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Population biology, dynamics and their implications for management of red bass: a large, long-lived reef fish.

Thesis submitted by

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in March 2005

for the degree of Doctor of Philosophy
in Marine Biology
within the School of Marine Biology and Aquaculture
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Abstract

The red bass, *Lutjanus bohar* (Forsskal 1775), is a large tropical reef fish that has a widespread circum-tropical distribution (Allen 1985). Preliminary research (Marriott 2002) done prior to this thesis identified that this species was potentially long-lived and slow-growing. Knowing this, the harvest of *L. bohar* by commercial fisheries is a cause for concern because populations of long-lived, slow growing species are typically more vulnerable to overfishing (e.g. Adams 1980; Musick 1999). This issue was investigated by addressing the following research objectives: (i) to investigate aspects of the population biology of *L. bohar*; (ii) to explore potential impacts of fishing on growth, size, and age structure of an exploited *L. bohar* population; and (iii) to explore the vulnerability of *L. bohar* populations to overfishing using an age-structured model and simulations.

Detailed studies of the population biology of *L. bohar* on the Great Barrier Reef provided support for the accuracy of initial estimates of age, and statistically justified a method of accepting estimates of age from repeated readings of otolith sections. The initial indication of relatively slow growth for this species was supported and the fit of the von Bertalanffy growth function (fork length-at-age) to samples from Lizard Island Region was: $L_t = 649.8\ (1 - \exp\ \{-0.093[t+2.500]\})$, with no detectable difference in growth between sexes. Sexual maturity was found to be reached relatively late in life, compared to other reef fish, with the length at 50% maturity (L_{50}) for females observed at 428.96 mm and the age at 50% maturity (a_{50}) at 9.39 years. The L_{50} and a_{50} for males could not be resolved but were indicated to be at a much smaller size and younger age than those observed for females. Oocyte development was asynchronous and ripe

females were sampled in 8 months of the year, indicating that *L. bohar* spawned multiple times over a protracted period during each year, over a long reproductive life. Estimates of batch fecundity were also relatively high, ranging from 1.02 x 10^3 to 3.13 x 10^6 eggs, and an exponential relationship with fish weight was indicated. All of these characteristics are consistent with a theoretical *K*-selected life history strategy, and one which is typically vulnerable to overfishing.

Comparisons of size and age structures sampled from regions of different historical fishing pressure in the Seychelles, where *L. bohar* is a major component of the fishery, indicated a top-down size-selective fishing impact in the historically harvested region. Interestingly, a larger length-at-age for older age groups was also observed for this region, which was atypical of a fishing impact. Predictions made using an age-structured stock assessment model and data of its historical harvest indicated that these differences in growth were not likely due to historical differences in fishing but to other region-specific factors. The age-structured modelling also facilitated the exploration of the fished population's vulnerability to overfishing and identified the potential importance of an inferred reduced availability to harvest of older age groups to its persistence, at least in the short term.

Results from this thesis have important implications for fisheries management. My results are applicable to managing the harvest of *L. bohar* in the Seychelles and the by-catch of *L. bohar* on the Great Barrier Reef where it has recently become a "no take" species. Issues identified for *L. bohar* could also be transferred to the harvest of other exploited species with similar life history characteristics, such as the red emperor (*Lutjanus sebae*) and mangrove jack (*L. argentimaculatus*), which are targeted by commercial and recreational line fishers on the Great Barrier Reef. This thesis also builds on developing theory concerning the impacts of fishing on species with different life history characteristics because *L. bohar* is an exploited species that is at one end of a theoretical continuum of life history strategies.

Acknowledgements.

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STATEMENT ON SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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Chapter 1: General Introduction.

1.1. The issue.

Fishing is one of the major factors that impacts on fish populations world-wide, frequently leading to localised depletion and stock collapse (e.g., Peruvian anchovy, *Engraulis ringens* (Glantz 1979; Pauly and Tsukayama 1987; Laws 1997); Atlantic herring, *Clupea harengus* (Saetersdal 1980; Saville and Bailey 1980); Atlantic cod, *Gadus morhua* (Hutchings and Myers 1994); orange roughy, *Hoplostethus atlanticus* (Clark and Tracey 1994; Kloser et al. 1996)). Fisheries biology is a doctrine which is traditionally considered to involve the description of individual fisheries in terms of the nature and dynamics of exploited fish stocks (Cushing 1968). This information is required for use in stock assessments to develop appropriate management strategies, usually on the basis of forecasts of the stock's relative resilience to, and predicted yield from, a range of possible harvest scenarios (Hilborn and Walters 1992).

Long-lived, slow-growing species generally are considered to be less likely to produce sustainable harvest yields than shorter-lived species (Adams 1980; Kirwood et al. 1993) and are most likely to be heavily impacted by fishing (e.g., Parent and Schriml 1995; Jennings et al. 1998; Musick 1999). The elevated risk of longer-lived, slower-growing species being "overfished" is an important global issue because such overfishing not only affects the yields and incomes of fishers, but can also have serious consequences for marine and aquatic ecosystems (e.g., Jennings and Lock 1996; Jennings and Kaiser 1998; Bellwood et al. 2004). The overall aim of this thesis was to explore developing theory linking the biology of an exploited fish population to its intrinsic vulnerability to being overfished. This was done by investigating the population biology, dynamics, and likely impacts of fishing on populations of a tropical reef fish suspected to be relatively long-lived and slow-growing.

1.2. Fish biology, population dynamics, and life history theory.

The need to quantify biological parameters for stock assessment has contributed greatly towards our current understanding of the biology of many exploited species (Cushing 1968). Growth, mortality, and stock size typically are the main determinants of a fishery's yield, whilst other aspects such as the timing of spawning and recruitment can be important in considering management measures (King 1995). Further, an understanding of changes in the size and other properties of an exploited population over time and in response to perturbations (i.e., population dynamics) are often implicitly assumed to enable better management of its harvest (Haddon 2001). A number of authors (e.g., Hoenig 1983; Roff 1984; Stearns and Koela 1986; Cury and Pauly 2000) have used results from such studies, often involving some form of "comparative approach" (Stearns 1992), to improve our general understanding of fish biology.

The observation of different biological characteristics in different fish species has been explained frequently by referring to terrestrial-based theories on inter-specific competition and ecological succession postulated by MacArthur and Wilson (1967). These authors observed that different species dominated at different stages of an ecological succession and categorised two major types: short-lived, fast-growing "*r*-selected" species; and long-lived, slow-growing "*K*-selected" species. It was later noted by Pianka (1970) that these concepts of *r*- and *K*-selection could be applied to the more general description of evolved biological strategies because a number of other biological and ecological attributes were observed to be correlated with each postulated response to natural selection. Pianka (1970) also postulated that there was more likely to be a “continuum” of evolved biological strategies in nature, ranging from strongly *r*-selected species to strongly *K*-selected species. Some attributes of marine species, however, such as broadcast spawning and a dispersive larval phase complicate induction from a theory that was originally developed for terrestrial organisms (King 1995).

More recently, many authors have referred to theory based on postulated intrinsic trade-offs between evolved life history traits (Stearns 1989; 1992) when attempting to explain observed aspects of biology. A number of principal life history traits are postulated to be key aspects of a species’ evolved life history strategy, including: size at birth; age at maturity; size at maturity; the number, size and sex ratio of offspring; age and size-specific reproductive investments; age and size-specific mortality schedules; and growth (Stearns 1992). This body of theory is referred to as “Life History Theory”. The quantification of a number of principal life history traits for a species can be used to build up a picture of the species’ life history strategy and thus can also be useful for independent tests of theory (Caley 1998).

Large, long-lived species generally have life history characteristics of slow growth (Pianka 1970), delayed maturity (Roff 1981), and a low average rate of natural mortality (Hoenig 1983). A delayed maturity is a life history strategy theoretically evolved to increase initial reproductive output, to reduce instantaneous juvenile mortality rates through improved quality of offspring or of parental care, and to increase later fecundity through longer growth (Stearns 1992). The trade-off of this strategy is that juveniles are exposed to mortality for a longer period before they reach maturity, which can reduce their chances of reproducing (Bell 1980). Increased fluctuation in the mortality of immature offspring has been postulated to select for reproduction over several years ("iteroparity"; Murphy 1968), and thus a longer reproductive life. Further, reproduction over many years of life has been postulated as a life history strategy evolved to decrease the mean and / or variance of highly unpredictable juvenile mortality ("bet hedging"; Stearns 1976; 1992). This body of widely accepted theory provides a context that can be useful for predicting fishing impacts because it provides insight into likely biological processes that can be assumed when information on an exploited species' population dynamics is limited.

1.3. The impacts of fishing.

Most fisheries selectively remove larger, older fish from populations (Russ 1991; Jennings and Lock 1996). In addition, the increase in mortality of all age groups results in a progressive reduction in the relative abundance of older individuals. A common direct and indirect impact of fishing is therefore a reduction in the number of older, larger fish in an exploited population (Cushing 1968). Over time, this can result in a reduction of the average size and age of fish within exploited populations (e.g., Ricker 1981; Beacham 1983).

Reductions in population size and density can also indirectly affect the phenotypic and / or genotypic expression of traits within a fished population. Changes in phenotype, known as "plasticity" (Bradshaw 1965), or genotype as a result of longer-term artificial selection on population traits (e.g., Law and Grey 1989; Sutherland 1990; Law 1991; Smith 1999; Conover and Munch 2002) can occur as a result of fishing. Detecting the effects of fishing on populations can be difficult, however, because it is possible for plastic changes in phenotype to mask underlying genetic changes in the population (Policansky 1993).

There are two conflicting theories about the likely impact of fishing on growth rates. It has been postulated by some authors (e.g., Eschenroder 1977; Gulland 1983; Pilling 1999) that a reduction in population density by fishing could result in a greater amount of resources available for growth per capita, allowing increased average growth as a phenotypically plastic response. This is possible because growth in size is one of the most plastic of the life history traits of fish (Weatherly and Gill 1987), but it is also debatable whether resources for growth would be limiting in such dynamic and “open” systems as the marine environment (Caley et al. 1996). Alternatively, fishing has been postulated to select for a reduced size-at-age within exploited populations because fishing typically removes the largest fish, and, thus, the fastest growers (e.g., Law 1991; Kirkpatrick 1993; Conover and Munch 2002). It is intuitive, then, that the impact of fishing on growth will depend intrinsically on how plastic or heritable growth is in the fished population.

Fishing also has been observed to impact on reproductive attributes of exploited populations. A decreased age-at-maturity could result from a reduced population density and concomitant plastic growth response or from fishing mortality selecting for a reduced size- and age-at-maturity (Trippel 1995). This is important because it has been demonstrated for some species that smaller, younger individuals are not capable of spawning as many gametes and are likely to produce less viable offspring than larger individuals (e.g., Mann and Mills 1979; Chambers and Leggett 1996; Kjesbu et al.

1996; Trippel et al. 1997; Marteinsdottir and Steinarsson 1998; Heyer et al. 2001; Palumbi 2004). The removal of larger spawners could also affect the average duration of spawning if larger individuals spawn for a longer period, reducing the probability that larval emergence will match peak abundances of zooplankton (Hutchings and Myers 1993).

The biological characteristics of an exploited population appear to be related to the magnitude of observed fishing impact (Rochet et al. 2000). For example, Musick (1999) showed that species with a relatively slow growth rate (i.e., a von Bertalanffy growth curvature parameter, *K*, of less than 0.1) were most severely impacted by fishing. Slow-growing species tend to mature later in life and thus have slower rates of population turnover (Krebs 1994) and are considered to be less able to sustain high rates of fishing mortality. Delayed maturity also results in a longer period where immature fish are potentially available to be harvested, which can decrease the probability of immature fish surviving to a reproductive age (Crouse 1999). Thus, populations of longer-lived, slower-growing, later-maturing, more "*K*-selected" species are intrinsically more vulnerable to overfishing.

There are several well known cases where long-lived species have been overfished, almost to the point of stock collapse. For instance, populations of orange roughy, which is suspected of living to over 100 years old (Smith et al. 1995), have suffered marked declines as a result of fishing on the Challenger Plateau fishery in New Zealand (Clark and Tracy 1994) and Australia (Kloser et al. 1996). Another example is the white sturgeon (*Acipenser transmontanus*), which has also been estimated to live to over 100 years old (Rein and Beamesderfer 1994) and has suffered an 88% decline in abundances through harvest throughout most of its range (Cech 1992). The red snapper, *Lutjanus campechanus*, (a congeneric of the focal species of this thesis) has been estimated to be relatively long-lived (up to 52.6 years; Wilson and Nieland 2001) and a recent assessment of an exploited stock in the U.S. Gulf of Mexico has suggested likely overfishing (Ehrardt and Legault 1996; Scott-Denton and Nance 1996). Comparative studies by Jennings et al. (1998; 1999) have also shown that populations of large, slower-growing, later-maturing species are those most heavily impacted by fishing.

It should also be noted, however, that there are several well documented cases of overfishing of shorter-lived stocks, such as the collapses of the Californian sardine and Peruvian anchovy fisheries (Hilborn and Walters 1992). Thus, the extent to which fish populations are affected by perturbations such as fishing can be attributed to many factors other than life history traits. For instance, the connectedness of species interactions and the type and magnitude of perturbation have been suggested by Pimm (1984) as important. Also, criteria including: rarity, range of distribution and endemism, and specialised habitat requirements, have been used by Musick et al. (2000) to define risk of extinction from overfishing.

The above points highlight the need for studies that quantify changes and / or differences in population parameters among areas exposed to different levels of fishing pressure (e.g., Jennings et al. 1995, 1998; Russ and Alcala 1998) or for experimental manipulations of fishing effort (e.g., Mapstone et al. 2004). Studies that have done this have reported greater declines in abundance and biomass for larger tropical reef fish than for smaller species in more heavily fished areas (Ault et al. 1998; Russ and Alcala 1998; Jennings et al. 1999).

1.4. The Study Species.

The subject species of this thesis is the red bass or twin-spot snapper, *Lutjanus bohar* (Forsskal 1775). *L. bohar* is a large reef fish that has a widespread tropical distribution (Allen 1985; Fig. 1.1.). It also has a notorious reputation for causing ciguatera fish poisoning throughout much of its distribution (Lewis 2001a) and its harvest varies accordingly. In the Seychelles, however, ciguatera poisonings are rare (Wheeler 1953) and *L. bohar* is one of the main harvest species (Government of Seychelles 2000; Table 1.1). Using a spatial comparative approach, Jennings et al. (1995; 1999) noted that in regions where it was fished, *L. bohar* exhibited a much lower population biomass than in areas where it was protected from fishing, possibly indicating a high susceptibility to fishing impacts.

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Figure 1.1. Global distribution of *Lutjanus bohar*. Distribution as indicated in Allen (1985). Approximate locations of the two geographic areas considered in this thesis (Seychelles, Great Barrier Reef) are also indicated (inset rectangles).

The population biology of *L. bohar* has been investigated previously by several authors (Wheeler 1953; Talbot 1960; Loubens 1980; Wright et al. 1986) but the studies have produced different descriptions of age and growth (Wright et. al. 1986). Only one study

(Loubens 1980) estimated fish age from transverse sections of otoliths, which is widely regarded as the most accurate method for ageing tropical and temperate fish (Secor et al. 1995), and from a relatively small sample size (n = 14) produced a maximum age of 38 years. Preliminary research done prior to this thesis also used otolith sections to estimate age for *L. bohar* and recorded a maximum age of 54 years (Marriott 2002). The above results suggest that populations of *L. bohar* might be vulnerable to fishing impacts because it appears to be an exceptionally long-lived and *K*-selected tropical species.

Table 1.1. Catch Statistics for the Seychelles Artisanal Line Fishery in 2000. Rankings are for annual landed catch from Whaler vessels (the predominant mode of fishing), recorded for individual species in tonnes. Source: Government of Seychelles (2000).

Rank	Species	Total Catch (tonnes)
1	*Carangoides fulvoguttatus*	679.7
2	*Carangoides gymnostherus*	659.4
3	*Aprion viriscens*	462.9
4	*Sphryaena jello*	171.8
5	*Lutjanus bohar*	127.5

1.5. Thesis Objectives.

The aim of this thesis was to explore developing theory linking the biology of an exploited fish population to its intrinsic vulnerability of being overfished. *L. bohar* was selected as the focal species for this study because it was suspected to be exceptionally long-lived and thus potentially "*K*-selected" and vulnerable to overfishing. Postulated correlates of *K*-selection (Pianka 1970) and trade-offs among life history traits (Stearns 1992) were also likely to be obvious and detectable if present.

The thesis addresses 4 primary objectives:

1. To thoroughly describe the population biology of *L. bohar*, including: validating the accuracy and precision of age estimation methods (Chapter 3); quantifying spatial variation in growth; testing for spatial, temporal and depth stratification in sampled size and age frequency distributions (Chapters 4 and 5); and describing aspects of reproductive biology (Chapter 6) for populations on the Great Barrier Reef (GBR), off north-eastern Australia;
2. To compare basic demographic characteristics of *L. bohar* populations between two geographically separated areas, the GBR and the Seychelles Republic off Africa (Chapter 5);
3. To explore potential impacts of fishing on growth, size and age structure of an exploited *L. bohar* population in the Seychelles Republic (Chapter 5).
4. To predict the relative vulnerability of an exploited *L. bohar* population to overfishing using an age structured stock assessment model and simulations (Chapter 7).

1.6. Rationale.

Aspects of population biology were explored in detail for GBR populations (Objective 1) to verify initial findings and inferences about *L. bohar* populations on the GBR (Marriott 2002). *L. bohar* was not a targeted species of commercial or recreational fisheries on the GBR because of a perceived risk of ciguatera poisoning. Therefore, sampling was extended to Seychelles' populations of *L. bohar* to address Objective 3 because *L. bohar* was not known to cause ciguatera in this geographic area and was a significant component of the artisanal fishery catch (Table 1.1). Objective 3 was addressed by comparing parameters and frequency distributions of samples from study regions of contrasting historical fishing pressure in the Seychelles. Objective 2 was a necessary corollary of this increase in geographic scope to verify the degree to which *L. bohar* showed similar life history characteristics in the two areas.

The Seychelles Fishing Authority was also able to provide historical catch and effort data, which provided scope for addressing Objective 4. A standard age-structured stock assessment model (Deriso et al. 1985) was used, which incorporated biological and fishery data collected from the exploited region to predict relative depletion. This model was also used to determine if parameter estimates from different areas had an influence on model predictions, and thus the potential significance of regional variation in growth on results for fisheries management. The model was then used to run simulations of the potential effectiveness of a minimum size limit management strategy and forecasted recovery of the population if harvest was stopped. This was done to obtain an indication of relative vulnerability of the exploited *L. bohar* population to overfishing by comparing outputs from different hypothetical harvest scenarios.

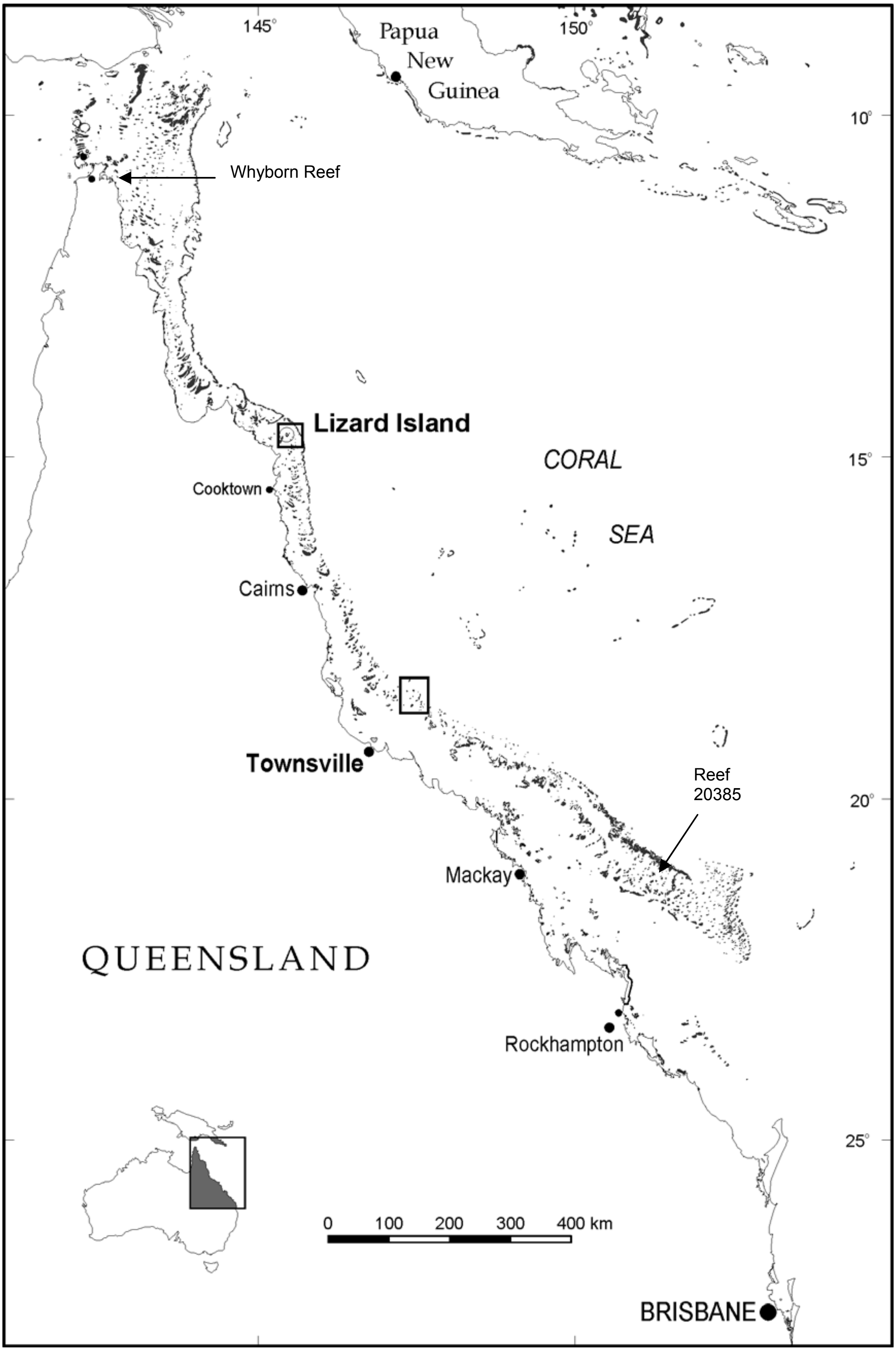
Chapter 2: General sampling methods.

2.1. Study Sites.

This thesis reports on the biology of *L. bohar* in two Geographic Areas (hereafter “areas”): the Great Barrier Reef in the Pacific Ocean, on the north east coast of Australia; and the oceanic banks of the Seychelles Republic in the Indian Ocean, off the east coast of Africa (Fig. 1.1).

2.1.1. Great Barrier Reef.

The Great Barrier Reef (GBR) is the largest chain of coral reefs in the world, consisting of nearly 3,000 emergent reefs (Maniwavie et al. 2002) and extending over 14 degrees of latitude from $9^{o}30'$S to $24^{o}30'$S (Lewis 2001b) along the east coast of Queensland (Fig. 2.1). Most of the GBR lies within both a Marine Park (339,750km^2) and World Heritage Area and is subject to multiple uses by international tourists and a coastal population that has a relatively low population density (Maniwavie et al. 2002). Although *L. bohar* has been recognized historically as a high risk species for causing ciguatera poisoning in Australia, it was commonly eaten by fishers and involved in few cases locally (Gillespie et al. 1986).



<u>Figure 2.1.</u> <u>The Great Barrier Reef</u>. Also shown are the two study regions: Lizard Island and Townsville (inset rectangles). Samples from the CRFFF collected between Whyborn Reef and Reef 20385

The Coral Reef Fin Fish Fishery (CRFFF) of the GBR has commercial, recreational, and charter fishing sectors and has seen marked changes recently, particularly as a result of the increasing sale of live reef fish to international markets (Mapstone et al. 2001). Annual catch (and effort) in the fishery has increased since 1996 from 3,061t of coral reef fish to 4,400t in 2001 (Queensland Fisheries Service 2002), in part because of higher prices offered by the live reef fish export market. As a result, a revised management plan for the CRFFF was implemented in 2004, which involves the regulation of annual catch by Individual Transferable Quotas. Commensurate with these regulations was the listing of *L. bohar* as a “no take” species, partly because of its perceived ciguatera risk. Catch statistics for *L. bohar* were not available from the GBR because it was generally not kept and, when it was, catches were reported only in the multi-species aggregate category of “mixed reef fish” (Mapstone et al. 1996). Anecdotal evidence, however, indicates that *L. bohar* has been only lightly harvested on the GBR.

2.1.2. Seychelles.

The Exclusive Economic Zone of the Seychelles Republic (Fig. 2.2) covers an area of 1,374,000 km^2 (Jennings et al. 2000) and is comprised of 115 islands (Blindloss et al. 2001). Coral reefs are located on several “shallow banks” that rise from a deeper (~200 m), extensive limestone shelf called the Mascarene Plateau which extends from 4^{o}S to 21^{o}S (Mees 1996). The shallow banks of interest in this study are the Mahe Plateau (41,338km^2) and the Amirantes Plateau (3,999km^2; Mees 1996).

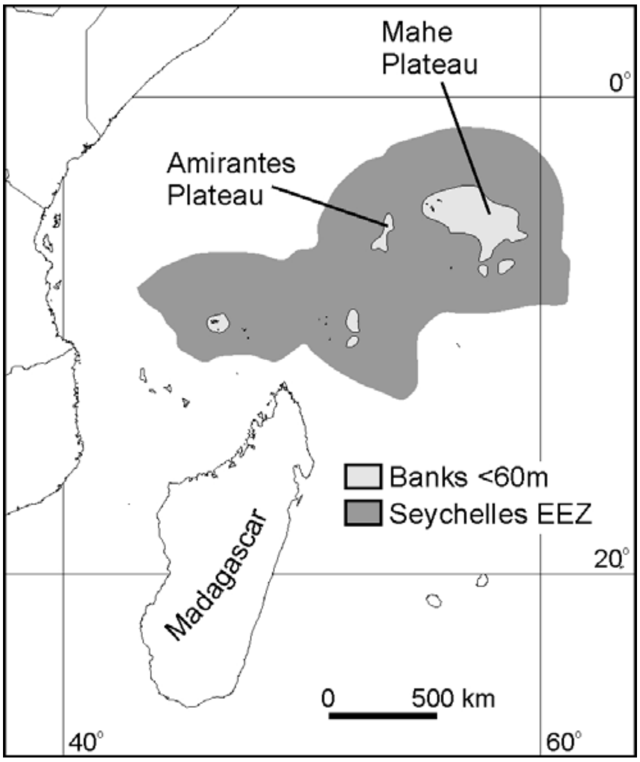


Figure 2.2. The Seychelles Exclusive Economic Zone (EEZ). Also shown are the two study regions: Amirantes Plateau and Mahe Plateau.

Fishing is the most significant exploitative activity in the Seychelles and, along with tourism, is the most financially important industry (Jennings and Marshall 1995). Historically, the fishing of demersal reef fish was confined to coastal areas of the central populated islands on the Mahe Plateau (Payet 1996), while only recently have more distant areas such as the Amirantes Plateau begun to be exploited (Jennings et al. 2000). This shift in fishing distribution was largely attributed to changes in the type of fishing vessel used, with most of the larger, more commercially important reef fish (including *L. bohar*; see Table 1.1) now caught by fishers operating from larger (~15 m in average length) Whalers and Schooners (2,875t and 192t in 2000, respectively: Government of Seychelles 2000). These vessels are better designed for longer fishing trips and are classified—for the purpose of catch assessment surveys by the Seychelles Fishing Authority (SFA)—as vessels with inboard engines. Whalers are ‘undecked’ or ‘partially-decked’ boats and Schooners are fully decked boats (Payet 1996).

2.2. General sampling methods.

Biological samples of *L. bohar* were gathered from four sources:

1) CRC Reef “Effects of Line Fishing” (ELF) Experiment catch surveys (GBR);
2) Catch samples from the CRFFF (GBR);
3) Catch samples from the Seychelles;
4) Spear-fishing (both areas).

2.2.1. CRC Reef ELF Experiment catch surveys.

Biological samples and associated field data from the GBR were collected from the CRC Reef ELF Experiment research surveys from 1995 to 2003. Sampling on ELF surveys involved a line fishing method that was standardised, uniformly distributed, and stratified by depth on six experimental reefs within four spatially separated clusters of reefs on the GBR (Mapstone et al. 2004; Fig. 2.3). The principal aim of the ELF Experiment, in conjunction with Management Strategy Evaluations, was to evaluate the resilience of harvested populations to fishing and evaluate the effectiveness of different spatial exclusion and effort control management strategies (Mapstone et al. 2004). The ELF Experiment involved temporal manipulations of pulsed fishing pressure, closure to fishing on individual coral reefs and monitoring effects on resident fish populations.

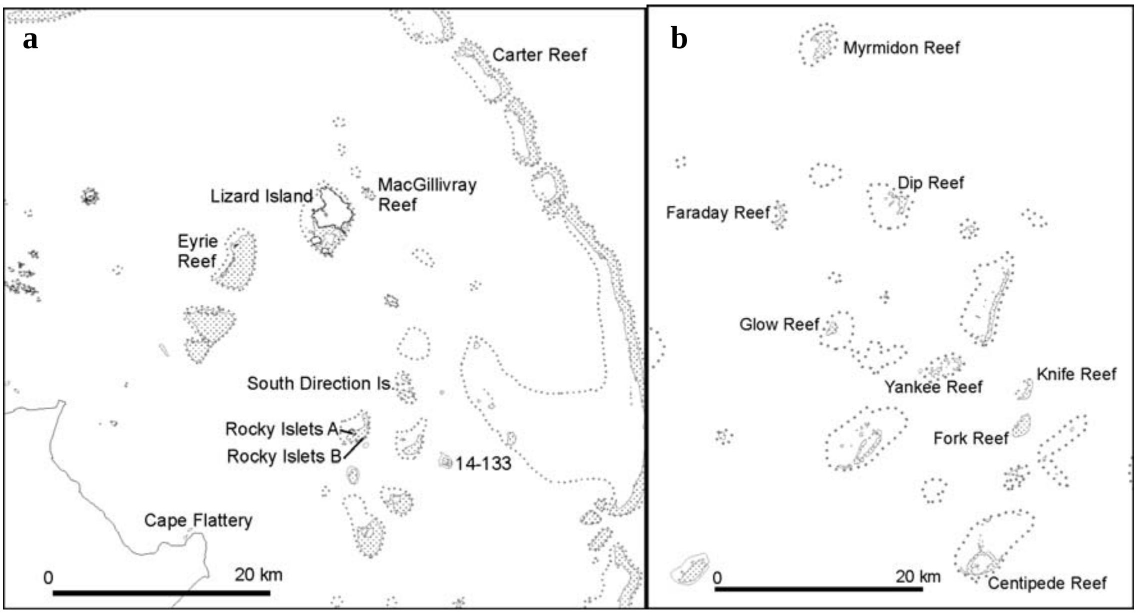


Figure 2.3. Reefs sampled in GBR regions. (a) Lizard Island Region; (b) Townsville Region. Refer to Fig. 2.1. for the location of these regions on the GBR.

The experimental design was replicated spatially for four clusters of reefs along the length of the GBR (Mapstone et al. 2004). Within each cluster there were three groups of treatment reefs and two replicate reefs per treatment (see Table 2.1 for sampling design). Prior to the ELF Experiment, the fishing of "Green Closed" (GC) and "Green Fished" (GF) reefs was prohibited and the fishing of "Blue Fished" (BF) reefs was permitted within the Marine Park. The timing of manipulated pulses of fishing effort differed among replicates of GF and BF reefs within clusters, and occurred for one year periods in 1997 and 1999 for all clusters. Fishing remained prohibited on GC reefs throughout the ELF Experiment. Fishing was prohibited on all treatment reefs from 2000 to 2003 and BF reefs were re-opened to fishing in 2003 or are due to be re-opened in 2005, depending on the timing of fishing manipulations for the experiment and subsequent spatial management strategies implemented for the Marine Park.

The Lizard Island and Townsville reef clusters (Fig. 2.3) were chosen to be the two GBR Study Regions (hereafter “regions”) for this thesis because the majority of *L. bohar* caught during catch surveys (98.9% for 1995 to 2001; n = 1,187) were sampled from them. Sampling was conducted each year from October to December (Austral spring; see Table 2.2 for sample sizes collected per year and region). Fish whole weights (g; 1999 to 2001) and fork lengths (mm; all years) were recorded and sagittal otoliths and gonads dissected from fish then stored in paper envelopes and vials of 10% phosphate buffered formaldehyde (UN 2209), respectively.

Otoliths were dissected from all *L. bohar* sampled from 1995 to 2003, with gonads collected only from those samples from 1999 to 2002. Otoliths (all years) and gonads (1999 onwards) were also collected on ELF pre- and post-manipulation catch surveys conducted in May 1997 (n = 41), August 1997 (n = 16), April 1998 (n = 33), February 1999 (n = 44), May 1999 (n = 35), August 1999 (n = 31) and March 2000 (n = 58). Some of these samples were used to supplement data from other sources (Section 2.2.2) to investigate seasonal trends in reproductive development and opaque increment deposition in otoliths.

Table 2.1. Sampling design for ELF Experiment: Lizard Island and Townsville regions. Adapted from Mapstone et al. (2004), showing reefs and regions relevant to this thesis only (i.e. Lizard Island and Townsville regions). Treatments comprised application of two processes, zoning and fishing, in different combinations in different years. Latitude and Longitude (Lat., Long.) at the centre of each cluster or reefs and the year in which they were fished intensively (if at all) are given.

Region / Lat., Long.	Treatment	Reef	Fished
Lizard Island	Green Closed (GC)	MacGillivray Reef	Not
		South Direction Island	Not
14°50’S, 145°30’E	Green Fished (GF)	Rocky Islets A	1997
		Eyrie Reef	1999
	Blue Fished (BF)	Rocky Islets B	1997
		14-133	1999
Townsville	Green Closed (GC)	Dip Reef	Not
		Glow Reef	Not
18°30’S, 147°30’E	Green Fished (GF)	Yankee Reef	1997
		Faraday Reef	1999
	Blue Fished (BF)	Knife Reef	1997
		Fork Reef	1999

Table 2.2. Samples collected in Austral spring (September to December) from all regions in each year. Lizard Island region samples include samples from ELF Experiment catch surveys (all treatments), speared samples from Lizard Island Region (2002; see Section 2.2.3.), and deep-water sampling (2003; see Section 2.2.2.). Townsville Region samples include samples from ELF Experiment catch surveys (all treatments) and those collected from a national spear-fishing competition held on Centipede reef (2001; see text). Other samples (n = 116) gathered from commercial line fishers on the GBR (i.e., the CRFFF; non-region specific) in spring (2001 to 2003) are not shown.

	GBR		Seychelles	
Year	Lizard	Townsville	Mahe Plateau	Amirantes
1995	53	97	-	-
1996	17	56	-	-
1997	54	32	-	-
1998	35	37	-	-
1999	45	52	-	-
2000	40	45	65	116
2001	78	62	-	-
2002	69	40	77	-
2003	88	-	-	-
Total	479	421	142	116

2.2.2. Catch samples from the CRFFF.

Monthly samples of gonads and otoliths were dissected from *L. bohar* caught by commercial fishers of the CRFFF for the purpose of investigating seasonal trends of reproduction and opaque increment deposition in otoliths. Where possible, measures of fork length (FL; mm) and whole weight (g) were recorded. Small numbers of *L. bohar* (n $\leq$ 10) were retained by three fishers on a monthly basis over a large fishing range on the GBR from Whyborn Reef (10°49'S, 142°46'E; Fig. 2.1) to Reef 20385 (20°57'S, 151°19'E; Fig. 2.1); from July 2001 to June 2002 (n = 279). An additional sample of *L. bohar* otoliths and gonads (n = 12) was also collected from the catch of the Australian Underwater Federation (AUF) National Spear-fishing Titles held on 28th November 2001 at Centipede Reef (Fig. 2.3b). Samples were gathered from this competition because large individuals of each species (including *L. bohar*) were targeted by spear-fishers, and larger *L. bohar* were less frequently sampled on the ELF Experiment catch surveys (see Chapters 4, 5).

A number of larger *L. bohar* caught by a deep-water line fisher were sampled from April to August 2003 (n = 23) to supplement monthly samples of otoliths and gonads. Otoliths were also dissected from all *L. bohar* caught on a fishing trip by this fisher in September 2003 (n = 34). Gonads were dissected from a sub-sample (n = 10) of this catch. Fishing took place 50 to 80 km south-south east of Lizard Island, in depths of 30 to 50 m.

2.2.3. Catch samples from the Seychelles.

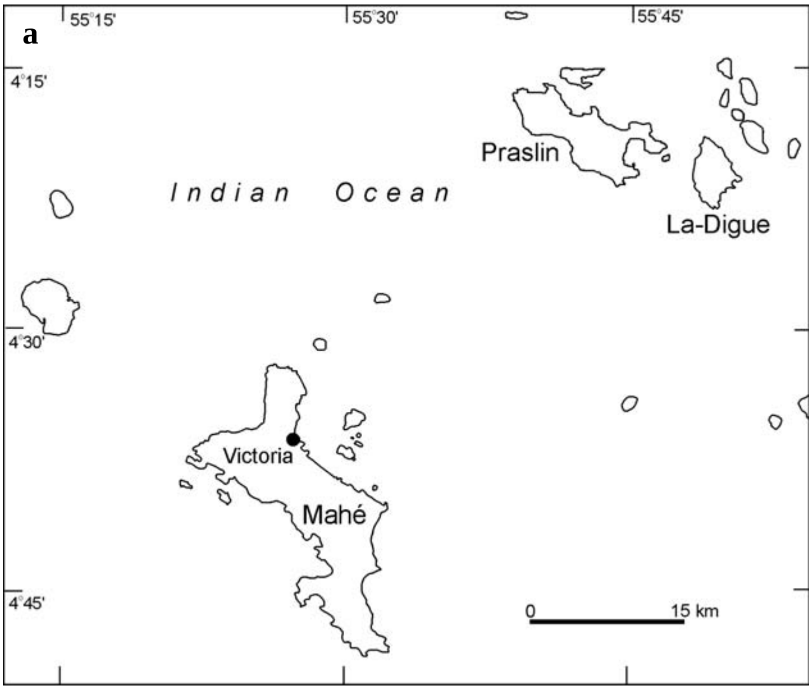
The majority of *L. bohar* from the Seychelles were sampled by the SFA. *L. bohar* otoliths and biological data were initially sub-sampled from the catch of artisanal fishers operating on the Mahe Plateau in September and October 2000 (Table 2.2). *L. bohar* were also randomly sampled, regardless of size, from artisanal fishery landings from the Mahe Plateau from February to April 2002 by the SFA for a representation of catch-at-age structure (n = 48). No more than 30 fish were sampled from each vessel per trip to distribute sampling effort across the catch of vessels from different areas and depths. Whole otoliths and field data (capture location, depth, fish length, fish weight) were sent from the Seychelles by the SFA to JCU for processing and age estimation (see Chapter 3).

These samples were supplemented with an additional sample (n = 77) of otoliths and biological data that were collected from the catch of fishers on the Mahe Plateau during a field trip to the Seychelles in November 2002. Otoliths were dissected and fish measurements recorded from the central markets in Victoria, where the majority of the catch landed at Mahe Island by the artisanal fishery was sold. Samples and data were also gathered from offloaded catch at "Oceania" cold stores at the primary landing site in Victoria (Fig. 2.4a). Measures of fork length (mm) and whole weight (g) were recorded.

L. bohar otoliths and biological data from the Amirantes Plateau were collected on catch surveys done by the SFA in September and November 2000 (n = 116). *L. bohar* were sampled by line fishing using bonito baits on size 13/0 and 14/0 tuna circle hooks. Catch samples were collected from five sites across the Amirantes Plateau: Remire (n = 39); Boudeuse (n = 33); D'Arros (n = 27); African Banks (n = 8); and Poivre (n = 8) (Fig. 2.4b).

2.2.4. Supplementary spear-fishing.

Since the hook size of the line fishing sampling method selectively excluded the smallest, youngest *L. bohar* from samples, small (juvenile) *L. bohar* were collected by spear-fishing from the Lizard Island region in October 2002 (n = 30) and the Amirantes Plateau in November 2000 (n = 3). *L. bohar* less than 300 mm fork length were targeted because this size approximated the size at full recruitment to the line fishing gear used on ELF Experiment catch surveys.



b

Figure 2.4. Sampling locations in the Seychelles. (a) Central granitic islands of the Mahe Plateau; most samples from the Mahe Plateau were gathered from the primary landing site and central markets at Victoria. (b) Amirantes Plateau. Refer to Fig. 2.2. for the location of these regions in the Seychelles EEZ. Fig. 2.4b from Tarbit (1980).

Chapter 3: Criteria for age estimation.

3.1. Introduction.

Estimating age from counts of growth increments on hard body parts of fish is subjective (Brothers 1987; Campana 2001) and can result in errors that influence our estimation of biological parameters (Barlow 1984) and age-based stock assessments (Powers 1983; Lai and Gunderson 1987; Eklund et al. 2000). The development of procedures to ensure the accuracy (reviewed in Campana 2001; Panfili et al. 2002) and precision (Beamish and Fournier 1981; Kimura and Lyons 1991; Campana et al. 1995; Hoenig et al. 1995; Morison et al. 1998) of fish aging, therefore, is vital to fisheries research and management and has received much attention over the last two decades.

Once a method has been validated (Beamish and McFarlane 1983) or quantified as a sufficiently accurate chronological measure (Francis et al. 1992), repeat age estimation is often done to ensure the method is applied consistently to produce reliable results. In high volume "production aging", an independent replicate subset of age estimates is often used to assess precision and detect if there were systematic differences (bias) in estimates between readings (Kimura and Lyons 1991; Morison et al. 1998). An alternative approach is to make independent repeat readings of all specimens and accept age estimates only when successive readings have been judged to reach a specified level of agreement. The criterion used for acceptance is largely arbitrary and varies among studies, but is commonly used. For example, Hesp et al. (2002) and Peres and Haimovici (2004) required repeat counts of annuli in otoliths to differ by no more than 2 and 0 annuli, respectively for a final age to be accepted. Crabtree et al. (1995) required repeat counts to differ by no more than 10% for acceptance. Usually, specimens are excluded from subsequent analyses (discarded) if ‘acceptable’ agreement between successive readings is not achieved, thereby losing potentially valuable data.

Although otoliths have been reported to be accurately readable chronometers for most temperate and tropical reef fish species so far examined (Secor et al. 1995; Choat and Robertson 2002), there exist particular difficulties in estimating age from the otoliths of long-lived fish (Beamish and Chilton 1982; Francis et al. 1992; Stevenson and Secor 1999; Andrews et al. 2001). For example, Hesp et al. (2002) reported that fewer older age estimates were accepted than younger age estimates while Rein and Beamesderfer (1994) observed larger discrepancies among repeated readings of older otoliths. Other studies (Lai and Gunderson 1987; Eklund et al. 2000) have observed that the variance of estimated ages increases with putative fish age.

Increasing discrepancies with age makes the choice of acceptance criterion for age estimates particularly important. For example, if the rate or magnitude of disagreements between repeated readings increases with putative fish age and a static (age-independent) criterion for accepting age estimates is adopted (e.g., requiring that repeated readings not differ by more than one or two), there will be a disproportionately high rate of discarding of older otoliths, particularly for long-lived species. This will lead to under-representation of older age groups in estimated population age frequencies, potentially causing bias in derived fishery statistics such as mortality and growth. Information about the relationship between aging imprecision (in the absence of bias) and putative age can be used to account for some of the uncertainties in age-structured stock assessment models (Fournier and Archibald 1982; Richards et al. 1992). This information could also potentially be used to determine which criterion is most appropriate for deciding whether to accept or discard age estimates from individual otoliths to minimise risks of discard-related biases in population samples.

In this chapter I demonstrate the use of empirical relationships between putative fish age and discrepancies between replicate readings of otoliths to develop an appropriate protocol for estimating age for *L. bohar*. The best fit relationship between reading discrepancies and putative age was used to infer the most likely error (imprecision) generating process. Using this knowledge, an “acceptable” rate of age-specific discrepancy between replicate readings could be established to result in precise age estimates. The influence of the area of sample collection (GBR, Seychelles) and preparation method for otolith sections on the relationships between reading discrepancies and age was also considered.

3.2. Theoretical Framework.

I considered three credible hypotheses to explain the influence of the number of increments counted on the probability of failing to achieve agreement between replicate readings, irrespective of the magnitude of discrepancies. The first (H_1) was that the probability of non-agreement (J) was constant and independent of the number of increments counted (putative age). The second (H_2) was that J changed with putative age based on the principle that interpretation errors could occur for each annulus with equal probability. The third hypothesis (H_3) was that J increased with putative age but the probability of misinterpreting each annulus increased as more annuli were counted. Graphical depictions of expected patterns in discrepancies with age for each hypothesis are shown in Figure 3.1a.

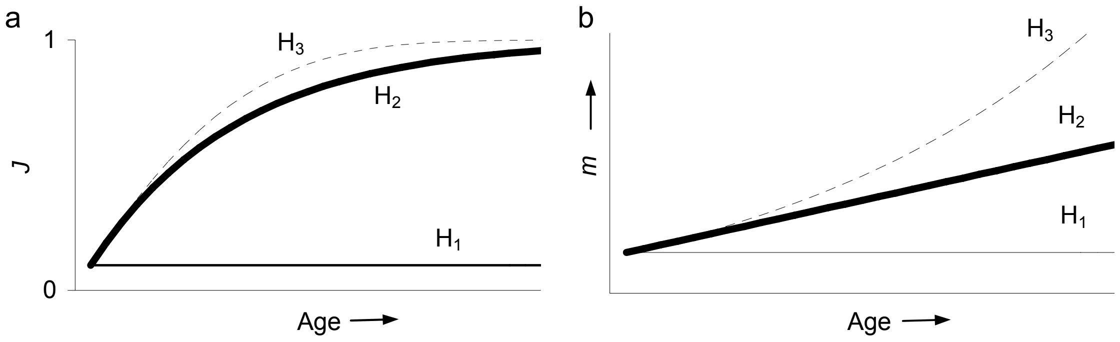


Figure 3.1. (a) Expected patterns in inter-read discrepancy with increasing fish age for 3 alternative hypotheses: H_1, the probability of not achieving an agreed age (*J*) did not change with putative fish age; H_2, *J* increased with putative age because errors made at all annuli were equi-probable; H_3, *J* increased with putative age at an increasing rate. (b) Predicted trend of mean magnitude of inter-read discrepancies (*m*) with putative age for each hypothesis, when errors were made.

H_1 was a plausible model for situations where discrepancies between readings arise principally because of difficulties in interpretation of specific features common to all otoliths, such as the first increment (e.g., Marriott and Cappo 2000) or final ("marginal") increment (e.g., Smith and Deguara 2003). H_2 would apply only if putative fish age does not influence the clarity or interpretability of growth increments in otolith sections and each increment had the same chance of misinterpretation. H_3 would indicate that growth increments become increasingly difficult to identify or interpret with increasing putative age, perhaps because of 'bunching' of increments deposited by older fish (e.g., Stevenson and Secor 1999; Manickchand-Heileman and Phillip 2000; Andrews et al. 2001).

The graphical form of H_1 was a horizontal line because *J* was constant with increasing putative age. The graphical form of H_2 represents a function derived from the binomial expansion. According to H_2, if *p* represented the probability that a growth increment (annulus) was interpreted differently between readings, then this probability, *p*, was the same for all annuli. Conversely, *q* was the probability for each annulus that it was interpreted in the second reading in the same manner as in the first, such that $p + q = 1$. From the binomial expansion, the probability of not achieving agreement (in this case having a discrepancy of at least 1) between successive readings (J) for a fish of putative age t is:

$$J_t = 1 - (1 - p)^t \qquad (3.1).$$

The graphical form of H_3 was similar to that of H_2 except that the rate or increase in probability of discrepancy was greater. If b is the rate at which the base probability of error (p) increased with each additional increment, then the probability of error for increment t, p_t, is

$$p_t = p(1 + b)^{t-1} \qquad (3.2)$$

and the probability of a discrepancy of at least 1 between successive readings was

$$J_t = 1 - \prod_{i=1}^{t} \left[1 - p(1 + b)^{(i-1)}\right] \qquad (3.3).$$

The expected magnitude (m) of discrepancy between successive readings of the same otolith also can be derived from each of the above models. For H_1, m was a constant, typically 1 or 2 depending on whether only one or both of the initial and marginal increments were difficult to interpret. Since p was constant for all t under H_2, the expected magnitude of discrepancies for each age was tp. Since I was dealing only with data that were discrepant though, the m for age 1 fish should have been 1 or more and thus a constant of 1 was added

$$m_t = tp + 1 \qquad (3.4)$$

(Fig. 3.1b). Under H_3, m was expected to increase roughly exponentially with the number of increments read and can be described by the function:

$$m_t = \left[p \sum_{i=1}^{t} (1+b)^{(i-1)} \right] + 1 \tag{3.5}$$

where;

b = the rate at which the probability of disagreement, p, increases with each additional increment in an otolith;

t = the number of increments in the otolith;

m = the expected magnitude of discrepancies between subsequent readings of the otolith.

The above models were selected as representations of H_1, H_2, and H_3 to comprise a biologically realistic set of candidate models for the description of observed trends in error (imprecision) with putative fish age. The best approximating model for observed trends in the rate (Fig. 3.1a) and magnitude (Fig. 3.1b) of imprecision were used to infer the most likely process of error generation from replicate readings of red bass otoliths. This model was then used as the basis for justifying an appropriate criterion for accepting or rejecting age estimates. If H_1 was most strongly supported, a static constant acceptance criterion would be appropriate for fish of all ages. If H_2 or H_3 were better approximations, however, then a constant or increasing rate criterion (with acceptable discrepancies being proportions of putative fish age) respectively would be more appropriate.

3.3. Methods.

3.3.1. Sample collection.

Biological samples of *L. bohar* and associated field data were collected from the GBR and Seychelles according to the sampling methods detailed in Chapter 2.

3.3.2. Sample processing and age estimation.

3.3.2.1. Whole otoliths.

Both sagittal otoliths were dissected from *L. bohar* in the laboratory. The left otolith from each fish was weighed (g) to four decimal places using a Sartorius Model BP61 measuring balance. A subset of otoliths collected from the GBR (n = 355) was then examined whole in immersion oil at low power magnification (40X) against a black background under reflected light. Opaque increments were enumerated along the distal surface, from the primordium to the outer dorsal or posterior margin for an initial estimate of fish age (years) (Fig. 3.2). The right otolith was weighed and used for age estimation when the left otolith had been damaged.

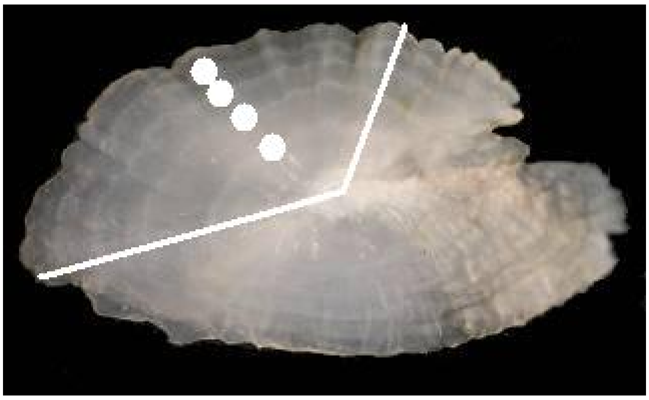


Figure 3.2. Whole otolith with reading axis and opaque increments counted for age estimation indicated. Otolith sampled from the GBR from a *L. bohar* individual of 383 mm FL.

3.3.2.2. Otolith Sectioning

Age estimates were then derived from the analysis of transverse sections of all otoliths (n = 1742) using a standard procedure (Ferreira and Russ 1994). Otoliths were sectioned in random order to ensure that any effects of sampling date or geographic area of collection were not confounded with any potential biases attributable to the order in which otoliths were sectioned and read.

3.3.2.3. Section Surface Preparation Methods

Otolith sections were further processed to improve the definition of opaque zones prior to repeat age estimation using one of four “secondary preparation methods”: acid etching; hand-polishing; mechanical-polishing; or acid etching followed by mechanical-polishing. Acid etching was done by placing one or two drops of 15% hydrochloric acid solution onto sections for approximately sixty seconds. Sections were viewed at 40X magnification with transmitted light, and if increments were not clearly discernable, this process was repeated. Hand-polishing involved rubbing hand-held otoliths against 1200-grade wet and dry emery paper on a flat surface under tap water. Mechanical polishing was done using a Kemet (300 series) variable speed lapping machine fitted with a disc of 1200-grade wet and dry emery paper and running tap water.

