E. Hall (Eds.)*, Age and Growth of Fish.* Iowa State University Press, Ames, Iowa, p3-14.

Carpenter, K.E. and G.R. Allen. (1989). *FAO species catalogue No.9. Emperor fishes and large eye breams of the world (family Lethrinidae). An annotated and illustrated catalogue of lethrinid species known to date.* FAO Species Synop, **125**(9), 118p.

CEFAS. (1997a). The use of otoliths to determine the age of snapper and grouper from the Seychelles and Mauritius fisheries. Preliminary report to MRAG Ltd on completion of Phase 1, 23pp.

CEFAS. (1997b). The validation of otoliths from *Pristipomoides filamentosus* and *Aprion virescens*. Second report to MRAG Ltd on completion of Phase 1, 20pp.

Cerrato, R.M. (1990). Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sci.* **47**: 1416-1426.

Church, A. (1989). Reproduction, age and growth of *Lethrinus chrysostomus*, Norfolk Island. PhD thesis, University of New South Wales, Australia.

Cortez-Zaragoza, E., P. Dalzell and D. Pauly. (1989). Hook selectivity of yellowfin tuna (*Thunnus albacares*) caught off Darigayos Cove, La Union, Philippines. *J. Applied Ichthyol.,* **1**: 12-17.

Craik, W.J.S. (1981). Recreational fishing on the Great Barrier Reef. *Proc. Int. Coral Reef Symp., 4th.* **1**: 47-52.

Cuellar, N., G.R. Sedberry, D.J. Machowski and M.R. Collins. (1996). Species composition, distribution and trends in abundance of snappers of the southeast USA, based on fishery-independent sampling. *In* Arreguin-Sanchez-F., J.L. Munro, M.C. Balgos and D. Pauly (Eds.), *Biology, Fisheries and Culture of Tropical Groupers and Snappers.* ICLARM, Manila, Philippines, 447pp.

Dalzell, P., S. Sharma and G. Nath. (1992). *Estimation of exploitation rates in a multispecies emperor (Pisces: Lethrinidae) fishery in Fiji, based on length frequency data.* South Pacific Commission, Noumea, New Caledonia, p43-50.

Davis, T.L.O. and G.J. West. (1992). Growth and mortality of *Lutjanus vittus* (Quoy and Gaimand) from the North West shelf of Australia. *Fish. Bull.,* **90**: 395-404.

DeMartini, E.E., F.A. Parrish and D.M. Ellis. (1996). Barotrauma-associated regurgitation of food: implications for diet studies of Hawaiian pink snapper, *Pristipomoides filamentosus* (Family: Lutjanidae). *Fish. Bull.,* **94**: 250-256.

Doherty, P. and A. Fowler. (1994). Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of 2 damselfishes. *Bull. Mar. Sci.* **54**(1): 297-313.

Doherty, P.J. (1982). Some effects of density on the juveniles of two species of tropical territorial damselfishes. *J. Exp. Mar. Biol. Ecol.,* **65**: 249-261.

Doherty, P.J. (1983). Tropical territorial damselfishes: Is density limited by aggression or recruitment? *Ecology.* **64**: 176-190.

Edwards, R.R.C. (1985). Growth rates of Lutjanidae (snappers) in tropical Australian waters. *J. Fish Biol.,* **26**: 1-4.

Erzini, K. (1991). Variability in length-at-age in marine fishes. PhD Thesis, Rhode Island University, Kingston, USA, 376pp.

Espinosa, L. and E. Pozo. (1982). Age and growth of the blackfin snapper (*Lutjanus buccanella*) at the southeastern Cuban shelf. *Rev. Cub. Invest. Pesq.* **7**(1): 80-100.

Everson, A.R., H.A. Williams and B.M. Ito. (1989). Maturation and reproduction in two Hawaiian Eteline snappers, Uku, *Aprion virescens*, and Onaga, *Etelis coruscans*. *Fish. Bull.* **87**(4): 877-888.

FAO. (1997). *FAO yearbook - Fisheries statistics; catches and landings, 1995.* FAO fisheries statistics, **80**(134). Food and Agriculture Organisation of the United Nations, Rome, 714pp.

FAO/SWIOP. (1983). Mauritius fisheries baseline study. FAO/SWIOP Document, OISO *RAF/78/065/WP/8/83*.

Favro, L.D., P.K. Kuo and J.F. McDonald. (1979). Population genetic study of the effects of selective fishing on the growth of trout. *J. Fish. Res. Board Can.* **36**(5): 552-561.

Ferreira, B.P. and G.R. Russ. (1992). Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces: Serranidae) from the central Great Barrier Reef, Australia. *Aus. J. Mar. Freshwater Res.* **43**: 1301-1312.

Ferreira, B.P. and G.R. Russ. (1994). Age validation and estimation of growth rate of the coral trout *Plectropomus leopardus* from Lizard Island, Northern Great Barrier Reef. *Fish. Bull.* **92**: 46-57.

Filipsson, O. (1989). The effects of fisheries on the size of fishes on mountain lakes. *Inf. Soetvattenlab. Drottingholm.* **3**: 1-18.

Flewwelling, P., N. Bonucci and C. Christy. (1992). Revision of fisheries legislation in the Seychelles. *FAO/UNTCP, TCP/SEY.0155/FL/10R/92/30*.

Fournier, D.A., J.R. Sibert, J. Majkowski and J. Hampton. (1990). MULTIFAN, a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for Southern Bluefin Tuna (*Thunnus maccoyii*). *Can. J. Fish. Aquat. Sci.* **47**(2): 301-317.

Fowler, A.J. (1995). Annulus formation in otoliths of coral reef fish - a review. *In* D.H. Secor, J.M. Dean and S.E. Campana (Eds.)*, Recent Developments in Fish Otolith Research*. Vol. 19. The Bella W Baruch Library in Marine Sciences, p45-63.

Fowler, A.J. and P.J. Doherty. (1992). Validation of annual growth increments in the otoliths of two species of Damselfish from the southern Great Barrier Reef. *Aus. J. Mar. Freshwater Res.* **43**: 1057-1068.

Fox, W.W. (1975). Fitting a generalized stock production model by least-squares and equilibrium approximation. *U.S. Fish. Bull.* **73**: 23-37.

Francis, R.I.C.C. (1990). Back-calculation of fish length - a critical review. *J. Fish Biol.* **36**: 883-902.

Francis, R.I.C.C., L.J. Paul and K.P. Mulligan. (1992). Ageing of adult snapper (*Pagrus auratus*) from otolith annual ring counts: validation by tagging and oxytetracycline injection. *Aus. J. Mar. Freshwater Res.* **43**: 1069-1089.

Francis, B., M. Green and C. Payne. (1993). *GLIM4: the statistical system for generalised linear interactive modelling.* Clarenden Press, Oxford, 821pp.

Fukuwaka, M. and M. Kaeriyama. (1997). Scale analyses to estimate somatic growth in sockeye salmon, *Oncorhynchus nerka*. *Can. J. Fish. Aquat. Sci.* **54**: 631-636.

Gabriel, K.R. (1978). A simple method of multiple comparison of means. *J, Amer. Stat. Assn.* **73**: 724-729.

Gauldie, R.W. (1988). Function, form and time-keeping properties of fish otoliths. *Comp. Biochem. Physiol.* **91A**(2): 395-402.