3.3.2.4. Assignment of nominal age estimates.

Fish age, in years, was then estimated by counting opaque increments along the ventral sulcus of otolith sections, from the primordium to the proximal surface margin, when viewed with transmitted light under low (40X) to medium (100X) power magnification (Fig. 3.3). Opaque increments were categorised as pseudo-annuli and excluded from estimates of age if their position or optical density relative to other opaque increments in the otolith was interpreted to be irregular. Where two or more opaque increments were interpreted to be confluent (Crabtree et al. 1995) they were grouped and interpreted as a single annulus. "Nominal" age was assigned to each individual otolith only on the basis of the number of annuli counted for the purpose of exploring effects on precision and likely acceptance of estimates from repeated age readings. Study of the periodicity of annulus deposition did not require the assignment of absolute estimates of fish age to otoliths, so nominal ages were also assigned for this purpose. Nominal ages were used principally for the grouping of otoliths for analysis.

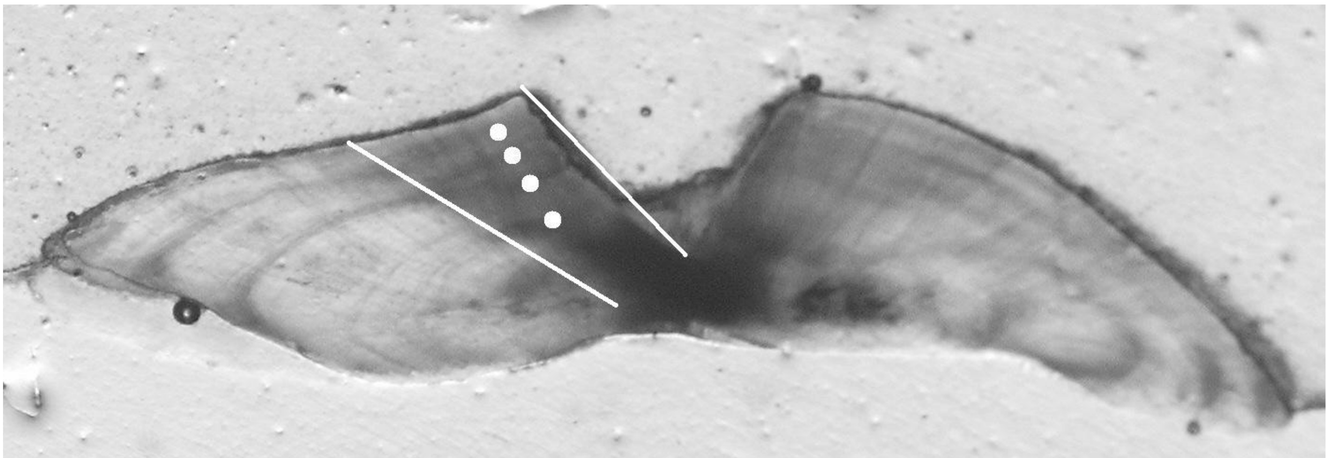


Figure 3.3. Transverse section of otolith with reading axis and opaque increments (annuli) counted for age estimation indicated. Otolith sampled from the GBR and prepared using hand-polishing. This otolith was dissected from a *L. bohar* individual of 296 mm FL.

3.3.3. Accuracy of Age Estimates – Increment Periodicity

3.3.3.1. Oxytetracycline Banding

Otoliths were stained with oxytetracycline (OTC) as a means of validating the accuracy of age estimates (Weber and Ridgeway 1962; Beamish and McFarlane 1983). Two *L. bohar* received intraperitoneal injections of OTC at a dosage of 50 mg kg^{-1} body weight shortly after capture and were kept in a large aquarium facility at James Cook University for a period of approximately 17 months, from November 1999 to April 2001. These fish were fed a varied diet of pilchards, squid, and small reef fish *ad libitum.* They were euthanized in 2001 to identify the position of OTC staining and subsequent otolith growth and deposited opaque increment(s) on otolith sections.

Seasonal patterns in daily water temperatures observed in the aquarium were very similar to those observed on outer reefs of the GBR (i.e., where *L. bohar* were sampled) throughout the course of the OTC experiment (Fig. 3.4). Noticable departures from outer reef water temperatures were observed on the 2nd June, 6th June, and 19th July 2000, when the water temperature in the aquarium was relatively low. These low temperatures coincided with low minimum air temperatures (9^{o}C, 11^{o}C, 13^{o}C, respectively) on these days, and the early time of day when water temperature readings were taken (0830 hrs, 0915 hrs, 0900hrs, respectively; Fig. 3.4). Several windows in the tank also allowed a natural day/night length cycle.

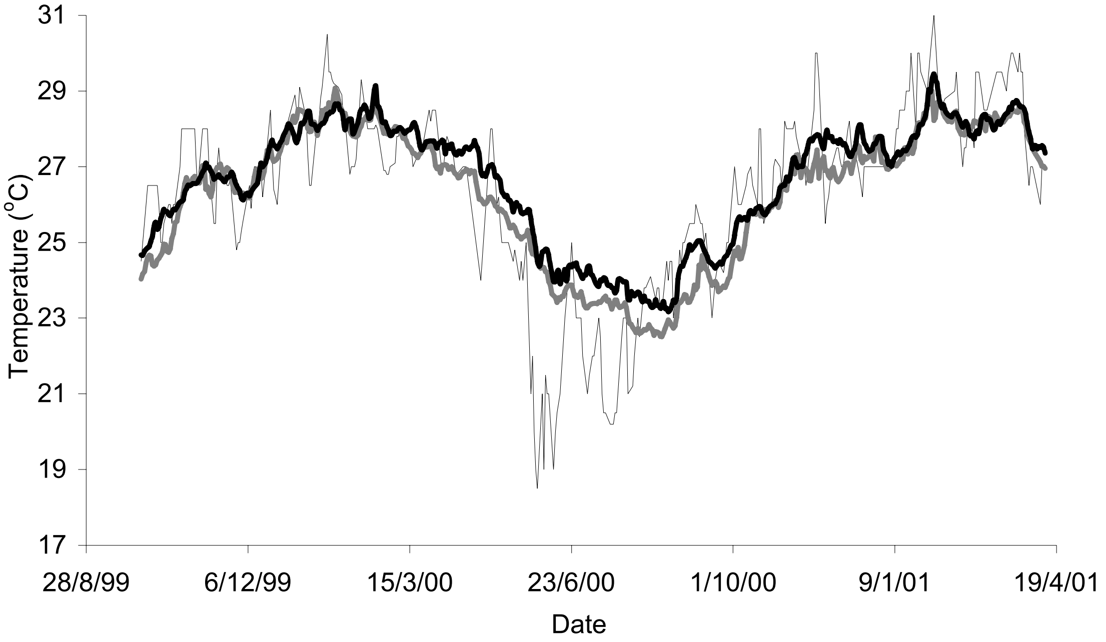


Figure 3.4. Temperature readings from aquarium used for OTC experiment. The thin black line represents daily water temperature readings from tank. Thick grey and black lines are daily water temperature readings from Myrmidon (Fig. 2.3b) and Carter (Fig. 2.3a) reefs on the Outer GBR (Steinberg and Burrage 2001), respectively. Temperature readings from the tank were recorded in the morning (0730 to 1200 hrs) and from the GBR were recorded at noon (1200 hrs). Aquarium temperature data were provided by the Marine and Aquaculture Research Facilities Unit at James Cook University.

3.3.3.2. Marginal Increment Analysis.

The relative distance from the marginal increment to the margin of otolith sections was quantified on a monthly basis to obtain further evidence of the periodicity of opaque increment deposition, and thus the accuracy of age estimates from otolith sections. Otoliths collected from monthly sampling were transversely sectioned for age estimation and secondarily processed by mechanical polishing or acid etching followed by mechanical polishing. The proportional method of Fowler and Short (1998) was used to calculate a marginal increment ratio (MIR) for otolith sections across a range of nominal age estimates. This approach was taken because it was not possible to obtain sufficient otoliths of single age groups over a full twelve months from each geographic area to examine age-specific marginal increments as recommended by Campana (2001).

Widths of marginal increments and penultimate increments were initially measured along the ventral sulcus of otolith sections viewed with transmitted light, but it was difficult to confidently discern opaque margins because of shadow effects (Gauldie 1988) and narrow increment widths. So, in a revised approach, otolith sections were viewed with reflected light against a black background and increment widths were measured at the ventral edge of otolith sections, along the axis from the ventral tip to the primordium. Opaque margins were judged to be more easily discerned, widths of full increment cycles larger, and thus measurement errors likely to be reduced (Cappo et al. 2000) using this method.

Electronic images of otolith sections were captured using the “Seqsnap” computer program (Version 1.0; Imaging Technology Inc). The width of the marginal increment and penultimate cycle (Fig. 3.5) were measured using “Image Tool for Windows” software (Version 3.00; UTHSCSA). The MIR was calculated as the width of the marginal increment divided by the width of the penultimate cycle.

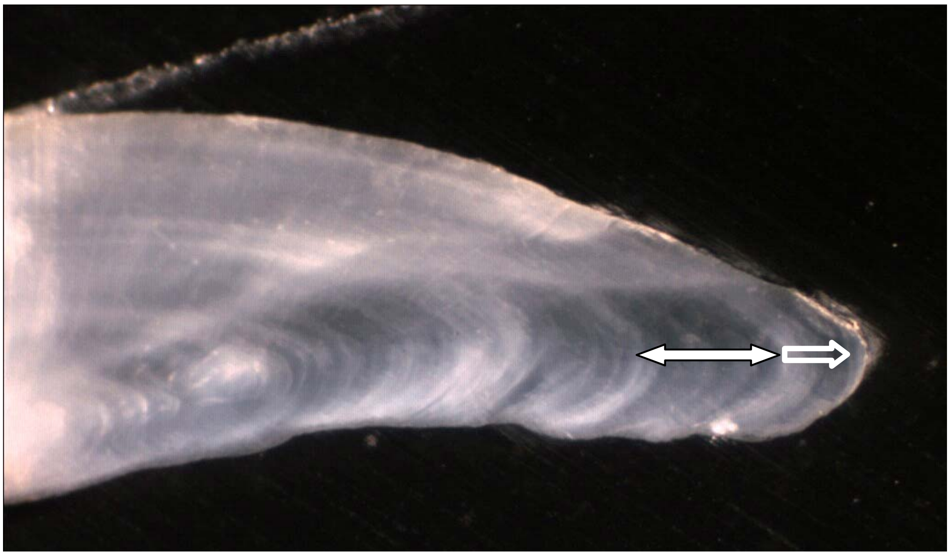


Figure 3.5. Penultimate cycle width (solid arrow) and marginal increment width (transparent arrow) as measured on otolith sections for the marginal increment analysis. This otolith section was collected in the Seychelles and was viewed under reflected light.

Means of MIRs were then calculated for each sample month and geographic area. Only otolith sections with nominal age estimates ranging from 4 to 10 years were measured for MIA. Successive opaque increments after the 10th annulus were not measured because they became obscured by “increment crowding” when viewed with reflected lighting (*pers. obs.*). Sections with nominal age estimates of less than 4 years were excluded because penultimate and marginal increments were judged to decrement markedly in width (Fig. 3.6), which would bias calculated mean MIR values downwards and thus underestimate the formation period.

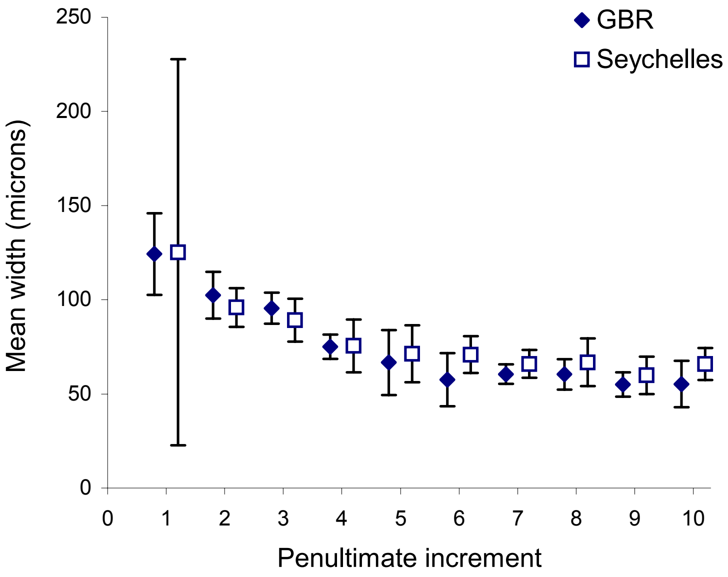


Figure 3.6. Penultimate increment widths as measured along the ventral sulcus. Measurements were recorded from viewing otolith sections with transmitted light at 100X magnification in a pilot study across a broader range of nominal age groups (see text). Error bars are 95% confidence intervals.

3.3.4. Agreement and Precision of Repeated Age Readings.

Age estimates from the first reading of otoliths were recorded as “nominal” ages. Up to 5 otolith sections, if available, were randomly selected from each nominal age group for each category of secondary preparation method and geographic area for a second reading. These otoliths were read in random order to ensure that estimates in the second reading were made without knowledge of those made in the first.

3.3.4.1. Influence of Area and Preparation Method.

Average Percent Error (APE; Eqn. 3.6; Beamish and Fournier 1981) was calculated for each otolith as an index of precision. Resultant APE scores were negatively skewed (skewness = +2.28 ± 0.09) and heteroscedastic ($F_{7,714} = 13.3$; p = 0.0001). Accordingly, the non-parametric Kruskal-Wallis test was used to test for the influence of area and secondary preparation method on APE. Dunn’s multiple comparison tests (Zar 1999) for tied rankings and uneven sample sizes among groups were used to investigate *a* *posteriori* the pattern in significant differences among the 8 combinations of area and preparation methods indicated by the Kruskal-Wallis test.

$$\text{APE} = \frac{1}{R}\sum_{h=1}^{R}\frac{\left|X_{gh} - X_{g}\right|}{X_{g}} \qquad (3.6)$$

where;

R = the number of times each fish was aged;

X_{gh} = the *h*th age estimate of the *g*th fish;

X_{g} = the average age calculated for the *g*th fish.

3.3.4.2. Rates of Agreement between Readings.

Data were pooled into nominal age bins (3 successive nominal year groups per bin) prior to calculating rates of non-agreement to provide larger sample sizes (nominally 15, see Table 3.1) for each category and improved resolution in estimates of non-agreement. The percentage of otoliths for which the two readings did not agree (PD) was then calculated for each nominal age bin from each geographic area and secondary preparation method.

These data were then analysed using analysis of covariance (ANCOVA) to investigate the influence of geographic area and method on PD, whilst accounting for nominal age bin (covariate). If plots of PD against nominal age bin indicated significant departures from linearity, a relevant linearizing transformation was applied prior to the ANCOVA. The ANCOVA was done to determine the validity of pooling data across factors because I considered that this would result in sufficient data to calculate PD for individual nominal age groups. A caveat, though, was that data from the acid-etched, machine-polished method could not be pooled with data from the plain, acid-etched method because many of these data were derived from the same otolith sections read independently. Accordingly, in cases where data were pooled across preparation methods, data from the acid-etched, machine polished method were excluded.

Table 3.1. Number of observations analysed for the Analysis of Covariance. Factors = Geographic Area (GBR, Seychelles) and secondary preparation method (acid etched (AE); hand polished (HP); machine polished (MP); acid etched then machine polished (AM)). Concomitant variable = nominal age. Pooled nominal age categories (bins) that were judged to have too few observations to sufficiently represent the percentage of data that did not achieve agreement from replicate reads are not shown here and were excluded from the analysis.

Age	GBR				Seychelles			
Bin	AE	HP	MP	AM	AE	HP	MP	AM
1-3	7	9	5	8	5	10	5	4
4-6	15	14	15	13	3	15	13	6
7-9	12	16	15	11	5	16	13	7
10-12	15	15	15	7	5	15	14	4
13-15	5	10	15	4	11	14	9	11

The models selected as representations of trends expected from each of the aforementioned error generating hypotheses (Table 3.2) were then fitted to observed PD on nominal age using non-linear regression in “SPSS for Windows” (Version 11.0; SPSS inc.) software. PD values calculated from less than 5 data were judged to be poor estimates and excluded from analysis.

Table 3.2. Candidate models used to investigate the likelihood of hypotheses about error generation processes leading to non-agreement between repeated readings of otoliths. PD was the percentage of otoliths per age bin for which repeated readings were discrepant. *J* = probability of not achieving an agreed age; *p* = probability that an annulus was interpreted differently between readings. *a, b, p* are model parameters, as described in text.

Hypothesis	Model	Functional Form	Constraints
H_1	*J* uniform	$PD = a$	None
H_2	*p* constant	$PD = 100 * [1-((1-p)^{t})]$	$0 \leq p \leq 1$
H_3	*p* increasing	$PD = 100 * [1-\prod_{i=1}^{t} (1-p(1+b)^{(i-1)})]$	$0 \leq p \leq 1; b > 0$

The statistical output on the fit of these models was used to calculate the Akaikes Information Criterion for small sample sizes (AIC_C; Burnham and Anderson 1998) to determine which of the models best explained the data and, by inference, which of the alternate hypothesis about the origin of aging errors was most likely. Models with an AIC_c value within two of that for the best approximating model were considered equally plausible as the best approximating model (Burnham and Anderson 1998).

3.3.5. Trends in inter-read discrepancy with nominal age.

Averages of observed inter-read discrepancies (IRD) were calculated from discrepant readings only, for each nominal age group. Empirical models for trends in observed magnitudes of IRD with nominal age group were then selected as representations of the functional forms of each aging error hypothesis (Table 3.3). AIC_C values were again calculated from the fit of these models to determine which one best explained these data. This was done as a “reality check” of my evaluation of the trend of PD with *t* to account for the prospect of Type II error in the former analysis.

Table 3.3. Candidate models used to describe the relationship between observed inter-read discrepancies (*IRD*) with nominal age (*t*). Each empirical model was the functional form of alternative theoretical models postulated for the error generating process. *a, b, p* are model parameters. See text for explanation of models and hypotheses.

Hypothesis	Model	Functional Form	Constraints
H_1	*J* uniform	IRD = a	None
H_2	*p* constant	IRD = $p(t-1)+a$	$0 \le p \le 1$
H_3	*p increasing*	IRD = $\left[p\sum_{i=1}^{t}(1+b)^{(i-1)} \right] + a$	$0 \le p \le 1$; $b > 0$

Model fits to data from different areas or preparation methods were then compared using ANCOVA following the application of any relevant linearizing transformation, if required.

3.4. Results

3.4.1. Accuracy of age estimates.

OTC injections for both fish resulted in a fluorescent mark on otolith sections when viewed with transmitted ultra-violet light under a compound microscope (Figs. 3.7, 3.8). One complete opaque increment and a margin of additional otolith material was visible between the OTC mark and the proximal edge of otoliths from both fish, indicating an approximately annual deposition rate of opaque increments during the 17 month growth period. The OTC mark was also in approximately the same position as the second last opaque increment on both otolith sections, indicating that these opaque increments were formed at approximately the same time as the OTC injection in both fish, in late October to early November, 1999.

This timing of opaque increment formation concurs with that suggested by the MIA in *L. bohar* otoliths from the GBR (Fig. 3.9a). Plots of mean MIR by month indicate annual cycles of opaque increment deposition in otoliths of nominally 4-10 year old fish from the Seychelles and the GBR (Fig. 3.9), although the distribution of MIR data with month is scattered and less convincing. Annual minimum mean MIR (approximating the time of increment cycle completion) occurred in November and December for both areas, although this was less defined for Seychelles' otoliths. An edge analysis revealed that opaque increments formed over a much longer period in the Seychelles (i.e., September to April) than on the GBR (i.e., October to January; Fig. 3.10).

There was a strong positive linear relationship between otolith weight and nominal age for both geographic areas (Fig. 3.11). This indicated that otolith growth persisted throughout life and that opaque increments were deposited in otoliths at a relatively constant rate with increases in otolith mass. Supportive evidence of an approximately annual periodicity of opaque increment deposition for a limited number of nominal age groups (Figs. 3.7, 3.8, 3.9) can therefore be extrapolated to other nominal age groups, assuming that increases in otolith mass continue at the same rate throughout life. The rate of increase in otolith mass with nominal age was higher in the Seychelles than on the GBR (Fig. 3.11). An age bias plot of estimated age from whole otoliths against age from sectioned otoliths demonstrated that readings from whole otoliths produced lower estimates than readings from otolith sections for *L. bohar* nominally older than 9 years (Fig. 3.12).

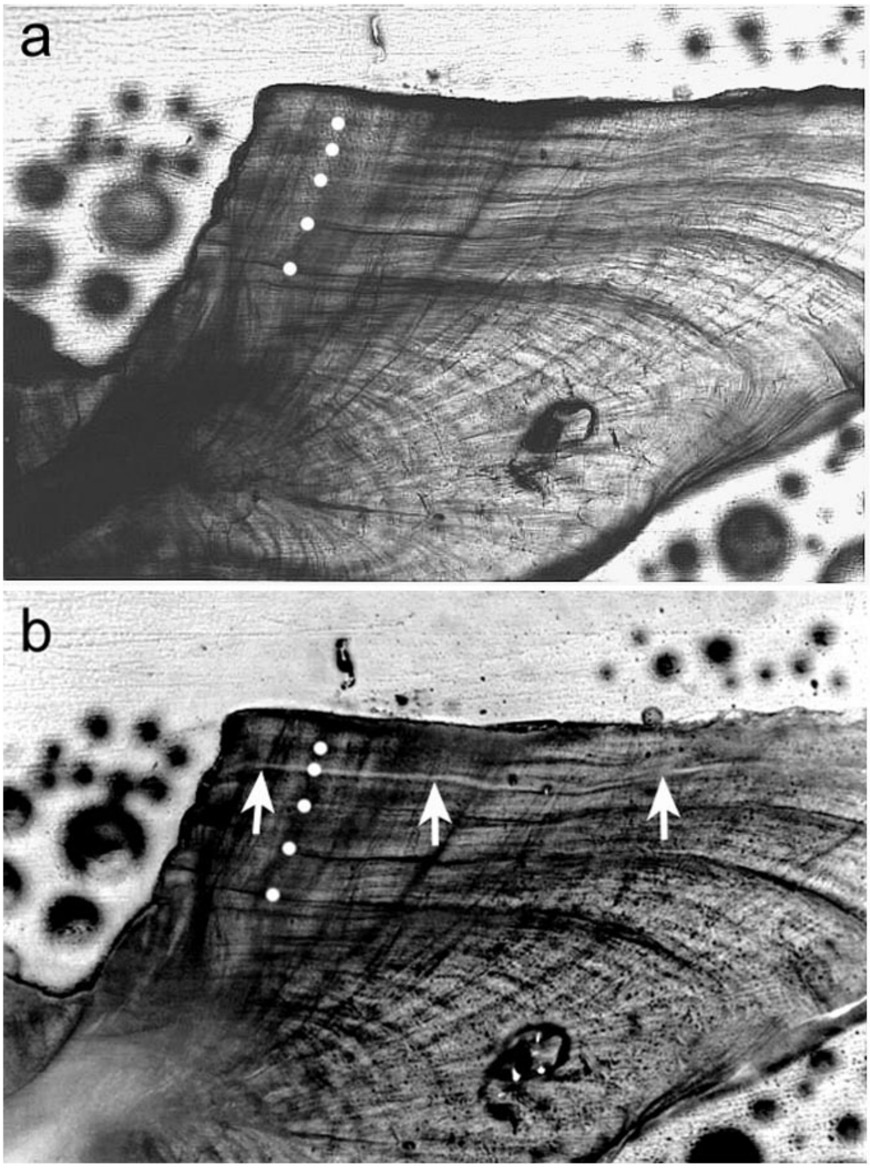


Figure 3.7. Position of opaque increments (a) and oxytetracyline (OTC) band (b) of a 447 mm FL individual estimated to be nominally 5 years of age. Growth period following OTC injection = approximately 17 months (30/10/99 – 5/4/01).

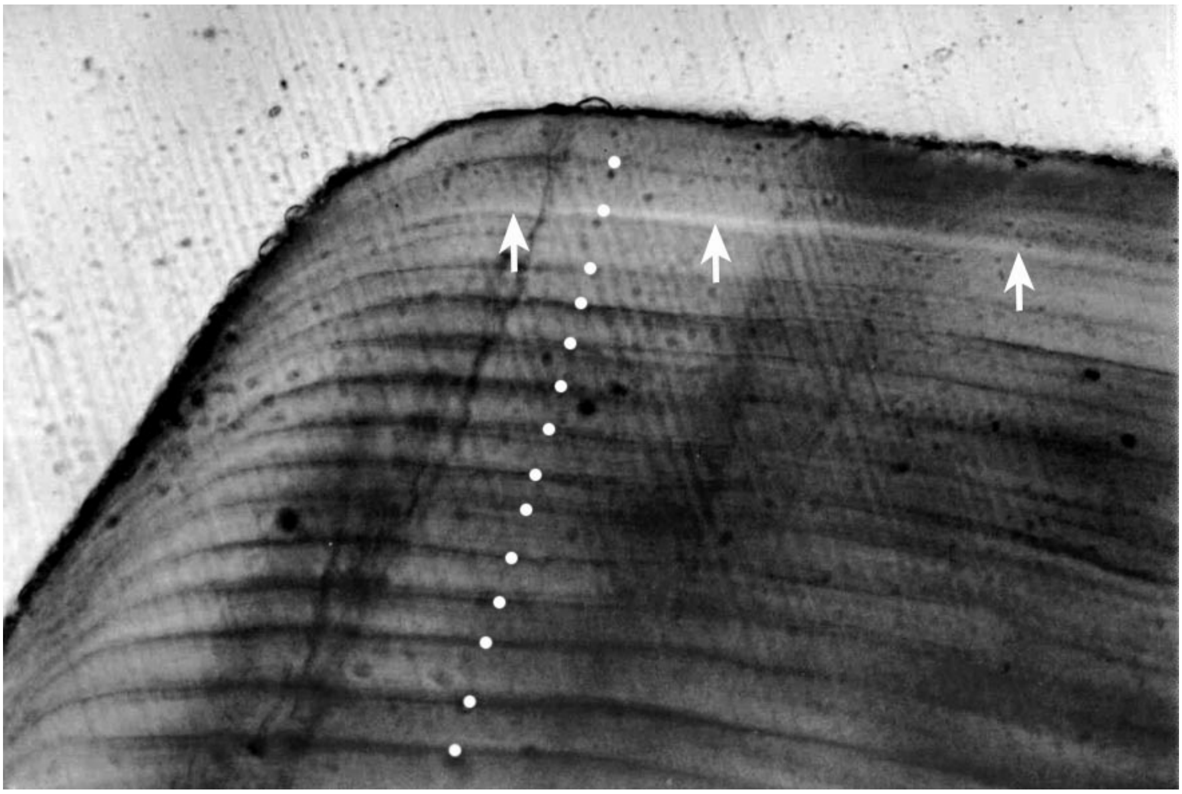


Figure 3.8. Position of oxytetracyline (OTC) band on the otolith section of a 650 mm FL individual estimated to be nominally 29 years of age. Growth period following OTC injection = approximately 17 months (5/11/99 – 9/4/01).

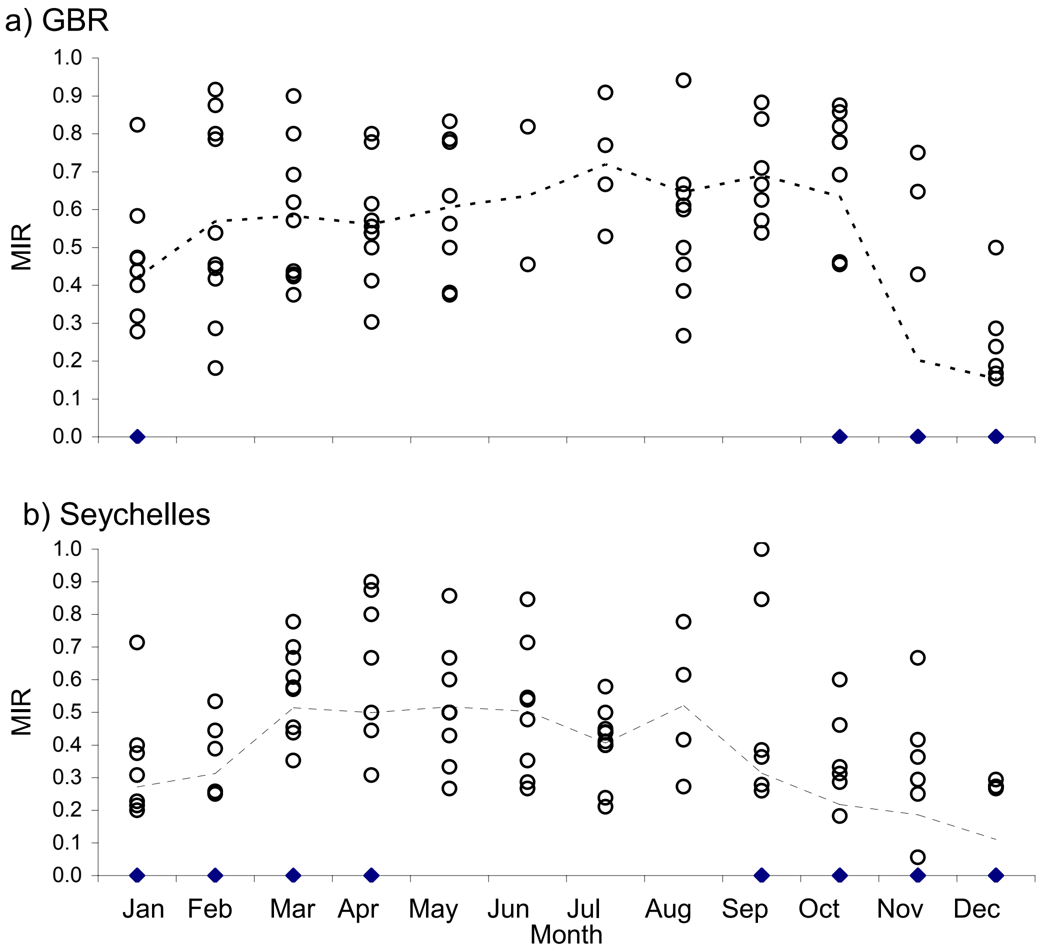


Figure 3.9. Marginal Increment Analyses plots of marginal increment ratios (MIR) for otoliths collected from the (a) GBR and (b) Seychelles. Open circles are data from otoliths with a transparent margin; filled diamonds are from otoliths with an opaque margin; and dashed lines are the mean MIR calculated per month.

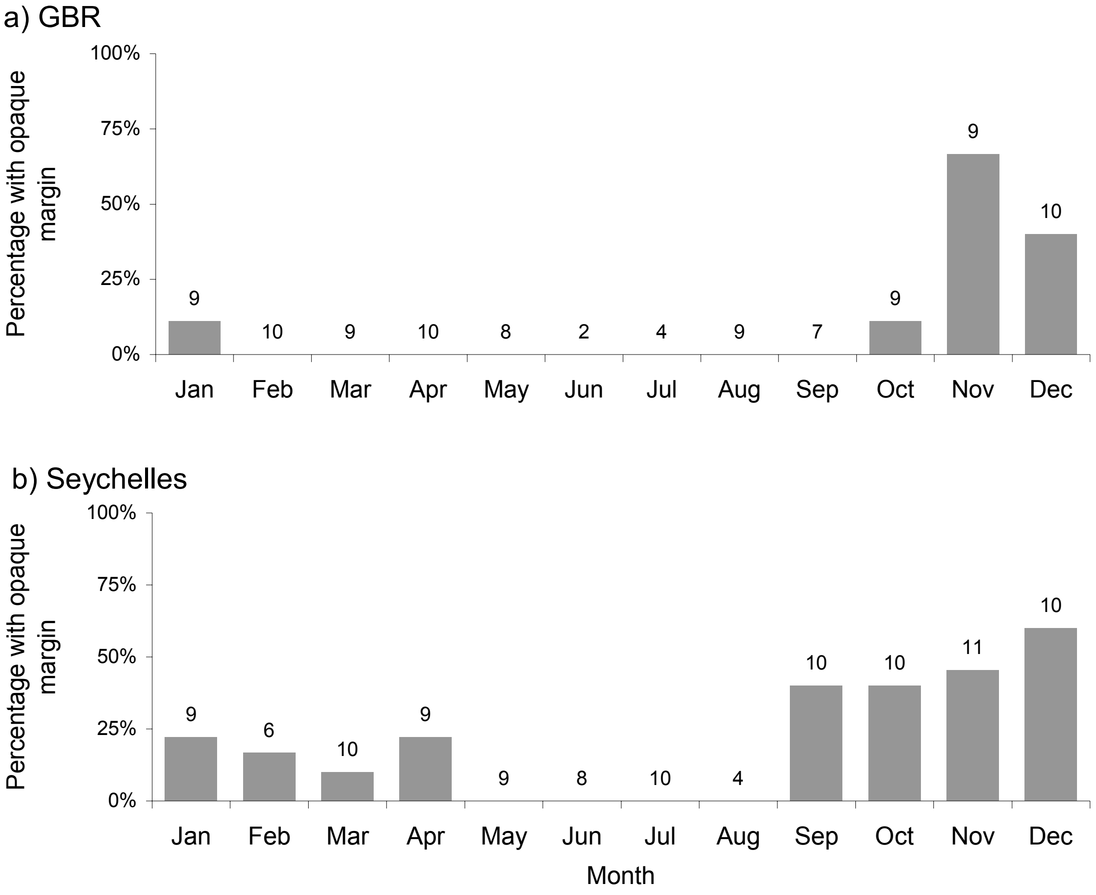


Figure 3.10. Edge analysis of otoliths from the GBR and Seychelles. Numbers denote sample sizes.

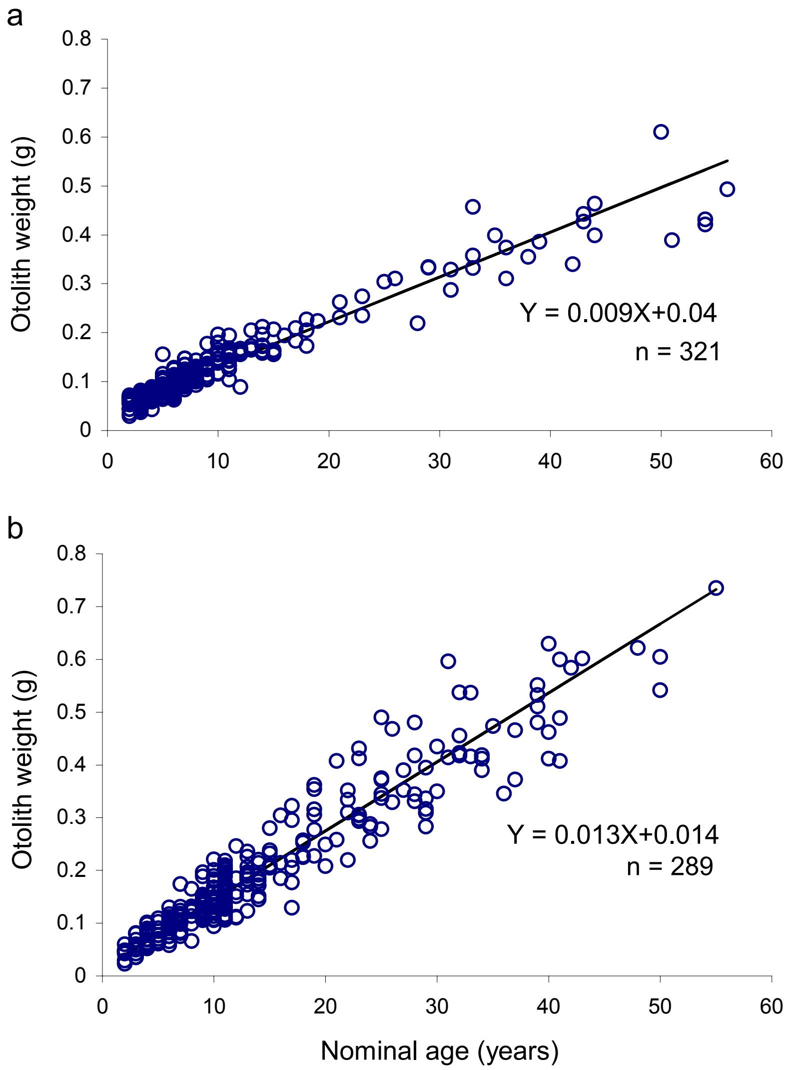


Figure 3.11. Model II regression of otolith weight on age for *L. bohar* from different areas (a) GBR; (b) Seychelles.

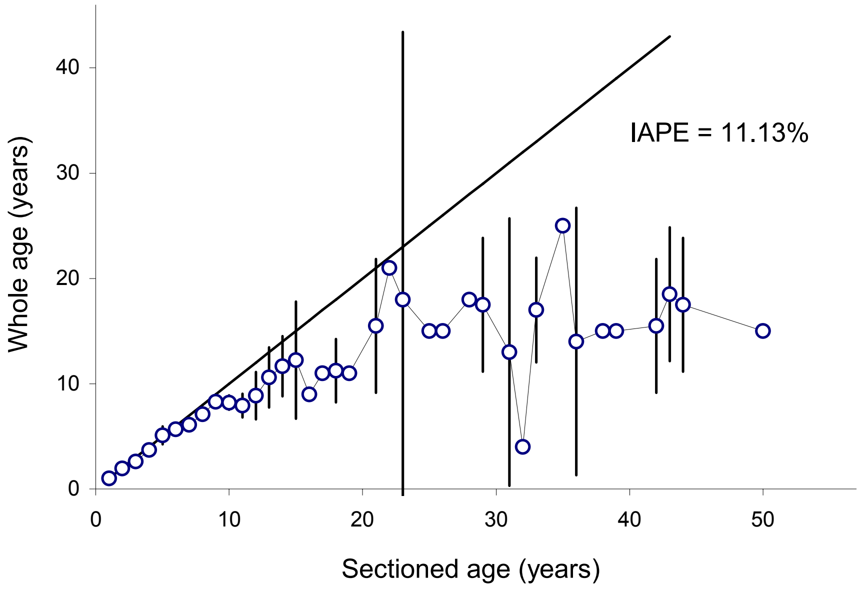


Figure 3.12. Age bias plot comparing nominal age estimates derived from whole and sectioned otoliths. Mean whole otolith age plotted against nominal age estimated from sectioned otoliths with corresponding 95% confidence intervals. The straight line through origin was the line of agreement between whole- and section-based estimates.

3.4.2. Precision: Influence of Geographic Area and Preparation Method.

Annuli on otolith sections from the Seychelles appeared faint relative to those from the GBR (Fig. 3.13.). Hand-polishing and machine-polishing appeared to improve the readability of annuli on GBR otoliths (Fig. 3.13c,e,g) but this was not as apparent on Seychelles otoliths (Fig. 3.13b,d,f,h). Some damage from acid-etching of an otolith section for too long can be seen in Figure 3.13a, which might also have contributed to a poorer readability of this method. These differences in readability are likely to affect the resulting precision of age estimates.

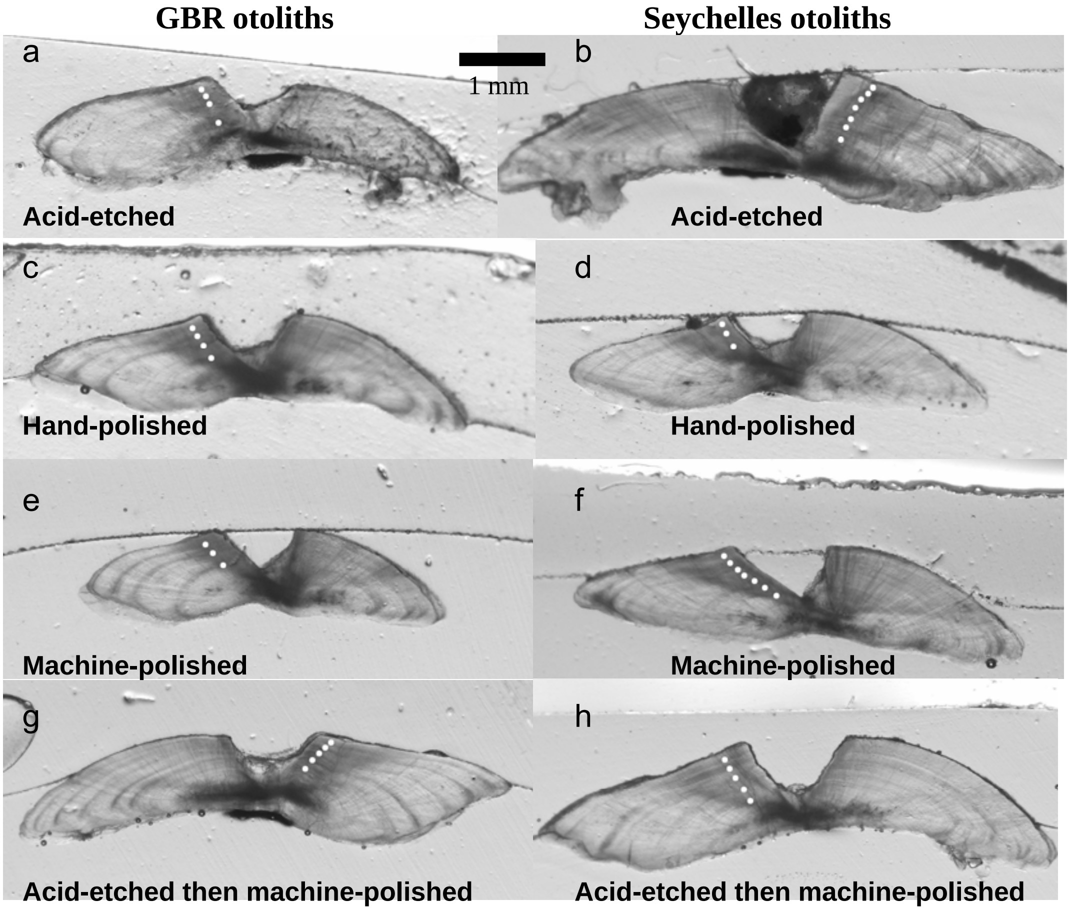


Figure 3.13. Transverse sections from each area prepared by each method. Areas (GBR, Seychelles) indicated on top of panel; section preparation methods (acid-etched, hand-polished, machine-polished, acid-etched then machine-polished) labelled for each otolith. White dots indicate positions of annuli along reading axis. Otoliths were dissected from *L. bohar* individuals of: a) 305 mm FL; b) 561 mm FL; c) 296 mm FL; d) 313 mm FL; e) 231 mm FL; f) 381 mm FL; g) 385 mm FL; and h) 412 mm FL.

Mean ranks of APE were found to differ significantly among the eight treatment groups (Kruskal Wallis test; $\chi_7^2 = 133.956$, $p < 0.001$), where “treatment groups” were two factor combinations of Geographic Area and Preparation Method. Multiple comparisons revealed that Geographic Area significantly affected precision, since mean ranks of APE were significantly higher for all four Seychelles treatment groups than for any of the GBR groups (Table 3.4). No apparent differences in mean rank between Preparation Methods within either Geographic Area were statistically significant.

Further, the order of methods was not consistent between areas. It was thus concluded that Preparation Method did not consistently or significantly influence APE.

Table 3.4. Dunn's multiple comparison tests. Treatment groups are combinations of Geographic Area: Great Barrier Reef (GBR), Seychelles (SC); and Preparation Method: acid-etched (AE), hand-polished (HP), machine-polished (MP), acid-etched followed with machine-polishing (AM). (a) Statistics: IAPE = Index of Average Percent Error (Beamish and Fournier 1981). Numbers in parentheses are standard errors of the estimates. (b) Test result: Non-parametric multiple comparisons (Dunn 1964 *in* Zar 1999) that account for tied rankings and unequal sample sizes among groups. Groups grouped by bold lines were not significantly different ($\alpha > 0.05$).

a) Statistics.

Treatment Group	n	IAPE		Mean Rank	
GBR-AM	56	2.24	(0.51)	226.20	(22.09)
GBR-AE	74	2.88	(0.44)	262.55	(19.71)
GBR-HP	98	3.22	(0.46)	269.25	(17.96)
GBR-MP	92	4.04	(0.60)	293.45	(19.20)
SC-MP	78	7.00	(0.73)	400.35	(22.75)
SC-AM	74	8.47	(1.00)	420.45	(23.12)
SC-HP	168	9.11	(0.71)	434.81	(14.98)
SC-AE	82	12.03	(1.34)	489.47	(19.90)

b) Test result.

	Most Precise							**Least Precise**
Area:	GBR	GBR	GBR	GBR	SC	SC	SC	SC
Method:	AM	AE	MP	HP	MP	AM	HP	AE

3.4.3. Trends in the proportion of agreement with nominal age.

Inspection of plots of PD for nominal age bins (Table 3.1) indicated no obvious departure from linearity among groups, so a 2-factor ANCOVA was done to compare the relationship among areas and preparation methods. Tests for homogeneity of slopes demonstrated that neither area ($F_{1,\,24} = 3.083$, p=0.092) nor preparation method ($F_{3,\,24} = 0.572$, p=0.639), nor their interaction ($F_{3,\,24} = 0.711$, p=0.555) significantly influenced the incline of this relationship. This result suggested that pooling of data across areas and preparation methods was valid, which resulted in sufficient data to analyse trends in PD with nominal age group (*t*) rather than bins of 3 nominal ages. The fit of empirical models to the relationship between PD and *t* and parameter estimates are shown in Table 3.5.

Out of the candidate models investigated, the "*p* constant" model, representing H_2, fitted the observed data best. This model provided a better description of the data than the "*p* increasing" (H_3) model because the difference in AIC_C was greater than two (Burnham and Anderson 1998). The predictive power of the "*p* constant" model was also reasonable because the coefficient of determination (R^2) explained 53.1% of the observed variability (Fig. 3.14). Importantly, the calculated AIC_C for the "*J*: Uniform" model was more than 10 higher than that calculated for the best approximating model, which was sufficient evidence to reject this model (Burnham and Anderson 1998).

Table 3.5. Model fits to variation in Percentage of Disagreement (PD) with nominal age group (*t*). The functional forms of each model and respective hypotheses are given in Table 3.2. Numbers in parentheses are standard errors of parameter estimates. Δ is the difference in AIC_C from that calculated for the best approximating model (**bold**). Calculated PD values were excluded from the analysis if calculated from fewer than 5 data or if estimated for *t* >41years (see text).

Model	n	*a*		*b*		*p*		R^2	AIC_C	Δ
p constant	37	-		-		0.09	(0.007)	0.53	**86.06**	0.00
p increasing	37			0	(0)	0.10	(0.010)	0.46	90.79	4.73
J: Uniform	37	73.98	(3.09)	-		-		0.00	98.23	12.17

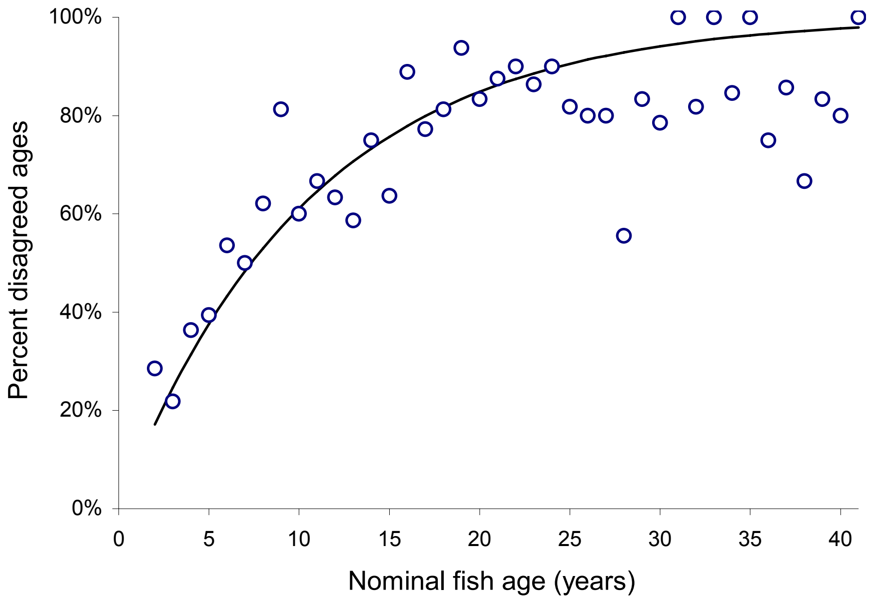


Figure 3.14. Fit of the "p constant" model to observed percentage of disagreed ages (PD) per nominal age (*t*).

The estimated value for parameter *p* was inferred as an approximation of the probability of misinterpreting any annulus on a *L. bohar* otolith section when relative frequencies (PD: %) in Figure 3.14 were equated to expected probabilities of disagreement between replicate age readings. At 0.09, $\hat{p}$ was not very high, but the cumulative effect of reading additional annuli was shown to result in a marked increase in the inferred probability of making an imprecise estimate of age (*J*). From Figure 3.14 it was shown that the inferred *J* continued to increase with an increasing number of annuli counted, to 84.8% (PD) after reading 20 nominal annuli. After this nominal age it is highly probable that replicate age readings will be discrepant (an inferred 84.8% to 97.9% chance from the observed range of data).

3.4.4. Trends in inter-read discrepancy with nominal age.

Since only those data arising from discrepancies between replicate reads (i.e., IRD > 0) were analysed, sample sizes were not sufficient for a full model 2-factor ANCOVA to test for the effects of area and preparation method. Accordingly, a main-effects only analysis was done. An initial inspection of plotted mean IRD against nominal age bin (5-9, 10-14, …, 35-39 years) indicated no significant departures from linearity, so no transformations were required.

Preparation Method was found to significantly influence the slope of mean IRD on nominal age bin ($F_{3,20} = 6.42$; $p<0.01$), but when the acid-etched followed by machine polished method (AM) was removed there was no significant effect of preparation method on slope ($F_{2,21} = 2.60$; $p = 0.107$). There was also no significant influence of area on slope ($F_{1,14} = 0.003$; $p = 0.96$) when AM data were excluded. Comparison of estimated marginal means of mean IRDs per nominal age bin and 95% confidence intervals adjusted for the influence of age, however, demonstrated significant differences among areas ($F_{1,10} = 4.709; p < 0.05$; Fig. 3.15a) and preparation methods ($F_{3,15} = 4.596; p < 0.05$; Fig. 3.15b). Adjusted mean IRDs from Seychelles' otoliths were significantly higher than those from GBR otoliths across preparation methods, while acid etched sections generated significantly higher mean IRDs than those generated from machine-polished sections when averaged across areas.

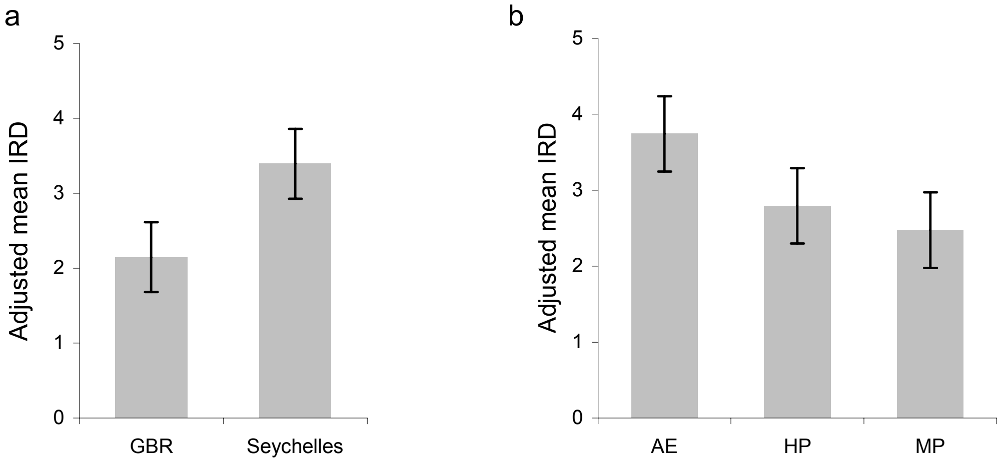


Figure 3.15. Estimated marginal means of mean inter-read discrepancies observed per nominal age bin from main effects model ANCOVA: (a) areas and (b) preparation methods: “AE” = acid-etched; “HP” = hand-polished; “MP” = machine-polished (MP). Error bars are 95% confidence intervals adjusted for the influence of the concomitant variable (nominal age bin).

Despite these differences in elevation among adjusted mean IRDs, the lack of significant differences in slope indicated that the best estimate of the trend in mean IRD with nominal age group, *t*, (excluding AM data and *t* with few data: $n < 4$) was the slope of the pooled data. Evaluation of fits of alternative models relating mean IRD to *t* was consistent with earlier interpretations from the analysis of trends in PD on *t*: that is, the "*p* constant" (H_2) model provided the best approximation of observations (Table 3.6). Although the “*p* increasing” model provided an equivalent fit in terms of calculated AIC_C (Table 3.6: $\Delta \leq 2$; Burnham and Anderson 1998), the estimate for the rate at which *p* increases with *t* was negligible and not significantly different from zero (i.e. $b = 0.025 \pm 0.029$SE).

Table 3.6. Model fits to mean inter-read discrepancy (IRD) with nominal age (*t*). The functional forms of each model and respective hypotheses are given in Table 3.3. Data have been pooled across Geographic Areas and Preparation Methods (excluding sections that were acid etched then machine polished). Numbers in parentheses are standard errors of the estimates. Δ was the difference in AIC_C from that calculated for the best approximating model (**bold**).

Model	n	*a*		*b*		*p*		R^2	AIC_C	Δ
p constant	33	0.959	(0.271)	-		0.107	(0.012)	0.73	**-4.15**	0.00
p increasing	33	1.273	(0.460)	0.025	(0.029)	0.064	(0.033)	0.75	-2.43	1.72
J: Uniform	33	3.171	(0.232)	-		-		0.00	12.76	16.31

The linear model predicts a mean IRD from replicate age readings of 0.96 increments for nominal age group 1, which will increase by 0.107 with each successive increase in nominal age, averaged across areas and preparation methods. This relationship (Fig. 3.16) provides a justification for establishing an acceptance criterion that is a constant proportion of putative fish age.

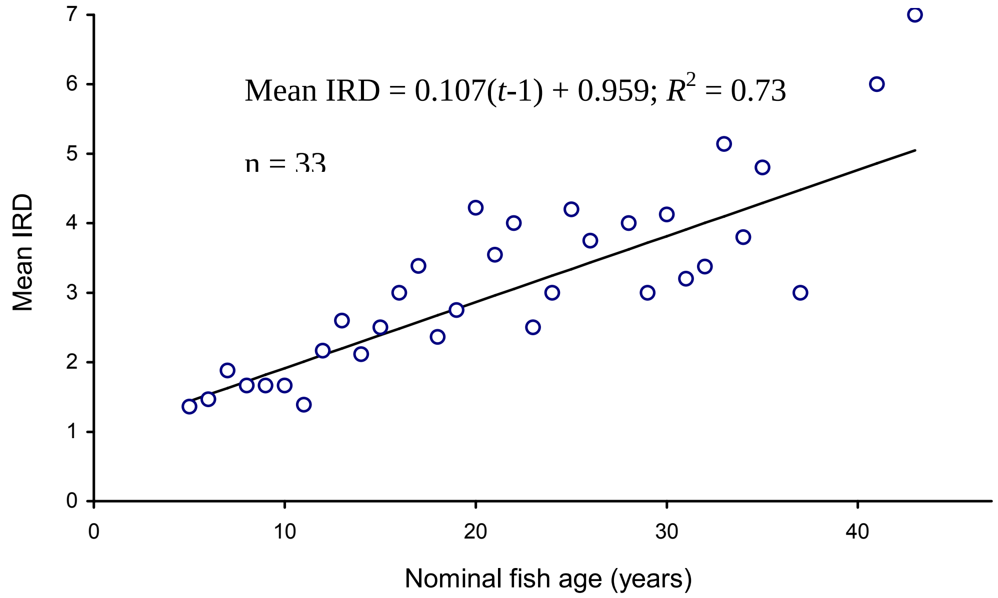


Figure 3.16. Fit of the linear model to observed mean inter-read discrepancy (IRD) with nominal fish age (*t*).

This observed trend in mean IRD was less precise for older age groups, however, because the standard error of IRD was shown to increase with nominal age (Fig. 3.17). This may be a simple result of the expected increase in variance with increasing nominal age (Fig. 3.18), which has been observed in other aging studies (Lai and Gunderson 1987; Eklund et al. 2000), and also of having fewer replicates in older nominal age groups.

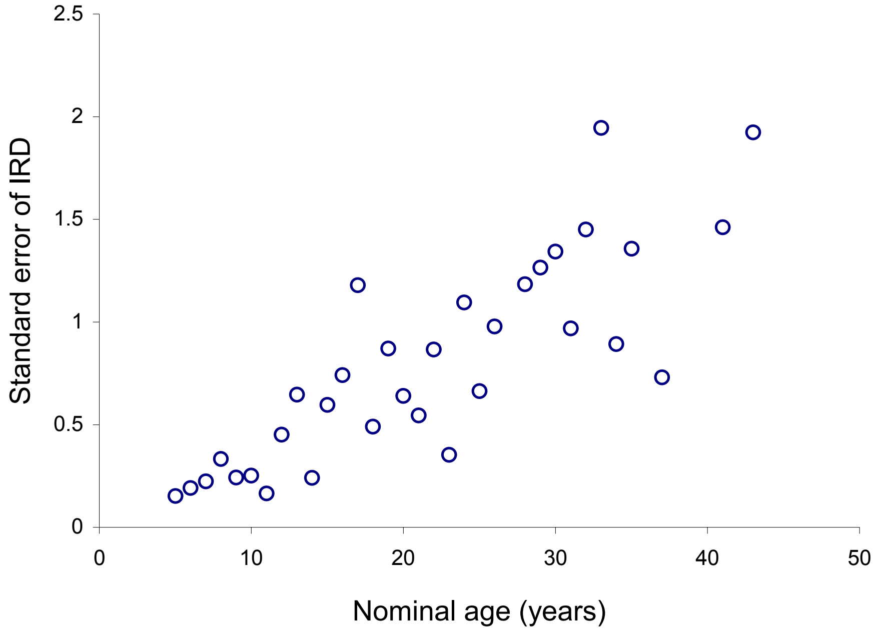


Figure 3.17. Standard error of inter-read discrepancies (IRD), indicating the precision of calculated mean IRD for each nominal age group (*t*). Data from acid etched then machine-polished method excluded.

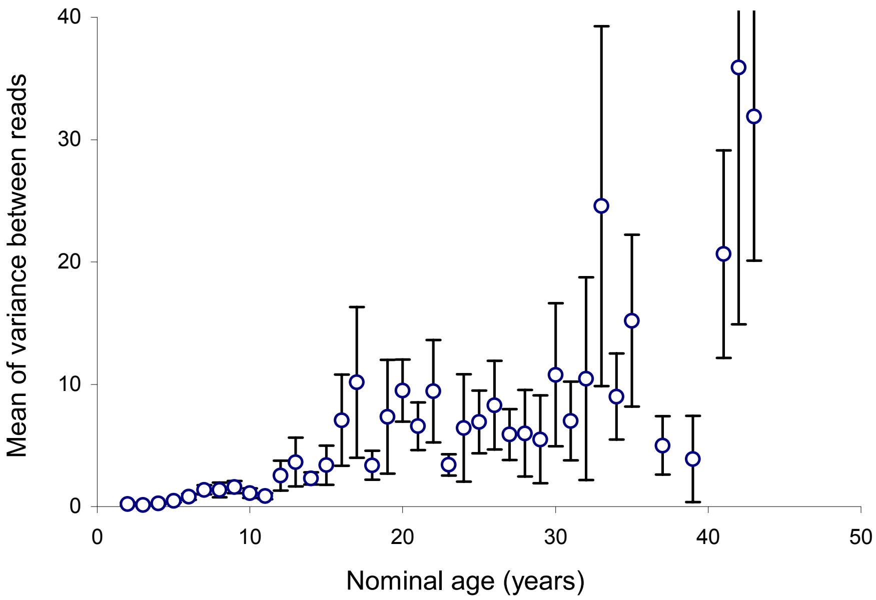


Figure 3.18. Mean of observed variances of age estimates among readings for nominal age groups. Error bars are standard errors about the estimates. Data from acid etched then machine-polished method excluded.

3.5. Discussion

3.5.1. Accuracy of age estimates.

Evidence from all validation studies supported the accuracy of the otolith section method for aging *L. bohar* sampled from the GBR and Seychelles. In addition, the importance of sectioning otoliths for estimating age of older *L. bohar* was demonstrated by the comparison of estimates from whole verses sectioned otoliths, where estimates from sectioned otoliths were double those from whole otoliths for the oldest age groups. Underestimation of age from readings of whole otoliths has been reported for many other teleosts, including tropical snappers (Rocha-Olivares 1998; Newman et al. 2000). The most likely explanation for the large observed discrepancy between methods was that growth additions on otoliths of older fish were linearly small and deposited on the proximal surface of the otolith and hence were more clearly visible on transverse sections (Brothers 1987).

The maximum nominal age estimate of 54 years indicates that *L. bohar* could be among the longest-lived of the lutjanids. Many other recent studies of lutjanids using otolith sections have reported maximum ages exceeding 30 years. Species include: *L. quinquelineatus* (31 years, Newman et al. 1996a); *L. peru* (31 years, Rocha-Olivares 1998); *L. erythropterus* (32 years, Newman et al. 2000); *Lutjanus campechanus* (52.6 years, Wilson and Nieland 2001); *L. malabaricus* (31 years, Newman 2002); *L. sebae* (34 years, Newman and Dunk 2002); and *L. argentimaculatus* (37 years, Russell et al. 2003). There is also much published evidence supporting the accuracy of tropical snapper age estimates from otolith sections, including studies that used bomb radiocarbon (Baker and Wilson 2001) and tetracycline marking and recapture (e.g., Cappo et al. 2000) methods, two of the most credible validation methods available (Campana 2001).

3.5.2. Percentage of Disagreements with Putative age.

Observed patterns in the frequency of discrepant readings with putative age most closely approximated those expected from a model in which the probability of growth increments being misinterpreted was constant for all growth increments (estimated to be approximately 0.09). The probability of recording discrepant estimates of age from replicate readings was demonstrated to increase as a function of the number of annuli counted (*t*) and the probability of not interpreting an annulus consistently (*p*), which was assumed to be the same for all annuli (H_2). The important implication of this is that the adoption of a traditional aging protocol (based on a static constant criterion of acceptance) would likely result in elevated discards of older otoliths and subsequent bias in derived fishery statistics such as mortality, longevity and growth. For example, in this study, adopting an acceptance criterion based on excluding otoliths for which repeat readings differed by more than one would result in exclusion from further analyses of 61% of fish nominally aged 10 years, 84.8% of fish aged 20 years and 97.7% of fish aged 40 years.

Other authors have simulated rates of random aging error with age to show that this can bias estimates of mortality from the average age method (Powers 1983), catch curve analysis (Barlow 1984), and optimum fishing mortality from yield per recruit analysis (Lai and Gunderson 1987). None of these studies, however, evaluated competing models for rates of aging error with age. The results from this study identify the best descriptive model of aging error with age for the aging methods used for *L. bohar*. From this evaluation it is possible to infer the biases likely to arise from the choice of alternative acceptance procedures. The investigation of the relationship between aging error rates and nominal age can also be useful for selecting the most appropriate acceptance procedure and thus minimise the likelihood of such procedural sources of bias.

It is important to note that in the analysis of the relationship between the percentage of disagreed ages (PD) and nominal age (*t*), all *t* above 41years were excluded because either the number of sample replicates per *t* was less than five or PD was 100%. As such, it was inferred that the age reader found it too difficult to achieve absolute agreement from replicate reads in otoliths nominally older than 41years and therefore there was likely to be no trend in PD with *t* above this "threshold" age. In reality there might or might not have been a trend, but the low number of sample replicates per *t* meant that the resolving power of the sampling strategy was not likely to detect a trend if it existed. Nevertheless, a very high rate of disagreement (approaching 100%) would be consistent with the preferred model for relating discrepancies to age, which showed the rate approaching its asymptote near 100% by nominal age 40 years (Fig. 3.14).

3.5.3. Inter-read Discrepancies with Putative age.

The magnitude of aging errors from replicate reads was observed to increase with nominal age, at a relatively constant rate. This result was consistent with that of Rein and Beamesderfer (1994) who also observed larger discrepancies among replicate sets of older age readings, but did not quantify this relationship. This result was also in line with theoretical expectations from the best approximating probabilistic model of aging error (H_2). The observed relationship therefore provided a justification for establishing an acceptance criterion that was a constant proportion of the number of annuli counted.

3.5.4. Effect of Geographic Area and Method.

Otoliths sampled from the Seychelles were read with lower precision than those from the GBR. This was most likely due to annuli on otolith sections from the Seychelles appearing to be fainter relative to those from the GBR (Fig. 3.13). This is consistent with a latitudinal effect on the readability of annuli, which has been posited for other species (Longhurst and Pauly 1987; Fowler and Doherty 1992; Choat et al. 2003; Smith and Deguara 2003). The most likely explanation for such an effect is that it is a manifestation of reduced seasonal climactic variation in lower latitudes resulting in a reduced contrast between translucent and opaque zones. This hypothesis, however, implies some causal link between opaque increment formation and seasonal environmental factors, which has not yet been verified (Fowler 1995).

Although marginal increment analyses of otolith sections from both geographic areas supported an annual cycle of opaque increment deposition in November and December, this was less distinct for those from the Seychelles. Opaque increments were observed to form over a longer period in otoliths from the Seychelles than those from the GBR. Opaque increments may form over a longer period in the Seychelles because of reduced seasonal amplitude in climactic variations that may trigger opaque increment deposition. Alternatively, increased errors in the identification of marginal increments in otoliths from the Seychelles due to the increased difficulty in identifying them could have resulted in an increased variability in MIR values recorded per month and a "smearing" of the annual mean MIR pattern. An increased slope of the otolith weight : sectioned age relationship for otoliths from the Seychelles provided additional evidence that opaque increment deposition in otoliths differs between populations from the GBR and Seychelles.

A higher observed mean IRD also was observed for age data from Seychelles otoliths. This was consistent with the inferred geographic difference in readability, since a lower aging precision could have been a manifestation of larger inter-read discrepancies. The general nature of trends in the rate and magnitude of discrepancies from replicate age readings with nominal age were similar, however, for otoliths collected from the different areas.

Although the difference in precision of age estimates from otolith sections prepared by different methods was shown not to be statistically significant, the “acid etched then mechanical-polished” method did result in a steeper rate of increase in observed mean IRD with nominal age bin. Approximately linear trends of mean IRD with nominal age bin were observed to not differ significantly in slope among the other methods. However, the mean IRD on nominal age bin was consistently significantly higher for data from the “acid-etched” method than from the “mechanical-polished” method. It is interesting that a consistent difference in mean IRD, yet a lack of detectable difference in precision, was observed between these methods. Also, methods were not consistently ranked in order of precision within area groupings, suggesting that observed differences in mean IRD among methods did not have a large influence on resulting precision.

3.5.5. Conclusion and the proposed agreement protocol.

Information about the relationship between aging imprecision (in the absence of bias) and putative age can be used to account for uncertainties in age estimation in age structured stock assessment models via aging error probability transition matrices (Richards et al. 1992). This is useful, as is the application of graphical and statistical measures for assessing imprecision and bias in age estimate data (Campana et al. 1995). Random aging errors are known to smooth differences in year class strength in sampled age frequency distributions (Kimura and Lyons 1991) and can bias some parameters directly with regard to certain modelling and statistical applications (Powers 1983; Barlow 1984; Lai and Gunderson 1987; Eklund et al. 2000). I have shown that the rate and magnitude of aging errors (random or biased) changed considerably with putative fish age and have argued that these patterns could result in serious biases when particular acceptance protocols are adopted.

This has wide ranging implications for studies that require the assignment of reliable age estimates to sample replicates, such as those modelling length-, percent maturity-, and fecundity-at-age trends and estimating mortality rates independently of applications where probability transition matrices can be applied. Many of these applications using age estimate data are studies of population biology, which can provide an important indication of potential harvest resilience of a stock (e.g., Musick 1999) prior to any formal assessment. An acceptance procedure is required that is consistent over all age groups and that is likely to result in unbiased estimates of age structure.

An allowable *rate*, rather than static constant, of discrepancy between replicate reads could be used as an acceptance criterion to avoid disproportionate discarding of sample replicates from any sampled age group (as evidenced by the support for H_2 in this case study). For aging of *L. bohar*, it was clear that the allowable discrepancy should be a constant proportion of putative fish age, after allowing for an initial offset of approximately 1.

In addition, it seemed appropriate to address a pre-set tolerance level of IRD that was considered acceptable in terms of the precision of the resultant data set. Under this approach, a standardised target level of precision across all age groups could be achieved whilst accounting for increasing PD and IRD with nominal age. Failing to include increasing magnitudes of errors with age, such as in many “static difference” acceptance procedures, would have likely resulted in the disproportionate discarding of older otoliths. The APE statistic (Beamish and Fournier 1981) provided a suitable criterion for calculating whether the observed IRD was acceptable for the purpose of achieving an agreed age, because it is widely used and explicitly related to fish age.

Although there is currently no general consensus in the literature for a maximum tolerable level of imprecision for age estimate data, Morison et al. (1998) expect an APE of less than 5% at the Australian Central Ageing Facility, while Campana (2001) stated that although an APE of less than 5.5% was frequently reported, many ageing laboratories set a target of 5% CV, which corresponds to 3.65% APE using his conversion formula. A critical level of 5% APE for agreement concurred with that of Morison et al. (1998) and required exact agreement among replicate age estimates for all fish estimated to be nominally 10 years or younger in the first read. Considering the relatively poor precision achieved for otolith sections from the Seychelles, this target level was more practical for *L. bohar* than the 3.65% APE recommended in Campana's (2001) review. Therefore, agreement of successive age estimates to within 5% APE was used for this study to minimise the number of otoliths discarded and, especially, those otoliths from older age groups.

Sampling a sufficient number of individuals from the largest, oldest age groups of a population is often cited as difficult in the biological and fisheries literature (Knight 1968; Hoenig 1983). The potential for increased discarding of samples from the oldest age groups due to an unjustified, inappropriate adoption of an acceptance protocol could accentuate this problem, particularly for long-lived species, which are typically vulnerable to overfishing (Musick 1999). This could lead to bias in stock assessments and inappropriate management advice for populations that are intrinsically vulnerable to overfishing. It is for these reasons the choice of criterion by which to accept age estimates should be based on the formalisation of a model for the error-generating process for each aging application—as it has been in this study—rather than the untested adoption of convention.

Chapter 4: Age-growth characteristics and within-Region effects.

4.1. Introduction.

Growth in body size is a major component of the biological production of a population (Hilborn and Walters 1992) and knowledge of growth is therefore critical for developing sustainable harvest strategies. Knowledge of the age and size structure of unexploited and exploited populations can be used to estimate rates of natural mortality (M) and fishing mortality (F; by subtracting M from total mortality, Z) respectively (Beverton and Holt 1957; Chapman and Robson 1960), which are key inputs to fisheries management. For example, estimates of M have historically been used to infer sustainable harvest yields directly (Gulland 1983) or used in combination with growth rate to predict optimal "yield per recruit" (Beverton and Holt 1957).

The tropical snappers (Lutjanidae) are typically long-lived, slow-growing reef fish with low rates of natural mortality (Manooch 1987). Lutjanids are also gonochoristic (Grimes 1987), and thus one might not expect female lutjanids to grow as quickly as males because females have greater energy requirements for reproductive development (Wootton 1985). However, since fecundity typically increases with size, there is a higher selective pressure for continued growth in females, but not in males, which predicts that females will grow to a larger size than males (Roff 1983), unless there is sexual selection for a larger male size (e.g., Hanson and Smith 1967; Perrone 1978). Previous studies of lutjanids have reported mixed results, with no sex-specific differences in maximum asymptotic length (L_∞) (e.g., Hood and Johnson 1998; Luckhurst et al. 2000; Newman et al. 2000; Patterson et al. 2001; Burton 2002; Newman and Dunk 2003), a longer L_∞ for females (e.g., Wilson and Nieland 2001; Russell et al. 2003), and a longer L_∞ for males (e.g., Davis and West 1992; Newman et al. 1996; Rocha-Olivares 1998; Claro et al. 1999; Newman et al. 2000; Burton 2001; Kritzer 2002). Previous studies of *L. bohar* have also reported mixed results for age-growth characteristics (Wheeler 1953; Talbot 1960; Loubens 1980; Wright et al. 1986) and of these, only one (Talbot 1960) noted no apparent difference in growth rate between sexes.

These different results for *L. bohar* among studies could be due to inconsistent methodologies or differences in local environmental factors (Wright et. al. 1986). Given the large differences in maximum age estimated from previous studies (i.e., 3 – 38 years) and this one (nominally 54 years), it was considered likely that the method of age estimation was responsible. The oldest estimates of age were obtained from otolith sections (Loubens 1980; this study). The accuracy of this method has been shown for this species (Chapter 3) and other long-lived congenerics (Cappo et al. 2000; Baker and Wilson 2001).

The aims of this Chapter were two-fold: (i) to describe basic age-growth characteristics for *L. bohar* under conditions of relatively low exploitation; and (ii) to explore the influence of sex and sampling regime on results. The “age-growth characteristics” investigated in this Chapter were for *L. bohar* from the Lizard Island Region and included: population age and size structure, growth (i.e., length-at-age), condition (i.e., weight-at-length), and mortality. The influences of sampling regime (ELF Experiment treatments, methods, depth, and year) and sex were explored to account for factors that could potentially influence results and thus, if ignored, confound inferences about life history strategy and harvest predictions. These results for *L. bohar* from the Lizard

Island Region will be used as a template for the broader spatial and temporal comparisons of age-growth characteristics in the next Chapter (5).

4.2. Methods.

4.2.1. Sample and data collection.

Samples from the Lizard Island Region were collected in the Austral spring, from 1995 to 2001 and in 2003, as described in Chapter 2. Sagittal otoliths were processed and read for age estimation according to the methods described in Chapter 3. Sex was determined from inspecting preserved gonads using microscopic (n = 60) or macroscopic (n = 182) characteristics. Medial transverse sections of gonad lobes were prepared for microscopic examination by dehydrating in alcohol, embedding in wax, histological processing, and then counter-staining with haemotoxylin and eosin according to the procedure outlined in Samoilys and Roelofs (2000). Sex was determined microscopically according to the type of gamete(s) and transverse gonad structure visible, as described by Nagahama (1983) and Reynaldo and Fumio (1995).

Sex was also determined macroscopically from inspecting freshly-dissected gonads in the field or preserved gonads in the laboratory. Colour was not a reliable indicator of sex because it varied with gonad development in both sexes (Table 4.1). To determine sex it was often necessary to cut transversely through one of the gonad lobes using a scalpel to observe the shape of the transverse section and internal gonad lobe characteristics (Table 4.1).

Table 4.1. Criteria for sex determination based on macroscopic characteristics of *L. bohar* gonads.

	Maturity	Macroscopic features
Ovaries	Immature	- White to beige - Rounded in cross-section - Distinctly thick gonad wall and granular internally
	Mature	- Beige to dark tan / orange - Often with brown speckles - Rounded in cross-section - Distinctly thick gonad wall and granular internally
Testes	Immature	- White to light grey - Strap-like
	Mature	- Pale pink to dark pink / grey - Triangular to occasionally rounded in cross-section - Not granular internally and often the central sperm ducts are visible as a lighter area.

Whole otolith readings (Chapter 3) of *L. bohar* less than 300 mm FL were done to identify individuals that had not formed, or had recently formed, the first annulus. The otoliths of these fish (n = 12) were then prepared for age estimation (days) according to the methods of Lewis and Mackie (2002). The approximate position of the otolith primordium was marked on the distal surface of left sagittal otoliths using a needle dipped in Indian ink and the otolith was then carefully embedded in clear casting polyester resin (UN 1866). After hardening, the blocks were ground and polished with 1200 grade wet and dry emery paper to ensure they could be squarely mounted for sectioning in the chuck of a Buehler Isomet low speed saw fitted with a rotating diamond tip blade.

A thin (350-400 μm) transverse section (including the otolith primordium) was cut from each block and manually polished on both sides using a series of wet polishing papers of decreasing coarseness (9, 5, and 3 μm). Polishing was ceased when it was judged that a clear, complete sequence of inferred daily increments could be seen along one axis, from the primordium to the outer edge of the otolith section. Live images of otolith sections were viewed at high power magnification (400X) using Optimus computer software and a compound microscope. Counts of presumed daily increments (i.e., microincrements; Fig. 4.1) were recorded using a hand counter. Up to three independent readings of each otolith were done and counts were accepted using the same method that was used for counts of annuli (Chapter 3). Accordingly, this assumed that the rationale for accepting counts from replicate reads of annuli also was appropriate for replicate reads of microincrements. Further, no validation was done to test the assumption that these microincrements were formed on a daily basis.

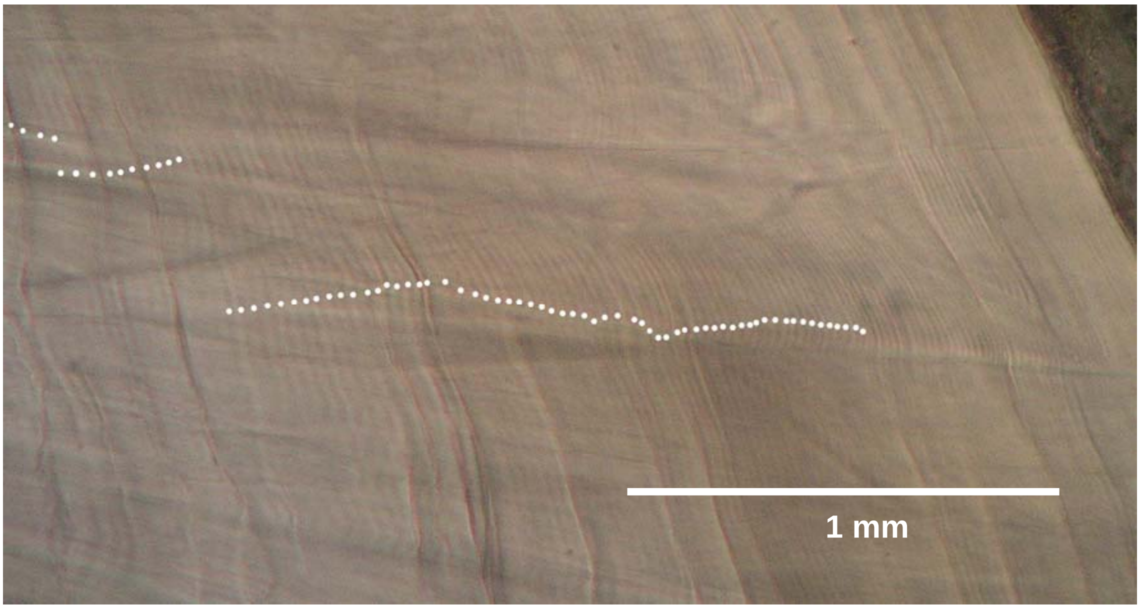


Figure 4.1. Microincrement structure of the transverse section of a sagittal *L. bohar* otolith. This image shows the field of view between the otolith primordium (bottom left) and the proximal surface (top right) on the ventral half of the otolith. White dots indicate positions of 75 microincrements. Microincrements were typically counted from the otolith primordium to the ventral tip for estimates of fish age in days. Image as viewed at 100X magnification.

These daily estimates of age were used to calculate age estimates (years) from counts of annuli according to the following procedure. Firstly, the daily estimates of age were converted to annual estimates of age , “∇”, by dividing by 365 (a standard calendar year). Secondly, the mean of these converted estimates, $\overline{\nabla}$, was calculated. Since all *L. bohar* for growth analyses were sampled at the same time of year (Spring), which also coincided with the approximate timing of annulus formation (Chapter 3), it was assumed that $\overline{\nabla}$ approximated the average annual age at which the first increment was deposited in all *L. bohar*. Thirdly, age estimates from counts of annuli were calculated by subtracting 1-$\overline{\nabla}$ from all annulus counts if $\overline{\nabla}$ was less than one, or adding $\overline{\nabla}$-1 if $\overline{\nabla}$ was greater than one.

4.2.2. Analyses: age and size of *L. bohar*.

Two sets of multi-factor ANOVAs were done to explore spatial, temporal and biological variation in age and size of *L. bohar* caught on catch surveys of the ELF Experiment. First, the influence of ELF treatment (GC, GF, BF; hereafter referred to as “zone”; see Chapter 2), sample year (1995 to 2001, 2003), and reef (the experimental unit: 2 nested within each zone) on mean age (years) and length (mm FL) were tested by 3-factor nested analyses [Year x Zone x reef(Zone)]. Second, the influences of sex, zone, and year on mean age and FL were tested by 3-factor analyses (Sex x Zone x Year). These separate 3-factor ANOVAs were done to avoid statistical zeros that would have occurred in 4-factor analyses (sex, zone, year, reef).

Model III Sums of Squares were used for ANOVA tests in “SPSS for Windows” (Version 11.0; SPSS inc.) software to account for uneven sample numbers per cell (n). Samples of *L. bohar* from Eyrie reef (GF zone) were excluded from the first ANOVA to avoid (3) statistical zeros in the analysis except for the 1996 Eyrie sample, which was used to replace a statistical zero of a GC reef in 1996 (Table 4.2). This substitution was based on the assumption that a sample from Eyrie reef was equivalent to a random sample from a GC reef in 1996, which was considered reasonable because GC and GF treatments were effectively equivalent in that year (see Table 2.1). Significant interaction effects were explored using single factor ANOVAs to test for the effect of one factor for each level of the other (interacting factor). Tukey's Honestly Significant Difference (HSD) tests for unbalanced designs (Tukey 1953; Kramer 1956 *in* Zar 1999) were then done to further explore effects detected from the ANOVAs.

Table 4.2. Frequency of *L. bohar* collected per zone, reef, and year from the Lizard Island Region during spring catch surveys of the ELF Experiment. Numbers represent frequencies of *L. bohar* with assigned age estimates. Each "zone" was a treatment of the ELF experiment (see Chapter 2 for details).

Zone	Reef	Year								Total
		1995	1996	1997	1998	1999	2000	2001	2003	
BF	14133	3	3	5	6	9	6	6	6	44
BF	Rocky Islets B	9	1	6	6	7	6	16	2	53
GC	MacGillivray Reef	7	0	15	6	6	12	16	19	81
GC	South Direction Island	9	2	15	5	12	4	8	5	60
GF	Eyrie Reef	2	4	0	0	0	2	1	10	19
GF	Rocky Islets A	16	2	6	1	3	7	13	10	58
Total		46	12	47	24	37	37	60	52	315

A 3-factor log-linear analysis was done by step-wise backward elimination (Gilbert 1981) to identify the relative importance of sex, zone and year, or their interaction, on sampled frequencies of *L. bohar*. This was done as an initial exploratory analysis to detect the gross influence(s) of sex and sampling regime on the number of *L. bohar* sampled prior to analyses of population age and size structure. The log-linear analysis was done for data collected from ELF Experiment spring catch surveys done in 1999, 2000, 2001 and 2003 because sex determination was attempted for all *L. bohar* gonads collected only in these years. The model with the fewest terms that was not significantly different from the full factor model, which included all terms and was thus identical to the original data matrix (Table 4.3), was accepted as the most parsimonious description of the frequency data.

Table 4.3. Frequency of *L. bohar* collected from the Lizard Island Region during spring catch surveys of the ELF Experiment per zone, sex, and year. Numbers represent frequencies of *L. bohar* for which sex was determined confidently from microscopic or macroscopic inspection of gonads. Frequencies shown for 1999, 2000, 2001 and 2003 because sex determination was attempted for all *L. bohar* gonads collected from ELF Experiment catch surveys done only in these years.

Zone	Sex	Year				Total
		1999	2000	2001	2003	
BF	Male	9	6	9	3	27
BF	Female	6	5	9	3	23
GC	Male	11	4	11	12	38
GC	Female	4	8	10	9	31
GF	Male	1	5	4	5	15
GF	Female	2	4	7	11	24
Total		33	32	50	43	158

Sampled *L. bohar* frequencies were then grouped into categories of FL (50 mm bins) and annual age for chi-square contingency table analyses done to test the effects of year, zone, and sex on FL and age group frequencies (Zar 1999). Successive categories of FL or age were pooled to ensure observed cell frequencies were at least two. Further pooling of successive FL or age groups was then done, if required, to meet the minimum observed cell frequency requirement of Roscoe and Byars (1971) (i.e., the average of cell frequencies in each contingency table was at least 6). If, after pooling, less than three FL or age groups remained, contingency table analyses were not done. If more than three FL or age groups remained, all satisfactory permutations of pooled age or FL categories for each contingency table analysis were tested. This was done to avoid potential biases arising from the selective pooling of FL or age groups.

The effect of year on the frequency of *L. bohar* collected per FL or age group from GC reefs was tested first. GF reefs had the same status and history as the GC reefs prior to manipulations of the ELF Experiment (see Table 2.1) and so pre-manipulation data from GF reefs were treated as GC reefs to increase the replicates per cell for this analysis. Data for 1996, 1998, and 2000 were excluded because sample numbers were too few. Sample numbers were also too few for testing the effect of year on FL or age group frequencies for other zones.

The effect of zone within survey year on the frequency of *L. bohar* collected per FL or age group was then tested. Tests were constrained to data collected in the same year because it was not appropriate to pool FL or age group frequencies across years in GF and BF zones due to the temporal manipulations of pulsed fishing effort in these zones (Chapter 2). The effect of sex on the frequency of *L. bohar* collected per FL or age group was then tested. The decision to pool FL or age group frequencies for testing effects of sex was based on the prior detection of interaction effects of sex with zone and/or with year from the log-linear analysis.

4.2.3. Analyses: Growth.

Single factor ANOVAs were done to compare mean FLs of common age groups among zones for each level of year and among years for each level of zone. Single factor ANOVAs were done to avoid statistical zeros that would have occurred in the corresponding 2-factor analysis. ANOVAs were done for those age groups most frequently sampled. Years or zones with statistical zeros were excluded. ANOVA tests for the effect of sex on the mean FL of common age groups were then done. FL-at-age data were pooled across years (and/or zones) for the test of sex if no effect of year (and/or zone) was detected in prior tests of year for each zone (and/or tests of zone for each year).

Growth trends were modelled by fitting the von Bertalanffy growth function to FL-at-age data. All models were fitted using the SPSS non-linear regression package. The von Bertalanffy model used was of the form:

$$L_t = L_\infty (1 - e^{(-K(t-t_0))}) \tag{4.1}$$

where;

L_t = FL of fish at age t;

t = age (years);

L_∞ = asymptotic length parameter (average maximum FL);

K = growth coefficient;

t_0 = theoretical age at zero length.

Estimates of L_∞ for *L. bohar* were converted from FL to total length (TL) for comparison with other published results for lutjanids using the FL : TL conversion function reported by Wright et al. (1986) (Eqn. 4.2).

$$\mathrm{FL} = 0.99\mathrm{TL} - 1.29 \tag{4.2}$$

where FL and TL are measured in cm. Estimates of L_∞ for other lutjanids reported in standard length (SL) or FL were converted to TL using the functions available on the Fishbase website (Froese and Pauly 2004).

The influence of zone and sex on the fit of the von Bertalanffy model to FL-at-age was investigated by statistically comparing fitted parameter estimates using Likelihood Ratio tests and 95% confidence regions according to the methods described by Kimura (1980). Likelihood ratio tests are valid only when models were fitted to the same range of data (Haddon 2001), so where differences in sampled age ranges were apparent, the older age groups were dropped from some samples such that all samples had the same age range.

"Coincident" likelihood ratio tests were done to assess overall similarity of model fits to FL-at-age among data sets ("treatment groups") grouped by levels of the tested factor. For example, for the test of zone, separate model fits to FL-at-age from each zone (GC, GF, BF) were compared. Likelihood ratio tests compared the combined residual variation from separate, unconstrained model fits to each treatment group (RSS_{Ω}) to that from model fits where parameter(s) were constrained for a specific hypothesis (RSS_{ω}; Kimura 1980). For the coincident test, the null hypothesis was that there was no difference in any of the parameters estimated among the separate model fits, so the RSS_{ω} was calculated from the combined residual variation when all parameters (i.e., L_{∞}, K and t_0) were constrained to the same estimates. For subsequent likelihood ratio tests the null hypothesis was that there was no difference in estimates of one parameter (e.g., L_{∞}) among the separate model fits, so the RSS_{ω} was calculated from combined residual variation when that parameter was constrained to the same estimate.

Alternatively, 95% confidence regions were representations of the uncertainty about fitted von Bertalanffy parameter estimates and thus confidence regions for each treatment group were derived from the entire set of data available per treatment group (i.e., not truncated as above). Cross-sections of the approximate 95% confidence regions of $\hat{L}_\infty$ and $\hat{K}$ for the fit to each treatment group were generated by conditioning on $\hat{t}_0$. These were then overlayed on the same plot to visually assess overlap and thus infer the significance of differences in model fit. These two-dimensional comparisons assumed that estimates of t_0 had no bearing on the constructed 95% confidence regions of $\hat{L}_\infty$ and $\hat{K}$ so were only done if there was no significant difference in $\hat{t}_0$ detected by the corresponding likelihood ratio test. These results could then be compared to those from likelihood ratio tests of $\hat{L}_\infty$ and $\hat{K}$ to evaluate the general robustness of the two sets of results.

Trends in weight-at-FL were described using the power function:

$$W = aL^b \tag{4.3}$$

where;

W = whole fish weight (g);

L = FL (mm);

a, b = model parameters.

Multi-factor ANCOVA tests were done following the linear transformation of weight-at-FL data to investigate the influence of zone and year, year and sex, and zone and sex, on *L. bohar* body condition. FL data were transformed by the exponent integer approximating $\hat{b}$ common to all fitted weight-at-FL relationships. The FL range of weight-at-FL data was also truncated prior to analysis where necessary to standardise the range of data compared among treatment groups.

Three 2-factor analyses were done in preference to one 3-factor ANCOVA because there were insufficient data to test for differences in slope across the three-way interaction of zone, sex, and year (Tables 4.2, 4.3). Single-factor ANCOVA tests were done to further investigate significant interaction effects from the multi-factor tests. The relationships of linear-transformed weight-at-FL data found to be significantly different from the *post-hoc* tests were then overlayed on the same plots for comparison.

4.2.4. Analyses: Mortality estimation.

Age data were pooled across those factors found not to have a significant effect on age frequencies, and the resulting distribution was used for a catch-curve analysis (Ricker 1975) to estimate the total mortality coefficient (Z) for the population. The catch-curve analysis involved fitting a linear regression to the natural-logarithm of the observed frequency of *L. bohar* sampled per age (dependent variable) on age (independent variable). The linear regression model was fitted to those data above and including the inferred “age at full recruitment” (t_r), which was the mode of the log-transformed catch-at-age frequencies.

The slope coefficient of the fitted linear regression (catch curve) was then taken as an estimate of Z. Mortality coefficients were also estimated using the published formulas of Pauly (1980) (Eqn. 4.4) and Hoenig (1983) (Eqn. 4.5), who quantified general relationships between mortality with von Bertalanffy growth model parameters and environmental temperature, and with maximum age, respectively.

$$\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log T \qquad (4.4)$$

$$\ln(Z) = 1.44 - 0.982 \ln(t_{\max}) \qquad (4.5)$$

where;

M = exponential coefficient of natural mortality;

L_∞ = von Bertalanffy model asymptotic length parameter (cm TL);

K = von Bertalanffy model growth coefficient;

T = mean environmental temperature (^{o}C);

Z = exponential coefficient of total mortality;

t_{max} = maximum estimated age (years).

An estimate of mean annual environmental temperature for Lizard Island Region was approximated to be 26.3^{o}C, which was the average of daily temperature readings taken at Carter Reef (Fig. 2.3a) in 2000 (Steinberg and Burrage 2001). Estimates of Z were assumed to approximate M when estimated for *L. bohar* sampled from GC zones (i.e., reefs closed to fishing).

4.3 Results.

4.3.1. Samples collected by different methods.

The FL frequency distributions obtained from different sampling methods demonstrated the effectiveness of spear-fishing and drop-line commercial fishing for supplementing the range of data from the ELF Experiment (Fig. 4.2). Spear-fishing was effective for targeting juveniles down to 114 mm FL and an estimated 147 days of age. Commercial drop-line fishing in deeper waters and closer to the outer GBR was effective for sampling proportionally more of the large *L. bohar,* up to 690mm FL and 44.46 years. Figure 4.2 shows how this additional sampling effort increased the FL range (232 mm

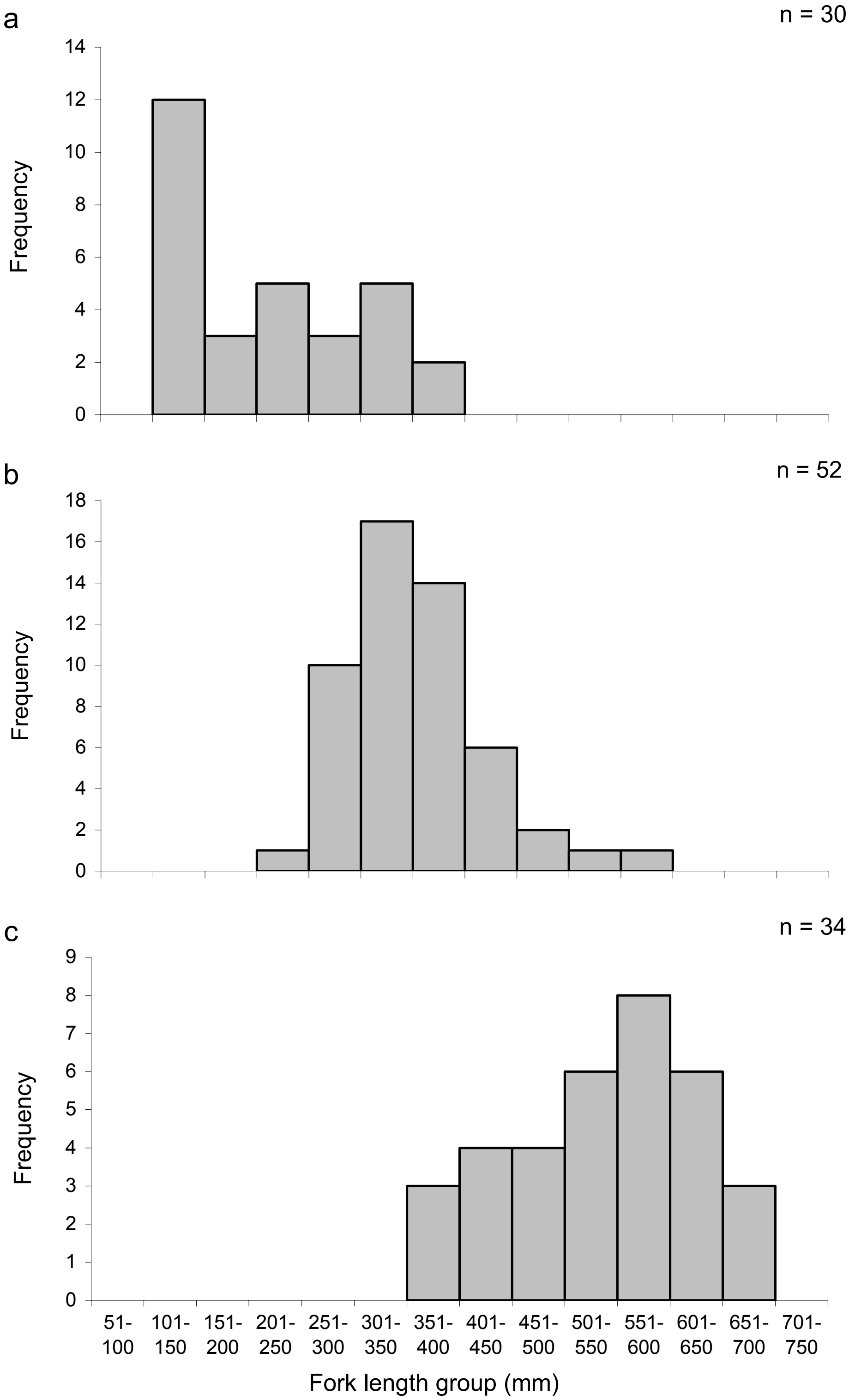


Figure 4.2. Length frequency distributions from using different sampling methods. All samples collected in Austral spring (September to October) in the Lizard Island Region. Samples in (a) represent targeted spearing of *L. bohar* < 300 mm FL in 2002 (to 9 m depth); samples in (b) and (c) collected in 2003 by line fishing from ELF catch surveys (0 to 30 m depth) and a commercial fishing operation (30 to 50 m depth), respectively.

to 593 mm FL) and age range (1.46 to 31.46 years) of the sample collected from the 2003 ELF catch survey; thereby increasing the range of FL-at-age data available for growth analysis (Section 4.3.3).

4.3.2. Age.

The age of *L. bohar* sampled from ELF catch surveys ranged from 1.46 to 43.46 years and was on average 6.57 ± 0.30 years old. *L. bohar* sampled from the BF zone appeared younger on average than those from GC and GF zones (Fig. 4.3a). The mean age of *L. bohar* was also observed to vary with sample year, ranging from 4.35 ± 0.43 years in 1999 to 10.32 ± 1.73 years in 2000, with no clear temporal trend (Fig. 4.3b). Females were slightly older on average than males (Fig. 4.3c).

Age data were log-transformed to remove skew and improve normality for analysis. Significant interactions of zone and year were detected, and there was no significant effect of reef within zone (Tables 4.4). Single factor ANOVAs provided insight into the origin of the Zone x Year interaction. An effect of year for all zones and an effect of zone in 1995, 1998, and 2003 (Table 4.4b) was detected.

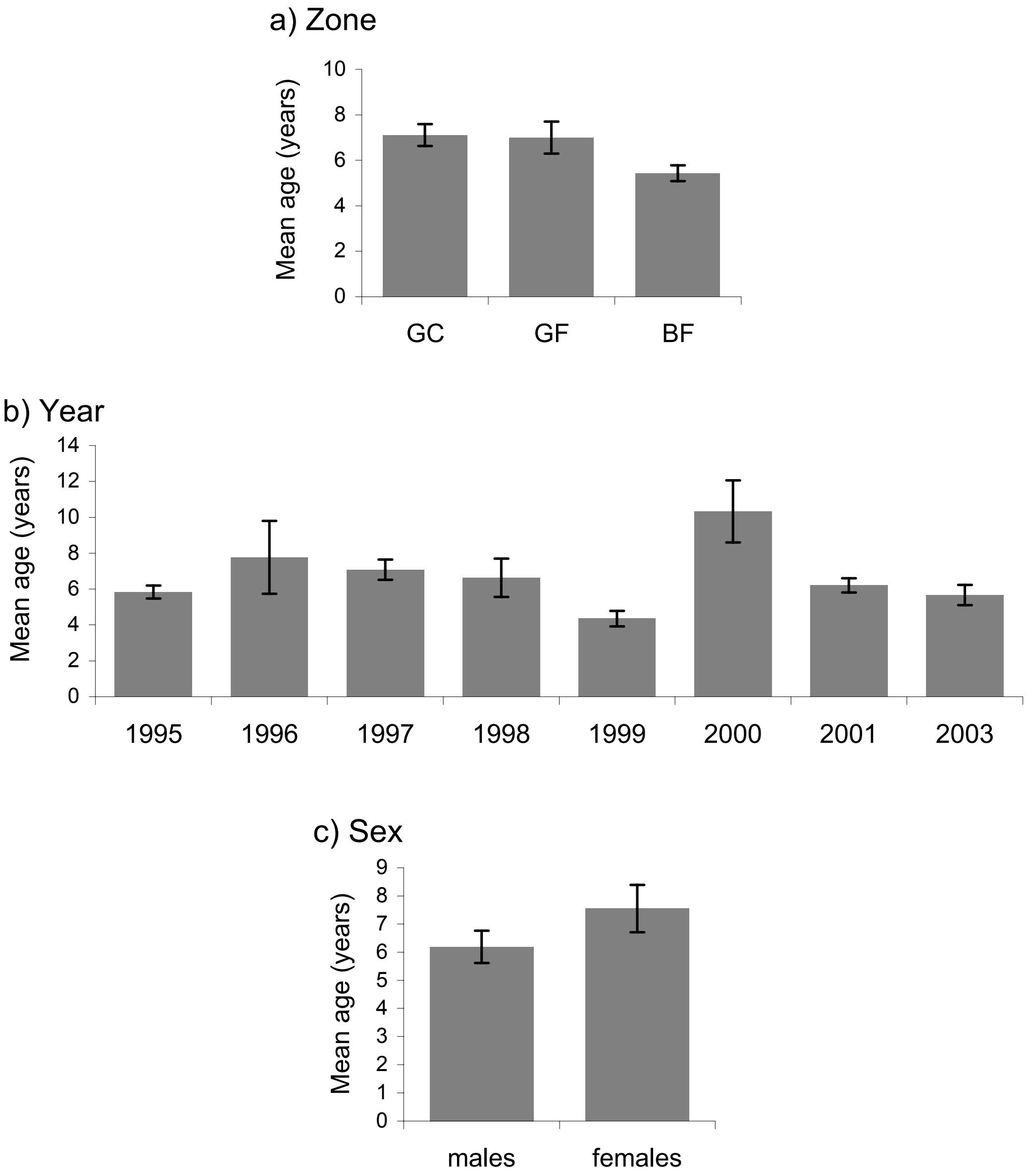


Figure 4.3. Mean age. Error bars are standard errors of mean age.

The multiple comparison tests revealed the nature of Zone effects for each year (Table 4.4c) and Year effects for each zone (Table 4.4d). Significantly younger ages were sampled from the BF zone than from the GC zone in all years where a zone effect was detected (Table 4.4c). A significantly older mean age from the GF zone than from GC and BF zones was detected in 1998, but this reflected the relatively old age (28 years) of only 1 replicate sampled from the GF zone in that year. Differences among years for each zone were variable: *L. bohar* sampled in 1999 were consistently among the

Table 4.4. ANOVA of zone, year, and reef (within zone) on average age of *L. bohar*. (a) ANOVA table from the multi-factor analysis (b) Results of single factor ANOVAs testing the effect of Year for each zone (Tests 1-3) and the effect of Zone for each year (Tests 4-11). ANOVA results significant at $\alpha = 0.05$ in **bold**. Tukey's HSD *post hoc* test for unbalanced designs among zones for each year (c) and among years for each zone (d). Groups joined by bold line were not significantly different ($\alpha = 0.05$). All tests done on log-transformed ages ($X' = \log_{10}(X + 1)$). * = Tukey's HSD tests only done for groups (Factor Levels) where a significant effect was detected by single factor ANOVAs.

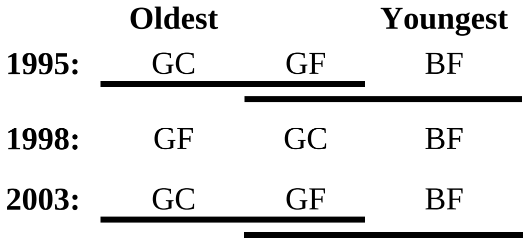
a) Multi-factor ANOVA.

	MS	d.f.	F	p
Zone	0.182	2	23.209	**0.015**
Year	0.146	7	13.818	**<0.001**
Zone x Year	0.062	14	5.808	**<0.001**
Year x Reef(Zone)	0.011	21	0.753	0.773
Reef(Zone)	0.008	3	0.557	0.64
Residual	0.014	168.45		

b) Single factor ANOVAs exploring the Zone x Year interaction.

Test	Factor Level	Factor Tested	F	df1	df2	p
1.	GC	Year	2.35	7	137	**0.027**
2.	GF	Year	3.54	7	50	**0.004**
3.	BF	Year	4.63	7	89	**<0.001**
4.	1995	Zone	4.41	2	41	**0.018**
5.	1996	Zone	2.26	2	10	0.155
6.	1997	Zone	1.28	2	44	0.288
7.	1998	Zone	23.20	2	21	**<0.001**
8.	1999	Zone	0.98	2	34	0.388
9.	2000	Zone	0.31	2	32	0.739
10.	2001	Zone	2.66	2	57	0.079
11.	2003	Zone	4.70	2	39	**0.015**

c) Post-hoc tests* comparing zones for each year.



d) Post-hoc tests* comparing years for each zone.