Gayanillo, F.C., P. Sparre and D. Pauly. (1994). FiSAT. The FAO-ICLARM Stock Assessment Tools (FiSAT) User's Manual. *FAO Computerised Information Series (fisheries), FAO Rome/ICLARM Contribution No. 1048*, 126pp

Gittinger, J.P. (1982). *Economic analysis of agricultural projects.* The John Hopkins University Press, Baltimore, Maryland, 445pp.

Grandcourt, E.M. (1995). Biomass, stock density and the maximum sustainable yield available to a line fishery for *Pristipomoides filamentosus* (Valenciennes, 1830) on the northwestern promontory of Saya de Malha bank. SFA Technical Report, *SFA/R&D/038.*

Grimes, C.B. (1987). Reproductive biology of the Lutjanidae: A review. *In* J.J. Polovina and R. S. (Eds.)*, Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Boulder, Colorado and London, p239-294.

Gulland, J.A. (1966). Manual of sampling and statistical methods for fisheries biology. Part 1. Sampling methods. *FAO Man. Fish. Sci.* **3**, 87pp.

Gulland, J.A. (1971). *The fish resources of the ocean.* Fishing News Books, West Byfleet, Surrey.

Gulland, J.A. (1983). *Fish stock assessment. a manual of basic methods.* FAO/Wiley Series on Food Agriculture Vol. 1, John Wiley and Sons, New York, 372pp.

Gulland, J.A. (1987). Length-based methods in fisheries research: from theory to application. *In* D. Pauly and G.R. Morgan (Eds.)*, Length-Based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Gulland, J.A. and L.K. Boerema. (1973). Scientific advice on catch levels. *Fish. Bull.* **71**(2): 325-335.

Gulland, J.A. and A.A. Rosenberg. (1992). A review of length-based approaches to assessing fish stocks. *FAO Fish. Tech. Pap.* **323**: 100pp.

Haight, W.R., D.R. Kobayashi and K.E. Kawamoto. (1993a). Biology and management of deepwater snappers of the Hawaiian archipelago. *Mar. Fish. Rev.* **55**(2): 17-24.

Haight, W.R., J.D. Parrish and T.A. Hayes. (1993b). Feeding ecology of deepwater lutjanid snappers at Penguin Bank, Hawaii. *Trans. Am. Fish. Soc.* **122**: 328-347.

Hamley, J.M. (1975). Review of gillnet selectivity. *J. Fish. Res. Board Can.* **32**: 1943-1969.

Hampton, J. and J. Majkowski. (1987). An examination of the reliability of the ELEFAN computer programs for length-based stock assessment. *In* D. Pauly and G.R. Morgan (Eds.)*, Length-based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Harding, J.P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. Mar. Biol. Assoc. UK.* **28**: 141-153.

Hardman-Mountford, N.J., N.V.C. Polunin and D. Boullé. (1997). Can the age of tropical species be determined by otolith measurement? A study using *Pristipomoides filamentosus* (Lutjanidae) from the Mahe Plateau, Seychelles. *Naga.* **20**(2): 27-31.

Hasselblad, V. (1966). Estimation of parameters for a mixture of normal distributions. *Technometrics.* **8**: 431-444.

Helser, T.E. and F.P. Alimeida. (1997). Density-dependent growth and sexual maturity of silver hake in the north-west Atlantic. *J. Fish. Biol.* **51**: 607-623.

Helser, T.E. and J.K.T. Brodziak. (1998). Impacts of density dependent growth and maturation on assessment advice to rebuild depleted U.S. silver hake (*Merluccius bilinearis*) stocks. *Can. J. Fish. Aquat. Sci.* **55**: 882-892.

Henderstrom, H. (1959). Observations on the age of fishes. *Rep. Inst. Freshwater Res. Drottingholm.* **40**: 161-164.

Hilborn, R. and C.J. Walters. (1992). *Quantitative fisheries stock assessment. Choice, dynamics, and uncertainty.* Chapman and Hall, New York, 570pp.

Hochberg, Y. (1974). Some generalisations of the T-method in simultaneous inference. *J. Multivar. Anal.* **4**: 224-234.

Hoenig, J.M., J. Csirke, M.J. Sanders, A. Abella, M.G. Andreoli, D. Levi, S. Ragonese, M. Al-Shoushani and M.M. El-Musa. (1987). Data acquisition for length-based stock assessment: report of working group 1. *In* D. Pauly and G.R. Morgan (Eds.)*, Length-Based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, 468p.

Holden, M.J. and D.F.S. Raitt. (1974). *Manual of fisheries science. Part 2. Methods of resource investigation and their application.* FAO Fish. Tech. Pap. 115 (Rev1). FAO. Rome, 214pp.

Holden, S., G. Kirkwood and M. Bravington. (1995). *Length Frequency Distribution Analysis - the LFDA package: user manual.* MRAG Ltd, London, 110pp.

Huntsman, G.R., C.S. Manooch and C.B. Grimes. (1983). Yield-per-recruit models of some reef fishes of the US South Atlantic bight. *Fish. Bull.* **81**(4): 679-695.

Isaac, V.J. (1990). The accuracy of some length-based methods for fish population studies. *ICLARM Tech. Rep.* **27**, 81pp.

Ivo, C.T.C. and S.C.A. Rocha. (1988). Hook selectivity in the Caribbean red snapper *Lutjanus purpureus* Poey, in northern Brazil. *Arq. Cienc. Mar.* **27**: 49-56.

Jennings, S. and J.M. Lock. (1996). Population and ecosystem effects of fishing. *In* N.V.C. Polunin and C.M. Roberts (Eds.), *Tropical Reef Fisheries*. Chapman and Hall, London, p193-218.

Jennings, S., S.S. Marshall and N.V.C. Polunin. (1996). Seychelles marine protected areas: comparative structure and status of reef fish communities. *Biological Conservation.* **75**: 201-209.

Jones, G.P. (1984a). Population ecology of the temperate reef fish *Pseudolabrus celidotus* (Pisces: Labridae). II. factors influencing adult density. *J. Exp. Mar. Biol. Ecol.* **75**: 277-303.

Jones, G.P. (1987a). Some interactions between residents and recruits in two coral reef fishes. *J. Exp. Mar.Biol.Ecol.* **114**: 169-182.

Jones, G.P. (1987c). Competitive interactions among adult and juveniles in a coral reef fish. *Ecology.* **68**: 1534-1547.

Jones, G.P. (1991). Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. *In* P.F. Sale (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, Inc, San Diego, California, p294-330.

Jones, R. (1984b). Assessing the effects of changes in exploitation pattern using length composition data (with notes on VPA and cohort analysis). *FAO Fish. Tech. Pap.* **256**. FAO, Rome, 118pp.

Jones, R. (1987b). An investigation of length composition analysis using simulated length compositions. *In* D. Pauly and G.R. Morgan (Eds.), *Length-Based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Jones, C.M. and B. Wells. (1998). Age, growth, and mortality of black drum, *Pogonias cromis*, in the Chesapeake Bay region. *Fish. Bull.* **96**(3): 451-461.

Kailola, P.J., M.J. Williams, P.C. Stewart, R.E. Reichelt, A. McNee and C. Grieve. (1993). *Australian fisheries resources.* Bureau of Resource Sciences, Department of Primary Industries and Energy, and Fisheries Research and Development Corporation, Canberra, Australia, 422pp.

Kerr, S.R. (1982). Estimating the energy budgets of actively predatory fishes. *Can. J. Fish. Aquat. Sci.* **39**: 371-379.

Kimura, D.K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fish. Bull.* **77**(4): 765-776.

King, M. (1995). *Fisheries biology, assessment and management.* Fishing News Books, Oxford, 341pp.

Kingsford, M.J. and M.H. Atkinson. (1994). Increments in otoliths and scales: how they relate to the age and early development of reared and wild larval and juvenile *Pagrus auratus* (Sparidae). *Aust. J. Mar. Freshwater Res.* **45**(6): 1007-1021.

Kirkwood, G.P. (1983). Estimation of von Bertalanffy growth curve parameters using both length increment and age-length data. *Can. J. Fish. Aquat. Sci.* **40**: 1405-1411.

Kirkwood, G.P., J.R. Beddington and J.A. Rossouw. (1994). Harvesting Species of Different Lifespans. *In* P.J. Edwards, R. May and N.R. Webb (Eds.), *Large Scale Ecology and Conservation Biology*. Blackwell Scientific Publications, p199-227.

Klein, M. (1992). Effect of exploitation on growth, age-structure and recruitment of an underfished population of European Whitefish. *In* T.N. Todd and M. Luczynski (Eds.), *Biology and Management of Coregonid Fishes - 1990*. Vol. 39, 3-4. Quebec City, p807-815.

Koslow, J.A., F. Hanley and R. Wicklund. (1988). Effects of fishing on reef fish communities at Pedro bank and Port Royal Cays, Jamaica. *Mar. Ecol. Prog. Ser.* **43**: 201-212.

Kristiansen, T.S. and T. Svasand. (1998). Effect of size-selective mortality on growth of coastal cod illustrated by tagging data and an individual-based growth and mortality model. *J. Fish Biol.* **52**: 688-705.

Kulbicki, M. (1988). Patterns in the trophic structure of fish populations across the SW lagoon of New Caledonia. *Proc. 6th Intl. Coral Reef Symp.*, p89-94.

Lablanche, G., G.D. Moussac and N. Jivan Shah. (1988). A summary description of the artisanal fisheries and resources for the Seychelles, in proceedings of the workshop on the assessment of the fishery resources in the south west Indian Ocean. FAO/UNDP. *RAF/79/065/WP/41/88/E*: 116-141.

Laevastu, T. (1992). Interactions of size-selective fishing with variations in growth rates and effects on fish stocks. *ICES-CM-1992/G:5.*

Lai, H.L., D.R. Gunderson, and L.L. Low. (1987). Age determination of pacific cod using 5 ageing methods. *Fish. Bull.* **85**: 713-723.

Landa, J. (1999). Density-dependent growth of four spot megrim (*L. boscii*) in the northern Spanish shelf. *Fish. Res.* **40**(3): 267-276.

Langi, S. (1990). The applicability of ELEFAN for use in analysing 3 species of deep-sea snappers (*Etelis corruscans*, *Pristipomoides flavipinnis* and *P. filamentosus*, Family Lutjanidae). *Fishbyte.* **8**(1): 21-25.

Langi, V.A. and S.A. Langi. (1989). Indicators of fishing pressure in the deepsea snapper fishery of the Kingdom of Tonga. *Fishbyte.* **7**: 15-17.

Langi, V.A., S.A. Langi and J.J. Polovina. (1992). Estimation of deepwater snapper yield from Tongan seamounts. *NAGA.* **15**(3): 32-35.

Latu, T. and S. Tulua. (1991). Stock assessment of deep water snappers and groupers in the Kingdom of Tonga. Interim Report 1986-1990. Fisheries Division Report.

Lebeau, A. and J.C. Cueff. (1975). Biologie et peche du capitaine *Lethrinus enigmaticus* (Smith, 1959) du banc de Saya de Malha (Ocean Indien). *Rev. Trav. Inst. Peches Marit.* **39**(4): 415-442.

Lebeau, A. and J.C. Cueff. (1976). Biologie et peche des Lethrinides sur les hauts-fonds de Saya de Malha. *Trav. et documents, ORSTOM.* **47**: 333-348.

Le Cren, E.D. (1958). Observations on the growth of Perch (*Perca fluviatilis*) over twenty-two years with special reference to the effects of temperature and changes in population density. *J. Anim. Ecol.* **27**: 287-334.

Liu, C.C. and S.Y. Yeh. (1991). Age determination and growth of red snapper (*Lutjanus sebae*) in the Arafura Sea off north Australia. *ACTA Oceanogr., Taiwan.* **26**: 36-52.

Lorenzen, K. (1996). A simple von Bertalanffy model for density-dependent growth in extensive aquaculture, with an application to common carp (*Cyprinus carpio*). *Aquaculture.* **142**: 191-205.

Lou, D.C. (1992). Validation of annual growth bands in the otolith of tropical parrotfishes (*Scarus schlegeli*, Bleeker). *J. Fish Biol.* **41**: 775-790.

Loubens, G. (1978). Biologie de quelque especes de poisson du lagon Neo-Caledonien. I. Determination de l'age (otolithometrie). *Cahiers ORSTOM, Series Oceanographie.* **16**: 263-283.

Loubens, G. (1980). Biologie de quelques especes de poissons du lagon Neo-Caledonien III. *Croissance. Cal. Indo-Pac.* **2**: 101-153.

Lowerre-Barbieri, S.K., J.M. Lowerre and L.R. Barbieri. (1998). Multiple spawning and the dynamics of fish populations: inferences from an individual-based simulation model. *Can. J. Fish. Aquat. Sci.* **55**: 2244-2254.

MacDonald, P.D.M. (1987). Analysis of length frequency distributions. *In* R.C. Summerfelt and G.E. Hall (Eds.)*, Age and Growth in Fish*. Iowa State University Press, Ames, p371-384.

MacDonald, P.D.M. and T.J. Pitcher. (1979). Age-groups from size frequency data: a versatile and efficient method for analysing distribution mixtures. *J. Fish. Res. Bd. Can.* **36**: 987-1001.

Mace, P.M. (1994). Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. *Can. J. Fish. Aquat. Sci.* **51**: 110-122.

Majkowski, J., J. Hampton, R. Jones, A. Laurec and A.A. Rosenberg. (1987). Sensitivity of length-based methods for stock assessment: report of working group 3. *In* D. Pauly and G.R. Morgan (Eds.)*, Length-Based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, p363-372.

Manickchand-Dass, S. (1987). Reproduction, age and growth of the lane snapper, *Lutjanus synagris* (Linnaeus) in Trinidad, West Indes. *Bull. Mar. Sci.* **40**(1): 22-28.

Manickchand-Heileman, S.C. and D.A.T. Philipp. (1996). Reproduction, age and growth of the Caribbean red snapper (*Lutjanus purpureus*) in waters off Trinidad and Tobago. *In* F. Arreguin-Sanchez, J.L. Munro, M.C. Balgos and D. Pauly (Eds.)*, Biology, Fisheries and Culture of Tropical Groupers and Snappers*. ICLARM, Manila, Philippines, 447pp.

Manooch, C.S. (1982). Ageing reef fishes in the Southeast fisheries centre. *In* G.R. Huntsman, W.R. Nicholson and W.W. Fox (Eds.)*, The Biological Basis for Reef Fishery Management. Proceedings of a workshop held October 7-10, 1980 at St. Thomas, Virgin Islands of the United States*. US Department of Commerce, National Oceanic and Atmospheric Administration, Beaufort, North Carolina 28516, p24-43.