	Oldest							**Youngest**
GC:	2000	1998	1996	1995	1997	2003	2001	1999
	—	—	—	—	—	—		
		—	—	—	—	—	—	—
GF:	1998	2000	2001	1995	1997	1996	1999	2003
	—	—	—					
		—	—	—	—	—	—	—
BF:	1997	2000	1996	2001	1995	1998	2003	1999
	—	—	—	—				
		—	—	—	—	—	—	
			—	—	—	—	—	—

youngest sampled and those from 2000 were consistently among the oldest sampled (Table 4.4d). There was also no significant effect of sex on mean age of *L. bohar* sampled on spring catch surveys, either alone ($F_{1,134} = 0.91$; p = 0.34) or in interaction with zone ($F_{2,134} = 0.50$; p = 0.61), year ($F_{3,134} = 0.79$; p = 0.50), or with zone and year ($F_{6,134} = 1.01$; p = 0.42).

Most *L. bohar* caught on ELF catch surveys were young relative to the maximum age sampled (43.46 years), with fish older than 15 years scarcely sampled (Figs. 4.4, 4.5, 4.6). More *L. bohar* and an older modal age (5.46 years) was sampled from the GC zone than from GF and BF zones (Fig. 4.4). The division of age frequencies by year did not result in any obvious temporal patterns (Fig. 4.5) but a highly variable modal age, ranging from 2.46 years in 1999 to 5.46 years in 1998. There was no obvious recruitment pulses except possibly of 2.46 year olds in 1999 (48.3% of sample), but sample numbers were typically low (i.e., n = 12 in 1996), so it is unlikely that there was sufficient resolution to detect such trends. There were also conspicuously more males sampled in the 1.46 to 3.46 age groups and more females sampled above 9.46 years of age from ELF catch surveys (Fig. 4.6).

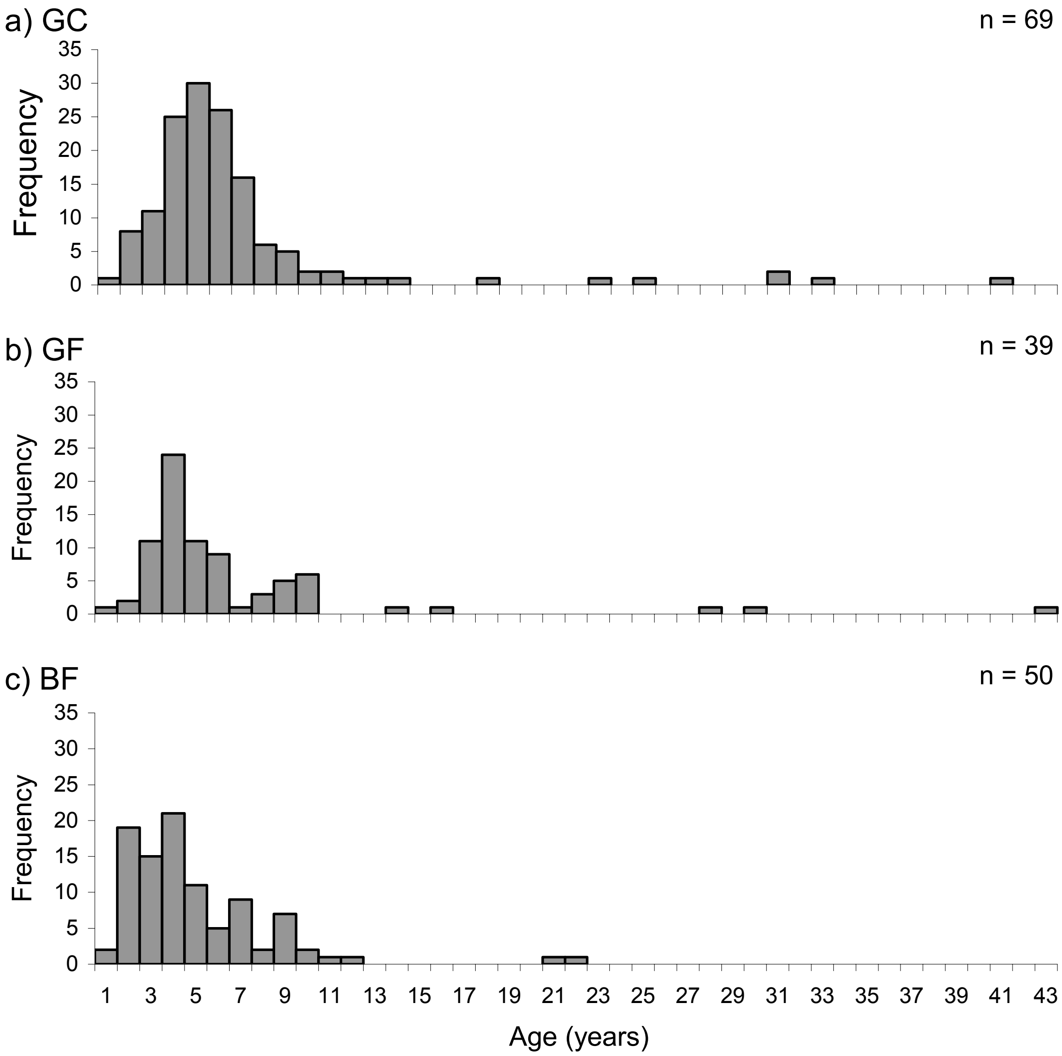


Figure 4.4. Age frequencies sampled from each zone. Data pooled across years, sexes.

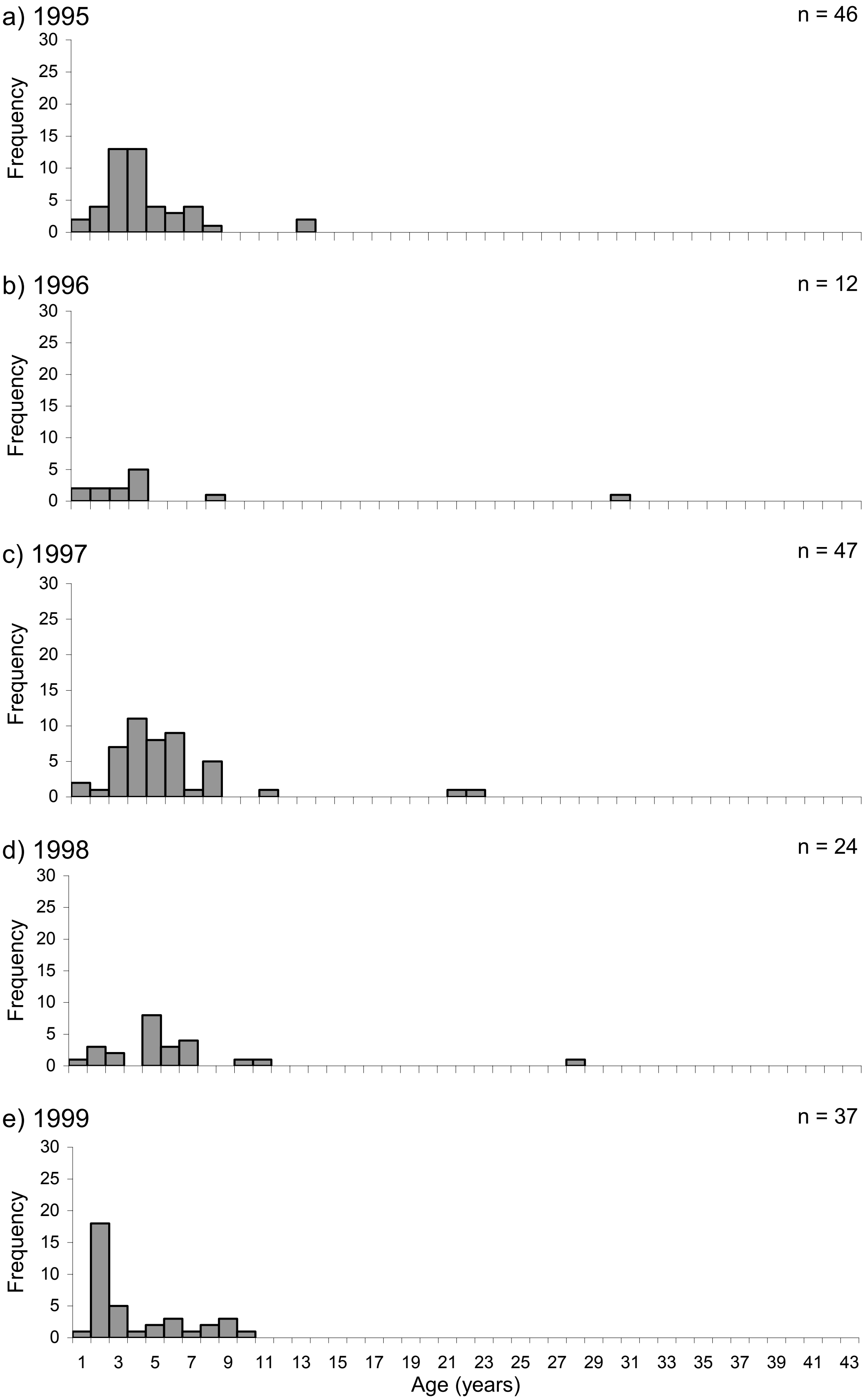


Figure 4.5. Age frequencies sampled each year. Data pooled across zones, sexes.

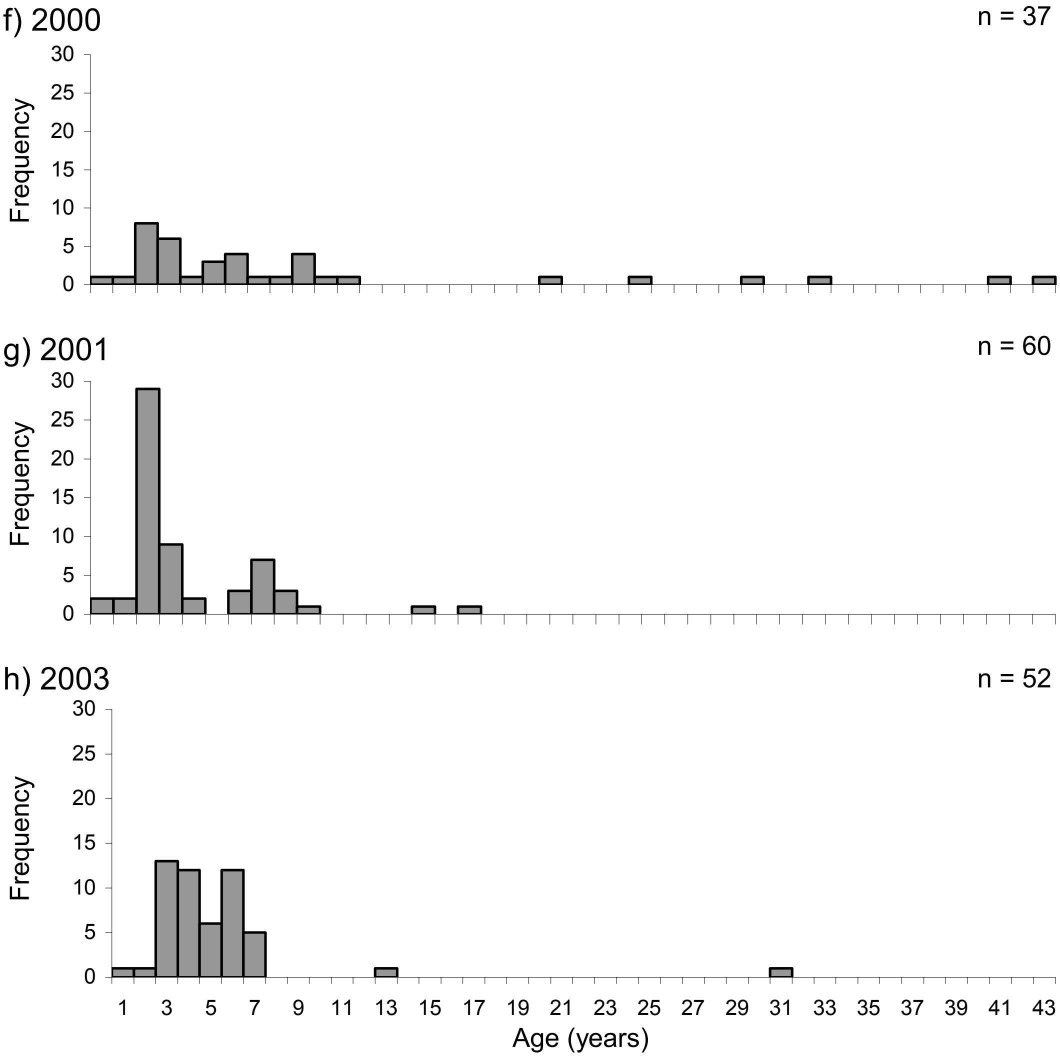


Figure 4.5. Age frequencies sampled each year (continued).

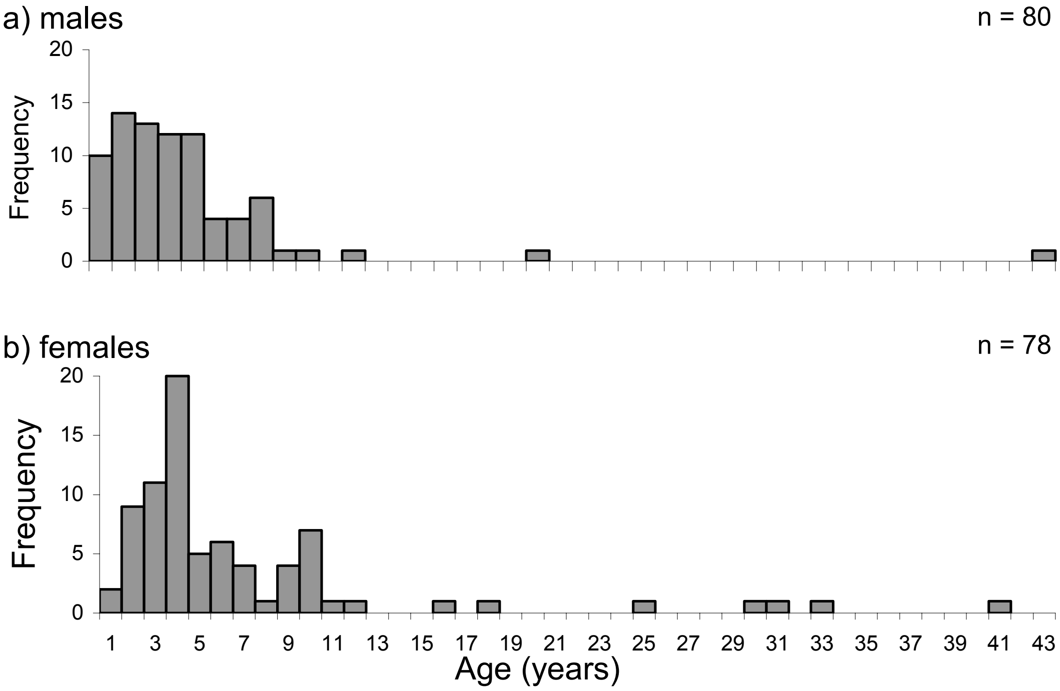


Figure 4.6. Sex-specific age frequency distributions. Data pooled across zones, years.

The most parsimonious log-linear model for the description of *L. bohar* frequencies per sex, zone, and year was comprised only of the main effect of zone (G^2_{21} = 30.10; p = 0.09). This demonstrated the over-riding importance of zone in explaining the frequency of *L. bohar* collected from the Lizard Island Region because the total frequency of *L. bohar* sampled from each zone accounted for most of the variability in the observed data matrix. This also indicated that the relative frequencies of *L. bohar* sampled per sex (i.e., the sex ratios) were not important and were thus inferred to be relatively uniform and to have remained relatively unaffected by zone or sample year. Many more *L. bohar* were sampled from the GC zone than from the BF and GF zones (Fig. 4.4).

Results from chi-square contingency table analyses of *L. bohar* age frequencies are shown in Table 4.5. Sample year was found to have no significant effect on age frequency distributions within the GC zone. Sample numbers were sufficient to compare age and FL frequency distributions between 2 zones in 2 years only. For 2001, age (Table 4.5; Tests 2a,b,c) frequency distributions were not significantly different between GC and BF zones. In 2003 though, a comparison of GC and GF zones revealed a significant difference (Table 4.5; Tests 3a,b). Age frequency distributions for GC and GF zones in 2003 are shown for visual comparison in Figure 4.7. In 2003 it can be seen that more young *L. bohar* were sampled from GF reefs and more older *L. bohar* were sampled from GC reefs, which is consistent with the trend observed in Figure 4.3.

Table 4.5. Chi-square contingency table analyses of age group frequencies. Analyses determine if observed relative frequencies by treatment group of the tested "Factor" were contingent upon "Age groups" for a subset of "Data." Age groups rounded to zero decimal places. Results significant at $\alpha = 0.05$ in **bold**.

Test	Factor	Data	Age groups	χ^2	df	P
1.	Year	GC	<5, 5, 6, 7+	17.17	12	0.143
2a.	Zone	2001: GC v BF	<5, 5, 6+	2.04	2	0.360
2b.	Zone	2001: GC v BF	<5, 5-8, 9+	2.54	2	0.280
2c.	Zone	2001: GC v BF	<6, 6-8, 9+	1.04	2	0.595
3a.	Zone	2003: GC v GF	<5, 5, 6+	7.46	2	**0.024**
3b.	Zone	2003: GC v GF	3, 4, 5+	7.63	2	**0.022**
4.	Sex	ELF: All	<3, 3, 4, 5, 6, 7-8, 9, 10+	13.61	7	0.059

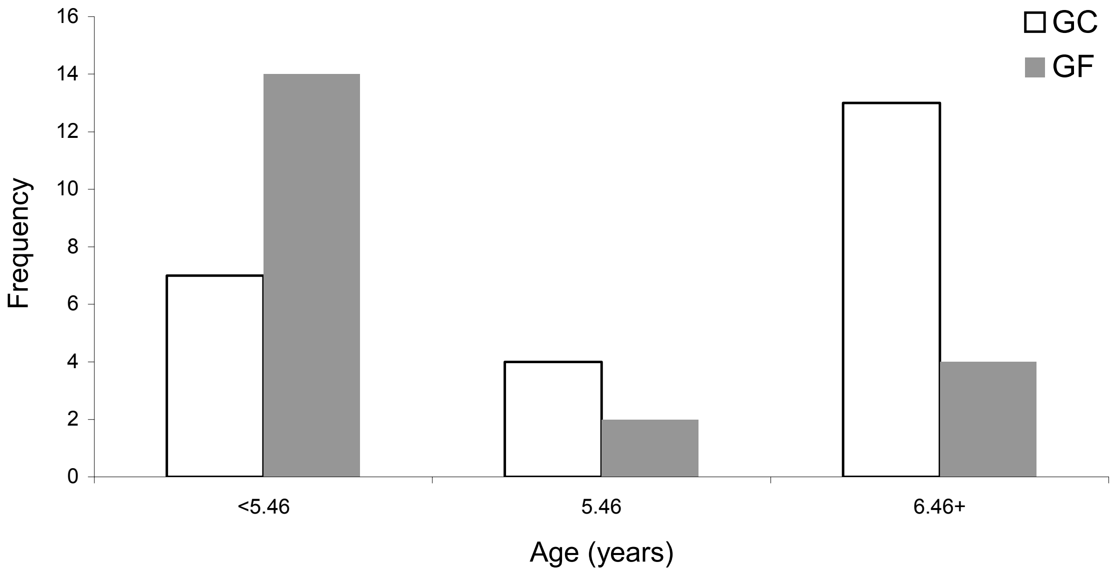
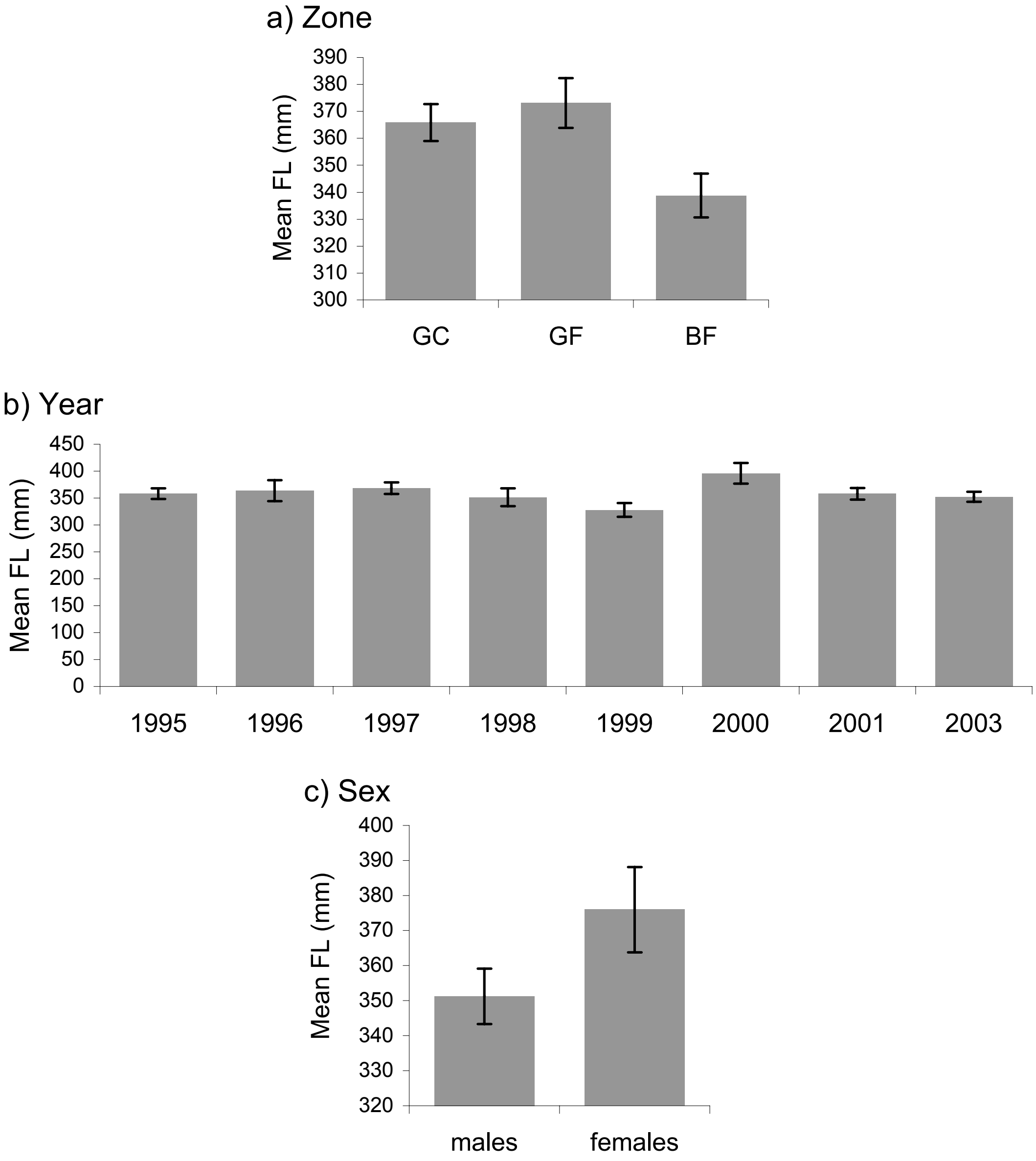


Figure 4.7. Comparison of sampled age frequency distributions of *L. bohar* between zones in 2003. Shown are frequency distributions of age group (GC age range: 3.46-31.46 years; GF age range: 3.46-7.46 years) that were used in chi-square contingency table analyses (Table 4.5, test 2a).

4.3.3. Fork length.

The FL of *L. bohar* sampled from ELF catch surveys ranged from 215 to 695 mm and was 360.23 ± 4.52 mm on average. *L. bohar* from the BF zone were noticeably shorter on average than those from the GC and GF zones (Fig. 4.8a). The mean FL by year appeared relatively stable, ranging from 327.76 ± 12.67 mm in 1999 to 395.87 ± 19.09 mm in 2000 (Fig. 4.8b). Also, females were noticeably longer on average than males (Fig. 4.8c).

FL data were square-root transformed to improve the normality of data for analysis. Significant interactions of zone and year were detected and there was no significant effect of reef within zone (Table 4.6). Single factor ANOVAs provided insight into the origin of the Zone x Year interactions. An effect of year for GF and BF zones and an effect of zone in 1995, 1998, 2001, and 2003 on mean FL (Table 4.4b) was detected.


a) Zone

b) Year

c) Sex

Figure 4.8. Mean fork length. Error bars are standard errors of the estimates.

Table 4.6. ANOVA of zone, year, and reef (within zone) on average FL of *L. bohar* (a) ANOVA table from the multi-factor analysis (b) Results of single factor ANOVAs testing the effect of Year for each zone (Tests 1-3) and the effect of Zone for each year (Tests 4-11). ANOVA results significant at $\alpha = 0.05$ in **bold**. Tukey's HSD *post hoc* test for unbalanced designs among zones for each year (c) and among years for each zone (d). Groups joined by bold line were not significantly different ($\alpha = 0.05$). All tests done on square-root transformed lengths ($X' = \sqrt{X + 0.5}$). * = Tukey's HSD tests only done for groups (Factor Levels) where a significant effect was detected by single factor ANOVAs.

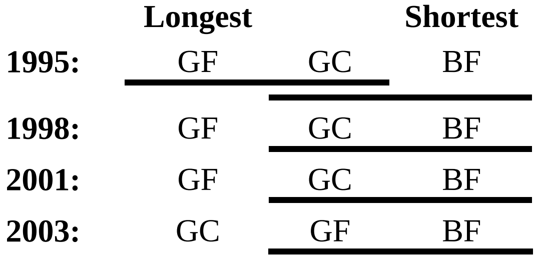
a) Multi-factor ANOVA.

	MS	df	F	p
Zone	19.593	2	5.246	0.104
Year	12.090	7	5.634	**0.003**
Zone x Year	8.016	14	3.735	**0.003**
Year x Reef(Zone)	2.146	21	0.837	0.672
Reef(Zone)	3.735	3	1.457	0.227
Residual	2.563	226.66		

b) Single factor ANOVAs exploring the Zone x Year interaction.

Test	Factor Level	Factor Tested	F	df1	df2	p
1.	GC	Year	1.20	7	168	0.304
2.	GF	Year	3.10	7	65	**0.007**
3.	BF	Year	2.85	7	94	**0.010**
4.	1995	Zone	3.83	2	48	**0.029**
5.	1996	Zone	0.29	2	14	0.755
6.	1997	Zone	0.78	2	51	0.462
7.	1998	Zone	8.47	2	29	**0.001**
8.	1999	Zone	0.89	2	41	0.420
9.	2000	Zone	0.63	2	34	0.539
10.	2001	Zone	3.94	2	70	**0.024**
11.	2003	Zone	5.37	2	40	**0.009**

c) Post-hoc tests* comparing zones for each year.



d) Post-hoc tests* comparing years for each zone.

	Longest							Shortest
GF:	1998	2000	2001	1995	1996	1997	1999	2003
BF:	1997	2000	1996	2001	1995	2003	1998	1999

The multiple comparison tests revealed the nature of Zone effects for each year (Table 4.6c) and Year effects for each zone (Table 4.6d). *L. bohar* were significantly shorter from BF than GF and/or GC zones in all years where an effect of zone was detected (Table 4.6c). There were no clear-cut patterns in mean lengths of fish among years for zones where a significant effect of year was detected (Table 4.6d). There was no significant effect of sex ($F_{1,134} = 2.80;$ p = 0.10), or of its interaction with zone ($F_{2,134} = 1.62;$ p = 0.20), year ($F_{3,134} = 1.89;$ p = 0.13), or year and zone ($F_{6,134} = 1.24;$ p = 0.29) on mean FL.

Most of the *L. bohar* sampled on ELF catch surveys were less than 450 mm FL with a modal FL group of usually 301-350 mm (Figs. 4.2, 4.9). Length frequencies from different zones shared a common modal FL group and were similar except for a higher number of *L. bohar* 251-300 mm FL long from the BF zone (Fig. 4.9). The modal FL group was 301-350 mm in five out of the eight length frequencies sampled in different years and there was no obvious temporal trend evident (Fig. 4.10). Length frequency distributions for males and females shared a common modal FL group, with more males sampled in the 251-300 mm FL group and more females sampled in the 451-500, 501-550, 551-600 and 651-700 mm FL groups (Fig. 4.11).

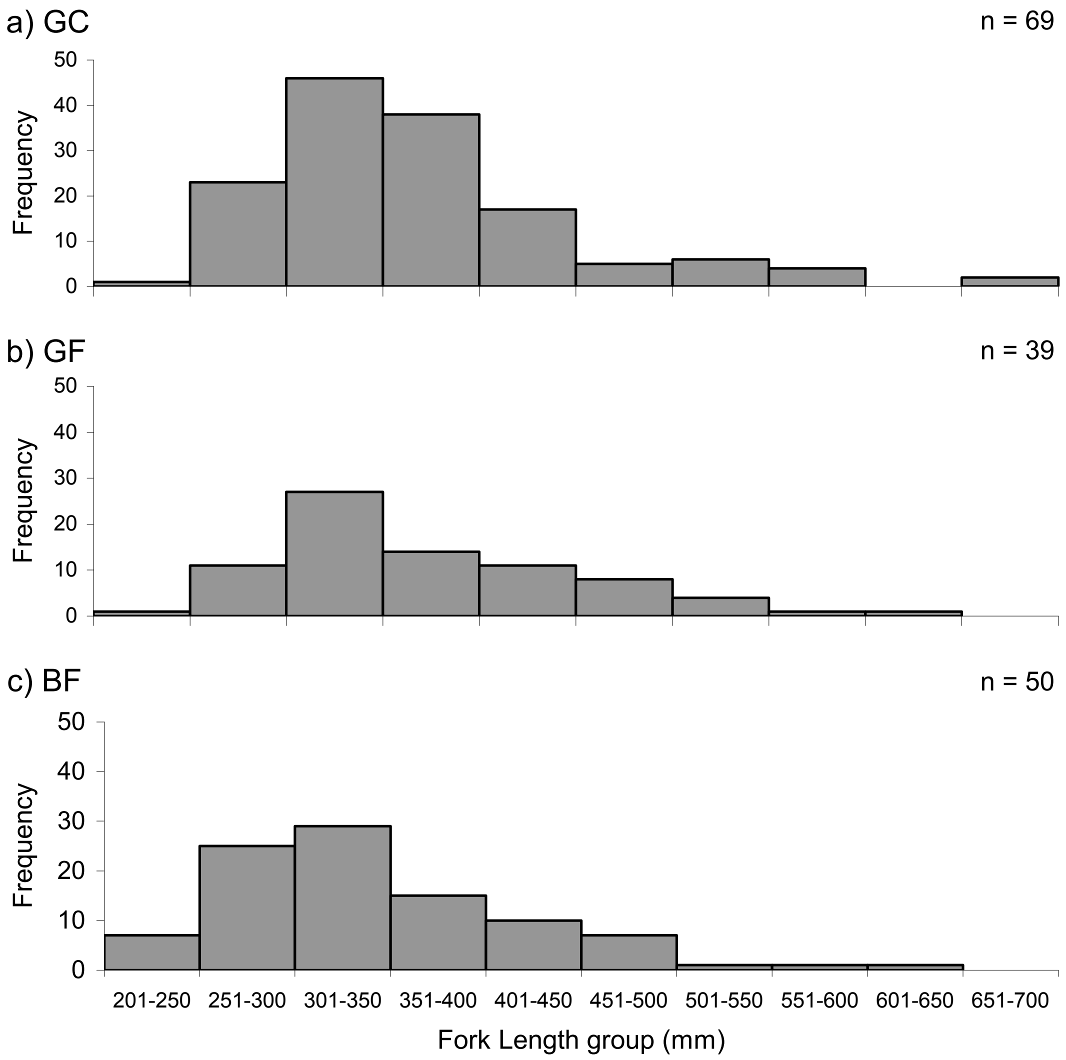
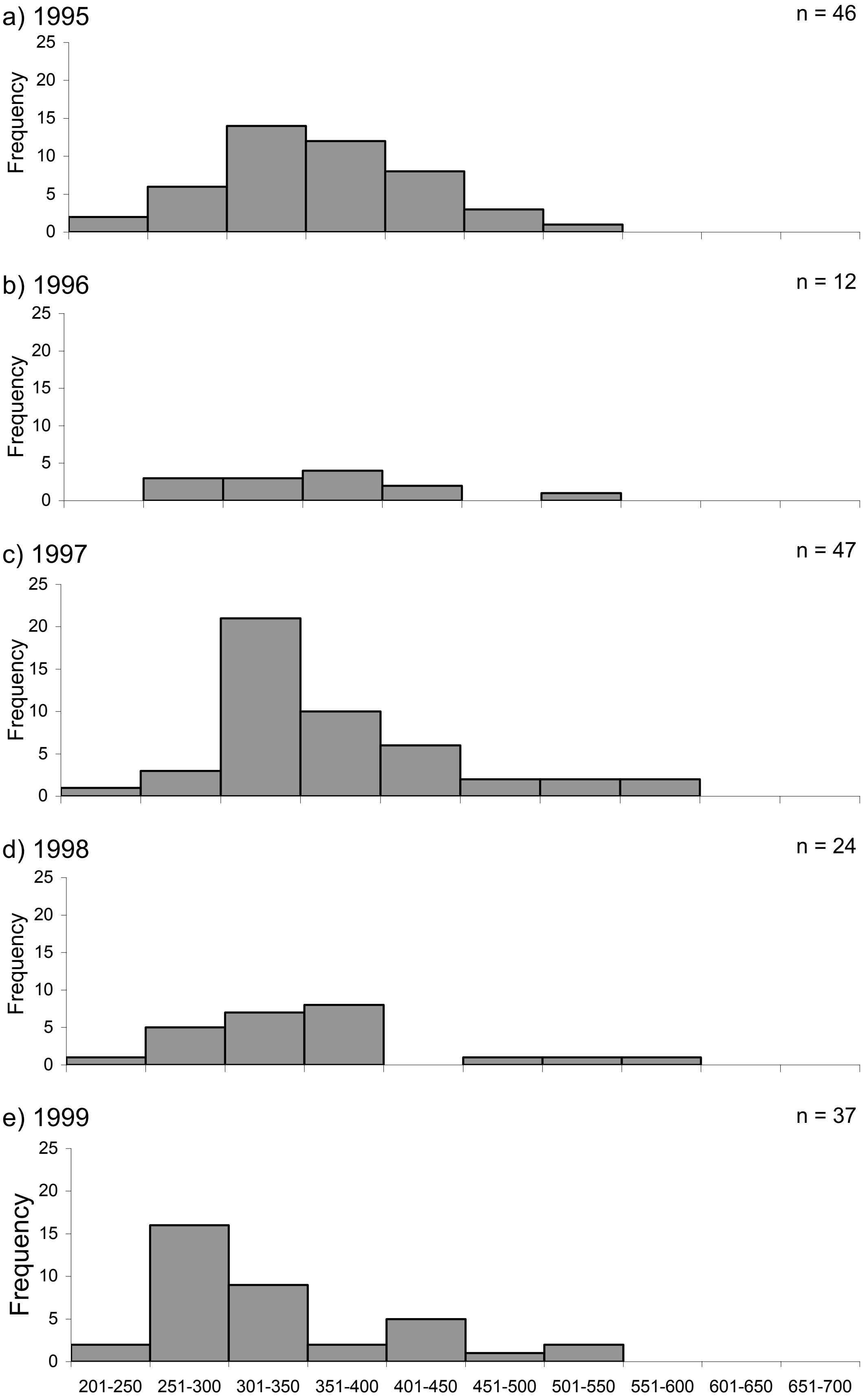


Figure 4.9. Size frequencies sampled from each zone. Data pooled across years, sexes.



<u>Figure 4.10.</u> <u>Size frequencies sampled each year.</u> Data pooled across zones, sexes.

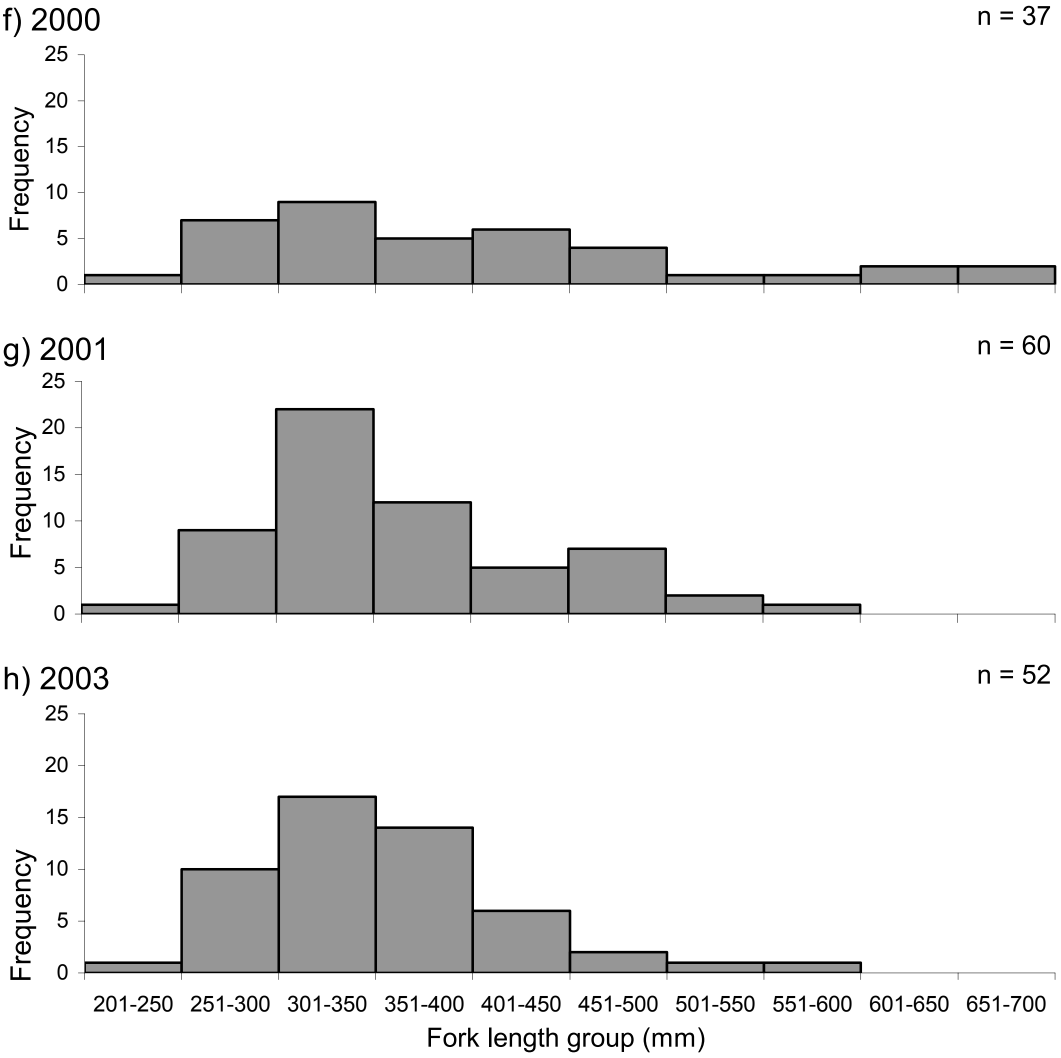


Figure 4.10. Size frequencies sampled each year. (continued)

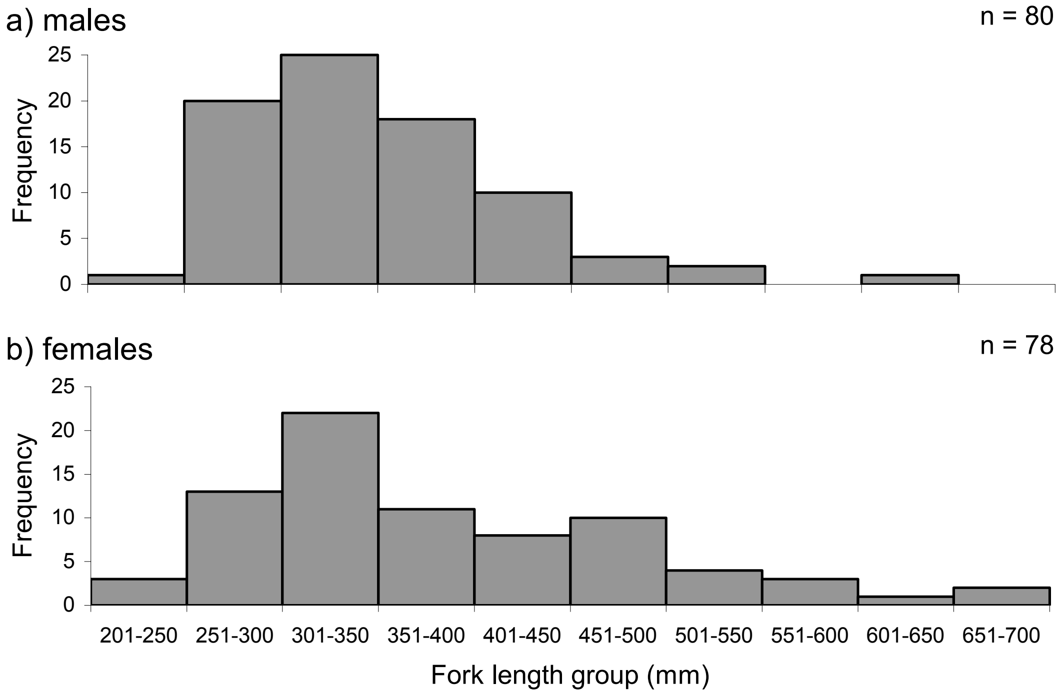


Figure 4.11. Sex-specific size frequency distributions. Data pooled across zones, years.

Results from chi-square contingency table analyses of *L. bohar* FL group frequencies are shown in Table 4.7. Sample year was found to have no significant effect on FL frequency distributions within the GC zone (Table 4.7; Test 1). Sample numbers were sufficient to compare FL frequency distributions between two zones in two years only. No significant differences were detected between zones (Table 4.7; Tests 1 to 3). As for the analysis of age frequency distributions, I assumed that zone and year also did not influence the frequency of *L. bohar* sampled per FL group per sex, and thus pooled data across zones and years to increase sample numbers for the analysis of sex. Sex-specific length frequency distributions were demonstrated to be significantly different (Table 4.7; Test 4).

Table 4.7. Chi-square contingency table analyses of FL group frequencies. Analyses determine if observed relative frequencies by treatment group of the tested “Factor” were contingent upon “FL groups” for a subset of “Data.” Results significant at $\alpha = 0.05$ in **bold**.

Test	Factor	Data	FL groups	χ^2	df	P
1.	Year	GC	<301, 301-350, 351-400, 401+	16.37	12	0.175
2.	Zone	2001: GC v BF	<301, 301-350, 351-450, 451+	0.39	3	0.942
3a.	Zone	2003: GC v GF	<351, 351-400, 401+	3.84	2	0.147
3b.	Zone	2003: GC v GF	<301, 301-400, 401+	2.84	2	0.242
3c.	Zone	2003: GC v GF	<301, 301-350, 351+	4.26	2	0.119
4.	Sex	ELF: All	<276, 276-300, 301-325, 326-350, 351-375, 376-400, 401-450, 451-525, 526+	18.22	8	**0.020**

I considered the lack of any significant effect of sex or year on the sampled age frequency of *L. bohar* from GC reefs as evidence to pool across these factors for a representation of sampled age structure (Fig. 4.12).

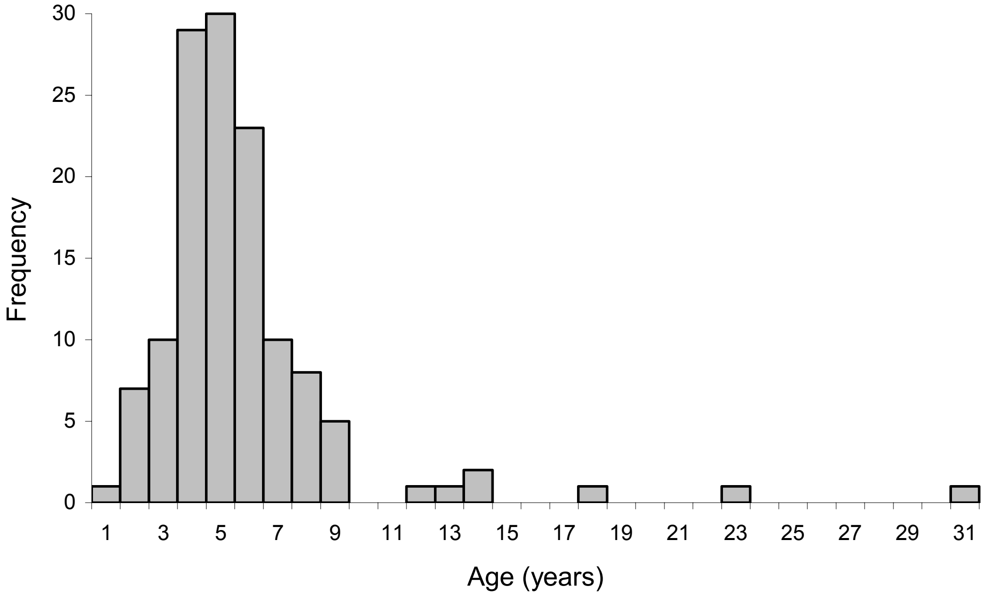


Figure 4.12. Age frequency distribution of *L. bohar* from GC reefs, Lizard Island Region. Data collected from spring catch surveys of the ELF Experiment, pooled across years and sexes. N = 130.

4.3.3. Growth.

4.3.3.1. Size-at-age.

Single factor ANOVA tests revealed no significant effect of year on mean FL-at-age within zones (Table 4.8). A significant effect of zone was detected only in 2000 (Table 4.8).

Table 4.8. Single-factor ANOVA test results comparing mean length for common age groups among years within zone and among zones within year. "Factor Level" was the level of zone or year within which the analysis was done. "N" = total sample number used in analysis. The "Antilog" transformation converts the fork length (after it has been divided by 100) to the exponent of base 10, to account for positive skew. Results significant at $\alpha = 0.05$ in **bold**.

Factor Level	Factor Tested	Dependent Variable	Common Age Group	N	F	df1	df2	p
GC	Year	FL	6.46	26	1.74	7	18	0.163
GF	Year	FL	4.46	24	0.95	5	18	0.472
BF	Year	FL	3.46	15	0.50	6	8	0.796
1995	Zone	FL	4.46	13	0.18	2	10	0.841
1995	Zone	FL	5.46	13	2.93	2	10	0.100
1996	Zone	FL	6.46	5	3.34	2	2	0.230
1997	Zone	FL	4.46	7	6.46	2	4	0.056
1998	Zone	FL	5.46	8	0.57	1	6	0.478
1999	Zone	$\text{Log}_{10}(\text{FL}+1)$	2.46	18	0.17	2	15	0.844
2000	Zone	FL	3.46	8	5.93	2	5	**0.048**
2001	Zone	Antilog (FL)	4.46	29	2.51	2	26	0.101
2003	Zone	FL	3.46	13	0.41	2	10	0.672

The lack of a significant effect of year on FL-at-age indicated that FL-at-age data could be pooled across years for subsequent analyses. Since pooling resulted in observed FLs for *L. bohar* of a common age group (4.46 years) in all combinations of sex and zone a 2-factor ANOVA test for these effects was done. No significant effect of sex ($F_{1,26} = 0.004$; p = 0.95) nor its interaction with zone ($F_{2,26} = 1.61$; p = 0.22) on the mean FL of 4.46 year olds was detected. There was also no significant effect of zone ($F_{2,26} = 2.83$; p = 0.08). Further, the repetition of this ANOVA for FL-at-age 4.46 with the exclusion of 2000 data, for which a significant effect of zone was previously detected (Table 4.8), demonstrated the same results for sex ($F_{1,21} = 0.39$; p = 0.54), zone

($F_{2,21} = 2.92;\ \text{p} = 0.08$), and the interaction of sex with zone ($F_{2,21} = 2.47;\ \text{p} = 0.11$). This indicates that the result for 2000 in Table 4.8 was perhaps aberrant and not indicative of any general zone effect. The lack of significant interaction between zone and sex was taken as supportive evidence for the pooling of FL-at-age data across sexes for comparing growth trends among zones and the pooling of FL-at-age data across zones for comparing growth trends between males and females in subsequent analyses.

4.3.3.2. Von Bertalanffy growth functions.

The R^2 values for the von Bertalanffy models fitted to FL-at-age data ranged from 0.83 to 0.95 (Table 4.9). Although the fit of the von Bertalanffy models were good for all FL-at-age data, the influence of zone, sex, and sample methods on the fitted parameter estimates was demonstrated. Model fits for GF, “ELF + spear”, “All” and Males data have the lowest $\hat{L}_\infty$ and $\hat{t}_0$ and BF and GC data have the highest $\hat{L}_\infty$ and the lowest $\hat{K}$ (Table 4.8). Differences in model fit arising from the use of data from different sampling methods are shown in Figure 4.13a, which demonstrates that smaller *L. bohar* collected by targeted spear-fishing result in a lower $\hat{t}_0$ (enlarged Fig. 4.13b) and $\hat{L}_\infty$ (enlarged Fig 4.13c) and a higher $\hat{K}$. The inclusion of samples from drop-line commercial fishing in deeper water had a smaller effect on parameter estimates, by lowering the $\hat{L}_\infty$ and raising the $\hat{t}_0$ marginally, but resulted in a higher R^2. The fit of the von Bertalanffy model to all data (Fig. 4.13d) demonstrated a relatively gradual curvature indicating slow growth that reached an asymptotic FL relatively late in life.

Table 4.9. Von Bertalanffy growth function parameters: Lizard Island Region. All samples collected in Austral spring (September to December), pooled across years. "All" = Data from ELF spring catch surveys plus supplementary data from spear-fishing ("spear") and commercial drop-line fishing ("deep").

Data	n	L_∞	SE	K	SE	t_0	SE	R^2
GC	141	677	(26)	0.079	(0.009)	-3.11	(0.64)	0.83
GF	77	646	(30)	0.101	(0.015)	-2.21	(0.67)	0.86
BF	96	711	(56)	0.071	(0.013)	-3.57	(0.65)	0.89
ELF = GC + GF + BF	314	674	(19)	0.082	(0.006)	-3.06	(0.36)	0.85
ELF + spear	343	646	(15)	0.099	(0.006)	-2.50	(0.22)	0.88
ELF + deep	347	661	(11)	0.085	(0.005)	-3.55	(0.317)	0.90
All = ELF + spear + deep	376	645	(9)	0.098	(0.004)	-2.54	(0.20)	0.91
Males	98	646	(28)	0.095	(0.011)	-2.67	(0.44)	0.87
Females	92	661	(13)	0.096	(0.007)	-2.81	(0.39)	0.95

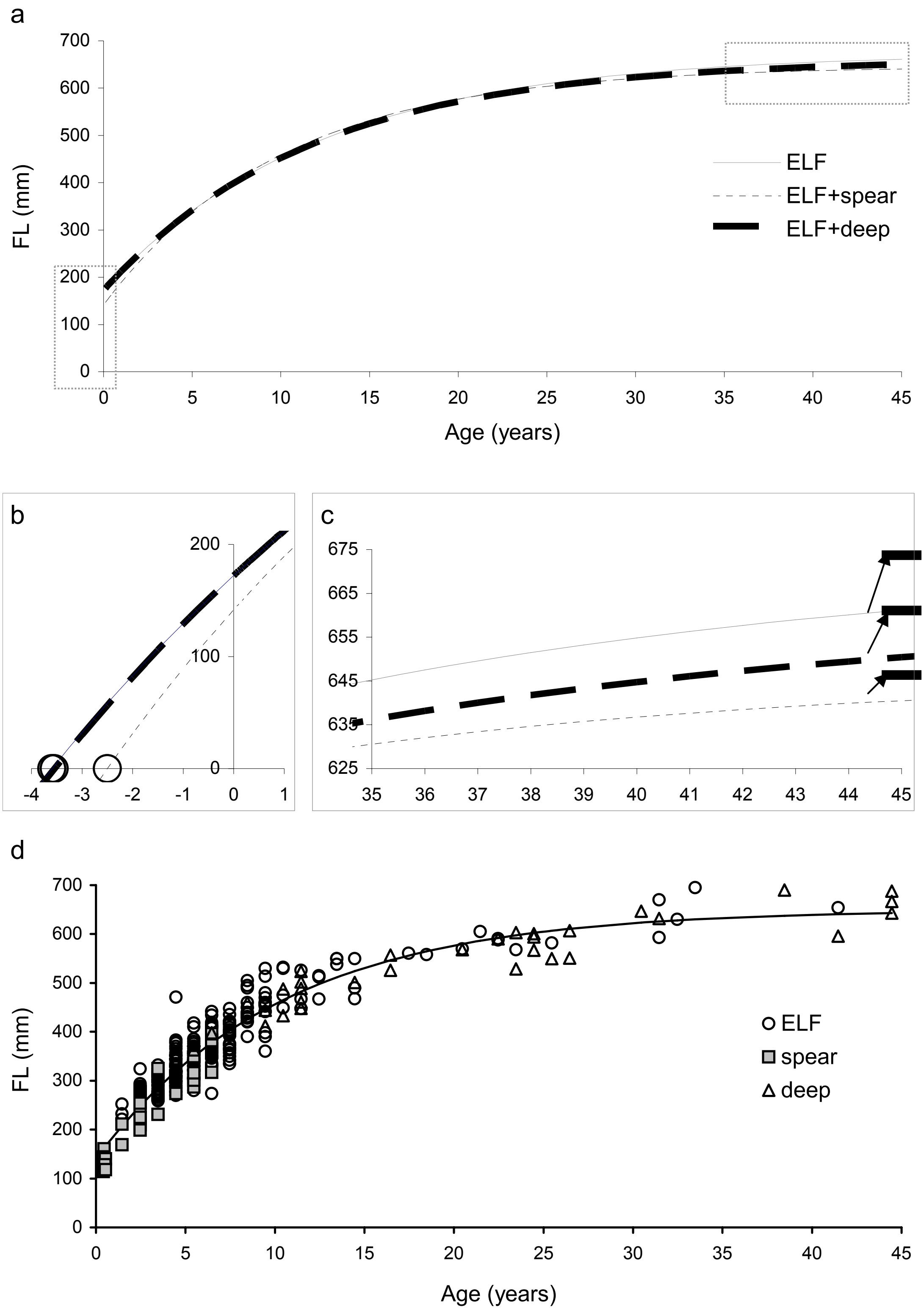


Figure 4.13. Fitted von Bertalanffy growth model to length-at-age data. The effect of including data from augmentative sampling methods ("spear" = targeted spear-fishing of juveniles; "deep" = sample from commercial drop-line fishing in deeper water) on parameter estimates are demonstrated in (a) and enlargements are provided for younger ages (b) and for older ages (c), to indicate model differences… *(Please see over).*

Figure 4.13. (Caption Continued):

…in estimates of $\hat{t}_0$ (open circles) and $\hat{L}_\infty$ (horizontal bars with corresponding arrows), respectively. The model fit to pooled data is shown in (d), with data coded for sampling method.