Manooch, C.S. (1987). Age and growth of snappers and groupers. *In* J.J. Polovina and S. Ralston (Eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management.* Westview Press Inc., Boulder, p329-363.

Manooch, C.S. and C.L. Drennon. (1987). Age and growth of yellowtail snapper and queen triggerfish collected from the US Virgin Islands and Puerto Rico. *Fish. Res.* **6**: 53-68.

Martinez-Garmendia, J. (1998). Simulation analysis of evolutionary response to size-selective harvesting with the use of an individual-based model. *Ecol. Model.* **111**(1): 37-60.

Mason, D.L. and C.S. Manooch. (1985). Age and growth of the mutton snapper along the east coast of Florida. *Fish. Res.* **3**: 92-104.

Mathews, C.P. (1974). An account of some methods of overcoming errors in ageing tropical and sub-tropical fish populations when hard tissue growth markings are unreliable and the data are sparse. *In* T.B. Bagenal (Ed.), *Ageing in fish*. Unwin Brothers Limited, Old Working, Surrey, England, p159-166.

Mathews, C.P. (1987). Fisheries management in a developing country: the most appropriate balance of size- and age-related methods for practical assessments. *In* D. Pauly and G.R. Morgan(Eds.)*, Length-based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

McPherson, G.R. and L. Squire. (1992). Age and growth of three dominant Lutjanus species of the Great Barrier Reef inter-reef fishery. *Asian Fish. Sci.* **5**(1): 25-36.

Mees, C.C. (1989). The artisanal fisheries of the Seychelles. SFA internal report, 12pp.

Mees, C.C. (1992). Seychelles demersal fishery: an analysis of data relating to four key demersal species. *SFA/R&D/019*, 143pp.

Mees, C.C. (1993). Population biology and stock assessment of *Pristipomoides filamentosus* on the Mahe Plateau, Seychelles. *J. Fish Biol.* **43**: 695-708.

Mees, C.C., G.M. Pilling and C.J. Barry. (1999). Commercial fishing activity in the British Indian Ocean Territory (Chagos Archipelago) inshore fishery. *In* C.R. Sheppard and M.R.D. Seaward (Eds.), *Ecology of the Chagos Archipelago*. Westbury Press, Otley, West Yorkshire, 350p.

Mees, C.C. and J.A. Rousseau. (1997). The potential yield of the lutjanid fish *Pristipomoides filamentosus* from the Mahe Plateau, Seychelles: managing with uncertainty. *Fish. Res.* **33**: 73-87.

Mees, C.C., R. Shotton and M. Margueritte. (1998). An inshore fisheries management strategy for Seychelles. *FAO/TCP/SEY/6713(A).* FAO, Rome, 118pp.

Millner, R.S. and C.L. Whiting. (1996). Long-term changes in growth and population abundance of sole in the North Sea from 1940 to the present. *ICES J. Mar. Sci.* **53**: 1185-1195.

Milton, D.A., S.A. Short, M.F. O'Niell and S.J.M. Blaber. (1995). Ageing of three species of tropical snapper (Lutjanidae) from the Gulf of Carpentaria, Australia, using radiometry and otolith ring counts. *Fish. Bull.* **93, 1**: 103-115.

Morales-Nin, B. (1988). Caution in the use of daily increments for ageing tropical fishes. *Fishbyte.* **6**(2): 5-6.

Morales-Nin, B. (1989). Growth determination of tropical marine fishes by means of otolith interpretation and length frequency analysis. *Aquatic Living Resources Nantes.* **2**: 241-253.

Morales-Nin, B. (1992). Determination of growth in bony fishes from otolith microstructure. *FAO Fish. Tech. Pap.* **322**. FAO, Rome, 51pp.

Morales-Nin, B. and S. Ralston. (1990). Age and growth of *Lutjanus kasmira* (Forskaal) in Hawaiian waters. *J. Fish Biol.* **36**(2): 191-203.

Morgan, G.R. (1987). Incorporating age data into length-based stock assessment methods. *In* D. Pauly and G.R. Morgan (Eds.)*, Length-based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Morel, M.H. (1989). Mauritius banks fishery study market considerations. SWIOP/MAFNR (1989) Proceedings of the seminar on the management of the banks handline fishery. *FAO/UNDP:RAF/87/008/WP/52/89/E*, 96pp.

Morgan, G.R. (1983). Application of length-based stock assessments to Kuwait's fish stocks. *International Centre for Living Aquatic Resources Management Newsletter.* **6**(4): 3-4.

MRAG. (1994). The Tongan deep reef-slope fishery - an analysis of data from 1987-1991. Technical report to the Government of Tonga, Ministry of Fisheries for the ODA DMSP Management of Tropical Multispecies Fisheries Project (R4584), 137pp.

MRAG. (1996a). Assistance in the analysis of Mauritian lagoon fishery data. Report on a consultancy to Albion Fisheries Research Centre, 18-28 November 1996, 65pp.

MRAG. (1996b). Management of multi-species tropical fisheries. A report to the Overseas Development Administration,193pp.

MRAG. (1996c). The Mauritian banks fishery: a review and spatial analysis. Technical report for the Management of Multi-Species Tropical Fisheries - Overseas Development Administration, Fish Management Science Programme Project R5484, 62pp.

MRAG. (1996d). The status of the Seychelles demersal fishery. MRAG Technical Report (R4584), 262pp.

MRAG. (1997a). The 1996 BIOT inshore observer programme. A report to the Commissioner for the British Indian Ocean Territory, 54pp.

MRAG. (1997b). The 1997 BIOT inshore observer programme. A Report to the Commissioner for the British Indian Ocean Territory, 56pp.

Mugiya, Y. and N. Watabe. (1977). Studies on fish scale formation and resorption - II. Effect of estradiol on calcium homeostasis and skeletal tissue resorption in the goldfish, *Carassius auratus*, and the killifish, *Fundulus heteroclitus*. *Comp. Biochem. Physiol.* **57A**: 197-202.

Mulligan, T.J. and B.M. Leaman. (1992). Length-at-age analysis: can you get what you see? *Can. J. Fish. Aquat. Sci.* **49**: 632-643.

Munro, J.L. (1983a). *Caribbean coral reef fishery resources.* ICLARM Study Reviews Vol 7. ICLARM, Manila, Philippines, 127pp.

Munro, J.L. (1983b). Epilogue: progress in coral reef fisheries research, 1973-1982. *In* J.L. Munro (Ed.), *Caribbean Coral Reef Fishery Resources*. Vol. 7. International Centre for Living Aquatic Resources Management, Manila, Philippines, p249-265.

Munro, J.L. and D.M. Williams. (1985). Assessment and management of coral reef fisheries: Biological, environmental and socioeconomic aspects. *Proc. Int. Coral Reef Congr., 5th.* **4**: 545-581.

Myers, R.A., J. Bridson and N.J. Barrowman. (1995). Summary of worldwide stock and recruitment data. *Can. Tech. Rep. Fish. Aquat. Sci.* **2024**(4): 327.

Myers, R.A. (1989a). Estimating bias in growth caused by size-selective fishing mortality. *ICES Council Meeting, 1989, collected papers. ICES-CM-1989/D:8*, 24pp.

Myers, R.F. (1989b). *Micronesian reef fishes.* Coral Graphics, Agana Guam.