Although the coincident likelihood ratio test of zone detected an overall effect on the fit of the von Bertalanffy model to FL-at-age, subsequent tests of zone for each model parameter did not (Table 4.10). This indicates that the result from the coincident test is probably not biologically meaningful. Further, no effect of sex on model fit was detected, either for the coincident or for the individual parameter tests (Table 4.10). The failure to detect a significant effect of zone or sex on the fit of the von Bertalanffy model supports the pooling of data across these factors for a general description of *L. bohar* growth in the Lizard Island Region (Fig. 4.13).

Table 4.10. Likelihood ratio tests comparing estimates of von Bertalanffy model parameters fitted to length-at-age data: Lizard Island Region. All samples collected in austral spring (September to December), pooled across years. 'Coincident' tests compare the fit of the von Bertalanffy model to pooled data with separate model fits to each data set. Other tests compare model fits when individual parameters were constrained to the same fitted values with separate model fits. Results significant at $\alpha = 0.05$ in **bold**.

Factor	Test	Age range	χ^2	df	p
Zone	Coincident	1.46 to 28.46	14.86	6	**0.021**
	L_∞ equal	1.46 to 28.46	1.28	2	0.528
	K equal	1.46 to 28.46	2.47	2	0.291
	t_0 equal	1.46 to 28.46	2.03	2	0.362
Sex	Coincident	0.4 to 44.46	7.18	3	0.066
	L_∞ equal	0.4 to 44.46	0.27	1	0.603
	K equal	0.4 to 44.46	0.0001	1	0.994
	t_0 equal	0.4 to 44.46	0.053	1	0.819

95% confidence regions of $\hat{L}_\infty$ and $\hat{K}$ for fits of the von Bertalanffy model to FL-at-age from different zones, pooled across sexes and years and for males and females, pooled across zones and years, are shown in Figure 4.14. Overlap of the 95% confidence regions for GC and BF zones (Fig. 4.14a) and for males and females (Fig. 4.14b) demonstrate no significant difference between growth curves fitted to these different data groups. The non-overlap of the GF 95% confidence region with those for GC and BF zones indicated differences in model fit. These confidence regions, however, span an overlapping range of L_∞ , and, for GC and GF zones, an overlapping range of K (Fig. 4.14a), which demonstrates no significant difference among these fitted parameter estimates. The 95% confidence regions for GF and BF zones demonstrated no overlap along the K axis, indicating a significant difference in the $\hat{K}$ fitted to GF and BF data.

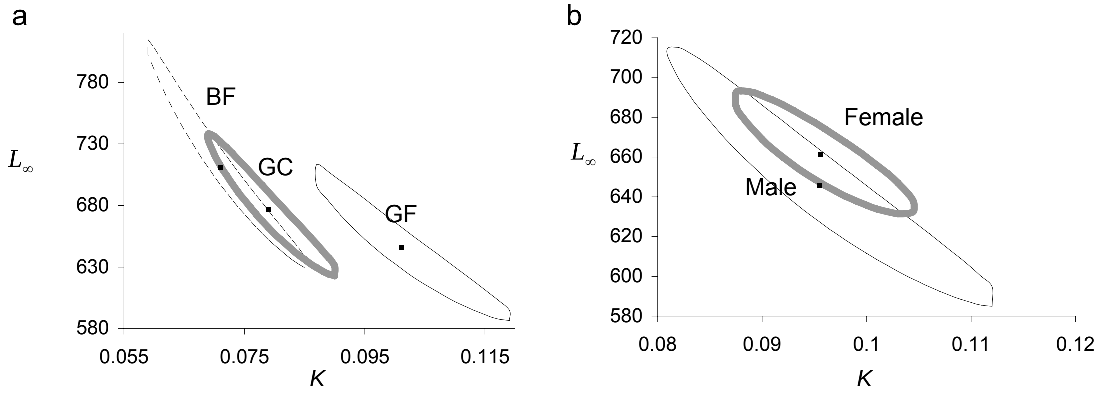


Figure 4.14. 95% Confidence regions for fits of the von Bertalanffy growth model parameters to different length-at-age data groups. 95% confidence regions for $\hat{L}_\infty$ and $\hat{K}$ for model fits to different zones, pooled across sexes and years (A) and sexes, pooled across zones and years (B) are shown.

The power function fitted weight-at-FL data exceptionally well, with all model fits having R^2 of 0.98 – 0.99. This indicated a very good description of the relationship and very little residual variation about fitted trends. The augmentation of ELF data by targeted spear-fishing of juveniles and the catch of a commercial deep-water drop-line fishing operation did not appear to have a large effect on parameter estimates (Table 4.11). All model fits presented in Table 4.11 assume no effect of year on weight-at-FL data.

Table 4.11. Power function parameters fitted to weight-at-FL data from different sample methods. All samples collected in Austral spring (September to December), pooled across years. "All" = Data from ELF spring catch surveys plus supplementary data from spear-fishing ("spear") and commercial drop-line fishing ("deep").

Data	n	*a*	SE	*b*	SE	R^2
ELF = GC + GF + BF	156	3.86×10^{-9}	(6.91×10^{-10})	3.266	(0.028)	0.99
ELF + spear	187	3.99×10^{-9}	(6.35×10^{-10})	3.261	(0.025)	0.99
ELF + deep	186	3.59×10^{-9}	(8.84×10^{-10})	3.276	(0.039)	0.98
All = ELF + spear + deep	218	3.70×10^{-9}	(8.19×10^{-10})	3.272	(0.035)	0.98

There was no significant effect of zone on the slope ($F_{2,107} = 0.29;$ p = 0.75) or intercept ($F_{2,107} = 0.01;$ p = 0.99) of the linear-transformed weight-at-FL relationship, nor was there any significant effect of the interaction of zone and year on its slope ($F_{4,107} = 1.47;$ p = 0.217) or intercept ($F_{3,107} = 0.63;$ p = 0.594). There was, however, a significant effect of year on slope ($F_{2,107} = 10.33;$ p < 0.001). The second two-factor ANCOVA revealed no significant effect of the interaction of year and sex on the slope ($F_{2,110} = 2.23;$ p = 0.113) or intercept ($F_{2,110} = 1.55;$ p = 0.218), nor of sex on its slope ($F_{1,110} = 0.63;$ p = 0.429) or intercept ($F_{1,110} = 0.01;$ p = 0.916). The third two-factor ANCOVA revealed a significant interaction effect of zone with sex on the slope ($F_{2,113} = 16.66;$ p < 0.001) of the weight-at-FL trend. The significant effect of year and the interaction effect of zone with sex on slope indicated that it was not valid to pool weight-at-FL data across zones and sexes for an overall description of the trend.

Results from the *post hoc* single-factor ANCOVA tests are presented in Table 4.12. Comparisons of weight-at-FL between males and females detected a significant difference in slope within the GC zone but not within BF or GF zones. *Post hoc* tests comparing zones within each sex, however, detected no significant effect on slope. The slope of weight-at-FL data collected in 2000 also differed from that collected in 1999 and 2001. All results in Table 4.12 that demonstrated no significant difference in slope also demonstrated no significant difference in intercept.

Table 4.12. Single factor ANCOVA tests for effects on the slope of linear-transformed weight-at-length data. Tests were done as *post hoc* comparisons to results of the multi-factor ANCOVA tests of zone, sex and year (see text). Dependent variable = fish weight (kg); independent variable = FL^3 (mm). Results significant at $\alpha = 0.05$ in **bold**.

Test	FL range (mm)	F	df1	df2	p
GC Males v GC Females	252 - 558	6.40	1	48	**0.015**
BF Males v BF Females	222 - 475	0.24	1	39	0.630
GF Males v GF Females	260 - 541	0.10	1	23	0.751
Males: Zone	244 – 450	0.15	2	53	0.149
Females: Zone	245 – 487	1.39	2	50	0.258
1999 v 2000	244 - 530	8.71	1	60	**0.005**
1999 v 2001	222 - 558	0.67	1	93	0.413
2000 v 2001	222 - 620	13.76	1	82	**<0.001**

Females from the GC zone were heavier than males when they reached a longer FL (Fig. 4.15a), but this difference in slope also appeared to be largely influenced by the 3 largest data points, which reduced the strength of this interpretation. Similarly, the effect of year on slope appeared to be driven by differences in weight-at-FL between groups for the longest fish, for which there were few data points (Figs. 4.15b,c). Given these effects of sex and year, separate fits of the power function for untransformed

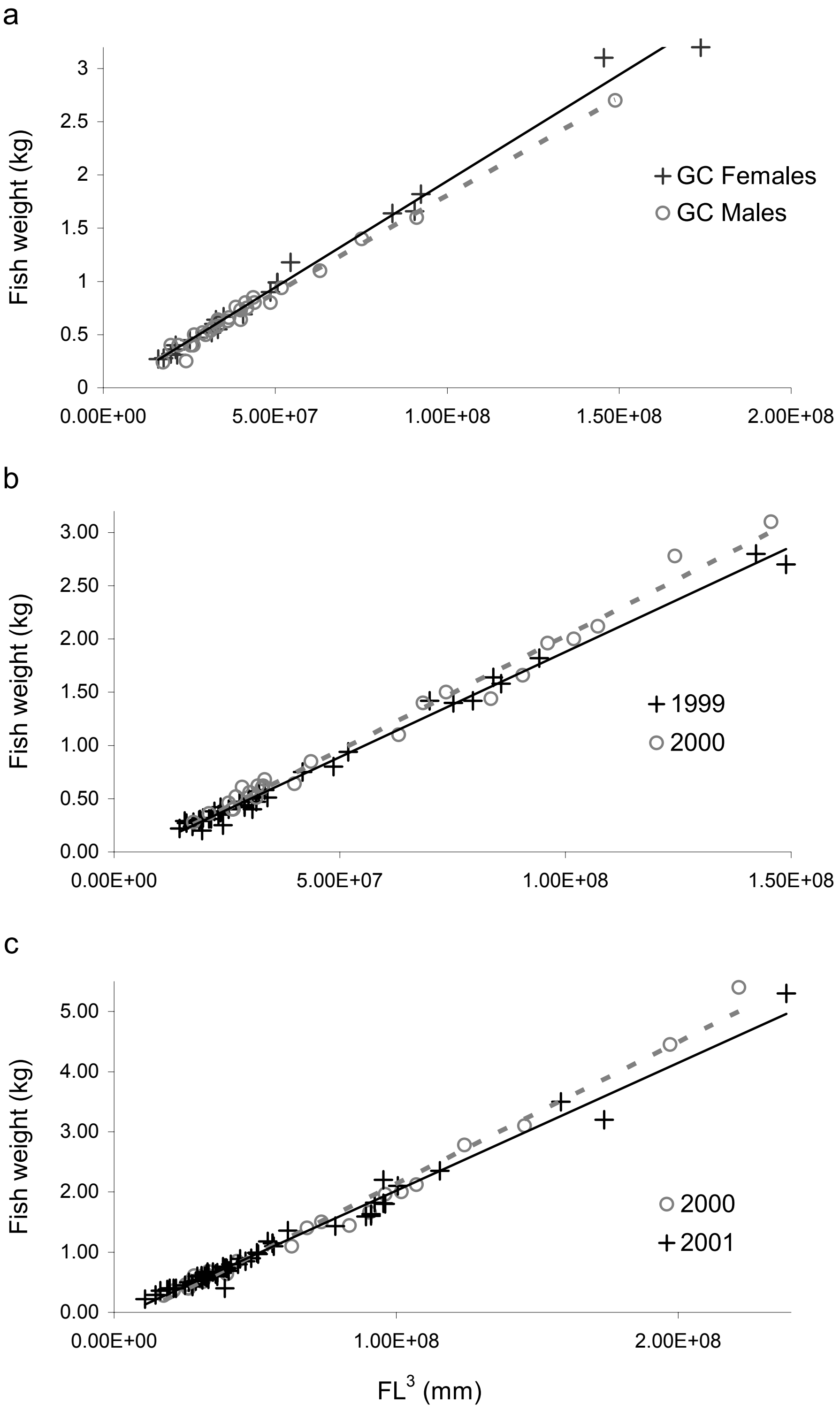


Figure 4.15. Comparisons of linear-transformed weight-at-length relationships for categories of sex and year. Graphs show significant differences detected from ANCOVA tests (see text; Table 4.11) at $\alpha = 0.05$.

weight-at-FL of males and females, pooled across the years where no significant differences were detected (i.e., 1999 and 2001), was done (Fig. 4.16).

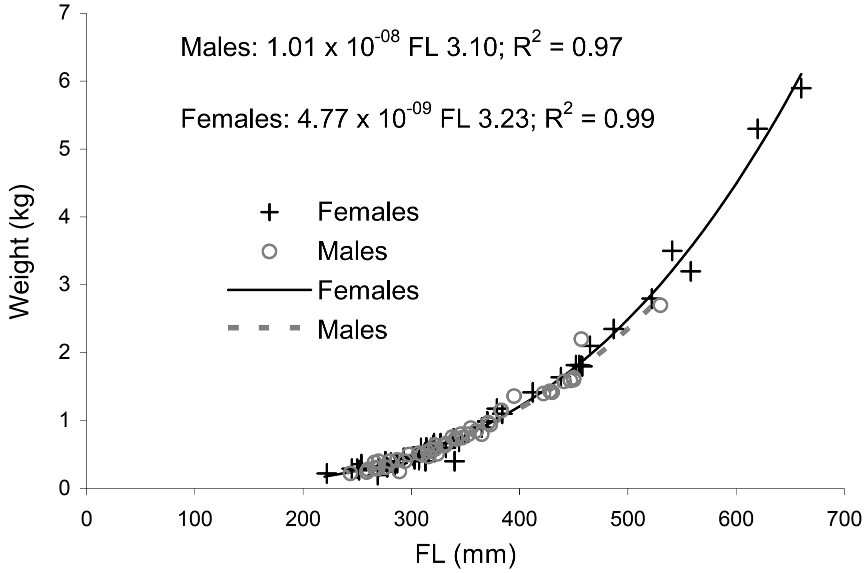


Figure 4.16. Power function fitted to weight-at-length data for males and females Data pooled across the two years for which the data did not differ (i.e., 1999 and 2001), ELF spring catch surveys.

4.3.4. Mortality.

The catch curve for the $\hat{t}_r$ of the 5.46 to 9.46 age groups from GC reefs (pooled over years) demonstrated a steep decline in the numbers at age, relative to the large age range sampled (Fig. 4.17). This was because relatively few *L. bohar* older than 9.46 years were sampled. The resulting $\hat{Z}$ from the catch curve was therefore relatively high, at 0.464 ± 0.049SE, compared to the Hoenig (1983) estimate based on the maximum estimated age (44.46 years; $\hat{Z} = 0.102$). The estimate of natural mortality ($\hat{M}$) using the Pauly (1980) method was 0.304.

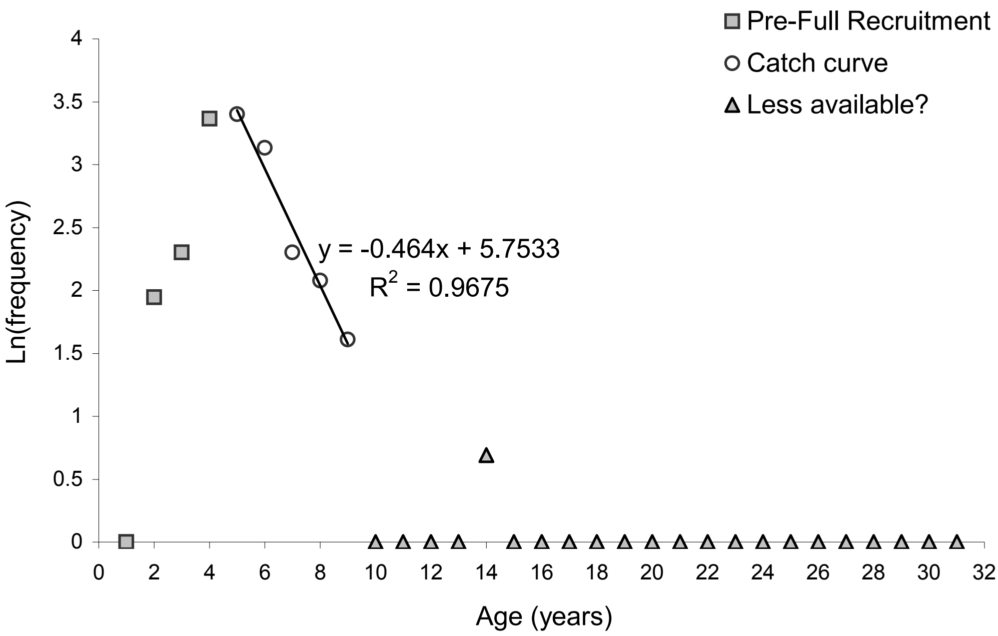


Figure 4.17. Catch-curve analysis of age frequency distribution sampled from GC reefs. The catch curve was not fitted to data where age groups were assumed to be not fully recruited (open circles) or available (filled triangles) to sampling done on ELF catch surveys.

4.4 Discussion

The detailed investigation of the influence of several factors on age and growth demonstrated some important constraints on the interpretation of data from the ELF Experiment, particularly with respect to the range of sizes and ages of *L. bohar* sampled. This analysis also provided insight into potentially important aspects of population dynamics and impacts of fishing that would not have been otherwise detected, although conclusions are tentative due to low sample sizes. Importantly, these results (i) elucidate those factors most likely to confound comparisons among populations if not taken into account and (ii) enable the presentation of age-growth characteristics of *L. bohar* from the Lizard Island Region whilst accounting for these potentially confounding effects. In the subsequent discussion I will focus on these latter two points.

4.4.1. Within-Region effects.

A summary of detected effects on age-growth results are presented in Table 4.12. An effect of zone was detected in most tests (except for tests on length group frequencies, fits of the von Bertalanffy growth model to length-at-age, and weight-at-length trends; Table 4.12.) and thus it is apparent that zone had an important influence on results. These effects of zone are likely to reflect impacts of fishing prior to (BF) and / or during (BF, GF) the ELF Experiment. Zone was demonstrated to significantly affect the fit of the von Bertalanffy growth model to length-at-age (Table 4.12.).

Table 4.13. Summary of factor effects on age-growth results. "S" = significant at $\alpha = 0.05$; "NS" = not significant at $\alpha = 0.05$; "-" = not tested.

Variable	Factors tested			
	Year	Reef (Zone)	Zone	Sex
Mean age	S	NS	S	NS
Mean FL	S	NS	S	NS
Frequency	NS	-	S	NS
Age frequency	NS	-	S	NS
FL group frequency	NS	-	NS	S
FL-at-age	NS	-	S	NS
Fit of von Bertalanffy growth model	-	-	S	NS
Weight-at-FL	S	-	NS	S

4.4.1.1. Fishing manipulations of the ELF Experiment.

No consistent effect of zone was detected among years except for the total frequency of *L. bohar* caught, with the most *L. bohar* caught from the GC zone. It is likely that the lower frequencies sampled from BF and GF zones reflected lower abundances in these zones than in the GC zone at the times of sampling. One plausible hypothesis to explain this result is that fishing manipulations of the ELF Experiment within the BF and GF zones (and not within the GC zone; see Table 2.1) caused depletions of *L. bohar* abundance in these zones.

Although there was no consistent effect of zone on mean age or mean length among years, *L. bohar* sampled from the BF zone were smaller and younger than those from GC and/or GF zones for all years where a significant effect of zone was detected. This also could reflect an impact of fishing, because fishing typically removes larger, older fish from populations (Russ 1991; Jennings and Lock 1996), which would reduce the population mean age or size. Larger, older fish are typically less abundant because they have been exposed to mortality for longer and therefore equal fishing mortality on all fully-recruited age groups removes older age groups more readily (Cushing 1968). The inferred reductions in abundance, mean age and mean size indicate that fishing might have also reduced the biomass of *L. bohar* in the BF zone. These results are perhaps surprising, considering the relatively light levels of fishing pressure suspected for the Lizard Island Region (Mapstone et al. 2004) and the propensity of fishers to avoid *L. bohar* on the GBR, and thus could indicate a high vulnerability of this species to fishing impacts. Other studies (Jennings et al. 1995; 1999) have indicated a high vulnerability of *L. bohar* populations to fishing impacts, with lower biomass estimates in all areas that were exposed to fishing relative to fishing exclusion zones, even for relatively lightly exploited areas.

The comparison of sampled age and length frequency distributions between zones within years, however, did not reflect this general trend. Although a fishing impact in the GF zone was indicated because fewer older *L. bohar* were sampled than from the GC zone in 2003, one would have also expected fewer older and larger *L. bohar* sampled from the BF than from the GC zone in 2001 to infer consistent fishing impacts among the fished zones. This is because BF zones (unlike GF zones) were fished prior to fishing manipulations of the ELF Experiment and because 2001 was near in time to the completion of fishing manipulations, when BF reefs were closed.

Nor were consistent results detected for the comparisons of mean length-at-age. No significant effect of zone was detected except in 1997 and 2000, suggesting that these effects might have reflected unknown effects unrelated to fishing, such as spatial variation in food availability (Weatherly and Gill 1987) or natural density-dependent processes (Forrester 1990). Also, although a significant effect of zone on the fit of the von Bertalanffy model to length-at-age was detected from the coincident test, subsequent likelihood ratio tests of each fitted parameter failed to detect an effect of zone. Further, a significant difference in *K* fitted to GF and BF data was demonstrated from plots of 95% confidence regions but not from likelihood ratio tests of *K*. Therefore, evidence of an effect of zone on growth was equivocal. Nevertheless, the detection of significant zone effects in some of these analyses warrants its consideration in subsequent studies of growth (e.g., Chapter 5).

4.4.1.2. Temporal effects.

Significant temporal variation was detected for mean age, mean length, mean length-at-age among zones and weight-at-length but there was no conspicuous trend apparent for any of these parameters over time. Interestingly, data collected in 2000 featured in all of these results: the mean age of *L. bohar* sampled in 2000 was consistently among the oldest of samples collected, in 2000 a significant difference in mean length-at-age 4 among zones was detected, and the weight-at-length relationship was steeper in 2000 than for samples collected in 1999 and 2001. It is possible that these effects reflected low precision, and thus, high inter-annual variation because of the low sample sizes. Accordingly, one hypothesis for these temporal effects is that the sample from 2000 sample was aberrant due to its low sample size and corresponding low precision for estimated parameters.

4.4.1.3. Selectivity of sampling methods.

Considering that the oldest estimated age from this region was 44.46 years, there were very few *L. bohar* sampled in the older ages from the ELF catch surveys. This indicates that either an exponential rate of mortality does not occur throughout life for this population or that the oldest individuals were not available to or selected by the ELF sampling method. The former explanation could be possible if only a small number of individuals survive up to some critical age or size at which they become less susceptible to mortality perhaps due to an ontogenetic shift in behaviour or habitat preference (Kingsford 1992; Luckhurst et al. 1992). The latter inference was supported by observed differences in the modes of length frequency distributions between samples from ELF surveys and from deeper water line fishing that was done closer to the outer-shelf. Differences in selectivity between the different sampling methods might also have affected this result because a different hook type (i.e., a 13/0 tuna circle hook vs 8/0) was used and a different time of operation (i.e., dusk to dawn vs post-dawn to pre-dusk) was adopted by the drop-line commercial fisher from which the deep sample was obtained.

The selectivity of the research line fishing method used on ELF catch surveys for larger, older juveniles was also clear since it was shown that targeted spear-fishing sampled those *L. bohar* that could not be sampled by line fishing. Including these data resulted in a noticeable shift in the fit of the von Bertalanffy growth model, with a reduction of $\hat{t}_0$ and a corresponding reduction of the length-at-age 0 (L_0) by 30.5 mm. Although this reduction in L_0 was desirable, the L_0 was still unrealistic at 141.7 mm FL, which was larger than 9 of the smallest *L. bohar* that were estimated to be 147 to 196 days old. This indicates that more spear-caught samples would be required to further correct this bias. The inclusion of spear-caught samples also resulted in a marked reduction in $\hat{L}_\infty$, which was surprising given that the largest length in the spear-caught sample was only 396 mm FL. This result was likely to reflect an effect of the spear-caught samples on estimates of K and / or t_0, which in turn affected the estimate of L_∞ because of strong correlations among these parameters. Strong correlation among parameters of the von Bertalanffy model has been previously noted by Bernard (1981).

Interestingly, the inclusion of the deep sample resulted in a smaller change in $\hat{L}_\infty$ when the von Bertalanffy model was fit to length-at-age than when the spear-caught samples were included. This indicates that the $\hat{L}_\infty$ from the initial fit to ELF data was a reasonable estimate, despite a conspicuous lack of data from older, larger *L. bohar*.

Knight (1968) and Francis (1988) previously emphasised the importance of sampling length-at-age data across the entire length range of a species to avoid biased extrapolations of $\hat{L}_\infty$. The augmentation of ELF data with data from larger, older fish of the deep sample in this study, however, had less effect on $\hat{L}_\infty$ than the apparent bias arising from length-at-age data collected for smaller, younger fish.

4.4.1.4. Sex.

No significant difference in the fit of the von Bertalanffy growth model or length-at-age between sexes was detected, which was consistent with the observation made by Talbot (1960), who used a different age estimation method (i.e., scales), for *L. bohar* off the coast of East Africa. This is also consistent with many other (previously cited) studies of lutjanids that reported no sex-specific difference in L_∞ and goes against the hypothesis that females should grow larger than males (Roff 1983). It suggests that there may be an alternative life history trade-off to account for the increased energy allocation to reproductive development in females, relative to males, such as a delayed age at first maturity in females (Bell 1980; Stearns 1992; see Chapter 6).

Finding more females to males in the larger length groups was consistent with the observation reported by Wright et al. (1986) for *L. bohar* populations in the Tigak Islands, Papua New Guinea. Despite this difference in sex ratio with size, however, there was no overall difference in sex ratio indicated. Other authors who have reported a biased sex ratio for lutjanids (either overall or with length group) have speculated that such patterns might have arisen because of sex-specific differences in longevity and mortality rates (e.g., Grimes and Huntsman 1980; Rocha-Olivares 1998), growth rates (e.g., Davis and West 1992), gear selectivity (e.g., Manickchand-Dass 1987; Zhao and McGovern 1997), or courtship and/or spawning behaviour (e.g., Kritzer 2002).

Excluding growth, which was found to be homogeneous between sexes, it was unclear which of these factors could have helped explain the relative rarity of larger and older male *L. bohar*. Also, the divergence in sex-specific size structures for longer length groups was not corroborated by the detection of similar differences for older age groups. This apparent inconsistency possibly arose because of the pooling of older age groups to obtain sufficient cell frequencies for analyses.

A significant effect of sex on the weight-at-length relationship was also detected for *L. bohar* sampled from the GC zone, but not in the other zones. However, inspection of weight-at-length trends indicated that the difference in slope was largely influenced by the three largest data points, but otherwise there was much overlap of data between sexes. Further, it is difficult to explain why a sex-specific difference in the condition of longer fish would have only occurred in the GC zone and not in the BF and GF zones, except for the possibility that fishing in the BF and GF zones might have removed a sex-specific difference in condition through size-selective harvest.

4.4.2. Age-growth characteristics of *L. bohar.*

4.4.2.1. Population age and size structure.

More *L. bohar*were sampled in the larger length groups of the deep sample, which is consistent with observations of Wright et al. (1986) for *L. bohar* populations in Papua New Guinea. Anecdotal reports from commercial line fishers on the GBR were consistent with this finding, although it was noted that larger, older specimens also can be caught in shallow waters (*pers obs.*; Wright et al. 1986). This result is also consistent with observations that many other lutjanids undertake cross-shelf ontogenetic migrations on the GBR, including *Lutjanus erythropterus* and *L. malabaricus* (Newman and Williams 1996), moving to deeper, further offshore waters as they grow.

The conversion of annulus counts to estimates of age was done using inferred daily increments, which was the best available evidence for assigning an average age at which formation of the first annulus was suspected to occur. This method assumed that *L. bohar* of all ages form annuli at the same time of year (Chapter 3) and that microincrements were formed on a daily basis, as has been demonstrated for other tropical reef fish (e.g., Victor 1983; Thresher and Brothers 1985; Thresher et al. 1989; Morales-Nin and Ralston 1990; Lou and Moltschaniwskyj 1992). It is acknowledged that there is uncertainty in this, because *L. bohar* could have bi-annual (Wheeler 1953) or year-round spawning (Talbot 1960), which suggests that offspring could have highly variable ages of first annulus deposition, up to about one year of age. There was no suitable evidence available for using alternative methods to assign an age of first annulus deposition to all fish (e.g., Fowler and Short 1998; Wilson and Nieland 2001), so this remains an area for further study.

4.4.2.2. Growth and condition trends.

The fit of the von Bertalanffy growth model to length-at-age indicated a relatively slow growth trend for *L. bohar* because of the relatively gradual curvature of the fit (i.e., low $\hat{K}$) and because the onset of asymptotic growth was apparent relatively late in life (~25-35 years). This growth curve is therefore not of the “square” type, as generalised by Choat and Robertson (2002) for some tropical reef fish, including acanthurids and some lutjanids, where young fish grow rapidly until they reach maturity and then rapidly reduce somatic growth. Rather, it is of the more familiar type where growth decrements gradually, as observed for *Plectropomus* species (Ferreira and Russ 1992; 1994) and some other lujanids, including *Lutjanus sebae* (Newman et al. 2000), *Pristipomoides multidens* (Newman and Dunk 2002) and *L. argentimaculatus* (Russell et al. 2003).

The $\hat{K}$ for *L. bohar* is similar to that reported from the only other study of *L. bohar* in which otolith sections were used to estimate age (0.11; Loubens 1980) and is much less than that reported by Wright et al. (1986; K = 0.27), who used length frequency analysis to assign age. This $\hat{K}$ is less than 0.1, which is consistent with growth described for populations of other species that demonstrated vulnerability to overfishing (Musick 1999). The only other studies of lutjanids that reported equivalently low estimates of K were on *Lutjanus purpureus* (0.09; Menenzes and Gesteira 1974), *L. analis* (0.1; Manooch 1987), and *L. griseus* (0.1; Manooch and Matheson 1981), which all reported much higher estimates of L_∞ (989 mm TL, 1178 mm FL (1089 mm TL), 890 mm TL, respectively) than reported for this study (664.07 mm TL).

The estimated $\hat{L}_\infty$ for the Lizard Island Region was smaller than that which Manooch (1987) cited Talbot (1960) as having reported for *L. bohar*, at 660 mm standard length (SL; 737.4 mm TL), but Talbot did not fit the von Bertalanffy model to length-at-age. This $\hat{L}_\infty$ was also much longer than the 520 mm SL (585.2 mm TL) estimate reported by Loubens (1980), but Loubens analysed a relatively small sample size (n = 14) and estimated L_∞ using a different method. Despite the high coefficients of determination

(R^2) for fits of the von Bertalanffy model, length-at-age was quite variable, with the lengths of 3.46 year olds ranging from 270 to 471 mm FL. Also, one 605 mm FL individual was estimated to be 21.46 years old, while another individual of 596 mm FL was estimated to be 41.46 years old. This high variability in length-at-age could not be explained by temporal variation, sex-specific growth or fishing intensity. Thus, although the trend of length-at-age for the population was well described, the prediction of age from fish length using the fitted von Bertalanffy model is highly uncertain.

The relationship of whole fish weight to length was very tight and showed relatively little variation at any point, indicating that fish weight could be predicted precisely from fish length. This result therefore negated the need to investigate the relationship between fish weight and age for this species. The only other weight-length relationship quantified for this species described a lighter weight at age for older fish in Papua New Guinea (Wright et al. 1986). It is difficult to determine if this is a regional difference in ontogenetic condition or if differences were due to seasonal variation in condition (Weatherley and Gill 1987) because it was not specified by Wright et al. (1986) at what time of year weight-at-length samples were collected.

4.4.2.3. Mortality.

The use of age data pooled across years without the confounding influence of zone (Fig. 4.4) produced a rather high estimate of mortality from catch-curve analysis (0.464; Fig. 4.10) given the high estimated longevity (44.46 years) and relatively slow average growth trend (K = 0.098) observed for *L. bohar* from this region. Further, this estimate was much higher than expected given the general trends revealed by Pauly (1980) and Hoenig (1983) for teleosts. Clearly, if *L. bohar* populations exhibit a conventional exponential decline in numbers over time due to natural mortality, as observed for other congenerics (e.g. Davis and West 1992; Newman 2002; Kritzer 2004), then this high catch curve estimate is likely to be an artefact of a reduced availability of older fish to the sampling method used for the ELF Experiment. This might be because of the limited depth range sampled combined with age- or size-specific depth distributions of *L. bohar* or changes in gear selectivity with size. For these reasons, I consider the Pauly and Hoenig estimates more plausible indicators of mortality rate for *L. bohar*.

4.4.3. Conclusion.

Factors to consider potentially having an influence on age-growth analyses in subsequent chapters include: zone for total frequency, mean age, mean length, age frequencies, and length-at-age; sex for length group frequencies and weight-at-length; and year for mean age, mean length, and weight-at-length, because significant effects were detected on results for the Lizard Island Region in this Chapter. Further, the effect of year on age and length frequency distributions for GF and BF zones was not investigated and thus should also be considered if sample sizes are sufficient, particularly considering that temporal manipulations of fishing were done within these zones during the sampling period. The use of different sampling methods improved the range of age and length data for analysis, resulting in improved descriptions of growth and an indication of the selectivity of ELF Experiment catch surveys and reduced availability of larger *L. bohar* to sampling.

Relatively slow growth and a likely low (i.e., Hoenig estimate) or moderate (i.e., Pauly estimate) rate of natural mortality indicate that *L. bohar* could be particularly vulnerable to overfishing. Adams (1980) has demonstrated that species with slow growth and slow rates of natural mortality are likely to produce lower harvest yields relative to shorter-lived, faster-growing species for a given harvest rate. In a simulation study, Kirkwood et al. (1993) provided supportive evidence of this and demonstrated that species with lower rates of natural mortality would be likely to take longer to recover from overfishing. Further, comparative studies have demonstrated that long-lived, slow-growing species generally have a high vulnerability to overfishing and fishing impacts (Parent and Schriml 1995; Jennings et al. 1998; Musick 1999). Results from this Chapter on general age-growth characteristics therefore provide further evidence to suggest that *L. bohar* populations are likely to be vulnerable to overfishing.

Chapter 5: Geographic, regional, and temporal variation in age-growth characteristics.

5.1. Introduction.

Coral reefs are classified as ‘multi-scalar’ systems for the study of reef fish ecology because ontogenetic, demographic, and ecological processes that have evolved within this environment occur over different spatial scales (Sale 1998). Reef fish demography may vary: within reefs (e.g. van Rooij et al. 1995), about islands (Aldenhoven 1986; Gladstone and Westoby 1988), between islands and reefs (Pitcher 1992; Newman et al. 1996b; Gust et al. 2002), and between largely dispersed geographic areas (Craig et al. 1999; Grandcourt 1999; Meekan et al. 2001). Studies of reef fish demography over multiple spatial scales (e.g. Pitcher 1992; Gust et al. 2002; Kritzer 2002; Williams et al. 2003) are necessary for determining which scale is most appropriate for fisheries management and to assess the generality of results obtained at just one or a few locations.

Comparison of demographics and population parameters between locations that have experienced different historical levels of fishing pressure has also been used to infer the relative magnitude of harvest impacts (e.g., Munro 1983; Ferry and Kohler 1987; Jennings et al. 1995; 1998; 1999). For instance, fishing pressure on *L. bohar* populations differs in many areas of the world because of it’s reputation for causing ciguatera fish poisoning in some areas (Lewis 2001a), such as on the GBR (Gillespie et al. 1986), and not in others, such as in the Seychelles (Wheeler 1953). Also, *L. bohar* was, and currently is, fished with different intensity in different regions of the

Seychelles (Government of Seychelles 2000) because some regions, such as the Amirantes Plateau, are remote to populated cities and villages (Jennings et al. 2000).

The failure to account in such comparisons for differences in other factors, such as habitat, history and/or larval supply, and the infringement of historical management regulations, however, could confound interpretations of fishing effects detected by this approach (Russ 2002). The potentially confounding influence of environmental or anthropogenic variables on the results of such “mensurative experiments” has been widely recognised (Hurlbert 1984). The interpretation of comparisons from a single time frame can also be misleading when significant temporal variation is characteristic of a population (e.g., because of variable recruitment) (Begg et al. 1999). Some recent longer term studies have demonstrated the benefits of collecting information on population demographics before, during, and after fishing pressure through the manipulations of marine reserves (Mapstone et al. 1996; 1997; 2004; Russ and Alcala 1996; 1998; 2003; 2004; Campbell et al. 2001).

Differences in naturally-occurring aspects of biology could also indicate different intrinsic levels of vulnerability to fishing impacts. For instance, long-lived, slow-growing species are most likely to be heavily impacted by fishing (Parent and Schriml 1995; Jennings et al. 1998; Musick 1999). Similarly, local differences between sites in population biology could indicate different local vulnerabilities to fishing impacts and thus may warrant consideration of region-specific management strategies (Grimes et al. 1987).

I explored spatio-temporal variation of *L. bohar* population biology and demography between and within the GBR and Seychelles: (i) to obtain an indication of the generality of age-growth results described in Chapter 4 and (ii) to infer the relative magnitude and/or likelihood of harvest impacts in regions where *L. bohar* has historically been fished to different extents. Information on spatio-temporal variability on the GBR was used to explore, to some extent, the validity of assuming regional uniformity in natural demographics that underpinned the mensurative "experiment" done in the Seychelles. The highly structured sampling frame of the ELF Experiment (Mapstone et al. 2004) provided scope for exploring the influence of spatio-temporal variation in demographics, while examining an area where *L. bohar* has historically been lightly fished compared to the heavily fished Seychelles populations. Aspects of growth, population structure, and morphology in both areas were also compared to determine the extent to which these widely-separated populations differed in population biology, and thus, in their likely vulnerability to fishing impacts.

5.2 Methods.

5.2.1. Sample and data collection.

Samples were collected as described in Chapter 2. Sample sizes collected each year from each zone (GC, GF, BF) per GBR region (Lizard Island Region, Townsville Region) on ELF Experiment spring catch surveys are shown in Table 5.1. The relative positions of reefs sampled within each zone across the GBR shelf were also recorded to assess the possible confounding influence of cross-shelf effects on interpretations of zone effects. The relative positions of reefs on the GBR shelf were calculated from measurements made on maps of the GBR Marine Park (GBRMPA 2002; Table 5.2).

Table 5.1. Samples collected on spring catch surveys of the ELF Experiment. GC, GF, and BF are zones of the ELF Experiment (see Chapter 2).

Year	Lizard Island Region			Townsville Region		
	GC	GF	BF	GC	GF	BF
1995	20	20	13	66	28	3
1996	5	8	4	24	19	13
1997	34	7	13	17	8	7
1998	16	7	12	22	10	5
1999	21	8	16	25	12	15
2000	16	12	12	23	13	9
2001	34	19	25	22	8	19
Total	149	81	95	199	98	71

Table 5.2. Relative position of reefs (within zones) sampled on the GBR for the ELF Experiment. Regions: “Liz” = Lizard Island Region; “Tsv” = Townsville Region. Straight-line distances from each respective ELF reef to the shore (“Shore to reef”) were estimated from measurements made on maps of scale 1:250,000 (GBRMPA 2002). The “Proportional distance across GBR shelf” was approximated as the “Shore to reef” distance divided by cross-shelf distances, estimated for transects of the GBR Depth and Elevation Model (Lewis 2001b), that passed through the centre of each respective study region (i.e., Liz: Transect #1475, ~56km; and Tsv: Transect #1875, ~125km). Reefs ranked in ascending order of Proportional distance across GBR shelf.

Region	Zone	Reef	Shore to reef (km)	Proportional distance across GBR shelf
Liz	GF	Rocky Islets A	16.0	0.29
Liz	BF	14-133	16.75	0.30
Liz	GF	Eyrie Reef	17.25	0.31
Liz	BF	Rocky Islets B	20.0	0.36
Liz	GC	South Direction Island	22.25	0.40
Liz	GC	MacGillivray Reef	33.5	0.60
Tsv	GC	Glow Reef	79.0	0.63
Tsv	GF	Yankee Reef	80.0	0.64
Tsv	BF	Fork Reef	82.9	0.66
Tsv	BF	Knife Reef	85.7	0.69
Tsv	GF	Faraday Reef	86.7	0.69
Tsv	GC	Dip Reef	92.4	0.74

Sagittal otoliths were processed to determine fish age according to the methods described in Chapter 3. Estimates of age in days for those *L. bohar* estimated to be less than 1 year old from the GBR (n = 12) and the Seychelles (n = 3) were made according to the method of Lewis and Mackie (2002) described in Chapter 4. The procedure for calculating age estimates from counts of annuli in Chapter 4 was also used for Seychelles otoliths. This was considered appropriate because the deposition of annuli in otoliths (Chapter 3) and sampling (Chapter 2) occurred at the same time of year in both areas (Chapter 3), Further, age estimates from counts of annuli were comparable between areas because the estimated time to formation of the first band was similar (Fig. 5.1).

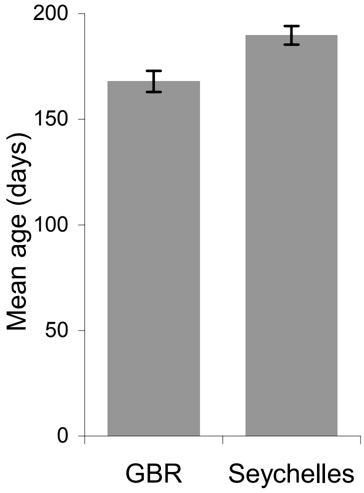


Figure 5.1. Mean estimated age from counts of microincrements on otolith sections of 0+ year olds. Error bars are standard errors of the estimates.

5.2.2. General analysis framework.

5.2.2.1. GBR analysis.

Tests of the effects of Region, Zone, and Year were initially done for data collected from ELF Experiment catch surveys to explore the significance of spatio-temporal variation on the GBR and general effects of the ELF Experiment design on results. Although the experimental units of the ELF Experiment were reefs, Reef(Zone) was omitted from tests because *L. bohar* were not sampled from all reefs in all years. Also, since Reef(Zone) was found not to have a significant effect on mean age or FL from the Lizard Island Region (Chapter 4), nor to have significant interaction effects with Year, Reef(Zone) was assumed not to have a confounding influence on analyses of this Chapter.

Three-factor analyses of Region, Zone, and Year were done where possible (i.e., for mean age, mean FL, and weight-at-FL) to facilitate the testing of interaction effects on results. Significant interactions were explored using single factor tests for the effect of one factor for each level of the other interacting factor(s). Non-significant effects were pooled in these analyses if the probability of a Type I error was greater than 0.25 (Winer 1971 *in* Underwood 1981). *Post hoc* tests were then done to detect differences among those groups for which significant effects were detected by the one factor tests (where there were more than two groups being compared).

5.2.2.2. Testing the effects of area and differences in historical fishing pressure.

Results from the GBR analyses also provided information to determine if it was valid to pool across years, zones, and/or GBR regions in subsequent analyses of Area effects (i.e., GBR v Seychelles). Table 5.3 shows the rationale for analyses done, based on the results of GBR analyses, to test the effect of Area and the effect of Fishing (i.e., the comparison of lightly fished Amirantes Plateau v the historically fished Mahe Plateau) in the Seychelles.

Table 5.3. Decision table for analysis of effects of Area and differences in historical fishing pressure in the Seychelles. Table indicates the general approach to analyses, but see text for specific details / variants of tests done. "Fishing effect Seychelles" = was there a significant difference detected between the lightly fished Amirantes Plateau (AP) versus the fully fished Mahe Plateau (MP)? "Liz" = Lizard Island Region; "Tsv" = Townsville Region. * = This test (i.e., fully fished components) was only done if no significant effect was detected from the test of lightly fished components (i). ** = GBR data from 2000 and 2001 only.

Decision Criterion	Effect(s) detected from GBR tests	Fishing effect Seychelles?	Analysis.
1.	None	Yes	1-factor: GBR v AP v MP
2.	None	No	1-factor: GBR v Seychelles
3.	Region	N/A	1-factor: Liz v Tsv v AP v MP
4.	Year	Yes	1-factor: [GBR 2000+2001] v AP v MP
5.	Year	No	1-factor: [GBR 2000+2001] v Seychelles
6.	Zone	N/A	2-factor: Area x Fishing
7.	Region x Year	Yes	1-factor:[Liz 2000+2001] v [Tsv 2000+2001] v AP v MP
8.	Region x Year	No	1-factor:[Liz 2000+2001] v [Tsv 2000+2001] v Seychelles
9.	Region x Zone	N/A	i. 1-factor: Liz GC v Tsv GC v AP *ii. 1-factor: Liz BF v Tsv BF v MP iii. 1-factor: AP v MP
10.	Zone x Year	N/A	2-factor: Area x Fishing**
11.	Region x Zone x Year	N/A	i. 1-factor: [Liz GC 2000+2001]v[Tsv GC 2000+2001]vAP *ii. 1-factor: [Liz BF 2000+2001]v[Tsv BF 2000+2001]vMP iii. 1-factor: AP v MP

Failure to detect any effect of Region, Zone, or Year meant that data could be pooled across all of these effects to test for differences between areas (Table 5.3, Criteria 1, 2). An effect of GBR Region meant that data from the Lizard Island Region and Townsville Region could not be pooled in subsequent analyses (Criteria 3, 7-9, 11). An effect of Year meant that one could not pool across years in subsequent analyses, so tests of GBR and Seychelles' data were done for data sampled over the same period in both regions (i.e., for data collected in 2000 and 2001; Criteria 4, 5, 7, 8, 10, 11). If single factor or *post hoc* analyses of GBR data detected no significant difference between 2000 and 2001 data then it was valid to pool across these years for tests of Area.

An effect of Zone detected in GBR analyses meant that it was not valid to pool across zones of the ELF Experiment in tests of GBR v Seychelles' data; so separate tests for groups of "like" historical fishing pressure were done. "Lightly fished" components were GC zones on the GBR and the Amirantes Plateau region in the Seychelles (Table 5.3, Criteria 9, 11, Test i). "Fully fished" components were BF zones on the GBR and the Mahe Plateau region in the Seychelles. Samples from the CRFFF were also included in the "fully fished" component from the GBR for some analyses. Tests using data from fully fished components for the effect of historical differences in fishing pressure between areas were done if it was determined that there was no significant effect of area for lightly fished components (Table 5.3 Criteria 9, 11, Test ii). The tests on lightly fished components determined to some extent the validity of testing for differences in fishing effects between areas by determining the significance of potentially confounding effects of natural variation between areas when fishing effects were presumed to be absent or very low.

Results for different Seychelles regions were compared to test for effects of historical differences in fishing pressure (i.e., the "Fishing" effect from the "mensurative experiment"). The interpretation of fishing effects from these tests were also dependant on results from the GBR analyses because the detection of regional variation in the absence of fishing suggested that one could not attribute differences between the Amirantes and Mahe Plateaux to fishing, natural spatial variation, or both.

5.2.3. Analyses: Comparing sampled age and length data.

Comparisons of mean ages and fork lengths (FL) were done using ANOVA tests and t-tests for independent samples in “SPSS for Windows” (Version 11.0; SPSS Inc.). A 3-factor ANOVA comparing Region (Lizard Island Region, Townsville Region), Zone (GC, GF, BF), and Year (1995 – 2001) was done to analyse GBR data (Region x Zone x Year). Model III sums of squares were used to account for uneven sample numbers among groups. Age and FL data were either log-transformed, square-root transformed or reciprocal-transformed where necessary to improve normality prior to analysis (Zar 1999). The degrees of freedom of t-tests were reduced to adjust for violation of the homogeneity of variance assumption where necessary (i.e., transformation of data did not render variances homogeneous). Tukey’s multiple comparison tests for unbalanced designs were used for *post hoc* tests (Tukey 1953; Kramer 1956 *in* Zar 1999).

A 3-factor log-linear analysis was done by step-wise backward elimination (Gilbert 1981) to identify the relative importance of Region (Lizard Island Region, Townsville Region), Year (1995 to 2001), or their interaction on the frequency of *L. bohar* sampled per FL or age group from GF zones prior to ELF Experiment manipulations (Table 2.1) and from GC zones. This was done as an initial exploration of spatio-temporal variation of sampled age and length frequency distributions from lightly fished components on the GBR. Data from experimental reefs and years subject to deliberate fishing were excluded. The model with the fewest terms that was not significantly different from the fit of the full factor model was accepted as the most parsimonious description of the frequency data (Gilbert 1981).

Some sample years (FL group frequency analysis: 1996; age frequency analysis: 1996, 1998, 2000) and age groups (see following) were excluded to reduce the number of sampling zeros in the observed data matrix. This was done in preference to the pooling of frequencies across successive categories because it retained a more biologically meaningful data structure for analysis (Fienberg 1970). The 3.46 to 9.46 year (inclusive) age groups were retained for analysis because few data were excluded and relatively few sample zeros remained compared to other combinations of age groups (Fig. 5.2). Remaining sample zeros were accounted for by the addition of a small constant (0.5) to all cell frequencies and a corresponding reduction in the degrees of freedom of the log-likelihood chi-square G^2 statistic (Fienberg 1970).

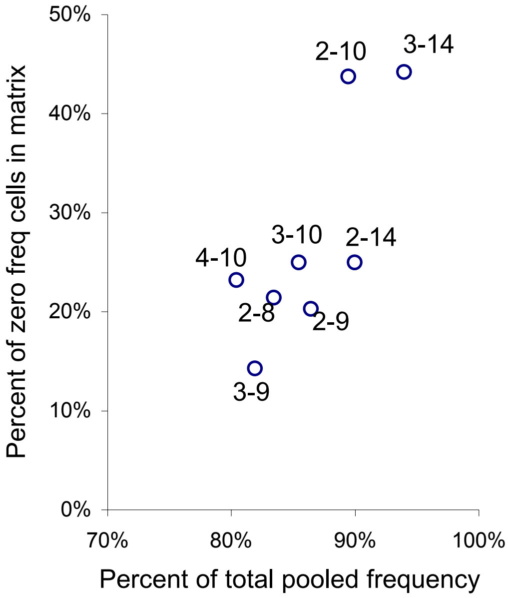


Figure 5.2. Criterion used to select age group range for spatio-temporal log-linear analysis of sampled age frequency distributions from GBR regions. Age estimates rounded to zero decimal places for simplicity. For the above alternative age group ranges there were minimal improvements in the percentage of total sample size included (pooled across sample years 1995, 1997, 1999, 2001 and GBR regions) with respect to the much larger changes in the percentage of sampling zeros present in respective observed data matrices. Therefore the 3.46-9.46 age group range was preferred because it had the lowest percentage of sampling zeros.