Nash, R.D.M., A.J. Geffen and G. Hughes. (1994). Individual growth of juvenile plaice (*Pleuronectes platessa* L.) on small Irish Sea nursery ground (Port Erin Bay, Isle of Man, UK). *Neth. J. Sea Res.* **32**(3-4): 369-378.

Newman, S.J. (1995). Spatial variability on the distribution, abundance, growth, mortality and age structures of tropical snappers (Pisces: Lutjanidae) in the central Great Barrier Reef, Australia. PhD thesis, James Cook University, Queenstown, Australia, 250pp.

Newman, S.J., D.M. Williams and G.R. Russ. (1996). Age validation, growth and mortality estimates of the tropical snappers *Lutjanus adetii* and *L. quinquelineatus* from the Central Great Barrier Reef, Australia. *Mar. Freshwater Res.* **47**: 575-584.

Okamoto, H. (1982). Deep bottom fish surveys in Hawaii. *NOAA 83050410*, 24pp.

Opic, P., F. Conand and P. Bourret. (1994). *Poissons commerciaux du Sud-Ouest de L'Ocean Indien.* ORSTOM Editions, 45pp.

Ottway, N.M. and J.R. Craig. (1993). Effects of hook size on the catches of undersized snapper *Pagrus auratus*. *Mar. Ecol. Prog. Ser.* **93**: 9-15.

Overholtz, W.J. (1989). Density-dependent growth in the northwest Atlantic stock of atlantic mackerel (*Scomber scombrus*). *J. Northwest Atl. Fisheries.* **9**: 115-121.

Panella, G. (1971). Fish otoliths: daily growth layers and periodical patterns. *Science.* **173**: 1124-1127.

Panella, G. (1974). Otolith growth patterns: An aid in age determination in temperate and tropical fishes. *In* T.B. Bagenal (Ed.), *The Ageing of Fish*. Unwin Brothers, Old Woking, England, p28-39.

Panella, G. (1980). Growth patterns in fish sagittae. *In* D.C. Rhoads and R.A. Lutz (Eds.), *Skeletal Growth of Aquatic Organisms*. Plenam Press, New York, p519-560.

Parker, D. (1990a). Techniques of cost benefit analysis. *In* Proceedings of the workshop on economic aspects of fisheries development and management. *RAF/87/008/WP/53/90/E.* SWIOP Document OISO, p67-84.

Parker, R.O. (1990b). Tagging studies and diver observations of fish populations on live-bottom reefs of the US southeastern coast. *Bull. Mar. Sci.* **46**(3): 749-760.

Parma, A.M. and R.B. Deriso. (1990). Dynamics of age and size composition in a population subject to size-selective mortality: Effects of phenotypic variability in growth. *Can. J. Fish. Aquat. Sci.* **47**: 274-289.

Parrish, F.A., E.E. DeMartini and D.M. Ellis. (1997). Nursery habitat in relation to production of juvenile pink snapper, *Pristipomoides filamentosus*, in the Hawaiian Archipelago. *Fish. Bull.* **95, 1**: 137-148.

Parrish, J.D. (1987). Trophic biology of snappers and groupers. *In* J.J. Polovina and S.V. Ralston (Eds.)*, Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Boulder, Colorado, p405-463.

Pauly, D. (1978). A preliminary compilation of fish length growth parameters. *Beruchte des Instituts fur Meereskunde an der Christian-Albrechts. Universitat Kil.* **55**: 200.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. CIEM.* **39**(2): 175-192.

Pauly, D. (1981). The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforschung/Reports on Marine Research.* **28**(4): 251-282.

Pauly, D. (1983). Length-converted catch curves. A powerful tool for fisheries research in the tropics (Part 1). *ICLARM Fishbyte.* **1**(2): 9-13.

Pauly, D. (1984). Fish population dynamics in tropical waters: a manual for use with programmable calculators. *ICLARM Stud. Rev.* **8**, 325pp.

Pauly, D. (1987). A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates. *In* D. Pauly and G.R. Morgan (Eds.)*, Length-based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Pauly, D., F. Arreguin-Sanchez, J.L. Munro and M.C. Balgos. (1996a). Biology, fisheries and culture of snappers and groupers: workshop conclusions and updates to 1996. *In* F. Arreguin-Sanchez, J.L. Munro, M.C. Balgos and D. Pauly (Eds.)*, Biology, Fisheries and Culture of Tropical Snappers and Groupers*. ICLARM, Manila, Philippines, 449pp.

Pauly, D. and N. David. (1980). An objective method for determining growth from length-frequency data. *ICLARM Newsletter.* **3**(3): 13-15.

Pauly, D. and N. David. (1981). A BASIC program for the objective extraction of growth parameters from length frequency data. *Meeresforschung/Reports on Marine Research.* **28**: 205-211.

Pauly, D., J. Moreau and F. Gayanilo. (1996b). A new method for comparing the growth performance of fishes, applied to wild and farmed Tilapias. *In* R.S.V. Pullin, J. Lazard, M. Legendre, J.B. Amon Kothias and D. Pauly (Eds.)*, The Third International Symposium on Tilapia in Aquaculture*. Vol. 41. ICLARM Conf. Proc., 575pp.

Pauly, D. and G.R. Morgan. (1987). *Length-based methods in fisheries research.* Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Petersen, C.G.J. (1891). Eine methode zur bestimmung des alters und des wuches der fische. *Mitt. Dtsch. Seefisherei.* II: 226-235.

Petersen, C.G.J. (1892). Fiskenes biologiske forhold i Holbaek Fjord, 1890-1891. *Beret. Danm. Biol. St.* **1**(1): 121-183.

Pitcher, T.J., A.E. Magurran and I. Winfield. (1982). Fish in larger schools find food faster. *Behavioural Ecology and Sociobiology.* **10**: 149-157.

Polovina, J.J. (1986). A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock. *Fish. Bull.* **84**(2): 423-428.

Polovina, J.J. (1987). Assessment and management of deepwater bottom fishes in Hawaii and the Marianas. *In* J.J. Polovina and S. Ralston (Eds.)*, Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview, Boulder, Colorado, p375-404.

Polovina, J.J. and S. Ralston. (1986). An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas. *Fish. Bull,.* **84**: 759-770.

Polunin, N.V.C. and C.M. Roberts. (1993). Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Mar. Ecol. Prog. Ser.* **100**: 167-176.

Pope, J.G. (1972). An investigation of the accuracy of virtual population analysis using cohort analysis. *ICNAF Res. Bull.* **9**: 65-74.

Pope, J.G. (1987). Two methods for simultaneously estimating growth, mortality and cohort size parameters from time series of catch-at-length data from research vessel surveys. *In* D. Pauly and G.R. Morgan (Eds.)*, Length-Based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resource Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Pope, J.A., A.R. Margetts, J.M. Hamley and E.F. Akyuz. (1975). Manual of methods for fish stock assessment. Part III. Selectivity of fishing gear. *FAO Fish. Tech. Pap.* **41** (Rev. 1): 46.

Posada, J.M. and R.S. Appeldorn. (1996). The validity of length-based methods for estimating growth and mortality of groupers, as illustrated by comparative assessment of the Creole fish *Parathias furcifer* (Pisces: Serranidae). *In* F. Arreguin-Sanchez, J.L. Munro, M.C. Balgos and D. Pauly (Eds.)*, Biology, Fisheries and Culture of Tropical Groupers and Snappers*. ICLARM, Manila, Philippines, 447pp.