Sampled frequency distributions of *L. bohar* were then constructed from 50 mm categories of FL and annual age groups and compared using the Kolmogorov-Smirnov 2-sample test (Sokal and Rohlf 1995). Since this test only allowed pair-wise comparisons of frequency distributions, further tests of GBR data (if required) were done first, followed by tests of like fishing groups between areas (i.e., Table 5.3, Criteria 9: tests i, ii) and the test comparing Seychelles' regions was done last.

5.2.4. Analyses: Comparing growth.

GBR data were analysed by a 2-factor ANOVA of GBR Region (Lizard Island Region, Townsville Region) and Zone (GC, GF, BF) of the mean FL for the age group with the greatest number of samples and least number of cell zeros across all levels of the tested factor(s) (Region x Zone). Subsequent ANOVA and *post hoc* tests proceeded as for comparisons of mean age and FL.

Growth trends were modelled by fitting the von Bertalanffy growth function (Eqn. 4.1) to FL-at-age data sampled from each region and area. Growth, in terms of body condition, was also modelled for weight-at-FL data sampled from each region and area using the power function (Eqn. 4.3). Models were fitted to FL-at-age and weight-at-FL data for zones, regions, and areas sampled during Austral spring months (September to December) to minimise inter-seasonal variation on average trends. Data were also pooled across years of sample collection to increase the number of replicates and thus the precision of growth parameter estimates, for each region and area.

The parameter estimates and associated growth model fits were compared among regions and areas using likelihood ratio tests and 95% confidence regions according to methods of Kimura (1980) as described in Chapter 4. First, the effect of Zone (GC, GF, BF) on the fit of the von Bertalanffy model to data from Townsville Region was tested, as it was for Lizard Island Region in Chapter 4. A significant effect of Zone was explored by further pair-wise likelihood ratio tests that adjusted the probability of Type I error using the Dunn-Šidák correction for experiment-wise error rate (Sokal and Rohlf 1995). Tests of Area and Fishing in the Seychelles, respectively, were then done using this sequence of tests.

Weight-at-FL trends were compared by linear-transforming the weight-at-FL data and then proceeding with ANCOVAs as done in Chapter 4. In all ANCOVAs, tests for effects on slope were done first, and if there was no significant difference then tests of effects on elevation were done (Zar 1999). A 3-factor ANCOVA comparing GBR Region (Lizard Island Region, Townsville Region), Zone (GC, GF, BF), and Year (1999 – 2001) was done first (Region x Zone x Year). Single-factor ANCOVA tests were then done to explore significant interactions, followed by pair-wise comparisons of slope or intercepts among groups for which significant effects were detected using the Dunn-Šidák correction for experiment-wise error rate.

5.3 Results.

5.3.1. Age and length.

5.3.1.1. Mean FL.

Inspection of the raw data, pooled across years of sample collection, revealed no consistent difference in mean FL between areas (GBR, Seychelles) or sites of different historical fishing pressure (Fig. 5.3). The mean FLs for the Townsville Region were highest compared to those from the Lizard Island Region and the Amirantes Plateau of the Seychelles. The mean FL for lightly fished components were higher than the fully fished components for the Lizard Island Region and Seychelles but not for the Townsville Region. Rather, consistent differences were more apparent among regions where mean FL was higher for *L. bohar* from the Townsville Region than those from the Amirantes Plateau, Lizard Island Region and Mahe Plateau (Fig. 5.3).

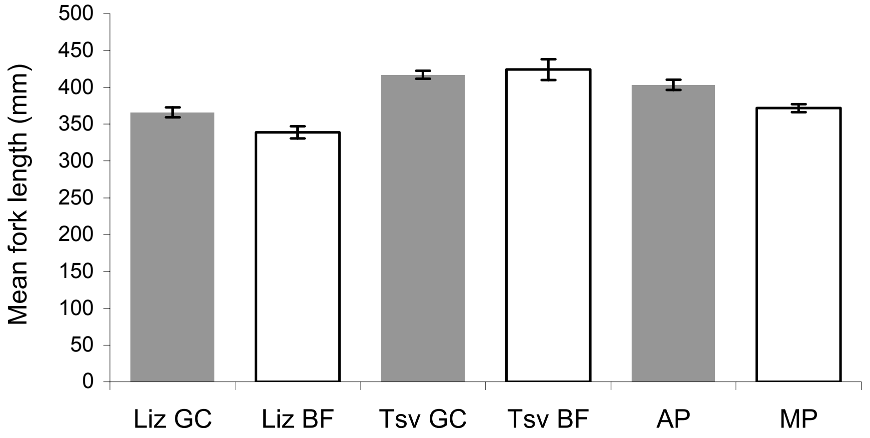


Figure 5.3. Mean fork length of data by region and historical fishing pressure. Grey bars are lightly fished components and clear bars are fully fished components. GBR: Tsv = Townsville Region; Liz = Lizard Island Region. Seychelles: AP = Amirantes Plateau; MP = Mahe Plateau; GC, BF are zones of the ELF Experiment: In GC zones fishing is not permitted and in BF zones fishing has been permitted (see Chapter 2). Error bars are standard errors of the estimates.

A significant effect of GBR Region on mean FL was detected and there were no significant Year, Zone, or interaction effects from the 3-factor ANOVA (Table 5.4). The subsequent single-factor test detected a significant difference in mean FL among GBR and Seychelles regions (Table 5.5a). *Post hoc* tests detected a longer mean FL from the Townsville Region than from the Lizard Island Region and Mahe Plateau and a shorter mean FL from the Lizard Island Region than from the Townsville Region and

Amirantes Plateau (Table 5.5b). No significant difference in mean FL was detected between Seychelles' regions.

Table 5.4. Analyses of mean FL, GBR. Results significant at $\alpha = 0.05$ in **bold**. The logarithmic transformation $X^1 = \log(X+1)$ was applied to normalise skew and kurtosis of FL data.

	MS	df	F	p
Region	0.462	1	54.11	**<0.001**
Zone	0.005	2	0.060	0.549
Year	0.015	6	1.74	0.109
Region x Zone	0.022	2	2.26	0.073
Region x Year	0.017	6	1.95	0.071
Zone x Year	0.012	12	1.27	0.233
Region x Zone x Year	0.012	12	1.37	0.175
Residual	0.009	645		

Table 5.5. Analyses on mean FL comparing both regions from each Area. Results significant in at $\alpha = 0.05$ in (a) in **bold**. The logarithmic transformation $X^1 = \log(X+1)$ was applied to normalise skew and kurtosis of FL data. (b) Tukey's HSD *post hoc* tests for unbalanced design where groups joined by bold line were found not significantly different ($\alpha = 0.05$). Regions: "Tsv" = Townsville Region; "AP" = Amirantes Plateau; "MP" = Mahe Plateau; "Liz" = Lizard Island Region.

a) Single Factor ANOVA of Region.

	MS	df	F	p
Region	0.247	3	28.94	**<0.001**
Residual	0.009	893		

b) Post hoc tests.

Longest **Shortest**

5.3.1.2. Mean age.

Inspection of the raw age data, pooled across all sample years, revealed no consistent differences in mean age between areas or sites of different historical fishing pressure (Fig. 5.4). The mean age from lightly fished components was highest for the Townsville Region, followed by the Amirantes Plateau and the Lizard Island Region (lowest). The mean age for lightly fished components was higher than the fully fished components for the Lizard Island Region and Seychelles (Fig. 5.4).

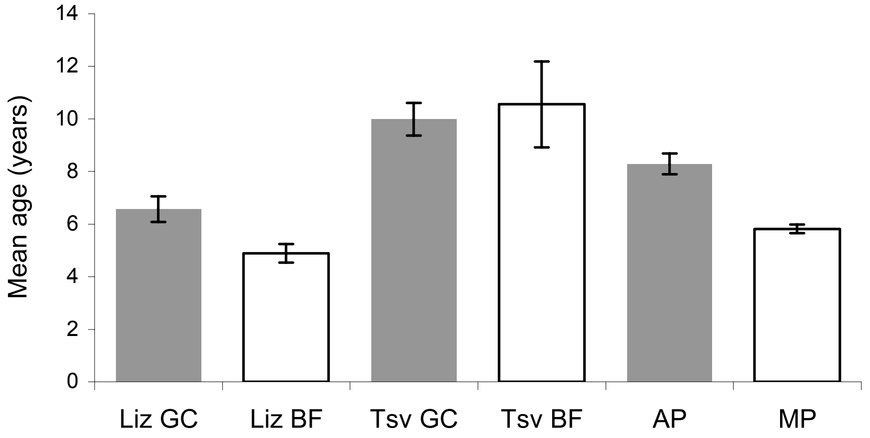


Figure 5.4. Mean age of data by region and historical fishing pressure. Grey bars are lightly fished components and clear bars are fully fished components. GBR: Tsv = Townsville Region; Liz = Lizard Island Region. Seychelles: AP = Amirantes Plateau; MP = Mahe Plateau; GC, BF are zones of the ELF Experiment: In GC zones fishing is not permitted and in BF zones fishing has been permitted (see Chapter 2). Error bars are standard errors of the estimates.

A significant 3-way interaction effect of GBR region with Zone and Year on mean age was detected (Table 5.6a). Subsequent single-factor tests of mean age detected: (i) an effect of Region for the GC zone in 1999 only; (ii) effects of Zone for Townsville Region (1999, 2000) and for Lizard Island Region (1995, 1998); and (iii) effects of Year for Lizard Island Region GC and GF zones (Table 5.6b). In 1999 a younger mean age was sampled from the Lizard Island Region (5.33 ± 0.59SE years) than from the Townsville Region (13.17 ± 3.02SE years).

Since no effect of Zone was detected consistently for 1997 groups ($\alpha > 0.25$), zones were pooled for the test of region for that year. *Post hoc* tests revealed these interaction effects were due to an older mean age sampled from the GC than from the BF zone for some years (1995, 1998) in Lizard Island Region (as found in Chapter 4), but no significant effects of Zone were detected for Townsville Region (Table 5.6c). The detection of Zone effects for Townsville Region from single-factor ANOVAs but not from the *post hoc* tests probably reflects the lower statistical power of the *post hoc* tests but also leaves the origin of the Zone effects uncertain. Differences among years for GC and BF zones in Lizard Island Region were not consistent and non-obvious apart from 1999 being among the youngest samples and 1996 and 2000 being among the oldest samples for both zones (Table 5.6c).

Table 5.6. Analyses of mean age, GBR. Test ordered in sequence done, from top to bottom of tables. “LF” = lightly fished component; “FF” = fully fished component; Regions: “Tsv” = Townsville; “Liz” = Lizard Island; Zones: GC, GF, BF (Chapter 2); Years: 1995 – 2001. Test results used as evidence to pool across factors at $\alpha = 0.25$ in *italics*. Results significant at $\alpha = 0.05$ in **bold**. The logarithmic transformation $X^1 = \log(X+1)$ was applied to normalise skew and kurtosis of age data. * = No test done because n=1 for one group. ** = Tukey’s HSD *post hoc* tests for unbalanced design among years for each zone and region combination © and among zones for each region and year combination (d) where a significant effect was detected by single factor ANOVAs (b). Groups joined by bold line were not significantly different ($\alpha = 0.05$).

a) Multi-factor ANOVA.

	MS	df	F	p
Region	0.168	1	3.42	0.065
Zone	0.180	2	3.66	**0.026**
Year	0.182	6	3.70	**0.001**
Region x Zone	0.111	2	2.26	0.105
Region x Year	0.070	6	1.42	0.204
Zone x Year	0.090	12	1.84	**0.040**
Region x Zone x Year	0.113	12	2.30	**0.007**
Residual	0.049	529		

Table 5.6.b) Single factor tests exploring the Region x Zone x Year interaction.

Factor 1 Level	Factor 2 Level	Factor Tested	Statistic	df1	df2	Value	p
Tsv	GC	Year	*F*	6	166	1.97	0.073
Tsv	GF	Year	*F*	6	72	1.38	0.234
Tsv	BF	Year	*F*	6	47	0.74	0.617
Liz	GC	Year	*F*	6	111	3.30	**0.005**
Liz	GF	Year	*F*	6	53	2.25	0.053
Liz	BF	Year	*F*	6	82	5.03	**<0.001**
Tsv	1995	Zone	*F*	2	85	0.53	0.589
Tsv	1996	Zone	*F*	2	41	0.58	0.563
Tsv	1997	Zone	*F*	2	21	0.82	*0.454*
Tsv	1998	Zone	*F*	2	26	0.23	0.795
Tsv	1999	Zone	*F*	2	30	4.31	**0.023**
Tsv	2000	Zone	*F*	2	40	4.02	**0.026**

Table 5.6.b) (Continued).

Factor 1 Level	Factor 2 Level	Factor Tested	Statistic	df1	df2	Value	p
Tsv	2001	Zone	*F*	2	42	0.24	0.786
Liz	1995	Zone	*F*	2	41	4.41	**0.018**
Liz	1996	Zone	*F*	2	10	2.26	0.155
Liz	1997	Zone	*F*	2	44	1.28	*0.288*
Liz	1998	Zone	*F*	2	21	23.20	**<0.001**
Liz	1999	Zone	*F*	2	34	0.98	0.388
Liz	2000	Zone	*F*	2	35	0.32	0.731
Liz	2001	Zone	*F*	2	57	2.66	0.079
All zones	1997	Region	*t*	69		-1.62	0.109
GC	1995	Region	*t*	75		-1.06	0.293
GC	1996	Region	*t*	22		0.84	0.410
GC	1998	Region	*t*	27		0.03	0.973
GC	1999	Region	*t*	35		-3.48	**0.001**
GC	2000	Region	*t*	37		-0.99	0.331
GC	2001	Region	*t*	42		-1.05	0.301
GF	1995	Region	*t*	40		-1.92	0.062
GF	1996	Region	*t*	22		-1.31	0.205
GF	1998	Region*	*t*	-		-	-
GF	1999	Region	*t*	5		0.36	0.736
GF	2000	Region	*t*	19		1.09	0.291
GF	2001	Region	*t*	20		-0.62	0.541
BF	1995	Region	*t*	13		0.99	0.342
BF	1996	Region	*t*	7		1.80	0.115
BF	1998	Region	*t*	15		0.90	0.384
BF	1999	Region	*t*	37		-0.87	0.392
BF	2000	Region	*t*	19		-0.90	0.379
BF	2001	Region	*t*	37		0.35	0.726

c) Post-hoc tests comparing years for combinations of Region and Zone.**

	Oldest						Youngest
Liz GC:	1996	2000	1998	1995	1997	2001	1999
	—	—	—	—	—	—	
			—	—	—	—	—
Liz BF:	1997	2000	1996	2001	1995	1998	1999
	—	—	—	—	—		
		—	—	—	—	—	
			—	—	—	—	—

d) Post-hoc tests comparing zones for combinations of Region and Year.**

	Oldest		Youngest
Tsv 1999:	GC	BF	GF
	—	—	—
Tsv 2000:	GC	BF	GF
	—	—	—
Liz 1995:	GC	GF	BF
	—	—	
		—	—
Liz 1998:	GF	GC	BF

The lack of difference between 2000 and 2001 for zones where an effect of Year was detected (Table 5.6c), however, indicated that age data from GBR regions could be combined for these years to compare with Seychelles' data sampled over the same period (i.e. 2000-01). Also, the lack of a Region effect in 2000 and 2001 (Table 5.6b) indicated that it was valid to pool across GBR regions for this period to compare with Seychelles data from the same years.

Although there was no significant effect of Area, there was a significant effect of historical Fishing on mean age (Table 5.7a). This indicated that the difference in mean age between lightly fished and fully fished components in the Seychelles (i.e., Amirantes Plateau v Mahe Plateau regions) and GBR (i.e., GC v BF zones) was consistent. *L. bohar* from fully fished components were shown to be significantly younger (6.82 ± 0.61 years) than from lightly fished components (8.37 ± 0.52 years) of both areas.

Table 5.7. Analyses of mean age, Areas. GBR regions and years were pooled for 2000 and 2001 to compare with Seychelles' data based on the results of Table 5.4(a, b, c) for the test of Area. Test of the effect of "Fishing" was based on the comparison of lightly fished and fully fished components of both areas (see text). The reciprocal transformation $X^1 = \frac{1}{X+1}$ was applied to normalise skew and kurtosis of age data.

a) Multi-factor ANOVA.

	MS	df	F	p
Area	0.005	1	1.93	0.166
Fishing	0.027	1	9.96	**0.002**
Area x Fishing	0.0001	1	0.05	0.822
Residual	0.003	278		

5.3.1.3. Size structure.

Inspection of length frequency data pooled across sample years revealed no clear effects of area or historical fishing pressure on the shape of length frequency distributions, apart from there being consistently fewer samples collected from fully fished components (Fig. 5.5). The modal FL group ranged from 301-350 mm (Lizard Island Region; Fig. 5.5a,b) to 351-400 mm (Townsville Region GC, Mahe Plateau; Figs. 5.5c,f) but it cannot be detected for the Townsville Region BF zone, which is platykurtic (Fig. 5.5d), or for the Amirantes Plateau sample (Fig. 5.5e). The FL range is also markedly lower for the Mahe Plateau distribution than for all other groups.

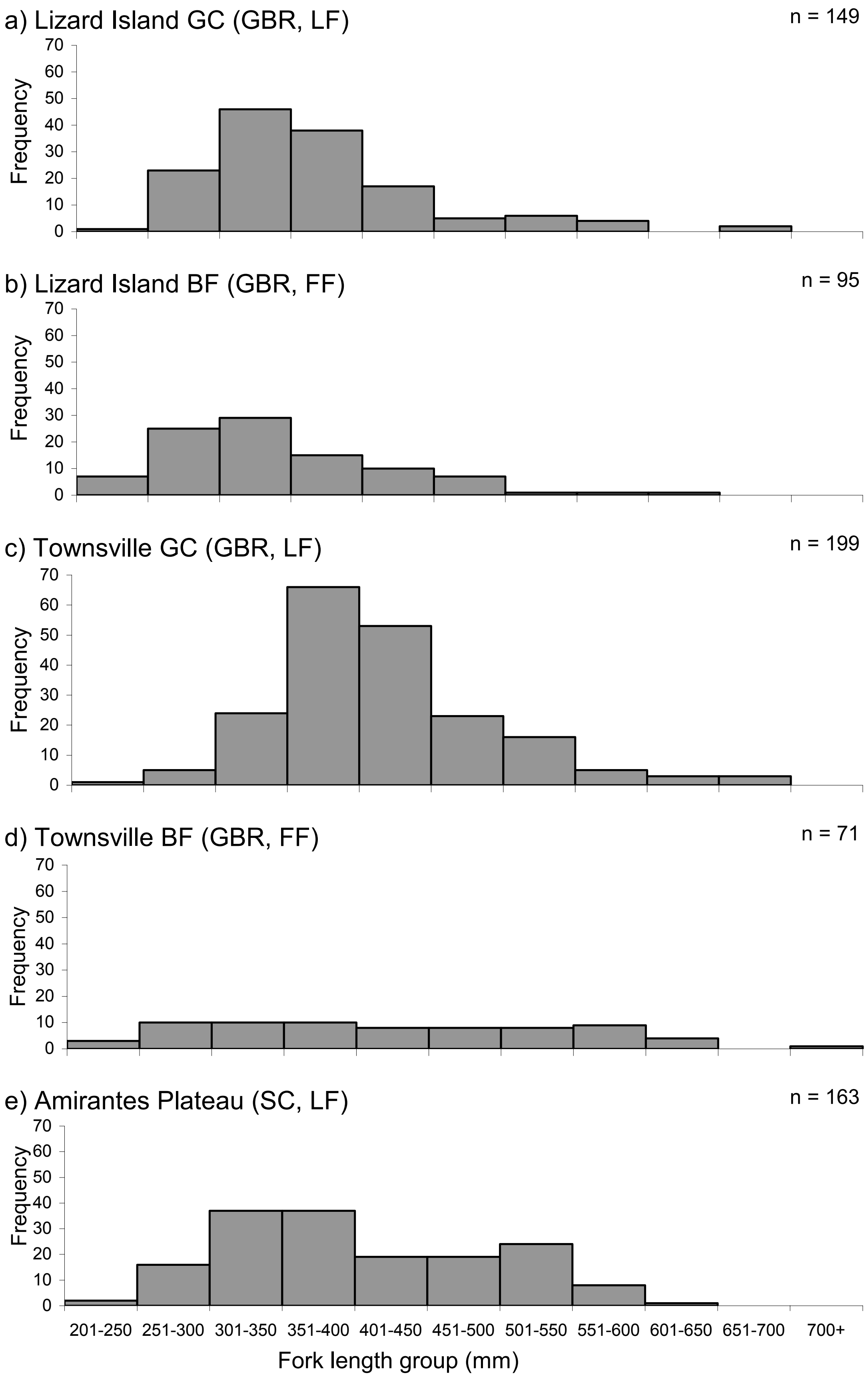


Figure 5.5. Length frequency distributions by region and historical fishing pressure. LF, FF = lightly fished and fully fished components; SC = Seychelles.

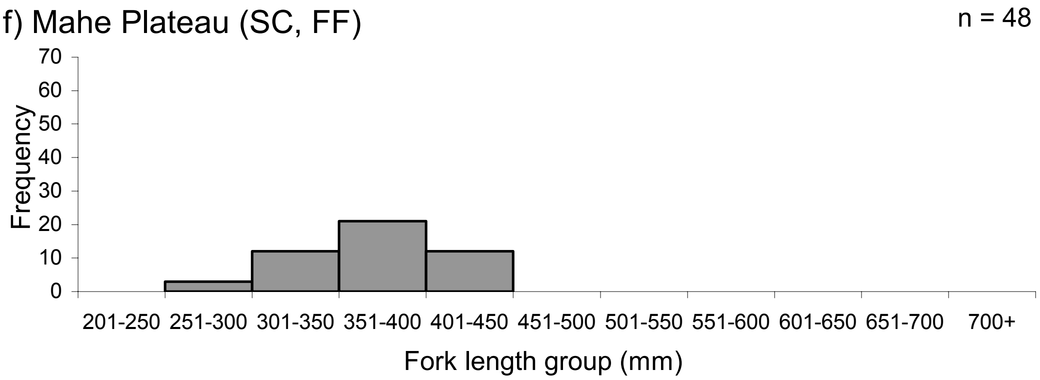


Figure 5.5. Length frequency distributions by region and historical fishing pressure. (continued).

The most parsimonious description of *L. bohar* FL frequencies from lightly fished components (GC zones) in both regions of the GBR was:

$$f(\text{FL}) = \text{FL x Region} + \text{Region x Year} + \text{FL x Year} + \text{FL} + \text{Region} + \text{Year};\ G^2 = 14.01 \quad (5.1).$$

The significant effects of Region and Year on FL frequencies meant that data from GBR regions could not be pooled and only GBR data collected in 2000 and 2001 could be considered for comparison with Seychelles' data. The effect of GBR Region on FL group frequencies is apparent where a larger modal FL group and more larger *L. bohar* were sampled from Townsville Region than from Lizard Island Region (Fig. 5.5). The effect of Year on FL group frequencies is apparent where a high proportion of *L. bohar* sampled in 1999 were smaller than 301 mm FL, a high proportion of the sample collected in 2000 were larger than 500 mm FL and a relatively high proportion of *L. bohar* sampled in 2001 were in the 301-500 mm FL group (Fig. 5.6).

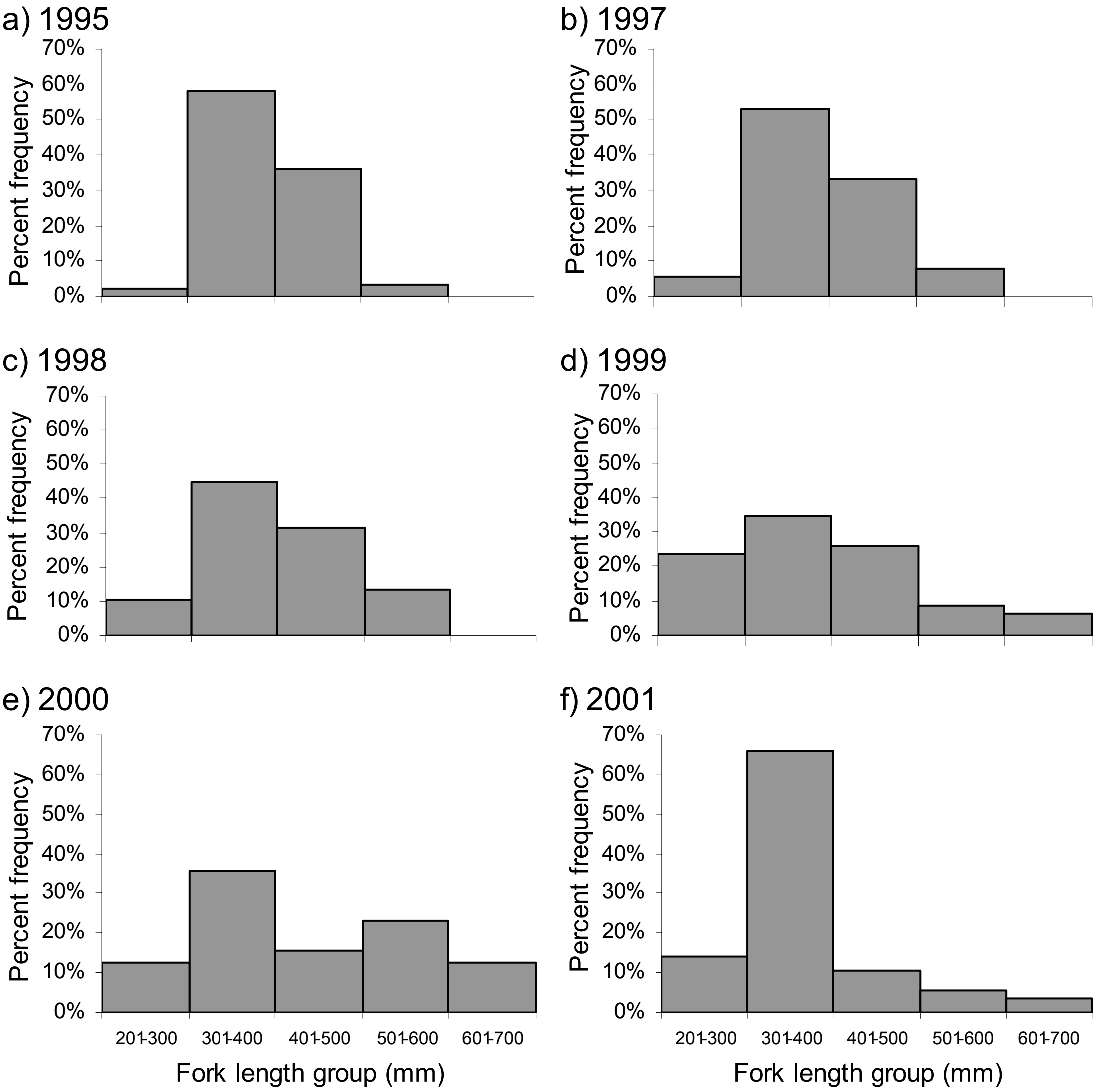


Figure 5.6. Effects of (a) Region and (b) Year on length groups sampled from lightly fished zones on the GBR. "Liz" = Lizard Island Region; "Tsv" = Townsville Region. Data in (a) pooled across years excluding 1996 (also excluded from log-linear analysis).

A detectable difference between 2000 and 2001 for GC zones (Test 1; Table 5.8) and a significant effect of GBR Region (Eqn. 5.1) meant that FL frequencies from GC zones for 2000 and 2001 could not be pooled for each GBR region to compare with data from the lightly fished component of the Seychelles (i.e., Amirantes Plateau). Comparisons of lightly fished FL group frequencies between areas did not produce consistent results because a significant difference was detected between Amirantes Plateau and Lizard Island Region GC zone in 2001 but not between Amirantes Plateau and Lizard Island

Region GC zone in 2000 or between Amirantes Plateau and Townsville Region GC zone samples (Tests 2-4; Table 5.8). The detected effect of Area is apparent where proportionally greater frequencies of larger (i.e., 351-500 mm FL) *L. bohar* were sampled from Amirantes Plateau than from Lizard Island Region in 2001 (Fig. 5.7). No significant difference was detected for FL group frequencies from fully fished components between areas (Tests 6-8; Table 5.8). There was also no significant difference for FL group frequencies between Seychelles' regions (Test 9; Table 5.8).

Table 5.8. Comparison of length frequency distributions. Tests numbered in order of sequence done. Significant differences detected from the Kolmogorov-Smirnov 2 sample test in **bold** at $\alpha = 0.05$. "Liz" = Lizard Island Region; "Tsv" = Townsville Region; "SC" = Seychelles area; "AP" = Amirantes Plateau; "MP" = Mahe Plateau; "LF" = lightly fished component; "FF" = fully fished component.

Test	Factor Level	Factor Level	Factor Tested	Groups compared	n1	n2	*D*
1.	GBR	GC	Year	2000 v 2001	39	44	**0.308**
2.	LF	2000	Area	AP v Liz GC 2000	16	163	0.140
3.	LF	2001	Area	AP v Liz GC 2001	24	163	**0.311**
4.	LF	2000	Area	AP v Tsv GC 2000	23	163	0.250
5.	LF	2001	Area	AP v Tsv GC 2001	20	163	0.136
6.	FF	2000	Area	MP v Liz BF 2000	12	48	0.250
7.	FF	2000	Area	MP v Tsv BF 2000	9	48	0.333
8.	FF	2001	Area	MP v Tsv BF 2001	17	48	0.353
9..	SC	-	Fishing	AP (LF) v MP (FF)	48	163	0.319

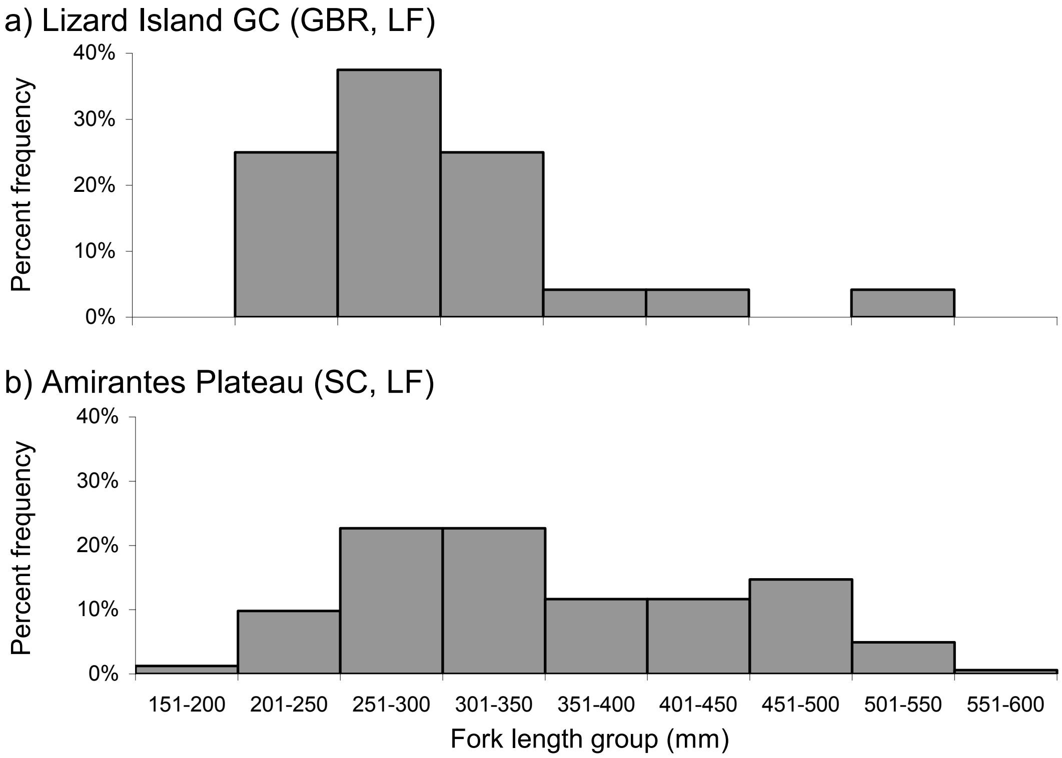


Figure 5.7. Effect of Area on length (FL) group frequencies sampled from lightly fished (LF) zones. Lizard Island Region GC zone sample collected in 2001; SC = Seychelles.

5.3.1.4. Age structure.

Modal ages were older, and the proportion of older fish sampled was higher, from lightly fished sites on the GBR, indicating an effect of fishing on age structure (Figs. 5.8a,b,c,d). In the Seychelles a greater age range and proportionally more *L. bohar* older than 8.52 years were sampled from the lightly fished Amirantes Plateau than from the fully fished Mahe Plateau; also suggesting a fishing effect (Figs. 5.8e,f). No consistent differences in age structure were apparent between areas, although the age structure for the Amirantes Plateau was distinctly different from all other regions, with no clear modal age apparent.

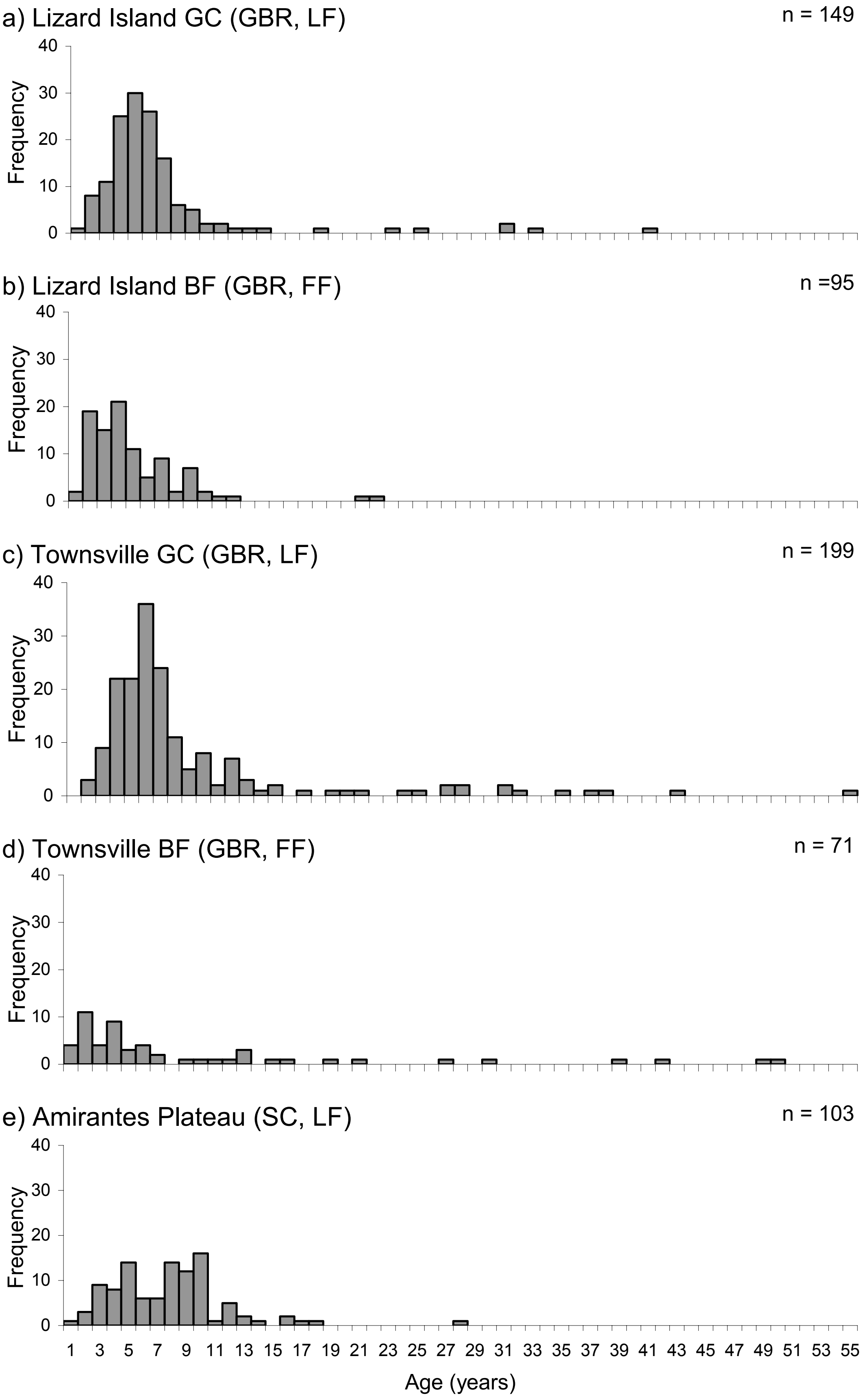


Figure 5.8. Age frequency distributions by region and historical fishing pressure.

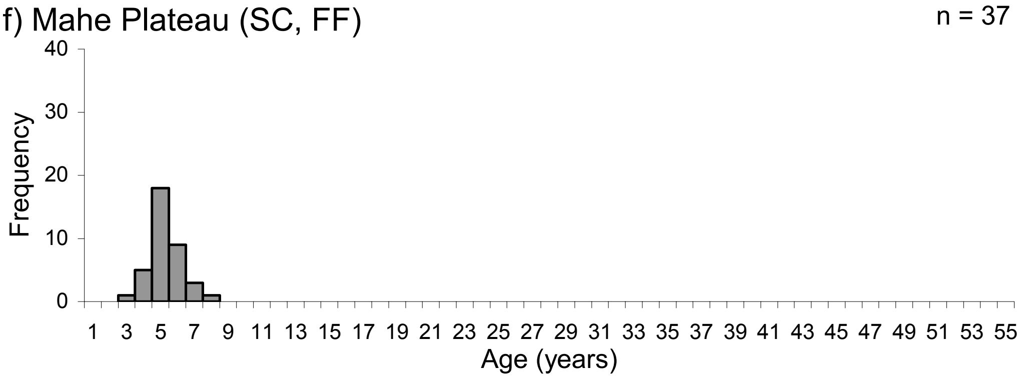


Figure 5.8. Age frequency distributions by region and historical fishing pressure. (continued).

The most parsimonious description of *L. bohar* age frequencies from lightly fished components of GBR regions was:

$$f(\text{Age}) = \text{Age x Region} + \text{Region x Year} + \text{Age} + \text{Region} + \text{Year};\ G^2 = 33.86 \qquad (5.2).$$

The significant effect of Region on age frequencies meant that GBR regions could not be pooled for the comparison with Seychelles' data. No significant effect of Year on age frequencies, however, meant that data could be pooled across years for further analysis. The effect of GBR Region on age group frequencies was apparent as there was an older modal age (6.46 years) and more fish older than 10.46 years sampled in the Townsville Region GC zone and more younger *L. bohar* (i.e., in 2.46 and 5.46 year groups) sampled in the Lizard Island Region GC zone (Fig. 5.8a,c).

Results from the comparison of lightly fished age frequencies detected significant differences between the Amirantes Plateau and both GBR regions (Tests 1, 2; Table 5.9). There was no clear modal age for the Amirantes Plateau, with a higher proportion of 8 to 10 year olds and *L. bohar* older than 20 years scarcely sampled (Fig. 5.8e). A significant difference between Seychelles regions was detected, where a greater age range and a greater proportion of older *L. bohar* were sampled from the Amirantes Plateau (Test 3, Table 5.9; Fig. 5.8e,f).

Table 5.9. Comparison of age frequency distributions. Tests numbered in order of sequence done. Significant differences detected from the Kolmogorov-Smirnov 2 sample test in **bold** at $\alpha = 0.05$. "Liz" = Lizard Island Region; "Tsv" = Townsville Region; "SC" = Seychelles area; "AP" = Amirantes Plateau; "MP" = Mahe Plateau; "LF" = lightly fished component; "FF" = fully fished component. * = Excluding 1996, 1998 and 2000 data because these weren't included in the log-linear analysis (Eqn. 5.2).

Test	Factor Level	Factor Tested	Groups compared	n1	n2	*D*
1.	LF	Area	AP v Liz GC*	88	103	**0.385**
2.	LF	Area	AP v Tsv GC*	111	103	**0.264**
3.	SC	Fishing	AP (LF) v MP (FF)	37	103	**0.517**

5.3.2. Growth.

5.3.2.1. Length-at-age.

The most frequently sampled age group of *L. bohar* was the 4+ (i.e., 4.46 year olds from the GBR and 4.51 year olds from the Seychelles) year group when data were pooled across regions, years, and zones on the GBR, and for the Amirantes and Mahe Plateaux, so this age group was used for tests on mean FL-at-age. From inspection of plots of mean FL-at-age 4+, pooled across sample years, there was no clear effect of area or historical fishing pressure (Fig. 5.9). Means for fully fished components were higher than lightly fished components of the Townsville Region and Seychelles, but not for the Lizard Island Region. Means for the Townsville Region were also higher than all other regions.

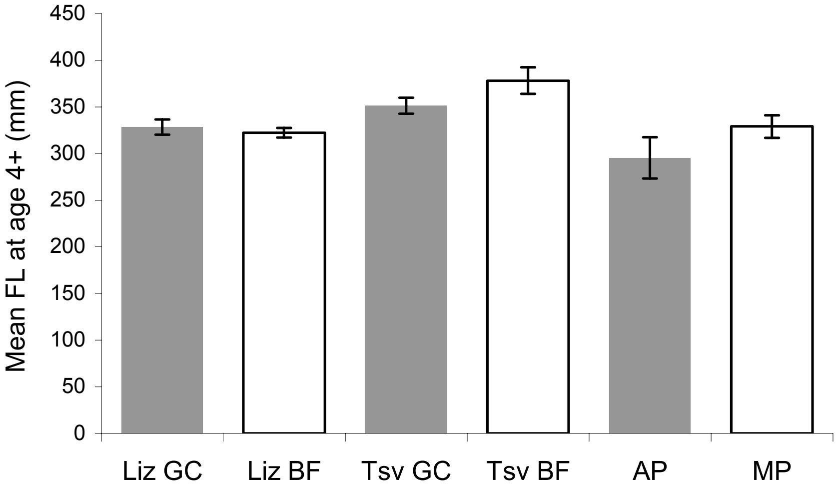


Figure 5.9. Mean fork length of 4+ year olds by region and historical fishing pressure. Grey bars are lightly fished components and clear bars are fully fished components. Tsv = Townsville Region; Liz = Lizard Island Region; AP = Amirantes Plateau; MP = Mahe Plateau; GC, BF are zones of the ELF Experiment (see Chapter 2). Error bars are standard errors of the estimates.

The 2-factor ANOVA of the effects of GBR Region and Zone showed no significant Zone or Zone x Region effect but a significant effect of Region on mean FL-at-age 4+ (Table 5.10). The subsequent single factor ANOVA among GBR and Seychelles regions also demonstrated a significant effect of Region, and *post hoc* tests revealed that the FL-at-age 5 from Townsville Region was consistently longer than that for all other regions (Table 5.10). There was no difference in FL-at-age 5 among the Lizard Island Region, Amirantes Plateau and Mahe Plateau regions.

Table 5.10. Tests of mean FL-at-age. Common age group used in tests =4+ years. Tests numbered in order of sequence done. “LF” = lightly fished component only. “FF” = fully fished component only. Test results used as evidence to pool across factors at $\alpha = 0.25$ in *italics*. Results significant at $\alpha = 0.05$ in **bold**. Abbreviations as in Table 5.9.

a) Multi-factor ANOVA (GBR).

	MS	df	F	p
Region	33,968	1	28.29	**<0.001**
Zone	1,249	2	1.04	0.357
Region x Zone	2,186	2	1.82	0.167
Residual	1,201	106		

b) Single factor test of Region (GBR, Seychelles).

	MS	df	F	p
Region	12,707	3	9.60	**<0.001**
Residual	1,323	126		

c) Post-hoc tests comparing regions (GBR, Seychelles).

Longest **Shortest**

$$\text{Tsv} \qquad \underline{\text{MP} \qquad \text{Liz} \qquad \text{AP}}$$

5.3.2.2. Fit of von Bertalanffy model to FL-at-age.

The von Bertalanffy growth model fitted well to FL-at-age data from all regions and zones of GBR regions, with R^2 ranging from 0.87 to 0.91 (Table 5.11; Fig. 5.10). There appeared to be an effect of area on growth, with a higher $\hat{L}_\infty$ fitted to the Seychelles data than the GBR data. The difference in $\hat{K}$ was relatively large between regions from the Seychelles. There also appeared to be an effect of zone on $\hat{K}$ and $\hat{t}_0$ for the Townsville Region, with $\hat{t}_0$ deviating from the origin by a relatively large extent for all model fits, as was observed in Chapter 4.

Table 5.11. Fit of the von Bertalanffy model to FL-at-age. "Liz" = Lizard Island Region; "Tsv GC" = Townsville Region GC zone; "Tsv BF" = Townsville Region BF zone; "Tsv GF" = Townsville Region GF zone; "AP" = Amirantes Plateau; "MP" = Mahe Plateau.

Data	n	$\hat{L}_\infty$	SE	$\hat{K}$	SE	$\hat{t}_0$	SE	R^2
Liz	376	645	(9)	0.098	(0.004)	-2.54	(0.20)	0.91
Tsv GC	173	622	(16)	0.078	(0.009)	-5.82	(1.07)	0.81
Tsv BF	54	631	(17)	0.117	(0.015)	-2.71	(0.72)	0.90
Tsv GF	77	625	(16)	0.086	(0.010)	-4.25	(0.87)	0.90
AP	73	678	(16)	0.103	(0.011)	-1.88	(0.51)	0.91
MP	129	774	(26)	0.074	(0.008)	-2.60	(0.67)	0.87
Pooled	892	671	(7)	0.090	(0.003)	-3.08	(0.21)	0.87

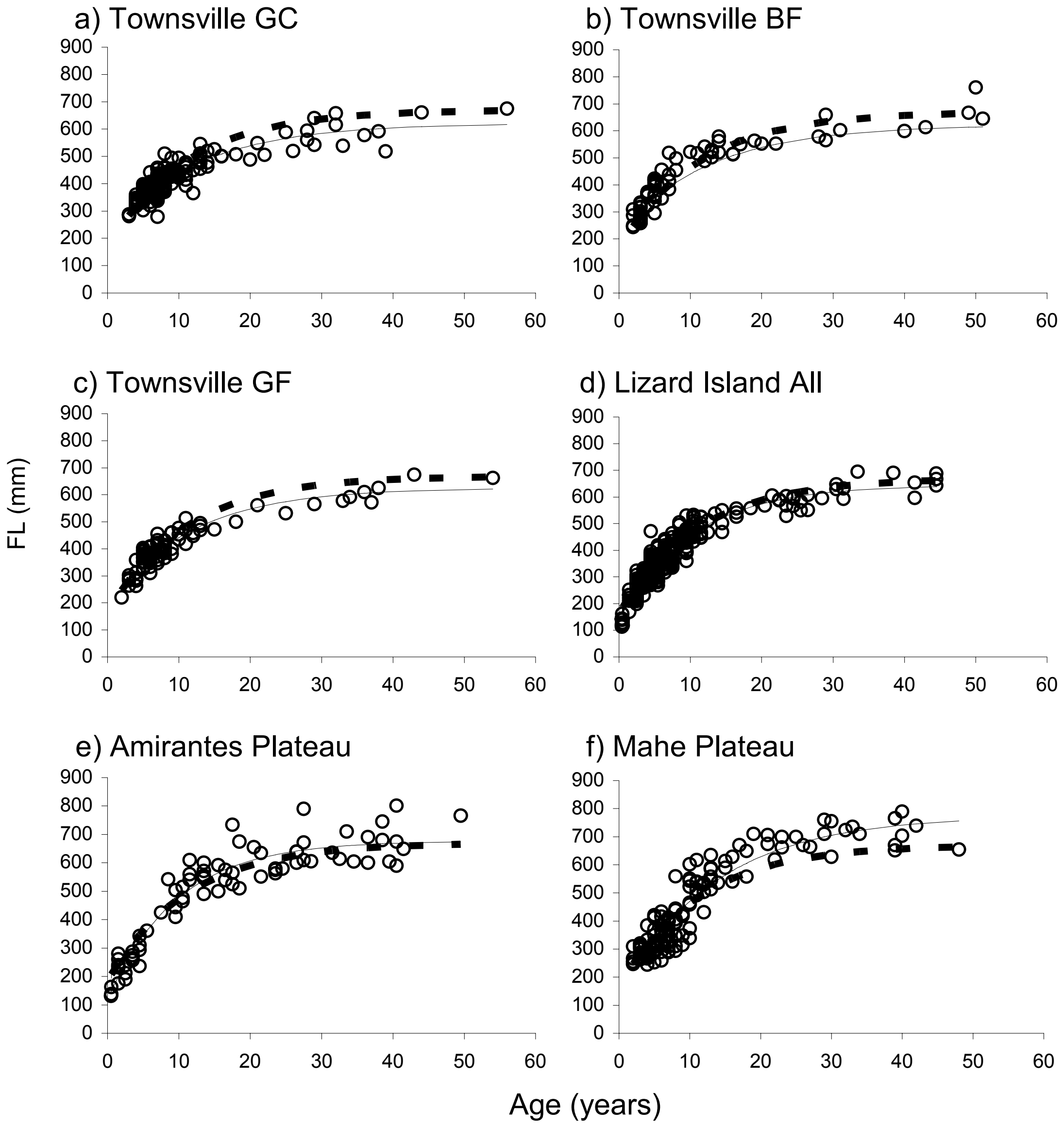


Figure 5.10. Length-at-age data and estimated von Bertalanffy growth curves for Townsville Region zones (a, b, c) and other regions (d, e, f). Solid line is the zone/region-specific fit of the von Bertalanffy model; dotted line is the fit to data from all regions (a common reference for comparison).

A significant effect of Zone was detected in the Townsville Region, with *post hoc* tests showing a significantly higher $\hat{K}$ and $\hat{t}_0$ for Townsville Region BF than for Townsville Region GC (Table 5.12a, b). Therefore zones were not pooled to compare von Bertalanffy growth model fit between areas. A significant difference in $\hat{K}$ and $\hat{t}_0$ was detected among lightly fished GBR and Seychelles regions, where higher $\hat{K}$ and $\hat{t}_0$

were estimated for the Amirantes Plateau than for the Lizard Island Region and Townsville Region GC zones (Table 5.12c, d). A significantly lower $\hat{t}_0$ was also estimated for the Townsville Region GC zone than for the Lizard Island Region GC zone (Table 5.12c, d). A comparison of von Bertalanffy model fits for fully fished components between areas was not done because significant differences between areas were detected for the lightly fished components.

Table 5.12. Analyses of fit of the von Bertalanffy model to FL-at-age. "LF" = lightly fished component only. "FF" = fully fished component only. Results significant at $\alpha = 0.05$ in **bold**. * = *Post hoc* tests used Dunn-Šidák correction for experiment-wise error rate, where groups joined by bold line are not significantly different ($\alpha = 0.05$). ** = See Chapter 4 for tests of zone for Lizard Island Region. Abbreviations as in Table 5.9.

a) Single factor tests of Zone for Townsville Region.**

Factor Level	Factor Tested	Test	χ^2	df	p
Tsv	Zone	Coincident	36.21	6	**<0.001**
Tsv	Zone	L_∞ equal	0.05	2	0.975
Tsv	Zone	*K* equal	6.33	2	**0.042**
Tsv	Zone	t_0 equal	7.36	2	**0.025**

b) Post-hoc tests* comparing Townsville Region zones.

Factor Tested	**Highest**		**Lowest**
***K*:**	BF	GF	GC
t_0:	BF	GF	GC

c) Single factor tests of Region (GBR, Seychelles).

Factor Level	Factor Tested	Test	Groups compared	χ^2	df	p
LF	Region	Coincident	Liz GC v Tsv GC v AP	102.24	6	**<0.001**
LF	Region	L_∞ equal	Liz GC v Tsv GC v AP	2.26	2	0.267
LF	Region	K equal	Liz GC v Tsv GC v AP	12.53	2	**0.002**
LF	Region	t_0 equal	Liz GC v Tsv GC v AP	31.61	2	**<0.001**

d) Post-hoc tests* comparing regions (GBR, Seychelles).