Press, W.H., S.A. Teukolsky, W.T. Vetterling and B.P. Flannery. (1996). *Numerical recipes in C. The art of scientific computing.* Cambridge University Press, 994pp.

Radtke, R.L. (1987). Age and growth information available from the otoliths of the Hawaiian snapper, *Pristipomoides filamentosus*. *Coral Reefs.* **6**: 19-25.

Radtke, R.L. and D.J. Shafer. (1992). Environmental sensitivity of fish otolith microchemistry. *Aus. J. Mar. Freshwater Res.* **43**: 935-951.

Ralston, S. (1980). An analysis of the Hawaiian offshore handline fishery: a progress report. *In* R. Grigg and R. Pfund (Eds.), Procedural Symposium on the status of resource investigation in the northwest Hawaiian Islands. *UNIHI-SEAGRANT-MR-8004*. p204-215.

Ralston, S. (1981). A study of the Hawaiian deepsea handline fishery with special reference to the population dynamics of opakapaka, *Pristipomoides filamentosus* (Pisces: Lutjanidae). PhD thesis, University of Washington, Seattle, WA, 205pp.

Ralston, S. (1982). Influence of hook size in the Hawaiian deep sea handline fishery. *Can. J. Fish. Aquat. Sci..* **39**(9): 1297-1302.

Ralston, S. (1987). Mortality rates of snappers and groupers. *In* J.J. Polovina and S. Ralston (Eds.)*, Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Boulder and London, p375-404.

Ralston, S. and K.E. Kawamoto. (1985). A preliminary analysis of the 1984 size structure of Hawaii's commercial opakapaka landings, and a consideration of age at entry and yield per recruit. Southwest Fish. Cent., Honolulu Lab., Natl. Mar. Fish. Serv., *NOAA Admin. Rep.*, H-85-1, p1-9.

Ralston, S. and K.E. Kawamoto. (1988). A biological assessment of Hawaiian bottomfish stocks, 1984-1987. Southwest Fish. Cent., Honolulu Lab., Natl. Mar. Fish. Serv., *NOAA Admin. Rep.*, H-88-8.

Ralston, S. and G.T. Miyamoto. (1981). Estimation of the age of a tropical reef fish using the density of daily growth increments. *Proceedings of the Fourth International Coral Reef Symposium, Manila, 1981.* **1**: 83-89.

Ralston, S. and G.T. Miyamoto. (1983). Analyzing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. *Fish. Bull.* **81** (3): 523-535.

Ralston, S. and H.A. Williams. (1988a). Age and growth of *Lutjanus kasmira*, *Lethrinus rubrioperculatus*, *Acanthurus lineatus* and *Clenochaetus striatus* in American Samoa. Administrative Report 11-18, Southwest Fisheries Centre: NMFS (Honolulu Lab), 11pp.

Ralston, S. and H.A. Williams. (1988b). Depth distributions, growth and mortality of deep slope fishes from the Marianas Archipelago. NOAA Technical Memorandum. *NMFS.NOAA-TM-NMFS-SWFC-113*: 47pp.

Ralston, S.R., R.M. Gooding and G.M. Ludwig. (1986). An ecological survey and comparison of bottomfish resource assessments (submersible versus handline fishing) at Johnston Atoll. *Fish. Bull.* **84** (1): 141-155.

Reay, P.J. (1972). The seasonal pattern of otolith growth and its application to back-calculation studies in *Ammodytes tobianus*. *J. Cons. perm. inte. Explor. Mer.* **34**: 485-504.

Reiman, B.E. and D. Myers. (1990). Kokanee population dynamics. Idaho Department of Fish and Game, Federal Aid in Sport Fish Restoration, Project F-73-R-12.

Reznik, D., E. Lindbeck and H. Bryga. (1989). Slower growth results in larger otoliths: An experimental test with guppies (*Poecilia reticulata*). *Can. J. Fish. Aquat. Sci.* **49**: 1801-1815.

Richards, L.J., J.T. Schnute, A.R. Kronlund and R.J. Beamish. (1992). Statistical models for the analysis of ageing error. *Can. J. Fish. Aquat. Sci.* **49**(9): 1801-1815.

Richter, H. and J.G. McDermot. (1990). The staining of fish otoliths for age determination. *J. Fish Biol.* **36**: 773-779.

Ricker, W.E. (1963). Big effects from small causes: two examples from fish population dynamics. *J. Fish. Res. Board Can.* **20**: 257-264.

Ricker, W.E. (1969). Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *J. Fish. Res. Board Can.* **26**: 479-541.

Ricker, W.E. (1975). Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* **199**: 382p

Ricker, W.E. (1992). Back-calculation of fish lengths based on proportionality between scale and length measurements. *Can. J. Fish. Aquat. Sci.* **49**: 1018-1026.

Rocha-Olivares, A. and V.M. Gomez-Munoz. (1993). Validation of otolith age determination of the Pacific red snapper *Lutjanus peru* (Perciformes: Lutjanidae) in La Paz Bay and adjacent waters, B.C.S, Mexico. *Cienc. Mar.* **19**(3): 321-331.

Rochet, M. (1998). Short-term effects of fishing on life history traits of fishes. *ICES J. Mar. Sci.* **55**: 371-391.

Rohlf, F.J. and R.R. Sokal. (1995). *Collection of tables to accompany biometry.* W.H. Freeman and Company, State University of New York, Stony Brook, 199pp.

Rosenberg, A.A. and J.R. Beddington. (1987). Monte-Carlo testing of two methods for estimating growth from length-frequency data with general conditions for their applicability. *In* D. Pauly and G.R. Morgan (Eds.)*, Length-based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Rosenberg, A.A., J.R. Beddington and M. Basson. (1986). The growth and longevity of krill during the first decade of pelagic whaling. *Nature.* **324**: 152-154.

Ross, M.R. and F.P. Almeida. (1986). Density-dependent growth of silver hakes. *Trans. Am. Fish. Soc.* **115**: 548-554.

Ross, M.R. and G.A. Nelson. (1992). Influences of stock abundance and bottom-water temperature on growth dynamics of haddock and yellowtail flounder on Georges Bank. *Trans. Am. Fish. Soc.* **121**(5): 578-587.

Rowling, K.R. and D.D. Reid. (1992). Effect of temporal changes in size composition on estimates of von Bertalanffy growth parameters for gemfish, *Rexea solandri*, Gempylidae. *Aus. J. Mar. Freshwater Res.* **43**: 1229-1239.

Russ, G.R. (1985). Effects of protective management on coral reef fishes in the central Philippines. *Proc. Int. Coral Reef Congr., 5th.* **4**: 219-224.

Russ, G.R. (1991). Coral reef fisheries: effects and yields. *In* P.F. Sale (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, London, 725pp.

Russ, G.R. and A.C. Alcala. (1989). Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar. Ecol. Prog. Ser.* **56**: 13-27.

Russ, G.R. and A.C. Alcala. (1998). Natural fishing experiments in marine reserves 1983-1993: roles of life history and fishing intensity in family responses. *Coral Reefs.* **17**(4): 399-416.

Russ, G.R., D.C. Lou and B.P. Ferreira. (1995). A long term study on population structure of the coral trout *Plectropomus leopardus* on reefs open and closed to fishing in the Central Great Barrier Reef. *CRC Reef Research Centre Technical Report No.3.*, 30pp.

Russ, G.R., D.C. Lou and B. Ferreira. (1996). Temporal tracking of a strong cohort in the population of a coral reef fish, the coral trout *Plectropomus leopardus* (Serranidae, Epinephelinae) in the Central Great Barrier Reef, Australia. *Can. J. Fish. Aquat. Sci..* **53**: 2745-2751.

Sadovy, Y., M. Figuerola and A. Roman. (1992). Age and growth of red hind *Epinephelus guttatus* in Puerto Rico and St Thomas. *Fish. Bull.* **90**(3): 516-528.

Sadovy, Y.J. (1996). Reproduction of reef fishery species. *In* N.V.C. Polunin and C.M. Roberts (Eds.)*, Tropical Reef Fisheries*. Chapman and Hall, London, p15-59.

Sainsbury, K.J. (1980). The effect of individual variability on the von Bertalanffy growth equation. *Can. J. Fish. Res. Aquat. Sci.* **37**: 241-247.

Salojaervi, K. and A. Mutenia. (1994). Effects of fingerling stocking on recruitment in the Lake Inari whitefish (*Coregonus lavaretus*) fishery. *In* I. Cowx (Ed.), *Rehabilitation of Inland Fisheries*. Fishing News Books, Oxford, p302-313.

Salvanes, A.G.V. and B.M. Balino. (1998). Productivity and fitness in a fjord cod population: an ecological and evolutionary approach. *Fish. Res.* **37**(1-3): 143-161.

Samboo, C.R. (1983). Banks fisheries: an appraisal. Proceedings of a seminar on marine fisheries development. University of Mauritius, 18-19 July 1983, 286pp.

Samboo, C.R. (1987). A preliminary review of the artisanal and banks fisheries of Mauritius. AFRC Report, *RD(F)/SU/87/2*.

Samboo, C.R. (1989). A re-appraisal of the banks fishery in Mauritius. *In* Proceedings of the seminar on the management of the banks handline fishery. SWIOP/MAFNR. *FAO/UNDP:RAF/87/008/WP/52/89/E*, 96pp.

Samboo, C.R. and D. Mauree. (1988). Summary of fisheries and resources information for Mauritius. *In* M.J. Sanders, P. Sparre and S.C. Venema (Eds.)*, Proceedings of the workshop on the Assessment of the Fishery Resources in the Southwest Indian Ocean*. p62-79.

Samoilys, M.A. (1988). Abundance and species richness of coral reef fish on the Kenyan coast: the effects of protective management and fishing. *Proc. Int. Coral Reef Symp. 6th.* **2**: 261-266.

Samuel, M. and C.P. Mathews. (1985). Validating the ageing of newaiby, hanoor and hamra in Kuwait. *In* C.P. Mathews (Ed.), *Final Report of The Proceedings of the 1984 Shrimp and Fin Fisheries Management Workshop*. Kuwait Inst. for Scientific Research, Safat, Kuwait, p56-66.

Schaeffer, M.B. (1954). Some aspects of the dynamics of populations important to the management of commercial marine fisheries. *Bull. Inter-Am. Trop. Tuna Comm.* **1**: 27-56.

Schnute, J. and D. Fournier. (1980). A new approach to length-frequency analysis: growth structure. *Can. J. Fish. Aquat. Sci.* **37**: 1337-1351.

Secor, D.H. and J.M. Dean. (1989). Somatic growth effects on the otolith - fish size relationship in young pond-reared Striped Bass, *Morone saxatilis*. *Can. J. Fish. Aquat. Sci.* **46**: 113-121.

Secor, D.H., J.M. Dean and S.E. Campana. (1995). *Recent Developments in Fish Otolith Research.* Belle W. Baruch library in marine science, University of South Carolina Press, Columbia, South Carolina, No.19, 735pp.

Seychelles Fishing Authority. (1990). *Seychelles artisanal catch assessment survey - Notes for* *implementation.* SFA, 39pp.

Seychelles Fishing Authority. (1991). Seychelles artisanal fisheries statistics for 1990. *SFA/R&D/016*, 94pp.

Seychelles Fishing Authority. (1995). 1995 annual report. *SFA/R&D/039*, 63pp.

Seychelles Fishing Authority (1998). Seychelles artisanal fisheries statistics for 1997. *SFA/R&D/045*, 90pp.

Shackell, N.L., W.T. Stobo, K.T. Frank and D. Brickman. (1997). Growth of cod (*Gadus morhua*) estimated from mark-recapture programs on the Scotian Shelf and adjacent areas. *ICES J. Mar. Sci.* **54**: 383-398.

Shepherd, J.G. (1982). A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *J. Con. Int. l'Explor. Mer.* **40**(1): 67-75.

Shepherd, J.G. (1987a). A weakly parametric method for the analysis of length composition data. *In* D. Pauly and G.R. Morgan (Eds.), *Length-Based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Shepherd, J.G. (1987b). Toward a method for short-term forecasting of catch rates based on length compositions. *In* D. Pauly and G.R. Morgan (Eds.), *Length-based methods in fisheries research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Shepherd, J.G., G.R. Morgan, J.A. Gulland and C.P. Mathews. (1987). Methods in analysis and assessment: report of working group 2. *In* D. Pauly and G.R. Morgan (Eds.), *Length-Based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Sirois, P., F. Lecomte and J.D. Dodson. (1998). An otolith-based back-calculation method to account for time-varying growth rate in rainbow smelt (*Osmerus mordax*) larvae. *Can. J. Fish. Aquat. Sci.* **55**(12): 2662-2671.

Smith, S.V. (1978). Coral reef area and the contribution of reefs to processes and resources of the world's oceans. *Nature.* **273**: 225-226.

Smith, A. and J.C. Wakefield. (1994). The hierarchical Bayesian-approach to population pharmokinetic modelling. *International Journal of Bio-Medical Computing.* **36**(1-2): 35-42.

Smith, M.K. (1992). Regional differences in otolith morphology of the deep slope red snapper *Etelis carbunculus. Can. J. Fish. Aquat. Sci..* **49**: 795-804.

Smith, M.K. and E. Kostlan. (1991). Estimates of age and growth of Ehu *Etelis carbunculus* in four regions of the Pacific from density of daily increments in otoliths. *Fish. Bull.* **89**: 461-472.

Sokal, R.R. and F.J. Rohlf. (1995). *Biometry: the principles and practice of statistics in biological research.* W.H. Freeman and Company, New York, 850pp.

Soriano, M., J. Moreau, J.M. Hoenig and D. Pauly. (1990). New functions for the analysis of two-phase growth of juvenile and adult fishes, with application to Nile perch. *ICES C.M. 1990/D:16*, 13pp.

Sparre, P. (1987). A method for the estimation of growth, mortality and gear selection/recruitment parameters from length-frequency samples weighted by catch per unit effort. *In* D. Pauly and G.R. Morgan (Eds.), *Length-Based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Sparre, P. and S.C. Venema. (1998). *Introduction to tropical fish stock assessment. Part 1, Manual.* FAO, Rome, 376pp.

Stearns, S.C. and R.E. Crandall. (1984). Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. *In* G.W. Potts and R.J. Wootton (Eds.), *Fish reproduction: Strategies and Tactics*. Academic Press, London, p13-33.

Susman, E.P., J.R. Murphy, G.O. Zerbe and R.H. Jones. (1998). Using a nonlinear nixed model to evaluate three models of human stature. *Growth development and ageing.* **62**(4): 161-171.