Factor Level	**Factor Tested**	**Highest**		**Lowest**
LF	***K*:**	AP	Liz GC	Tsv GC
LF	**t_0:**	AP	Liz GC	Tsv GC

A significant difference in von Bertalanffy growth model fit was detected between Seychelles regions, with a higher $\hat{L}_\infty$ and lower $\hat{K}$ for the fully fished Mahe Plateau than for the lightly fished Amirantes Plateau (Table 5.13; Fig. 5.11). A comparison of 95% confidence regions between Seychelles' regions was done because there was no significant difference in $\hat{t}_0$ between these model fits (see Chapter 4).

Table 5.13. Comparison of the fit of the von Bertalanffy model to FL-at-age between Seychelles' regions. Results significant at $\alpha = 0.05$ in **bold**. "SC" = Seychelles area. "Fishing" effect tested because regions compared have known differences in historical fishing pressure, assuming detected effects not confounded by other factors (see text).

Factor Level	Factor Tested	Test	χ^2	df	p
SC	Fishing	Coincident	13.29	3	**0.004**
SC	Fishing	L_∞ equal	10.43	1	**0.001**
SC	Fishing	K equal	4.07	1	**0.044**
SC	Fishing	t_0 equal	1.53	1	0.216

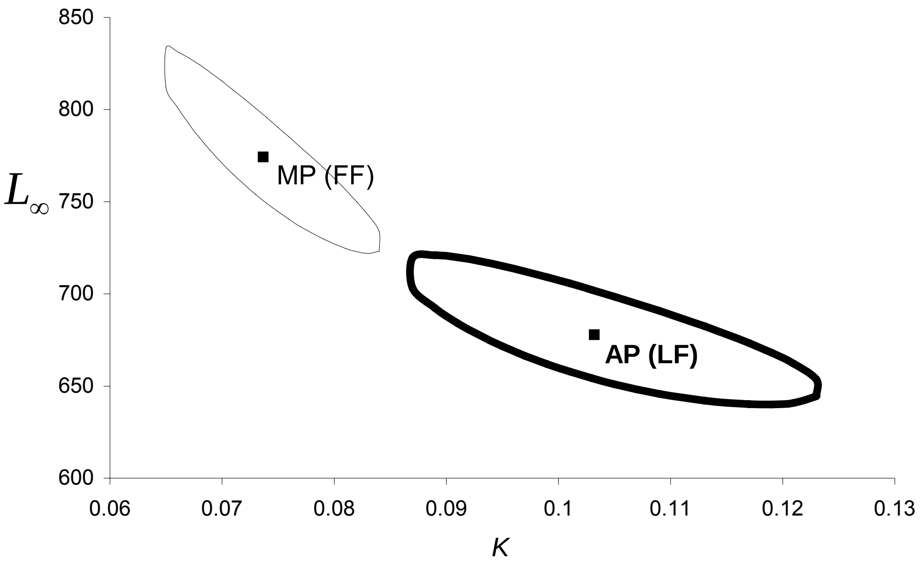


Figure 5.11. 95% Confidence regions for fits of the von Bertalanffy growth model parameters to length-at-age from different Seychelles' regions. "MP" = Mahe Plateau; "AP" = Amirantes Plateau; "FF" = fully fished component; "LF" = lightly fished component. The confidence regions shown were from fits of the von Bertalanffy model to FL-at-age from different regions where no significant difference in $\hat{t}_0$ was detected.

5.3.2.3. Fit of the power function to weight-at-FL.

Weight demonstrated an exponential increase with FL, which was similar among areas and sites with different historical fishing pressure (Fig. 5.12). There is minor residual variation about power models fitted to data partitioned by region and historical fishing pressure and about the model fitted to all data, indicating strong similarity in weight at FL trends among groups (Fig. 5.12).

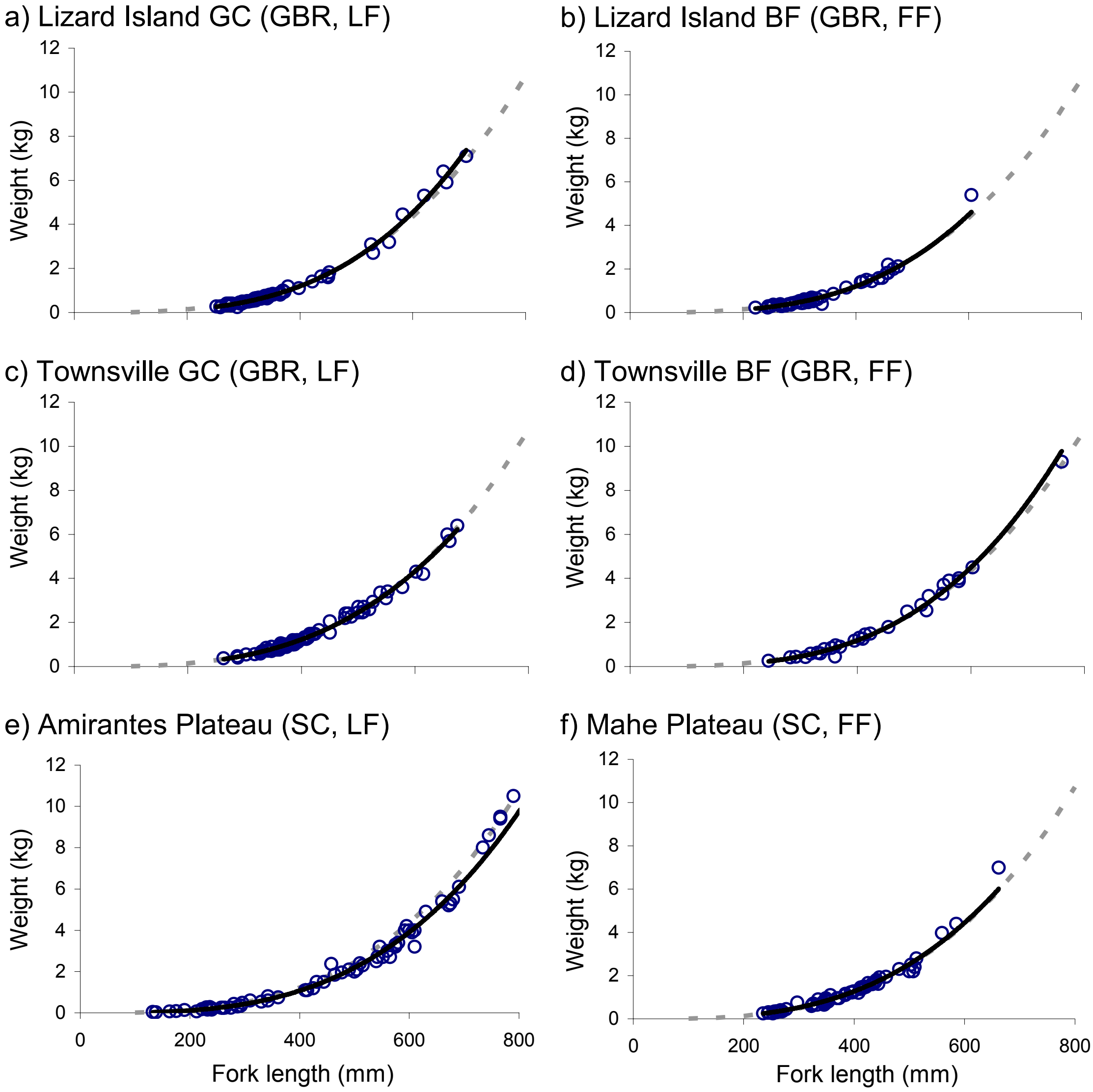


Figure 5.12. Weight-at-length data and trends by region and historical fishing pressure. Data pooled over all sample years, sexes. LF = lightly fished components; FF = fully fished components; SC = Seychelles; GC, BF are zones of the ELF Experiment (Chapter 2). Solid line is the fitted power function to each data group; lighter dashed line is the fit of the power function to all data for reference.

The interactions between GBR Region and Zone and between Zone and Year significantly affected the slope of the linearised weight : FL regression (Table 5.14a). Subsequent single-factor tests detected: (i) an effect of Zone on slope for both GBR regions; (ii) an effect of GBR Region on slope for GF and BF zones but not for the GC zone; (iii) an effect of Year for GC and BF zones but not for the GF zone; and (iv) an effect of Zone in 2000 but not in 1999 or 2001 (Table 5.14b,c). *Post hoc* tests revealed a steeper slope for BF zone than for GC zone data in both GBR Regions and a steeper slope for BF zone than for GF zone data in Townsville Region only (Table 5.14d). A steeper slope of the weight : FL regression was observed for Lizard Island Region GF zone ($\hat{\beta} = 2.07 \times 10^{-8}$) and BF zone ($\hat{\beta} = 2.30 \times 10^{-8}$) than for Townsville Region GF zone ($\hat{\beta} = 1.98 \times 10^{-8}$) and BF zone ($\hat{\beta} = 2.15 \times 10^{-8}$), respectively. *Post hoc* tests also revealed that 2000 data had a steeper slope than data collected in 1999 and 2001 and BF zone data had a steeper slope than GC and GF zones in that year (Table 5.14d).

Table 5.14. Tests of linear-transformed weight-at-FL relationships: GBR. Regions: "Liz" = Lizard Island Region; "Tsv" = Townsville Region. Zones: GC, GF, BF (Chapter 2). Results significant at $\alpha = 0.05$ in **bold**. Non-significant effects of slope were also non-significant effects of intercept. * = *Post hoc* tests used Dunn-Šidák correction for experiment-wise error rate, where groups joined by bold line were not significantly different ($\alpha = 0.05$).

a) Multi-factor ANCOVA.

	MS	df	F	p
Slope effects.				
Region	0.009	1	0.83	0.364
Zone	0.074	2	6.90	**0.001**
Year	0.261	2	24.21	**<0.001**
Region x Zone	0.040	2	3.67	**0.027**
Region x Year	0.020	2	1.87	0.157
Zone x Year	0.044	4	4.10	**0.003**
Region x Zone x Year	0.015	4	1.40	0.234
Residual	0.011	199		

b) Single factor ANCOVAs exploring the Region x Zone effect on Slope.

Factor 1 Level	Factor 2 Level	Factor Tested	F	df1	df2	p
Liz	All years	Zone	5.98	2	118	**0.003**
Tsv	All years	Zone	5.55	2	105	**0.005**
GC	All years	Region	1.76	1	108	0.187
GF	All years	Region	8.45	1	47	**0.006**
BF	All years	Region	4.42	1	68	**0.039**

c) Single factor ANCOVAs exploring the Zone x Year effect on Slope.

Factor 1 Level	Factor 2 Level	Factor Tested	F	df1	df2	p
Liz+Tsv	GC	Year	11.11	2	106	**<0.001**
Liz+Tsv	GF	Year	1.16	2	45	0.322
Liz+Tsv	BF	Year	15.38	2	66	**<0.001**
Liz+Tsv	1999	Zone	2.77	2	76	0.069
Liz+Tsv	2000	Zone	8.42	2	55	**<0.001**
Liz+Tsv	2001	Zone	1.32	2	86	0.273

d) Post-hoc tests*

Factor 1 Level	**Factor 2 Level**	**Slopes Compared** **Steepest**		**Gentlest**
Liz	**All years:**	BF	GF	GC
Tsv	**All years:**	BF	GC	GF
Liz+Tsv	**GC:**	2000	1999	2001
Liz+Tsv	**BF:**	2000	1999	2001
Liz+Tsv	**2000:**	BF	GC	GF

A significant difference in the slope of the weight-at-FL data was detected between the Amirantes Plateau and Mahe Plateau (Table 5.15, Test 1), with *L. bohar* above about 400 mm FL from the fully fished region being heavier than those from the lightly fished region (Fig. 5.13). The effects of GBR Region, Zone, and Year on slope meant that data could not be pooled across these factors to compare with linearised weight : FL regressions of Seychelles' data. Therefore data for like levels of historical fishing and sampled during the same period (2000-01) were used for these tests. Further, since 2000 data were not consistent with 1999 and 2001 results in Table 5.14 and were indicated to be aberrant from analyses in Chapter 4, 2000 data were excluded. There was no significant difference in the slope or intercept of weight : FL regressions among GBR and Seychelles' regions, for tests of lightly fished (Table 5.15, Tests 2, 3) or fully fished (Table 5.15, Tests 4, 5) components.

Table 5.15. Single factor tests of the effect of region on linear-transformed weight-at-FL relationships. "SC" = Seychelles area; "LF" = lightly fished component; "FF" = fully fished component; "AP" = Amirantes Plateau; "MP" = Mahe Plateau; "Liz GC 2001" = 2001 Lizard Island Region GC zone data; "Tsv GC 2001" = 2001 Townsville Region GC zone data. Results significant at $\alpha = 0.05$ in **bold**.

Single-factor ANCOVAs.

Test	Factor Level	Factor Tested	Parameter	Groups compared	F	df1	df2	p
1.	SC	Fishing	Slope	AP (LF) v MP (FF)	17.6	1	94	**<0.001**
2.	LF	Region	Slope	Liz GC 2001 v Tsv GC 2001 v AP	2.69	2	59	0.076
3.	LF	Region	Intercept	Liz GC 2001 v Tsv GC 2001 v AP	0.25	2	59	0.780
4.	FF	Region	Slope	Liz BF 2001 v Tsv BF 2001 v MP	0.84	2	41	0.438
5.	FF	Region	Intercept	Liz BF 2001 v Tsv BF 2001 v MP	1.79	1	41	0.188

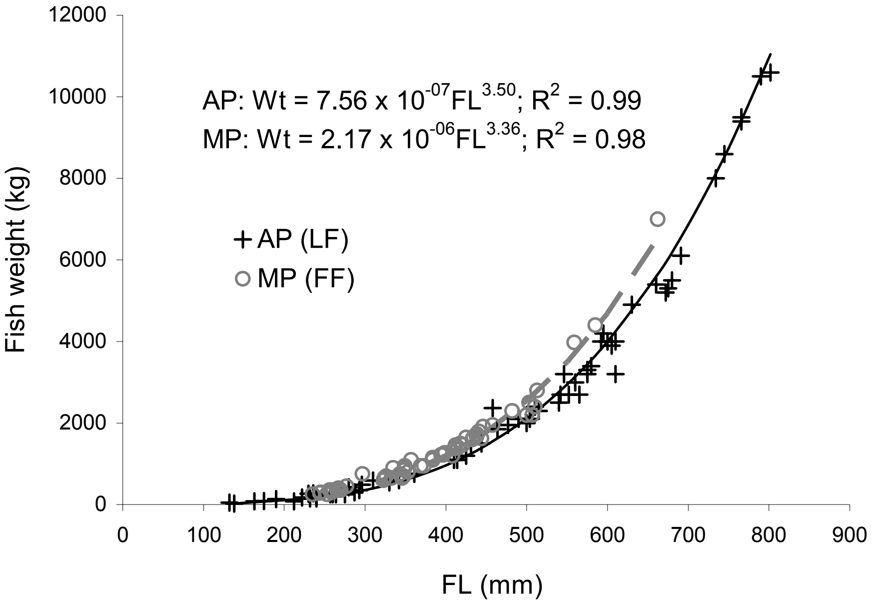


Figure 5.13. Power function fitted to weight-at-length data for *L. bohar* sampled from different regions in the Seychelles. Abbreviations as in Table 5.13.

5.4. Discussion.

A lower mean age in historically fished components of both areas was consistent with an effect of fishing, because fishing typically removes older fish from fished populations (Cushing 1968). Interestingly, there was no significant difference in the mean FL or FL frequency of *L. bohar* sampled from sites of different historical fishing pressure, which suggests that the larger size classes of *L. bohar* were not removed by fishing. A higher asymptotic FL (L_∞) and a steeper curvature of the weight-at-FL trend in the Mahe Plateau were unlikely impacts of fishing but could reflect a density-dependent growth response of *L. bohar* to depletions caused by fishing in this region. These differences in mean age, growth, and weight-at-FL, however, could be attributed to other factors because they were also demonstrated to vary regionally on the GBR, where *L. bohar* have been exposed to light levels of fishing. The effects of temporal, regional, and geographic variation and of different levels of fishing are summarised in Table 5.16. In general, it was found that *L. bohar* populations on the GBR and in the Seychelles were similar in many aspects, and results that indicate potential influences of environmental factors or fishing are discussed in the following sections.

Table 5.16. Summary of results. "S" = significant at $\alpha = 0.05$; "NS" = not significant at $\alpha = 0.05$; "-" = not tested; "LF" = lightly fished component; "FF" = fully fished component. * = A significant effect of Fishing was detected for the 2 factor ANOVA of Fishing and Area, whilst no effect of Area, nor its interaction with Fishing was detected, indicating that the detected effect of Fishing was the same in both areas. ** = Differences were not consistent for comparisons of each GBR region with Seychelles' data. *** = Only detected for GF and BF zones and not for the GC zone.

Variable	GBR			Seychelles Region (LF v FF)	Area	
	Region	Zone	Year		LF	FF
Mean FL	S	NS	NS	NS	NS	NS
Mean age	S	S*	S	S*	NS	NS
FL group frequency	S	NS	S	NS	S**	NS
Age frequency	S	-	NS	S	S	NS
FL-at-age	S	NS	-	NS	S**	S**
Fit of von Bertalanffy growth model	S	S	-	S	S	-
Weight-at-FL	S***	S	S	S	NS	NS

5.4.1. Spatio-temporal variability and implications for the "mensurative experiment."

5.4.1.1. Population structure.

Regional differences in FL were apparent in samples from lightly fished (GC) zones on the GBR but were not reflected in fish age. This pattern might indicate region specific growth in FL; possibly due to variation in environmental factors or availability of resources (see Section 5.4.1.2.). Proportionally greater frequencies of larger and older *L. bohar,* however, were also sampled from the Townsville Region than from the Lizard Island Region. Given that reefs sampled in the Townsville Region were proportionally further offshore across the GBR shelf than Lizard Island Region reefs (Table 5.2), this may reflect a cross-shelf cline in population size (and age) structure. Such a cline would be consistent with a hypothesis of ontogenetic tendency off-shore migration, as found for several other lutjanids (Newman and Williams 1996). Although a north-south cline in population size structure is also possible, the analysis of size structure at different cross-shelf positions within the Lizard Island Region (Chapter 4) was consistent with the cross-shelf hypothesis.

Other explanations have been postulated for regional variation in reef fish population structure on the GBR. Newman et al. (1996) and Kritzer (2002) speculated that variable recruitment might partly explain differences in population age structures detected for small lutjanids at different reefs and regions on the GBR. Hart and Russ (1996) speculated that the presence of Crown of Thorns Starfish (*Acanthaster plancii*) might have indirectly resulted in more food for the surgeonfish, *Acanthurus nigrofuscus,* to grow to a larger average size on some reefs. Williams et al. (2003) conjectured that regional differences in food availability interacting in combination with density-dependent processes could explain overall regional trends in growth, mortality and age structure observed for red throat emperor (*Lethrinus miniatus*). Regional differences in many post-settlement processes, or their interaction (Jones 1991), could have contributed to this result for *L. bohar*.

Mean FL and length frequency distributions were similar between lightly fished components of Townsville Region and the Amirantes Plateau whilst the *L. bohar* from Lizard Island Region were smaller on average than those from the Amirantes Plateau. Whilst this pattern in length of *L. bohar* indicates considerable similarity between some regions in each area, it is not clear whether the regional variation from the GBR has an analogue in lightly fished parts of the Seychelles.

Population age structures were consistently different between the Amirantes Plateau and GBR Regions. A lack of difference in mean age between areas but the detection of a difference in age structure indicated a difference in the shape of age frequency distributions. Since no clear exponential decline in age structure after the inferred modal age of "full recruitment" (Ricker 1969) was demonstrated for the Amirantes Plateau, it could be inferred that this sample might not have been representative of the total population. If not, it could have been reflecting an effect of larger temporal variation in recruitment of local environmental conditions on cohort strength and/or imprecision and non-uniform distribution of sampling effort in the Amirantes Plateau.

In this study, the spatial scale of regions (< 3^o latitude or longitude) and areas (> 10^o of latitude and longitude) differed by an order of magnitude, as did the difference between distances separating regions within areas (< 4^o latitude or longitude) and separating areas (> 80^o longitude). There have been few other studies that have compared population structures between sites separated by tens of degrees of latitude and/or longitude. Grandcourt (1999) also compared population structures of a reef fish (*Lethrinus nebulosus*) between the Seychelles and GBR and surmised that a greater proportion of larger *L. nebulosus* were sampled in the Seychelles because they were collected from deeper depths than were sampled on the GBR. Meekan et al. (2001) postulated that differences in age structure observed for species of damselfish (*Stegastes* sp.) between sites separated by 11° to 31° of longitude were most likely due to either differences in local mortality rates due to predation or more sporadic and variable recruitment at sites near the edge of the species' range. On the other hand, Choat et al. (2003) observed that age structures and maximum ages of the Caribbean stoplight parrotfish, *Sparisoma viride,* were very similar among all study sites, including two that were separated by approximately 14° of latitude.

5.4.1.2. Growth.

A number of reasons could explain observed regional variation in growth on the GBR. A shorter maximum size (Atkinson 1994) and faster growth rate (Pauly 1980) is theoretically expected for populations in lower latitudes. On the GBR, however, the opposite of this trend was observed for average length-at-age (4+ year olds) and no significant differences were apparent for average maximum FL (L_∞) and growth rate (*K*). Regional differences in length-at-age could be attributed to cross-shelf effects, as inferred for *L. bohar* population structure and as observed for the growth of parrotfish (Scaridae) populations by Gust et al. (2002). Other factors, such as region-specific density-dependent processes (Forrester 1990), selection for a larger body size due to local predation pressure (Kritzer 2002), food availability (Weatherley and Gill 1987), or sampling bias (Brown and Sumpton 1998; Chapter 4) could also be responsible.

A higher growth rate (*K*) for *L. bohar* from the Amirantes Plateau than from the GBR was consistent with the hypothesis of increasing growth rate with decreasing latitude (Pauly 1980). However, the higher $\hat{t}_0$ for *L. bohar* from the Amirantes Plateau than from GBR regions was not consistent with this hypothesis, which may indicate other influences, including sampling bias (Chapter 4), on the fit of the von Bertalanffy model. It is possible, therefore, that such effects on $\hat{t}_0$ also could have affected $\hat{K}$ between areas because of the strong correlation among parameters of the von Bertalanffy model (Bernard 1981).

The only other study to compare growth trends between GBR and Seychelles fish populations was that of Grandcourt (1999), who found a higher L_∞ for Seychelles populations of *L. nebulosus* than for GBR populations, but no significant difference in *K*. He speculated that observed differences in asymptotic length could be attributed to either different sampling depths or differences in productivity between insular Seychelles and continental GBR populations; a generalisation made by Grimes (1987) for all lutjanids. Increased productivity also could have contributed to faster growth rates of *L. bohar* on the Amirantes Plateau and hence the higher observed $\hat{K}$. No difference in L_∞ was detected for *L. bohar* between GBR regions or between areas, demonstrating that this parameter was not significantly affected by natural variation in the studied regions.

Effects of Region, Zone, and Year on weight-at-length data from the GBR were ambiguous, with no consistent effects evident for any of these factors. A steeper increase in weight-at-length from fully fished (BF) than from lightly fished (GC) zones, however, was found whenever an effect of zone was detected, and, therefore, may reflect an effect of fishing (see Section 5.4.2.2.). Despite these effects for GBR data though, there were no significant effects of area on weight-at-length detected.

5.4.2. Inferred fishing impacts.

In the following section I discuss results from the “mensurative experiments” comparing areas and Seychelles regions to infer effects of historical fishing pressure. These tests assumed that effects of fishing were not confounded by differences in environmental factors or any other factors between regions. Given the results of the spatio-temporal analyses of lightly fished components, these assumptions are revisited in Section 5.4.3.

5.4.2.1. Population structure.

There were proportionally fewer older *L. bohar* in the fully fished Mahe Plateau than the lightly fished Amirantes Plateau. The results from analyses of mean age were consistent with this result because they detected *L. bohar* from the fully fished Mahe Plateau, were younger on average. These results are consistent with a typical fishing impact because fishing typically removes the largest, oldest fish (Russ 1991; Jennings and Lock 1996). Despite this, no significant effect on length frequency distribution or on mean length was detected.

The failure to detect clear, consistent differences between areas in fully-fished components of *L. bohar* populations could indicate that the *L. bohar* populations were sensitive to fishing impacts, over a wide range of historical fishing pressure. Other studies that estimated the biomass of *L. bohar* in sites of different fishing intensity in the Seychelles (Jennings et al. 1995) and Fiji (Jennings et al. 1999) have also found that *L. bohar* biomass was low in all sites where it was fished, regardless of relative fishing pressure, and was only detectably higher in sites that were completely protected from fishing. Alternatively, the relatively high fishing pressure on target species of the

CRFFF could also result in high fishing mortality rates of *L. bohar* on the GBR through incidental catch and release, potentially resulting in similar fishing impacts on the GBR as observed on the Mahe Plateau.

Mapstone et al. (2004) found significantly higher CPUE, mean age and mean lengths for the two main target species of the CRFFF, *Plectropomus leopardus* and *Lethrinus miniatus,* in GC than BF zones as part of the ELF Experiment. These results indicated the effectiveness of the management zones for controlling fishing effort. Results were variable by year and region, however, with no significant differences detected for the Lizard Island Region and significant differences for the Townsville Region detected only in some years (Mapstone et al. 2004). Mapstone et al. (2004) reasoned that these regional differences were related to differences in historical fishing effort rather than confounding effects, such as illegal fishing, in some GC zones. That is, lower levels of fishing effort in the Lizard Island Region were suspected to be responsible for the lack of contrast between GC and BF zones in this region as opposed to the other four regions of the ELF Experiment (Mapstone et al. 2004).

5.4.2.2. Growth.

Slower growth is a frequently reported effect of fishing. It has been postulated that the selective removal of faster-growing individuals by fishing could result in the increased relative contribution to subsequent generations by the slower-growing fish that are left behind, and if growth is a heritable trait this could result in the evolution of slower growth in fully fished populations (Law 1991; Kirkpatrick 1993; Conover and Munch 2002). Alternatively, it has been postulated that a shorter length-at-age might only reflect the composition of those individuals not removed by fishing and thus does not necessarily reflect an evolved change in growth, known as the "Phenomenon of Apparent Change in Growth Rate" (PACGR; Moulton et al. 1992). Although a reduced K for the fully fished region compared with the lightly fished region was consistent with this postulate, a longer L_∞ was not and was thus atypical of a fishing impact.

A longer L_∞ in the Mahe Plateau was not consistent with the expected effect of fishing on growth. An alternative theory postulated for a longer length-at-age in a more heavily-fished population is a density-dependent growth response to fishing (Gulland 1983; Policansky 1993). Underwater visual census surveys of the Mahe and Amirantes Plateaux revealed substantial differences in population density between regions, with much lower density for the Mahe Plateau (J. H. Choat and A. Ayling, *unpublished data*). It is therefore possible that fishing could have reduced the density of older *L. bohar* (or their competitors) on the Mahe Plateau, resulting in more food available *per capita* for these older age groups and thus resources available for increased growth (and average FL). The heavier body condition observed for longer *L. bohar* from the Mahe Plateau (Fig. 5.13) could also have resulted from higher consumption rates by older fish (Weatherley and Gill 1987) than on the Amirantes Plateau.

Inspection of plots of length-at-age and fitted von Bertalanffy growth curves (Fig. 5.9), however, shows considerable overlap in the range of length-at-age for older age groups, with greater variation in length-at-age of older age groups (i.e., 20 - 50 year olds) from the Amirantes Plateau than from the Mahe Plateau. Relatively small fish (i.e., 500 - 650 mm FL) rarely were sampled for older age groups from the Mahe Plateau. This appears to account for the larger L_∞ than for the Amirantes Plateau data, and the overall difference in model fit between regions. There is considerable overlap in length-at-age for younger age groups (i.e., < 20 years old), as indicated by the lack of detectable difference in the length-at-age of 4+ year olds between Seychelles' regions. Therefore, the difference in K between the Seychelles regions is inferred to have been driven by the different fitted L_∞ to older age groups, because K is strongly correlated with L_∞ (Bernard 1981).

5.4.3. Conclusions.

Insight into the generality and variability of demographic patterns and processes for lightly fished components of *L. bohar* populations indicated the extent to which conclusions from the "mensurative experiment", testing for the effects of historical fishing pressure, were valid. Significant temporal variation in mean age, length frequency and weight-at-length on the GBR indicated that results from any comparison of those variables between regions or areas for a single time frame would be unreliable. This demonstrated a source of uncertainty in results from the mensurative experiment in the Seychelles, where temporal variation was not assessed. The detection of differences in mean length, length frequency, age frequency, length-at-age of 4+ year olds, and t_0 for lightly fished components between GBR regions also demonstrated the potential for natural regional variation to significantly influence results, independently of historical regional differences in fishing intensity. Alternatively, no significant regional variation detected for L_∞ and weight-at-length of lightly fished *L. bohar* on the GBR meant that there was no evidence to indicate that natural, region-specific variation on these metrics might have influenced results from the mensurative experiment.

Fishing effects detected from the mensurative experiment are therefore to be treated with caution. Observed fishing effects on mean age and age frequency were typical.

An effect of fishing on L_∞, however, was large and atypical, where a larger L_∞ was observed in the fully fished region. The possibility that fishing may affect the length of fish in older age groups, and thus, affect predictions of fishing impacts, warrants further consideration and will be explored in the modelling chapter. Comparison of results from fished components in the Seychelles with those from the GBR failed to detect any consistent difference, which indicated that similar fishing impacts on population structure might have occurred in areas where *L. bohar* has not been as heavily fished.

Differences in population age structure and aspects of growth (*K*) of lightly fished *L. bohar* between areas indicated that intrinsic differences in demography and biology might also exist between these widely separated populations. The lack of consistent differences in all other aspects (mean length, mean age, length frequency, weight-at-length), however, indicated that there was also considerable similarity in population characteristics. Overall, these results indicated that much of the information gained from detailed biological studies on the GBR could be used with reasonable confidence to estimate aspects of *L. bohar* population dynamics in the Seychelles. Hence, this study provided insight into the credibility of using biological information from one area, such as the GBR, to predict the vulnerability of *L. bohar* populations to fishing impacts and overfishing in another, such as the Seychelles.

Chapter 6: Reproductive parameters of GBR populations.

6.1. Introduction.

Although many aspects of biology and ecology have been supported from the study of marine life (Roff 1984; Stearns and Koela 1986), theories and concepts were initially developed from studies of terrestrial systems. The concepts of "*r*-selection" and "*K*-selection" were developed from theory concerning ecological succession in terrestrial environments (MacArthur and Wilson 1967) particularly the colonisation of islands. Pianka (1970) initially put forward the idea of categorising life history strategies based on concepts of *r*- and *K*-selection, with *K*-selection favouring slower development, greater competitive ability, lower resource thresholds, delayed reproduction, larger body size, and repeated reproductions.

From a review of studies using induction, theoretical modelling and experiments, Stearns (1992) proposed that *r*-*K* selection was not as appropriate to the understanding of life history theory as were the intrinsic trade-offs between life history traits. Examples of such trade-offs are a delayed age and larger size at first reproduction and a higher initial fecundity for slower initial growth rate, and a longer reproductive life for those species demonstrating a higher mean or variance of juvenile mortality rates (i.e. 'bet hedging' theory; Stearns 1976). In species with promiscuous mating and external fertilisation strategies such as fish, males are expected to mature at a smaller size and younger age than females because of higher energy requirements for reproductive development in females (Stearns 1992).

Knowledge of the life history characteristics of an exploited fish population can provide some indication of its likely vulnerability to overfishing (Parent and Schriml 1995; Jennings et al. 1998; Musick 1999). A delayed age at first reproduction, for instance, equates to a longer generation time, which predicts a lower potential intrinsic rate of population increase (Krebs 1994) and thus slower rates of replenishment of numbers lost to fishing mortality. A longer generation time is also likely to result in a slower response to selective pressures (Charlesworth 1980), such as those imposed by size-selective harvest (Sutherland 1990; Trippel 1995), which could potentially act to compensate for deleterious fishing impacts (Rochet et al. 2000). Further, a delayed age at first reproduction leaves juveniles vulnerable to fishing mortality for a longer period prior to their first spawning (Crouse 1999), reducing the current spawning potential of the population and future recruitment. Thus, populations that can be harvested at a young age, but mature at a relatively old age are predicted to be extremely vulnerable to overfishing (Myers and Mertz 1998).

Tropical snappers (Pisces: Lutjanidae) are generally considered to be gonochoristic, highly fecund species (Grimes 1987) which have relatively protracted spawning seasons (e.g., Druzhinin 1970). The aim of this chapter was to quantify aspects of reproductive biology for *Lutjanus bohar* on the GBR to determine if reproductive characteristics conformed to theoretical expectations, given the high longevity (Chapter 3), slow growth (Chapters 4 and 5), and relatively large size of this species. Given these traits and according to bet hedging theory, *L. bohar* should demonstrate a relatively late age and size at maturity, high initial fecundity, and an extended spawning season. Also, given the similar growth rates observed for males and females (Chapter 4), one would expect females to mature later in life and at a larger length than males because of the higher energy requirements for reproductive development in females (Wootton 1985).

These results will be used to describe, more completely, the population biology and dynamics of *L. bohar*. Trends in reproductive contribution by size and age were described to predict, with greater confidence, how fish populations might respond to and be impacted by size-selective fishing mortality. This information will also be used in Chapter 7 to develop an age-structured model to predict the response of *L. bohar* populations to fishing pressure.

6.2 Methods

6.2.1 Preparations for age and maturity estimation.

Samples of *L. bohar* were gathered from ELF Experiment catch surveys and from catch samples from the CRFFF on the GBR as described in Chapter 2. Fish age (years) was estimated from transverse sections of sagittal otoliths using methods detailed in Chapter 3. Fish age was also estimated in days for a sub-sample of *L. bohar* estimated to be less than 1 year old (n = 12) and birth dates were back-calculated using methods detailed in Chapter 4. The larval period was estimated for some (n = 6) of this sub-sample from counts of presumed daily rings to the inferred “settlement mark”, as identified and interpreted by Victor (1982).

Preserved gonads were removed from vials of formalin in the laboratory, padded dry on tissue paper, and then weighed to the nearest 0.01 g. Where both gonad lobes were not complete due to damage during collection, one intact lobe was weighed separately and this weight was doubled to obtain an estimate of total gonad weight (*GW*). If both lobes were damaged, no weight was recorded and the sample was excluded from analyses requiring gonad weight. Medial transverse sections of gonad lobes were prepared for microscopic examination by dehydrating in alcohol, embedding in wax, histological processing, and then counter-staining with haemotoxylin and eosin according to the procedure outlined in Samoilys and Roelofs (2000) (n = 532). The number of specimens processed by histology per sampling method, year, month, and sex are given in Table 6.1.

Testes were classified as mature where spermatozoa were visible in either the lobules or central efferent ducts (Murphy and Taylor 1990). There was not enough visual evidence, however, to confidently discern between inactive immature and inactive mature males for this species. The relative width of the central efferent duct was recorded as either “narrow” or “distended,” as a proportion of the testis lobe width in Transverse Section (TS), to investigate whether post-spawned males only had distended central efferent ducts (Fig. 6.1).

Classification of ovaries into different stages of reproductive development was based on the most advanced stage of oocyte development (West 1990; Table 6.2). Stages of oocyte development were consistent with those initially described for the flounder, *Liopsetta obscura*, by Yamamoto (1965) and later generalised for all teleosts (Wallace and Selman 1981; Fig. 6.2). Unfortunately, oocyte development stages more advanced than primary yolk (Yamamoto 1965: stages 5 to 11) could not be reliably discerned on histological sections for *L. bohar* because many of the large ovaries were not placed in fixative immediately following capture or were incompletely penetrated by fixative, leading to the deterioration of central tissues. Therefore, all ovaries with oocyte stages in true vitellogenesis (Wallace and Selman 1981) or more advanced stages were conservatively grouped into the “ripe” category (Table 6.2).

Table 6.1. Number of histological samples processed. All gonad sample replicates processed from CRFFF samples collected between July 2001 and June 2003. All gonads sample replicates processed from ELF catch surveys were collected between February 1999 and March 2000. Specimens for other months and years were processed to supplement sample sizes for reproductive seasonality or maturity analyses (in italics, lighter font). Histological samples from spear-fishing (n = 30) and unknown sex determination not shown. See Chapter 2 for sampling methods.

	Method:	CRFFF						ELF catch surveys							
	Year:	2001		2002		2003		1999		2000		2001		2002	Total
Month	Sex:	F	M	F	M	F	M	F	M	F	M	F	M	F	
1				6	5										11
2				4	5			11	14						34
3				10	15			5	6		1				37
4				3	8					26	13				50
5				1	1	2	4	16	4						28
6				1	2	6	2	4	2						17
7		4	4												8
8		6	12			*3*		9	6						36
9		8	8			*11*		4							31
10		14	24	1				9	13	*20*	*1*	*9*	*1*		92
11		22	11					25	8		*1*	*24*	*13*	*26*	130
12		7	8					6	2						23
Total:		61	67	26	36	22	6	89	55	46	16	33	14	26	532

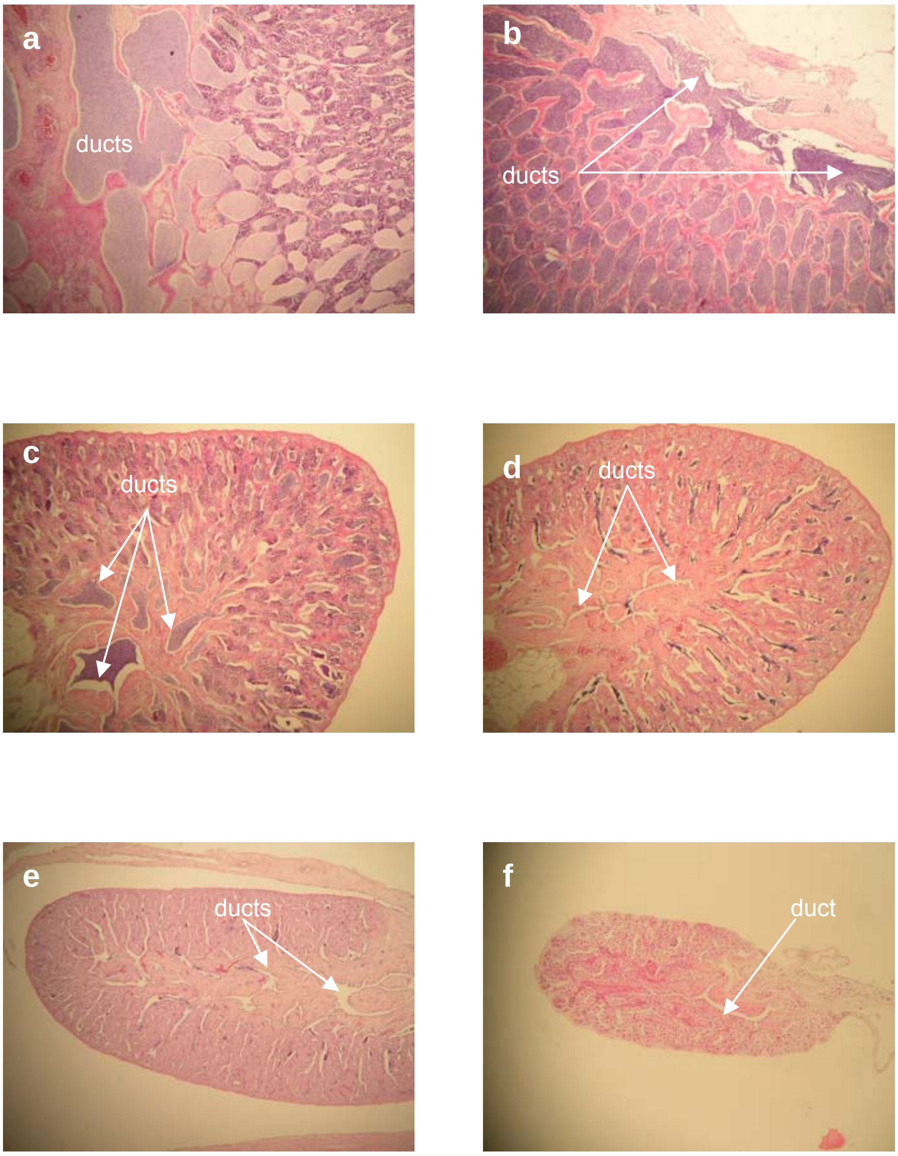


Figure 6.1 Position and structure of central efferent ducts on transverse sections of testis lobes. "Distended" ducts of individuals: (a) 760 mm, (b) 415 mm, and (c) 288 mm FL; and "Narrow" ducts of individuals (d) 364 mm, (e) 362 mm, and (f) 139 mm FL. Spermatozoa present in efferent ducts and lobules of (a) to (e). The section of a testis lobe for the 139 mm FL individual sampled by spear-fishing from Lizard Island Region in October 2002 (f) is shown to demonstrate the shape of relatively narrow ducts that was common in sections from all immature males.

Table 6.2. Histological criteria used for the classification of reproductive phases of *L. bohar* ovaries.

	Stage		Histological criteria
Inactive	Immature	-	Most advanced oocyte: chromatin nucleolus, early or late perinuceolus.
		-	Relatively thin ovarian wall.
		-	Lamellae well packed.
	Resting	-	Most advanced oocyte: early or late perinuceolus.
		-	Brown bodies may be visible.
		-	Relatively thick ovarian wall.
		-	Lamellae not well packed.
Active	Ripening	-	Most advanced oocyte: yolk vesicle.
	Ripe	-	Yolk globule stage oocytes present.

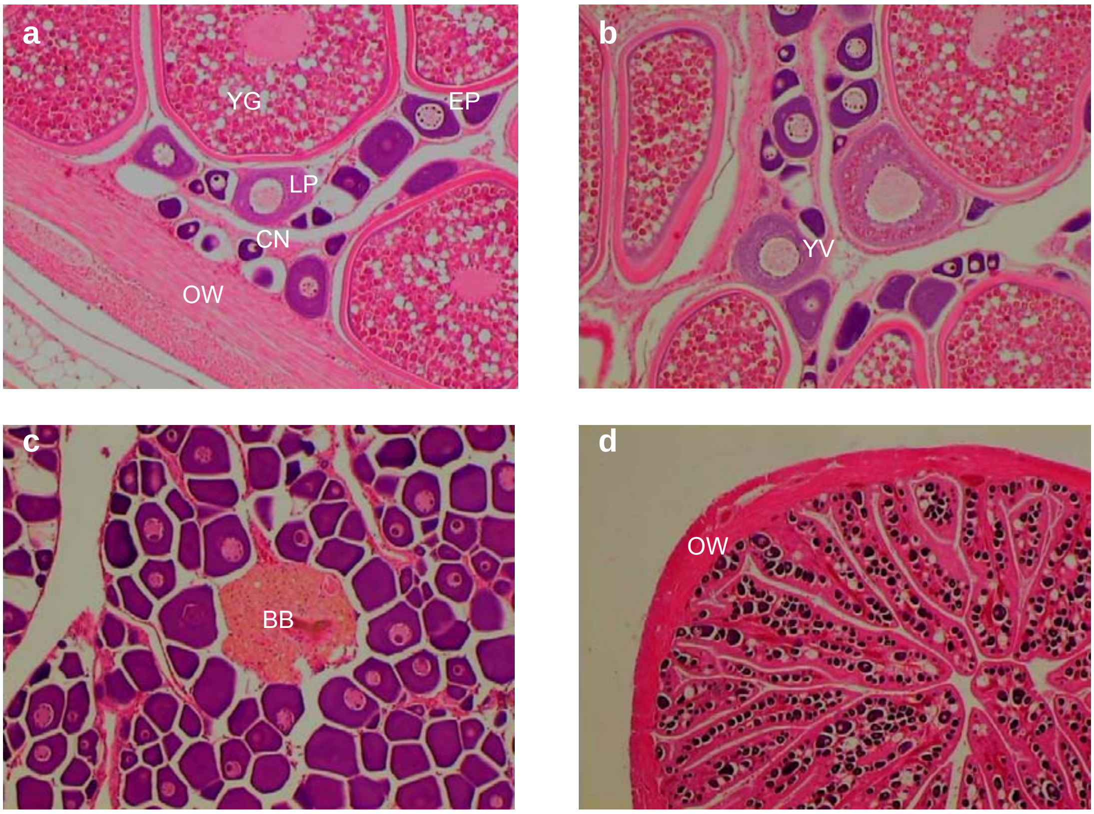


Figure 6.2 Histological criteria used to assign ovarian maturity in *L. bohar*. Oocyte stages: CN = Chromatin Nucleolus; EP = Early Perinucleolus; LP = Late Perinucleolus; YV = Yolk Vessicle; YG = Yolk Globule. OW = Ovarian Wall; BB = Brown Body. a, b = ripe ovary; c = mature resting; d = immature ovary.

To distinguish between immature females and mature inactive (resting) females, some additional criteria were used. These were the presence of brown bodies (Ferreira 1993; Fig. 6.2c), relative thickness of the ovarian wall (Burton et al. 1997) and whether the lamellae appeared to be well packed or vacuolated (Ferreira 1995; Samoilys and Roelofs 2000). Brown bodies are suspected to have originated from atretic vitellogenic oocytes (Ferreira 1993) because they are comprised of lipofuscin, a by-product of lipid degeneration, and vitellogenic oocytes are the only ovarian structures that contain lipids (S. Adams *pers comm.*).

6.2.2. Batch fecundity estimation

"Batch fecundity" is the number of hydrated oocytes released per spawning (Hunter et al. 1992). Most reef fish studied to date, including lutjanids, are indeterminate or batch spawners, characterised by asynchronous oocyte development (Sadovy 1996). Thus, a reliable method of identifying the most advanced oocyte stage to count in order to estimate batch fecundity was required. This was done by using measures of the diameter of different oocyte stages recorded whilst viewing each ovary TS.

The Optimas program was used to capture and display digital images of transverse sections of a sub-sample of ripe ovaries as viewed with a compound microscope at 40X magnification. Only those ovaries from females collected in month(s) of the inferred peak spawning season (as determined from the analysis of seasonal trends in ovarian maturity; n = 34; FL range: 386 – 667 mm) were analysed to estimate batch fecundity because this was the time when the greatest proportion of sampled ovaries were likely to be ripe and so give reliable estimates. Oocyte diameters were measured within digital images or "frames" (1806 x 1354 μm) captured without reference to oocyte characteristics from 5 uniformly distributed sites within the lamellae of each transverse ovarian section.

Within each frame the maximum diameter was measured of the closest oocyte—irrespective of developmental stage—to a pre-selected random coordinate (x, y; scaled to the dimensions of each frame). Oocyte diameters were only measured if the nucleus was clearly visible and if that particular developmental stage had not been measured previously in the frame. Measures were taken until one of each visible oocyte development stage (chromatin nucleolus, early perinucleolus, late perinucleolus, yolk vesicle, yolk globule) had been recorded per frame. The overlap of 95% confidence intervals of the means of average oocyte diameters for each oocyte development stage was then assessed graphically to determine if oocyte stages could be distinguished reliably on the basis of size alone.

Batch fecundity was estimated using the gravimetric method of Hunter et al. (1985). Wedges of ovarian tissue were cut from preserved ovarian lobes, blotted dry, and then weighed to the nearest 0.0001 g. These wedges were taken from three equidistant positions (anterior, medial, and posterior) along the length of an ovary lobe. These wedge sub-samples were no larger than one-eighth of the area of the lobe cross section or no heavier than 0.2 g, to maintain feasible processing and counting within available time constraints.

Whole oocytes were extracted from ovary wedges by firstly soaking in 15 to 20 drops of glycerine in a glass Petri dish for 15 minutes and then adding a further 10 drops of glycerine and lightly tapping the wedge with blunt forceps. Whole oocytes could then be pipetted onto a Bogorov tray and viewed at low power magnification using a dissecting microscope with a reflected light against a black background. It was difficult to extract all of the oocytes from the ovarian lamellae, however, and the remaining oocytes were teased apart from lamellar tissue using dissecting needles under the microscope.

Counts of hydrated and yolk globule oocytes were then made using a hand counter. Yolk globule oocytes were identified on the basis of size. Hydrated oocytes, which could not be identified on histological sections due to poor preservation, were identified whole as transparent oocytes that were much larger than yolk globule stage oocytes. This was consistent with Everson et al. (1989), who identified and counted hydrated oocytes for two confamilial species. Since it was not appropriate to use counts of yolk globule oocytes for estimates of batch fecundity (Hunter et al. 1985), counts of hydrated oocytes (when available) were used.

Oocyte counts from each wedge sample were then converted into numbers per gram to estimate the number per ovary using the formula:

$$BF_{est} = \frac{n_w}{WW} \times GW \tag{6.1}$$

where;

BF_{est} = estimate of batch fecundity;

n_w = number counted per wedge sample;

WW = preserved ovary wedge weight (g);

GW = preserved gonad weight (g).

6.2.3. Analyses.

Gonads were not collected from all *L. bohar* because of damage during filleting or logistical constraints during the ELF catch surveys. In order to increase the number of replicates for analyses, therefore, samples were often pooled across years into categories of month. For instance, November comprised samples collected in 1999, 2001, and 2002 from catch surveys of the ELF Experiment and in 2001 from the CRFFF (Table 6.1). This pooling of samples across years and sampling methods was based on the assumption that there was no significant influence of inter-annual environmental factors or sampling method on observed reproductive characteristics.

The proportions of each assigned ovarian stage were plotted for each calendar month for mature females to examine seasonal patterns in the ovarian development of mature females and thus inferred spawning activity. The pattern of inferred spawning activity over the lunar cycle was also investigated by categorising specimens on the basis of sample date into four respective phases of the lunar cycle (first quarter, full moon, second quarter, new moon) as done by Samoilys (1997). Samples were constrained to the same approximate time of year—25th October to 30th November—to reduce possible confounding effects of seasonal influences and because samples were collected from all lunar phases within this range of dates, pooled across sample methods and years (1995-2003).

Maturation schedules for female and male *L. bohar* collected in the peak spawning period (as determined from the analysis of seasonal trends in ovarian maturity) were determined from plots of the observed percentages of mature fish for each FL group.

Maturity analyses were constrained to the peak spawning period to reduce the number of histological distinctions made between inactive immature and inactive mature (Resting) females, which is difficult (Ferreira 1995). Further, constraining the maturity analyses to those samples collected for one season or sample month was considered likely to reduce potential confounding variation in reproductive status from seasonal growth in FL. The logistic model was used to estimate maturity following:

$$P_x = \frac{100}{1 + e^{(aL+b)}} \qquad (6.2)$$

where;

P_x = the predicted percentage of fish mature in each FL group;

a,b = model parameters;

L = the FL group (mm).

From these trends, a population estimate of the mean FL at which 50% of females and males had reached maturity (L_{50}) was calculated by the formula:

$$L_{50} = \frac{-b}{a} \qquad (6.3)$$

after Everson et al. (1989). The shortest recorded FL of those mature fish sampled (L_{min}) and the longest recorded FL of immature fish ($L_{\max\_im}$) were also noted. The ratio of the L_{min} and L_{50} as a proportion of the longest FL sampled (MAXFL) was also calculated for comparison with published estimates for other species and previously reviewed trends for the lutjanids by Grimes (1987).

These methods were also used to estimate the mean age at which 50% of females and males reached maturity (a_{50}), and the youngest age of mature ($a_{\min}$) and the oldest age of immature ($a_{\max\_im}$) males and females. Age data were pooled across months, in addition to pooling across years and sampling methods, because it was assumed that seasonal effects on annual age-based estimates would be negligible.

Since whole fish weights (*TW*) were not available for all fish, *TW* was estimated from the FL measurement of each fish using the fitted regressions of *TW* on FL (Chapter 5). This formula was also used to convert observed *TW* into estimates of FL, to assist with interpretation of observed trends. The significance of correlations between *GW* and *TW* for each sex-specific maturity stage was explored and model II linear regressions were fitted to describe significant linear relationships because similar types of measurement error were present for related variables (Laws and Archie 1981). This was done to identify changes in gonad growth that could be related to the onset of maturity in males and females and to determine whether relative reproductive output of males and females increased with body size. Analysis of covariance (ANCOVA) tests were done for the effects of sex and maturity stage on the slope and intercept of linear relationships over similar data ranges, according to the procedures described in Chapter 4.