Talbot, F.H. (1960). Notes on the biology of the Lutjanidae (Pisces) of the East African coast, with special reference to *L. bohar* (Forskal). *Ann. S. Afr. Mus.* **45**: 549-573.

Thompson, R. and J.L. Munro. (1974). The biology, ecology and biomonics of the snappers, Lutjanidae. *In* J.L. Munro (Ed.), *Caribbean Coral Reef Fishery Resources*. Vol. 7. International Centre for Living Aquatic Resources Management, Manila, Philippines, p94-109.

Thompson, R. and J.L. Munro. (1983a). The Biology, ecology and bionomics of the hinds and groupers, Serranidae. *In* J.L. Munro (Ed.), *Caribbean Coral Reef Fishery Resources*. Vol. 7. International Centre for Living Aquatic Resources Management, Manila, Philippines, p59-81.

Thompson, R. and J.L. Munro. (1983b). The biology, ecology and bionomics of the snappers, Lutjanidae. *ICLARM Stud. Rev.* **7**: 94-109.

Thompson, W.F. and F.H. Bell. (1934). Biological statistics of the Pacific halibut fishery. 2. Effects of changes in intensity upon total yield and yield per unit of gear. *Rep. Int. Fish. (Pacific Halibut) Comm.* 8, 49pp.

Uchida, R.N. (1986). Berycidae. *In* R.N. Uchida and J.H. Uchiyama (Eds.), *Fishery Atlas of the Northwestern Hawaiian Islands. NOAA Tech. Rep. NMFS* **38**, p78-79.

van der Knapp, M., Z. Waheed, H. Shareef and M. Rasheed. (1991).Reef fish resources survey in the Maldives. *BOBP/WP/64MDV/88/007*, 61pp.

van Leeuwen, P.I. and A.D. Rijnsdorp. (1986). The analysis of the growth of turbot by back-calculation of otoliths. *ICES CM 1986/G:50*, 17p.

Van Oosten, J. (1923). The whitefishes (*Coregonus clupeaformis*). A study of the scales of whitefishes of known ages. *Zoologica.* **2**: 381-412.

Van Oosten, J. (1929). Life history of the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. *Fish. Bull.* **44**: 265-428.

Venema, S.C., J. Christensen and D. Pauly. (1988). Contributions to tropical fisheries biology. Papers prepared by the participants at the FAO/DANIDA follow-up training courses on fish stock assessment in the tropics. Hirtshals, Denmark, 5-30 May 1986 and Manila, Philippines, 12 January-6 February 1987. *FAO Fish Rep.* **289**, FAO, Rome, 519pp.

Vilizzi, L. and K.F. Walker. (1999). Age and growth of the common carp, *Cyprinus carpio*, in the River Murray, Australia: consistency of age interpretation, and growth models. *Env. biol. fish.* **54**: 77-106.

von Bertalanffy, L. (1934). Untersuchugen uber die gesetzlichkeiten des wachstums. 1. Allgemeine grundlagen der theorie. *Roux'Arch. Entwicklungsmech. Org.* **131**: 613-653.

VonRosen, D. (1997). On moments of the inverted Wishart distribution. *Statistics.* **30**(3): 259-278.

Wakefield, J.C., A.F.M. Smith, A. Racinepoon and A.E. Gelfand. (1994). Bayesian-analysis of linear and nonlinear population models by using the Gibbs sampler. *Applied Statistics.* **43**: 201-221.

Walker, S. (1996). An EM Algorithm for nonlinear random effects models. *Biometrics.* **52**: 934-944.

Walters, C.J. and J.R. Post. (1993). Density-dependent growth and competitive asymmetries in size-structured fish populations: A theoretical model and recommendations for field experiments. *Trans. Am. Fish. Soc.* **122**(1): 34-45.

Wang, Y. and N. Ellis. (1998). Effect of individual variability on estimation of population parameters from length-frequency data. *Can. J. Fish. Aquat. Sci.* **55**(11): 2393-2401.

Watson, M., D. Righton, T. Austin and R. Ormond. (1996). The effects of fishing on coral reef fish abundance and diversity. *J. Mar. Biol. Assoc. UK.* **76**(1): 229-233.

Weatherly, A.H. and H.S. Gill. (1987). *The biology of fish growth.* Academic Press, London and New York, 291pp.

Wetherall, J.A., J.J. Polovina and S. Ralston. (1987). Estimating growth and mortality in steady-state fish stocks from length-frequency data. *In* D. Pauly and G.R. Morgan (Eds.), *Length-Based Methods in Fisheries Research*. Vol. 13. International Centre for Living Aquatic Resources Management, Manila, Philippines and Kuwait Institute for Scientific Research, Safat, Kuwait, 468pp.

Williams, D.M., S.J. Newman, M. Cappo and P.J. Doherty. (1995). Recent advances in the ageing of coral reef fishes. *In* P. Dalzell and T.J.H. Adams (Eds.), *South Pacific Commission and Forum Fisheries Agency Workshop on the Management of South Pacific Inshore Fisheries. Manuscript Collection of Country Statements and Background Papers*. Vol. 2. SPC, Noumea, New Caledonia, p667-671.

Williams, H.A. and M.K. Lowe. (1997). Growth rates of four Hawaiian deep slope fishes: a comparison of methods for estimating age and growth from otolith microincrement widths. *Can. J. Fish. Aquat. Sci.* **54**: 126-136.

Williams, T. and B.C. Bedford. (1974). The use of otoliths for age determination. *In* T.B. Bagenal (Ed.), *Ageing of fish*. Unwin, Surrey, p114-123.

Wootton, R.J. (1976). *The biology of sticklebacks.* Academic Press, London, 171pp.

Worthington, D.G., P.J. Doherty and A.J. Fowler. (1995a). Variation in the relationship between otolith weight and age: implications for the estimation of age of two tropical damselfish

(*Pomacentrus moluccensis* and *P. wardi*). *Can. J. Fish. Aquat. Sci.* **52**: 233-242.

Worthington, D.G., A.J. Fowler and P.J. Doherty. (1995b). Determining the most efficient method of age determination for estimating the age structure of a fish population. *Can. J. Fish. Aquat. Sci.* **52**: 2320-2326.

Wright, A., P.J. Dalzell and A.H. Richards. (1986). Some aspects of the biology of the red bass *Lutjanus bohar* (Forskal) from the Tigak Islands, PNG. *J. Fish Biol.* **28**: 533-544.

Yamamoto, S. and N. S. (1996). Growth and development of a bimodal length-frequency distribution during smolting in a wild population of white-spotted char in northern Europe. *J. Fish Biol.* **48**: 68-79.

Yeh, S.Y., C.Y. Chen and H.C. Lui. (1986). Age and growth of *Lutjanus sebae* in the waters off northwestern Australia. *Oceanogr. Taiwan. Sci. Rep.* **16**: 90-102.

Zhao, B.X., J.C. McGovern and P.J. Harris. (1997). Age, growth and temporal change in size at age of the vermillion snapper from the South Atlantic Bight. *Trans. Am. Fish. Soc.* **126, 2**: 181-193.

Zivkov, M.T., T.A. Trichkova and G.N. Raikova-Petrova. (1999). Biological reasons for the unsuitability of growth parameters and indices for comparing fish growth. *Env. biol. fish.* **54**: 67-76.