6.3 Results.

6.3.1. Seasonal and lunar trends in inferred spawning.

Ripe females were collected in 8 of the 12 months, indicating that females may have a protracted spawning season (Fig. 6.3), assuming that spawning was imminent for females with ripe ovaries. Unfortunately, however, the sample sizes were low, being less than 10 for 7 of the 12 months. Also, oocyte stages more advanced than yolk globule (i.e., “migratory nucleolus” and “hydrated” oocytes; Samoilys and Roelofs 2000) could not be confidently discriminated on histological sections because large ovaries were often poorly preserved. There appeared to be a high amount of reproductive activity in November (~88% of mature ovaries were either Ripening or Ripe) compared to other months for which reasonable sample sizes were available (April, May, August-November), possibly indicating a period of peak spawning.

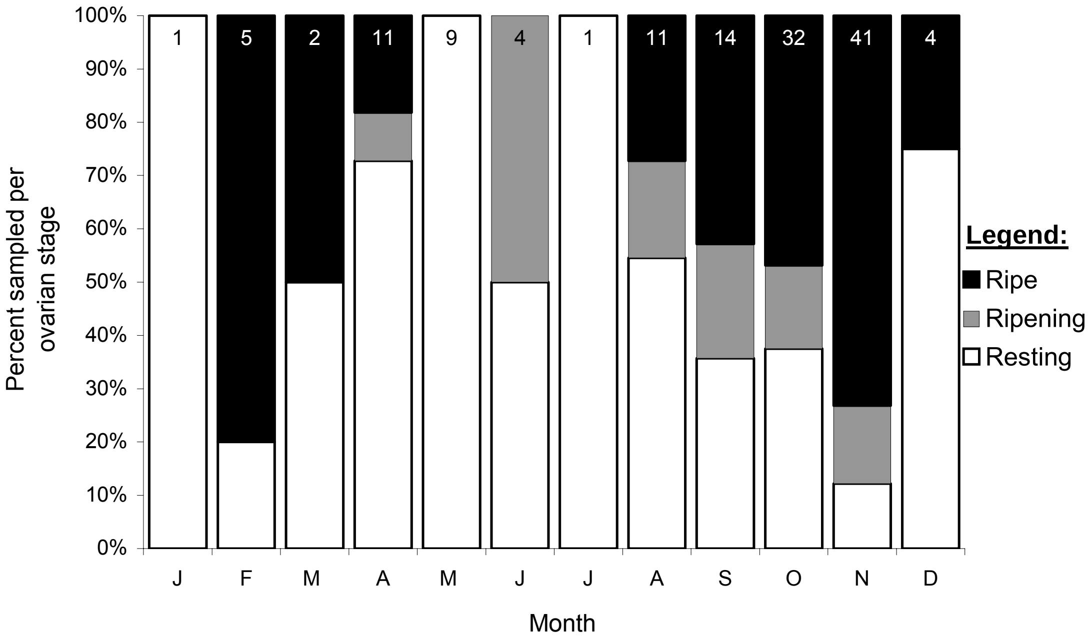


Figure 6.3 Percentage of mature ovarian stages collected per sample month. Data pooled across years 1999 to 2003, within calendar months. Number of sample replicates collected per calendar month (n) indicated inside top end of each respective bar. Ovarian stages as assigned from histology.

Age estimates of 0+ year olds speared in October 2002, ranging from 102 to 149 days, were used to estimate the back-calculated birth (hatching) dates, ranging from 12th April to 29th May, 2002. This result suggests that spawning of this sample occurred in early May, which increases the number of months of inferred spawning activity to 9. The average estimated larval duration for some of these specimens was 45 days (± 3 SE). If this is typical for fish spawned throughout the year, then it would be expected that the recruits from peak spawning in November would settle in mid- to late-summer (December – February). There was no obvious pattern across the lunar cycle within this peak spawning period, however, because ripe ovaries were sampled in all lunar phases (Fig. 6.4).

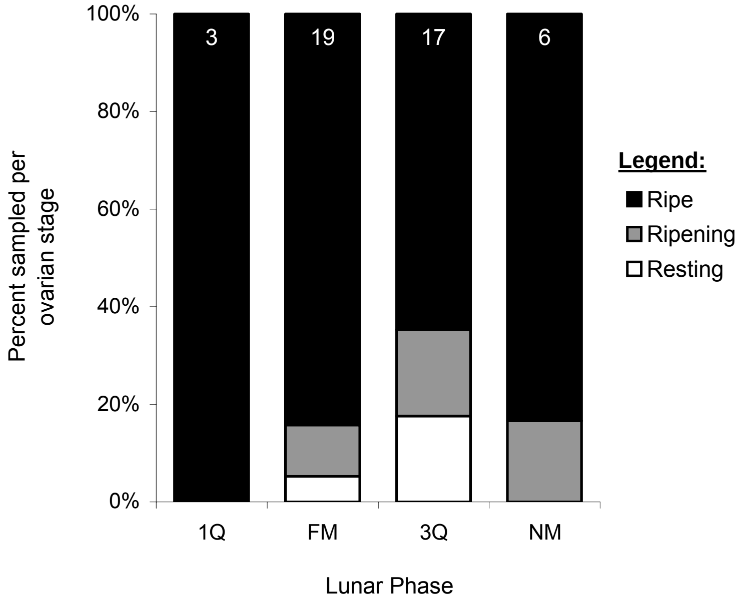


Figure 6.4. Percentage of mature ovarian stages collected per lunar phase. "1Q" = First Quarter; "FM" = Full Moon; "3Q" = Third Quarter; "NM" = New Moon. Samples collected on dates between 25th October and 30th November but pooled across sample years (1999 to 2003) within lunar phases. Number of sample replicates collected per lunar phase (n) indicated inside top end of each respective bar. Ovarian stages as assigned from histology.

6.3.2. Maturity.

Maturity analyses of FL were done for November because this was inferred to be the peak spawning period (Fig. 6.1). The logistic function demonstrated a good fit for percent maturity data for females ($R^2 = 0.995$), although it should be noted that the curve was only fitted to 5 data (Fig. 6.5a). The corresponding L_{50} estimate was ~428 mm FL, which equates to about 8 years of age. The logistic function also demonstrated good fit for the percent of females mature at age ($R^2 = 0.964$) and produced an older $\hat{a}_{50}$ (than the converted $\hat{L}_{50}$) of 9.39 years (Fig. 6.5b). All ovaries from females older than 12.46 years were classified as mature.

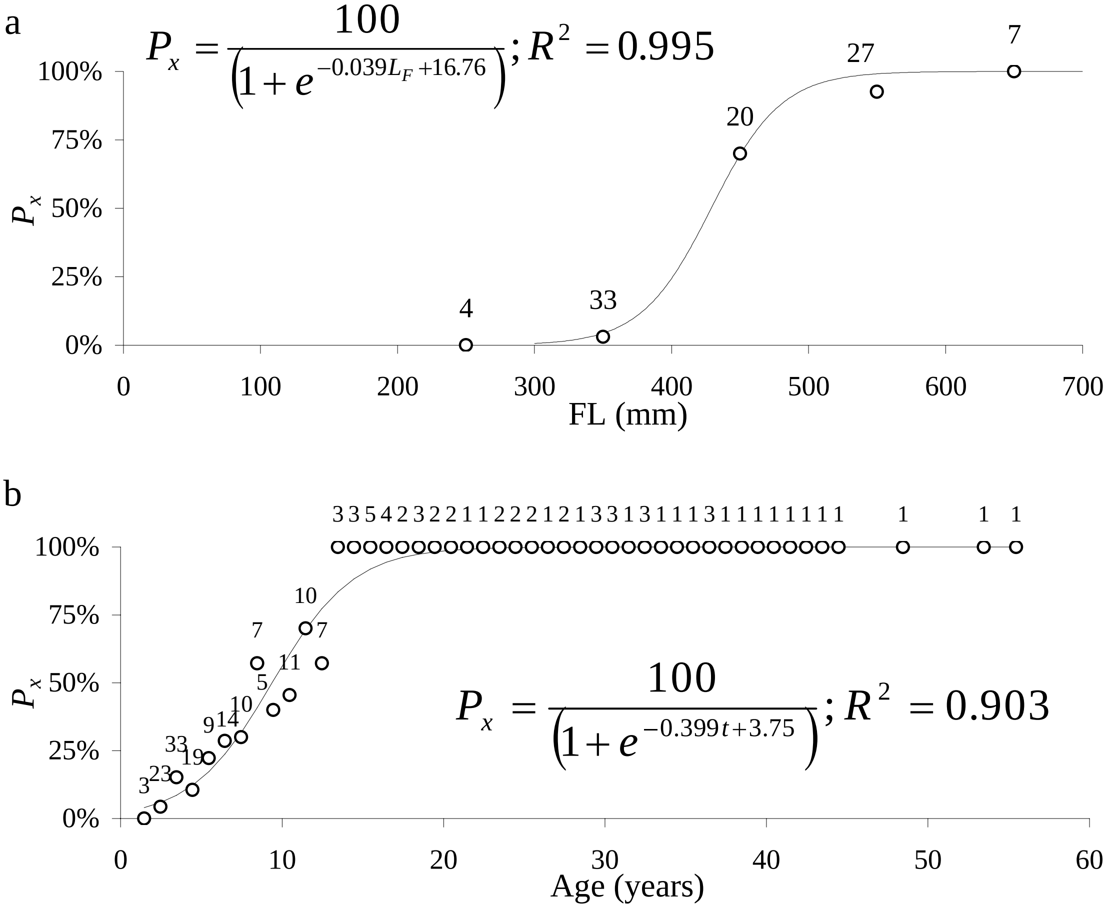


Figure 6.5 Maturation schedules for female *L. bohar* from the Great Barrier Reef. (a) Percent mature at FL; (b) Percent mature at age. P_x = predicted percentage of fish mature in each FL/age group; L = FL group (categories of 100mm FL); *a* = age group (categories of annual age estimates). Data in (a) for November only (pooled across sample years). Data in (b) pooled across all calendar months, years. Number of replicates for each plotted point indicated.

Unfortunately, there were not enough immature males collected to determine a maturation schedule for male FL (8.33% of total N for November calendar month) or age (11.30% of total N). From an inspection of $L_{\min}$, $L_{\max\_im}$, $a_{\min}$, and $a_{\max\_im}$ statistics in Tables 6.3 and 6.4, however, it appeared that males matured over a shorter (but overlapping) range of FL and younger overlapping age range than females. It is also possible that males could mature at a smaller size because the smallest mature male was also the smallest sampled in November.

Table 6.3 Maturity at FL statistics for females and males collected in November. 'MAXFL' = Maximum observed FL of both sexes (760 mm); 'L_{min}' = Minimum observed FL mature; '$L_{\max\_im}$' = Maximum observed FL immature; '$\hat{L}_{50}$' = Predicted FL at which 50% of observed sample replicates mature. Samples pooled across years. * Maturity schedule (and thus L_{50} estimate) could not be achieved for males.

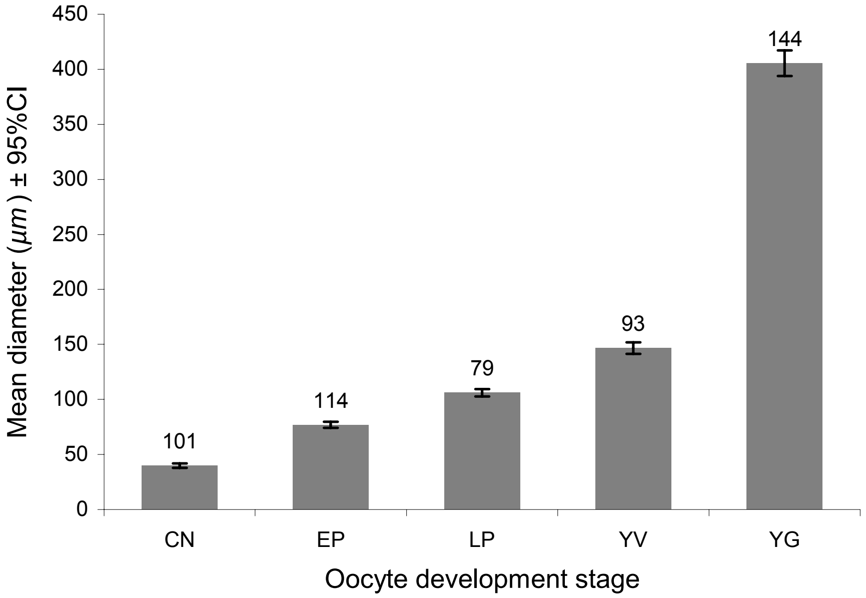
Statistic	Females	Males
Number of replicates	91	60
Total percent mature	49.45%	91.67%
L_{min} (mm)	386	248
L_{min} / MAXFL	0.51	0.33
$\hat{L}_{50}$ (mm)*	428.96	-
L_{50} / MAXFL	0.56	-
$L_{\max\_im}$ (mm)	510	451
Size range (mm FL)	287-675	248-760

Table 6.4. Maturity at age statistics for females and males. 'a_{min}' = Minimum observed age mature; '$a_{\max\_im}$' = Maximum observed age immature; '$\hat{a}_{50}$' = Predicted age at which 50% of observed sample replicates mature. Samples pooled across months and years. * Maturity schedule (and thus $\hat{a}_{50}$) could not be achieved for males.

Statistic	Females	Males
Number of replicates	209	177
Total percent mature	46.41%	88.70%
$a_{\min}$ (years)	3	2
$\hat{a}_{50}$ (years)*	9.39	-
$a_{\max\_im}$ (years)	13	11
Observed age range	2 - 56	1 - 50

6.3.3. Batch fecundity.

Female *L. bohar* had asynchronous oocyte development, as there were multiple developmental stages of oocytes simultaneously present in ovaries (Fig. 6.2). The diameter widths of oocytes from the different development stages were significantly different ($F_{4,526} = 1758$; $p < 0.001$; Fig. 6.6). There was no significant correlation between the size of the most advanced oocyte stage (i.e., mean diameter of Yolk Globule oocytes) with age ($r = 0.22$; p = 0.36), *TW* ($r = -0.17$; p = 0.44), or FL ($r = 0.04$; p = 0.82).



<u>Figure 6.6.</u> <u>Average diameters of different oocyte development stages.</u> 'CN' = chromatin nucleolus; 'EP' = early perinucleolus; 'LP' = late perinucleolus; 'YV' = yolk vesicle; 'YG' = yolk globule stage oocyte. Number of observations for each development stage indicated above each column. Error bars are 95% confidence intervals about the means. Oocyte diameters measured on histological sections of Ripe females collected in November.

The observed size range of yolk vesicle (YV) oocytes was 102 to 212 μm and of yolk globule (YG) oocytes was 182 to 550 μm. Following the exclusion of 3 replicates with a smaller observed mean size of YG oocytes, the remaining size range of YG oocytes was 281 to 550 μm. On the basis of this evidence it was decided that YG oocytes could be reliably discerned from other oocyte developmental stages on the basis of size alone and were identified as whole oocytes approximately 300 μm in diameter.

Unfortunately, hydrated oocytes were only found in one ovary. This specimen was sampled from the catch of an AUF spearfishing tournament (Chapter 2) held on Centipede Reef from 1000 to 1400 hours on 28th November 2001. This female was 542 mm long and estimated to be 11.46 years old. Counts of YG and hydrated oocytes are provided in Table 6.5, along with estimates of batch fecundity calculated from the hydrated oocyte counts. Given that the mean estimate of batch fecundity has low precision (CV = 20.3%), the variation in estimates from anterior, medial and posterior wedge samples is considered important. Therefore, only the full range of batch fecundity estimates for this individual will hereafter be considered.

Table 6.5. Counts of vitellogenic and hydrated oocytes and estimate of batch fecundity for one female *L. bohar.* * Batch fecundity estimate calculated from hydrated oocyte count using Eqn. 6.1.

Wedge sub-sample	Yolk Globule oocyte count	Hydrated oocyte count	Batch Fecundity estimate*
Anterior	201	141	62,506
Medial	195	84	46,242
Posterior	175	40	29,990
Mean:	190.33	88.33	46,246
Standard Error:	7.86	29.24	9,387

6.3.4. Morphometric indicators of relative reproductive output.

Significant positive correlations were revealed between *GW* and *TW* for females (r = 0.787; p < 0.001) and males (r = 0.807; p < 0.001), indicating a greater batch fecundity for larger fish. There were significant differences in linear trends of *GW* on *TW* for different female maturity stages, with a difference detected in slope ($F_{1,36} = 26.87;\ p <$ 0.001) between Inactive and Ripe stage females, and no difference in slope ($F_{1,24} = 3.77;\ p = 0.064$) but a difference in intercept ($F_{1,24} = 17.17;\ p < 0.001$) detected between Ripening and Ripe females. Differences in *GW* on *TW* trends were also detected between sexes, where the slope for mature males was less steep than for Ripe ($F_{1,43} = 10.66;\ p = 0.002$) and Ripening ($F_{1,8} = 8.05;\ p = 0.022$) females, but not different for Inactive females ($F_{1,77} = 0.0004;\ p = 0.984$), and the Y-intercept was lower ($F_{1,77} = 44.43;\ p < 0.001$) for mature males than for Inactive females. The trends described by fitted Model II regressions are shown in Figure 6.7.

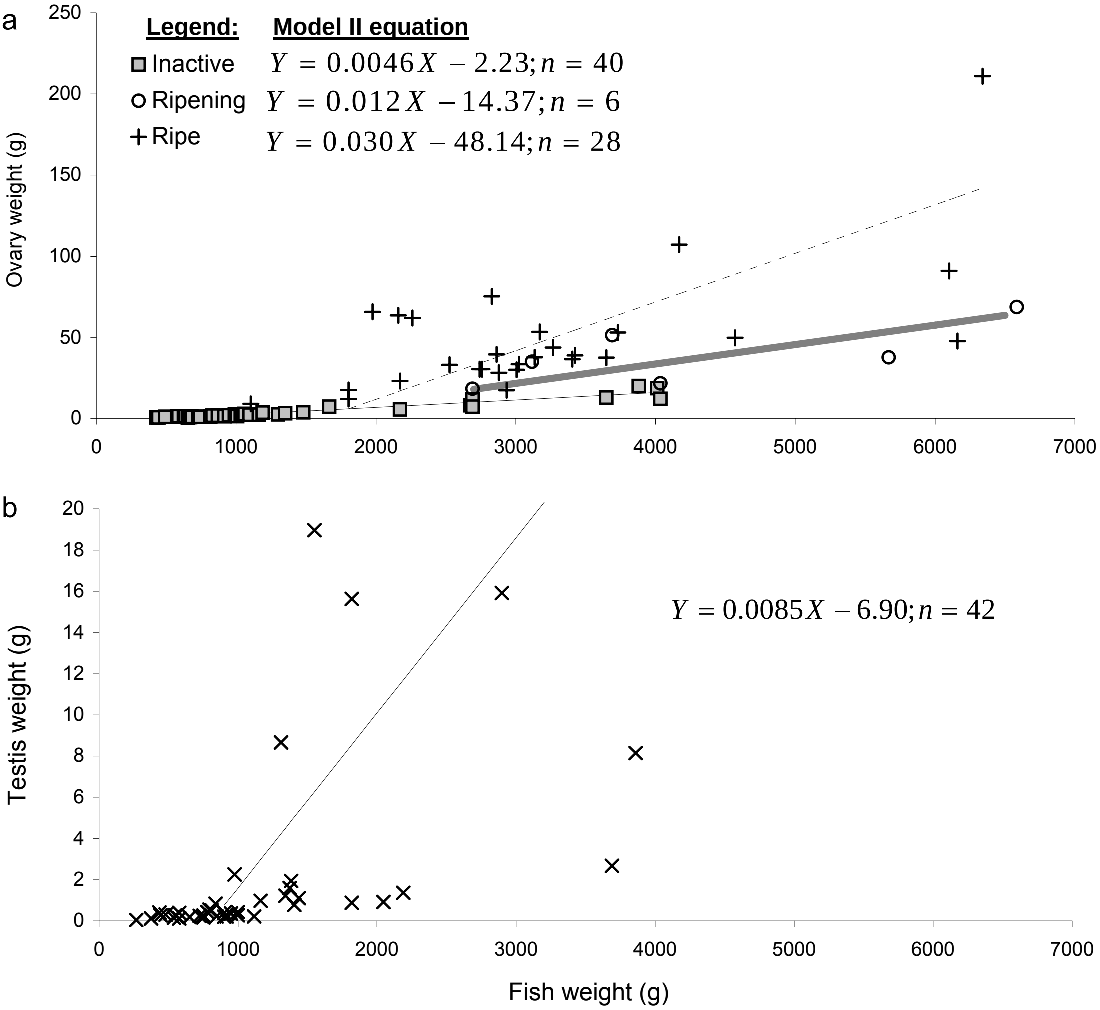


Figure 6.7. Relationships of preserved gonad weight to length-converted whole fish weight. (a) Model II regressions of ovary weight on fish weight for different maturity stages. (b) Model II regression of testis weight on fish weight. Equations for Model II regressions and sample sizes shown. Data for November, pooled across sample years.

Further, the departure of Y-intercepts for Ripening females, Ripe females and mature males from the origin demonstrates that ovaries and testes do not grow isometrically with *TW* (deVlaming et al. 1982). That is, larger mature males and females have proportionally heavier gonads. The difference in slope detected for Active (Ripe and Resting) versus Inactive trends indicated an effect of maturity stage on ovarian weight, and thus the intersection of fitted stage-specific Model II regressions indicated the *TW* at which the rate of allometric ovarian growth changes, on average. The *TW* at which the Inactive and Ripening trends intersect was 1640.54 g (436.78 mm FL) and the

Inactive and Ripe trends intersection was 1807.48 g (450.24 mm FL), which was only slightly heavier (and longer) than size at $\hat{L}_{50}$.

For mature males, there also was a marked increase in testis weight on *TW* apparent for some individuals from 974.16 g *TW* (371 mm FL). This size was also within the range of an observed increase above 50% of males with relatively distended central efferent ducts with FL, which was inferred to indicate relative reproductive output (Fig. 6.8).

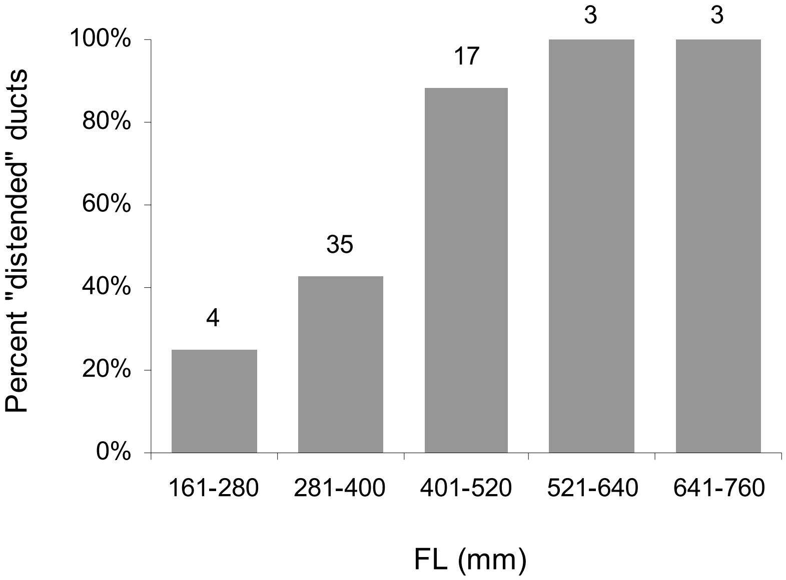


Figure 6.8. Percentage of males with distended central efferent ducts, per FL group. Duct width classified as narrow or distended relative to testis lobe width; see Fig. 6.1. Data for November only. Number of replicates for each FL group indicated.

6.4. Discussion.

Female *L. bohar* matured at a relatively large size and old age, were likely to be reproductively active over many months, and matured at a larger size (and older age) than males. Results with respect to reproductive mode were consistent with findings for other lutjanids including no evidence of hermaphroditism (Grimes 1987) and asynchronous oocyte development (Sadovy 1996). An estimate of batch fecundity was similar to or lower than previous estimates for closely related species and a positive linear relationship of ripe ovary weight with body weight indicated that batch fecundity is likely to increase with fish size and age.

6.4.1. Seasonal and lunar trends in reproductive activity of females.

Reproductive readiness in 8 sample months was demonstrated for female *L. bohar*. Inferred peak spawning in November coincided with the start of the summer monsoon and was consistent with results from previous studies in East Africa (Talbot 1960; Nzoika 1979), Palau (Johannes 1981), and Papua New Guinea (Wright et al. 1987). This spawning pattern has also been reported for other lutjanids (Manickchand-Dass 1987; Davis and West 1993), whilst a protracted spawning season has been speculated by Grimes (1987) to be a general trend for lutjanids that inhabit offshore and insular environments. Wheeler (1953) inferred two peak spawning seasons for *L. bohar* in the Seychelles: one at the start (October and November) and end (March) of the monsoon season. The duration of the spawning season on the GBR could not be estimated with confidence though, due to low sample sizes collected for some months.

It seems likely that *L. bohar* spawn multiple times each year because ripe females were sampled in most months. Other criteria that have been cited as indicative of multiple or 'fractional' spawning include: (i) large individual variation in gonad weight; (ii) multiple modes of developing oocytes; and (iii) a relatively light ovary weight relative to body weight (Grimes and Huntsman 1980). Evidence of criteria (i) and (ii) were observed in this study (Figs. 6.7 and 6.2, respectively) and the mean percentage of ovary to body weight in ripe females (in November) was also low (1.5% ± 0.15 SE) compared to that reported by Grimes and Huntsman for the lutjanid *Rhomboplites aurorubens* (2.4%), for which they suggested was light enough to indicate multiple spawning.

Johannes (1978) noted that most tropical marine fish species had lunar reproductive rhythms, and lutjanid spawning events have frequently been reported to coincide with full and new moon periods (Grimes 1987). Spawning aggregations of *L. bohar* are well known by traditional fishers to occur in Palau (Johannes 1981) and the Solomon Islands (Johannes and Hviding 2000) during full moon periods, and inferred courtship activity was also observed in a large aggregation of *L. bohar* in the full moon lunar phase in Palau (L. Squire, *pers. obs.*). The only recorded observations of spawning events by lutjanids to date were during the full moon (Wicklund 1969; Heyman et al. 2001) and third quarter moon (Carter and Perrine 1994; Heyman et al. 2001; Sala et al, 2003) phases. No obvious trend of spawning activity with lunar phase, however, was evident in this study, possibly due to the small sample sizes.

Poor preservation and low sample numbers of mature females meant that seasonal and lunar patterns in *L. bohar* spawning could not be precisely determined. Hydrated oocytes and post-ovulatory follicles are more precise indicators of spawning events than the criteria used in this study. This is because they indicate imminent spawning (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Hunter and Macewicz 1985) and that spawning has recently occurred (Hunter and Macewicz 1985; Davis and West 1993; Samoilys and Roelofs 2000), respectively. These criteria were not used in analyses because it is uncertain to what extent poor preservation caused deterioration in post-ovulatory follicles or advanced stage oocytes, which could potentially bias results; particularly for those samples that were not immediately preserved due to logistical constraints.

One individual with hydrated oocytes that were identified from the examination of whole oocyte characteristics was sampled during the full moon phase of the lunar cycle in November, the inferred period of peak spawning. Nine other mature females were sampled from the same reef on the same day, ranging from 514 to 659 mm FL: seven had ripe ovaries, two had migratory nucleolus stage oocytes present (Stage 8 of Yamamoto 1965), and three were the only females sampled with post-ovulatory follicles present. This was a more precise indication of spawning events that was consistent with previous evidence of *L. bohar* spawnings during the full moon period elsewhere and results of the seasonal analysis indicating that *L. bohar* spawns in November on the GBR.

6.4.2. Maturity.

Females matured relatively late in life, at an estimated age of 9.39 years. The L_{50} estimate (428 mm FL) was less than but similar to previous maturity estimates for *L. bohar* of 445 mm SL (479 mm FL; Talbot 1960), 450 mm FL (Wright et al. 1986), and 510 mm (length measure unspecified; Wheeler 1953). This study was the first to determine maturity using histology, which is the most accurate method of assessing ovarian maturity (West 1990). Therefore, these differences in reported lengths at maturity could be due to either regional variation or different methods of estimating maturity.

The proportions of L_{min} and adjusted L_{50} of maximum observed length (0.51 and 0.56 respectively; Table 6.3) fell within both the offshore and deep-water habitat categories generalised for lutjanids by Grimes (1987). Males, however, matured at a much smaller size than females, and it was not possible to resolve an average length at maturity estimate for males for the sampled size range. Talbot (1960) also reported that testes containing mature sperm were found in *L. bohar* males as small as 270 mm SL (291 mm FL) and that “ripe” males longer than 450 mm SL (485 mm FL) had much larger testes that were full of sperm. He speculated that the small males were not likely to be capable of spawning.

The estimated average age of maturity of 9.39 years is older than any other published for lutjanids to date, with the next oldest estimate reported by Russell et al. (2003) for *Lutjanus argentimaculatus* (7 years). Older published estimates for teleosts include those for the wreckfish, *Polyprion americanus* (8-10 years; Sedberry et al. 1999), Pacific rockfishes (Sebastinae; 6-12 years; Echeverria Wyllie 1987), hapuku, *Polyprion* *oxygeneios* (10-13 years; Francis et al. 1998), and orange roughy, *Hoplostethus atlanticus* (~25 years; Smith et al. 1995), which are all relatively long-lived species.

6.4.3 Relative reproductive output.

The changes in testis morphology with fish size was also observed by Talbot (1960), who noted a marked increase in testis size and sperm volume in larger male *L. bohar*. This demarcation between the postulated precocious non-spawning males and some of the larger presumed spawning males, however, occurred at a smaller size than observed by Talbot (~400 mm FL). Even if "functional" maturity for males does occur at this larger size, it is important to note that it would still be a smaller average length at maturity than for females, and thus would correspond with theoretical expectations.

An estimated batch fecundity of 29,990 to 62,506 ova for one female *L. bohar* was within the range reported for two smaller lutjanids (*L. vittus* Davis and West 1992; *L. guttatus* Rojas 1997) and one similar-sized lutjanid (*L. campechanus* Collins et al. 2001), but was an order of magnitude lower than the range reported for *Lutjanus argentimaculatus* (i.e., 2.5×10^5 – 4.0×10^6 ; Russell et al. 2003), another similar-sized lutjanid. Earlier estimates of fecundity for lutjanids (i.e, Rangarajan 1971, Grimes and Huntsman 1980; Manickchand-Dass 1987) were not comparable because they quantified estimates of the standing stock of vitellogenic oocytes within ovaries, which is not appropriate for indeterminate spawners (Hunter et al. 1985). The only other fecundity estimate for *L. bohar* was that of Wheeler (1953), who counted 2,250,000 ova in an ovary, which is much higher than the estimate for this study, although it is unknown if this was an estimate of batch fecundity or a count of the standing stock of vitellogenic oocytes. These results are also not comparable because batch fecundity is likely to change with fish size and no information on the size of this specimen was provided by Wheeler.

An indeterminate fecundity for *L. bohar,* with multiple spawnings over an extended period each year, suggests that this species could have a high annual fecundity. Annual fecundity for indeterminate spawners requires multiplying batch fecundity by some estimate of annual spawning frequency (Hunter et al. 1985). An estimate of spawning frequency was beyond the sampling frame of this study though, because repeated sampling of the population on sub-daily and daily intervals is required during a period of peak spawning (Hunter and Macewicz 1985). Instead, this study was an initial exploration of seasonal spawning pattern on the GBR and so was important in identifying the period(s) when *L. bohar* spawn. Further study to determine the annual fecundity of *L. bohar* would involve fine-scale sampling of *L. bohar* over a full lunar cycle, as done by Davis and West (1993) for *Lutjanus vittus* on the North-West Shelf, during a period of peak spawning. From this study, there was sufficient evidence to indicate that such sampling on the GBR should be done in November.

The positive linear relationships of ovary weight with body weight suggested that the potential number of ova spawned per batch increased at an increasing rate as females grow larger. This is suspected because larger ovaries are capable of ovulating more ova. This could indicate the importance of larger adults to the reproductive output and subsequent recruitment of *L. bohar* populations. Other factors such as spawning frequency and maternal effects are also likely to influence the reproductive contributions of females. Some studies of lutjanids have suggested that older females spawn more frequently (Collins et al. 2001), larger females spawn over a longer period (Kritzer 2004) and average trends in fecundity (Cueller et al. 1996; Russell et al. 2003) change at different times through the spawning season. Further, it is widely held that larger, older females are capable of producing more viable offspring by producing larger ova, resulting in better larval quality (e.g., Chambers and Leggett 1996; Kjesbu et al. 1996; Trippel et al. 1997; Marteinsdottir and Steinarsson 1998; Heyer et al. 2001; Palumbi 2004).

6.4.4. Conclusions and implications for management.

Expected correlates of *K*-selection were demonstrated, including delayed reproduction for females and iteroparity. Other predictions derived from current life history theory were also supported, albeit to varying degrees. For instance, although these results indicate a higher absolute size at first reproduction and initial fecundity for *L. bohar,* these results were not so different to those of closely related species when compared as a proportion of maximum length or when compared with species of a similar size. Also, although there was some indication that females matured at a larger size and older than males, there was much overlap in the size and age ranges of maturing males and females. The prolonged period of spawning identified here for *L. bohar* on the GBR is consistent with predictions from bet hedging theory for a longer-lived, repeat-spawning species, but this was also acknowledged to be a general trend for insular and offshore distributed lutjanids (Grimes 1987).

Trends from analyses of ovarian weights, testis weights, relative widths of central efferent ducts, and batch fecundity indicated that there may be potentially important paternal and maternal influences on recruitment. In a recent article, Palumbi (2004) noted that the use of standard fisheries models that don’t account for maternal influences could result in mis-management and over-exploitation of fisheries that remove larger, older individuals from populations. For instance, the Plan Development Team (1990) for the South Atlantic Fishery Management Council demonstrated, using data for *L. campechanus*, that fishing impacts on population fecundity were likely to be much higher if the larger individuals removed by fishing also produced the bulk of eggs and sperm.

Alternative fisheries models have been proposed to account for maternal effects. For instance, Hilborn and Walters (1992) recommended that a fecundity-at-age relationship, if available, should be used for calculating the spawning stock contribution to subsequent recruitment. Also, Marshall et al. (1999) suggested the use of an index of total liver weight of mature females to better predict the total viable egg production from gadoid stocks.

The attributes of reproductive biology described in this study indicate that populations of *L. bohar* are likely to be highly vulnerable to fishing impacts and overfishing. However, it has also been postulated, through theoretical modelling (Kirkwood et al. 1993) and analysis of temporal trends in catch-at-age (Secor 2000), that an accumulation of older age groups in longer-lived populations may better buffer an exploited stock against catastrophic events, such as recruitment failure. This is another hypothesis of a long-lived life history strategy termed “the storage effect” (Warner and Chesson 1985), which could negate some of the predicted deleterious impacts of fishing if the older age groups are unfished and remain relatively stable, perhaps because of unavailability to a fishery because of ontogenetic shifts in habitat use (such as movement to deeper water with age or size).

This was a possibility for *L. bohar* because a greater proportion of larger, older fish appeared to reside in deeper, offshore waters (Wright et al. 1986; Chapter 4) and thus might have been less available to fishing. Alternatively, larger older *L. bohar* may not have been targeted in some areas due to concerns about ciguatera poisoning, which is known to be more likely when larger fish are eaten (Randall 1980). This presents an interesting and unique scenario to consider for the management of exploited *L. bohar* populations.

Chapter 7: Predicting vulnerability to fishing impacts and overfishing.

7.1. Introduction.

The direct reduction of the number of older, larger fish (Cushing 1968) by fishing can have indirect effects on genetic and/or phenotypic characteristics within exploited populations (Law and Grey 1989; Reznick et al. 1990; Sutherland 1990; Law and Rowell 1993; Policansky 1993; Trippel 1995; Rochet et al. 2000; Conover and Much 2002). Models used for stock assessment often make many and varied simplifying assumptions, including that aspects of biology remain constant over time usually due to a lack of information about the dynamics of an exploited population. Thus, it is unknown if, and by how much, such indirect (and frequently unaccounted for) impacts of fishing might affect model predictions used for stock assessment and fisheries management.

The removal of larger fish from populations by fishing may select for a reduced average size at age in exploited populations over time (e.g., Kirkpatrick 1993; Law and Rowell 1993; Conover and Munch 2002). A smaller size at age, however, may reflect the resulting size at age composition of an exploited population because of the selective removal of larger, older fish by fishing and thus may not necessarily reflect an evolved change (Moulton et al. 1992). An increased size at age is an alternative postulated impact of fishing because a reduction in population density by fishing could invoke a density-dependent growth response (Eschenroder 1977; Gulland 1983; Policansky 1993). There also could be changes in other aspects of biology concomitant with a change in average size at age owing to evolved trade-offs with other life history traits (Stearns 1989; 1992) such as the age at first maturity (Trippel 1995). Such changes in aspects of biology could have potentially large impacts on rates of population turnover and sustainable harvest yields (Kirkwood et al. 1993).

Perceived rates of such phenomena could provide an indication of the relative ability of species to “compensate” for the deleterious impacts of fishing (Rochet et al. 2000), but it is also possible that such phenomena could distort perceptions of the relative ability of stocks to withstand such impacts. For instance, biological compensatory responses in length-at-age could bias estimates of depletion from retrospective harvest analysis if current length-at-age information used in the analysis was assumed invariant for the harvest period (Punt and Smith 2001).

In this chapter, I aimed to explore the potential implications of an increase in average asymptotic length, L_∞, as a possible effect of fishing (see Chapter 5), on estimates of depletion for an exploited stock of *L. bohar* using an age-structured stock assessment model. The plausibility of an increase in L_∞ as density-dependent growth response of older age groups to fishing was explored by comparing the predicted growth trend to that currently observed for the exploited population. I also aimed to use the model to simulate (i) recovery if harvest was ceased, (ii) future depletion if fishing continued at current levels and (iii) future depletion if fishing continued at current levels and an appropriate minimum size limit was implemented.

7.2. Methods.

7.2.1. General Approach

A standard 'Catch-At-AGE ANalysis' (CAGEAN) model (Deriso et al. 1985) was used, which incorporated biological and fishery data collected from an exploited region (Mahe Plateau) and a lightly fished region (Amirantes Plateau) in the Seychelles, to predict relative depletion. Specifically, growth parameter estimates from the different study regions were used to explore potential influences of harvest-induced density-dependent changes in growth parameters. The model was also used to assess the effect on predictions of biomass depletion of growth parameters from different regions that were assumed to be invariant with harvest. Thus, this approach facilitated the exploration of potential implications of alternative hypotheses for observed regional differences in growth: (i) that growth on the Mahe Plateau was different because of a density-dependent response to harvest depletion in this region only; and (ii) that regional differences in growth were due to factors other than historical differences in fishing pressure.

This approach provided scope for objectively exploring alternative credible scenarios for the impacts of fishing, whilst constraining model predictions to within "reasonable" bounds. A range of alternative model scenarios were explored to unravel effects of interactions among explored factors on predictions of the relative vulnerability of *L. bohar* populations to future overfishing. The stock assessment model could then also be used to forecast future recovery if harvest were stopped and the potential effectiveness of management strategies to further explore likely vulnerability to overfishing. However, since catch data used to fit model parameters were relatively scant, emphasis was placed on the relative estimates of depletion rather than estimates of absolute biomass.

7.2.2. Model inputs.

Biological parameters used as inputs for the age-structured stock assessment model were estimated from Chapters 4, 5, and 6 and presented in Table 7.1.

Although significant differences in $\hat{a}\_wt$ and $\hat{b}\_wt$ were indicated between Seychelles' regions ($p < 0.001$; Fig. 5.11) these differences were less conspicuous on plots than observed regional differences in fork length (FL)-at-age (Fig. 5.8). Thus, for simplicity, the effect of regional variation in weight-at-FL was not explored. Therefore $\hat{a}\_wt$ and $\hat{b}\_wt$ were estimated for data pooled across Seychelles' regions.

Table 7.1 Biological input parameters for the age-structured model. FL = Fork length (mm); L_∞ , K, t_0 are parameters of the von Bertalanffy growth model.

Parameter	Description	Estimate	SE	CV (%)	Region / Area	Source
a_wt	Parameters of the power function of weight (g) at length (FL)	4.16×10^{-6}	1.29×10^{-6}	31.0	Seychelles (Area)	Chapter 5
b_wt		3.238	0.048	1.5		
L_∞	Average asymptotic length (FL).	774.19	26.03	3.4	Mahe Plateau (Region)	Chapter 5
K	Growth coefficient (FL-at-age (years)).	0.074	0.008	10.8	Mahe Plateau (Region)	Chapter 5
t_0	Theoretical age at zero length (years).	-2.60	0.668	25.7	Mahe Plateau (Region)	Chapter 5
L_∞	Average asymptotic length (FL).	677.88	16.18	2.4	Amirantes Plateau (Region)	Chapter 5
K	Growth coefficient (FL-at-age (years)).	0.103	0.011	10.7	Amirantes Plateau (Region)	Chapter 5
MaxFL	Maximum observed FL from Seychelles.	850	-	-	Seychelles (Area)	This Chapter
Max age	Maximum observed age (years), to the nearest 10 year age group.	50	-	-	Seychelles (Area)	Chapter 5
M	Exponential coefficient of natural mortality.	0.0906	-	-	Seychelles (Area)	Hoenig (1983)
α _mat	Parameters of the logistic model fitted to the percentage of females mature at FL (100 mm bins).	-0.039	0.009	23.1	GBR (Area)	Chapter 6
β _mat		16.76	4.097	24.4		
h	Steepness parameter of the Beverton-Holt stock-recruitment function.	0.95	-	-	None	Myers et al. (1999), Francis (1992)
a_select	Parameters of the logistic model fitted to calculated selectivity coefficients at age.	-0.3335	4.10×10^{-4}	0.12	Mahe Plateau (Region)	This Chapter
b_select		99.9997	6.26×10^{-6}	6.26×10^{-6}		

The estimate for "*Max age*" was selected as an approximate estimate of longevity, and represents the number of age groups explicitly modelled. The "*MaxFL*" parameter was the maximum observed FL of *L. bohar* sampled from the Seychelles, and was used as an upper bound for a postulated density-dependent increase in FL-at-age (Section 7.2.4). The "*Max age*" estimate was used to predict an estimate of *M* using Hoenig's (1983) formula.

Parameters 'α _mat' and 'β _mat' were estimated from the maturity-FL schedule observed for females on the GBR (Chapter 6) as a conservative estimate of maturity for *L. bohar* populations in the Seychelles, assuming that maturity at length trends were similar in both areas. The parameter for the initial steepness of the Beverton-Holt stock recruitment function, *h* (Mace and Doonan 1988), was estimated to be 0.95, which was reported by Myers *et al.* (1999) for lutjanids (*L. campechanus, L. synagris*) in the Gulf of Mexico. This steepness estimate was also used by Francis (1992) for another long-lived teleost, orange roughy (*Hoplostethus atlanticus*), which effectively results in a constant predicted rate of recruitment with varying spawning stock size except when the spawning stock is depleted to very low levels. This seemed a reasonable approximation for *L. bohar*, given its estimated longevity and the lack of any available evidence to the contrary.

Catch and effort data from the artisanal fishery (Fig. 7.1; Table 7.2) were provided by the Seychelles Fishing Authority (SFA) and gleaned from technical reports (de Moussac 1988; Mees 1989; Mees 1992; SFA 2001; see Chapter 2 for descriptions of the fishery and study regions). Detailed sector- and region-specific catch and effort data were also provided by the SFA from 1994 to 2001. Length frequency distributions of catch were provided from the Catch Assessment Surveys (CAS) conducted by the SFA from 1994 to 1997 (monthly sample sizes in Table 7.3), which involved random sampling of boxes of landed catch, stratified by boat category and landing site (Mees 1996). The Mahe Plateau length-at-age sample, analysed in Chapter 5, could not be used to construct an age-length key for converting catch lengths to estimated ages because the length range of this sample (278-448 mm FL) did not span the range of catch-at-length data (240-822 mm FL). Therefore, recorded lengths in catch samples were converted to ages using the inverse of the von Bertalanffy function (Sparre and Venema 1992):

$$\hat{a}_{y,l} = t_0 - \frac{\ln\left(1 - \frac{l_y}{L_{\infty y}}\right)}{K_y} \qquad (7.1)$$

where;

$\hat{a}_{y,l}$ = estimated age for a given length *l*, in year *y*;

l_y = observed length (FL, mm) in catch sample in year *y*;

$L_{\infty y}$ = von Bertalanffy growth parameter (mean asymptotic length) for year *y*;

K_y = von Bertalanffy growth parameter (growth coefficient) for year *y*.

Observed lengths were converted to estimates of age only for the first 25 age groups because growth increments of FL above 25 years were less than 5 mm per year (Fig. 7.2). This was arbitrarily determined as the threshold minimum length increment for predicting age reliably before errors in length measurement were likely to substantially affect the uncertainty of length-to-age conversions. On this basis, observed catch frequencies were pooled for all fish aged to be above 25 years for sampled catch-at-age frequency distributions.

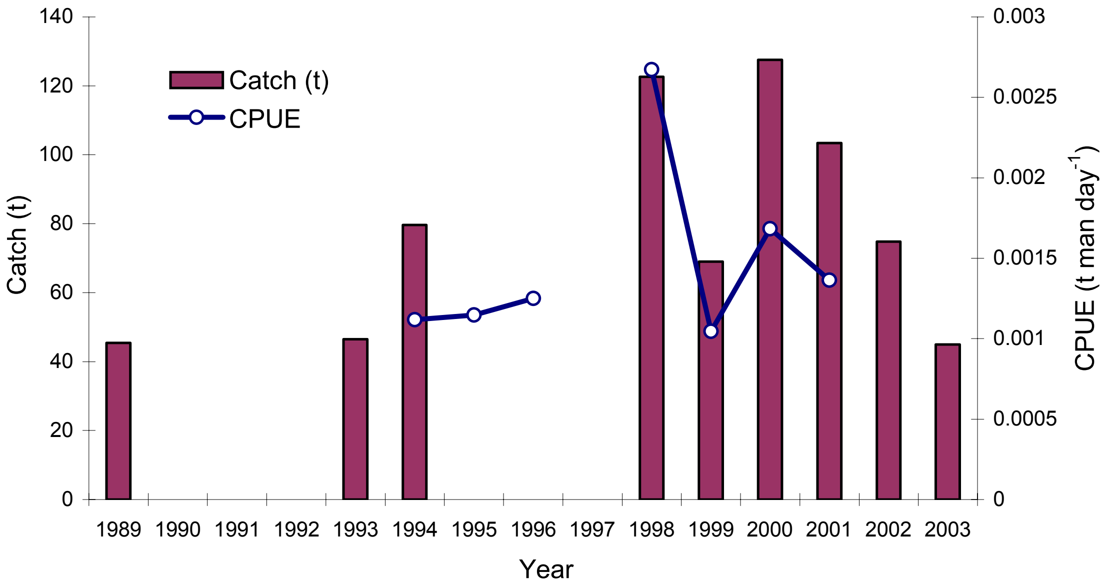


Figure 7.1. Catch and catch rate (CPUE) trends of *Lutjanus bohar* in the Seychelles artisanal fishery Catches are annual landings, in tonnes (T), provided by Government of Seychelles (2000) for primary landing sites. CPUE data provided from detailed region- and sector-specific Catch Assessment Surveys (CAS), where "man day" represents the average number of fishers fishing per day multiplied by the number of days fished per year. CPUE data excluded for 1997 due to low sample sizes.

Table 7.2. Catch, effort and CPUE of *L. bohar* on the Mahe Plateau. Catch and effort statistics provided by SFA. CPUE calculated from region- and sector-specific CAS data, also provided by SFA.

Year	Catch (t)	Effort (man days)	CPUE (t man day^{-1})
1989	45	44,898	-
1993	46	48,434	-
1994	80	46,426	1.12×10^{-3}
1995	-	-	1.15×10^{-3}
1996	-	-	1.25×10^{-3}
1997	-	-	-
1998	123	48,120	2.67×10^{-3}
1999	69	47,400	1.04×10^{-3}
2000	128	45,357	1.68×10^{-3}
2001	103	48,226	1.36×10^{-3}
2002	75	39,287	-
2003	45	34,693	-

Observed catch-at-age frequencies from annual sampling were scaled up to estimates of total catch-at-age using the standard formula (Megrey 1989):

$$C_{a,y} = O_y \left(\frac{H_{a,y}}{W_a} \right) \tag{7.2}$$

where;

$C_{a,y}$ = observed catch-at-age *a*, in year *y*;

O_y = estimated total catch for year *y* (g);

$H_{a,y}$ = observed fraction of age *a* fish in catch sample of year *y*;

$W_{a,}$ = average weight of fish of age *a* (g).

Table 7.3. Sample sizes of catch-at-length data collected from SFA Catch Assessment Surveys

Month	1994	1995	1996	1997	Total
Jan	-	85	707	139	931
Feb	-	17	364	278	659
Mar	-	522	69	56	647
Apr	3	180	170	50	403
May	-	64	520	113	697
Jun	-	31	46	-	77
Jul	-	-	43	-	43
Aug	-	-	90	-	90
Sep	101	-	2	-	103
Oct	96	-	27	-	123
Nov	26	-	255	-	281
Dec	530	44	43	-	617
Total:	756	943	2336	636	4671

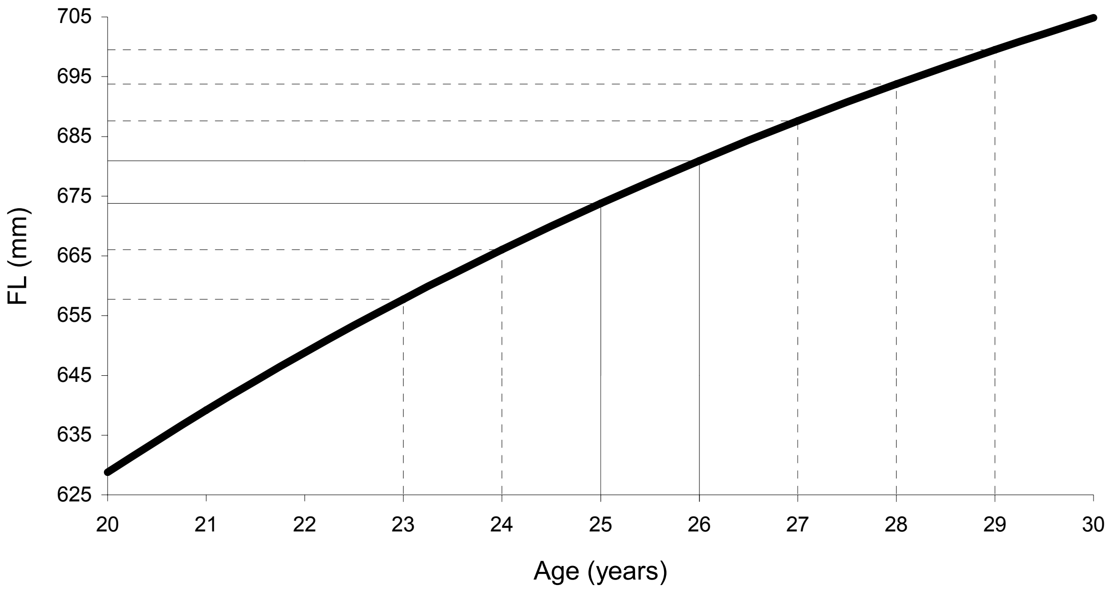


Figure 7.2 Intervals between expected lengths from the von Bertalanffy function used to convert catch-at-length categories to catch-at-age. Solid lines bracket the smallest interval between age groups that was ≥ 5 mm FL, which was used as an arbitrary criterion to group catch frequencies into a "plus-group" for the purpose of converting catch-at-length to catch-at-age frequencies.

As for catch-curve analysis, the inferred "age at full recruitment" (t_r) to the fishery was determined as the highest value of the natural log-transformed catch-at-age frequencies (Ricker 1975). Selectivity coefficients for age groups up to (but excluding) t_r were calculated as the ratio of observed catch frequency divided by the frequency expected to have encountered fishing gear, ζ . Expected frequencies of ζ were approximated by back-calculating from t_r the number of fish expected to be caught in the sample given the estimated M and the observed catch frequency of *L. bohar* at age t_r:

for $a = t_{r\text{-}1}$:
$$\zeta_{t_r-1} = \frac{\zeta_{t_r}}{e^{-M}} \qquad (7.3)$$

for all $a < t_{r\text{-}1}$:
$$\zeta_{a-1} = \frac{f(a)}{e^{-M}} \qquad (7.4)$$

where;

ζ_{t_r} = the observed catch frequency of age t_r fish, which was used to scale expected frequencies of fish younger than t_r, given the assumed natural mortality function, to those that would correspond to a representative sample from the population;

$f(a)$ = the frequency of *L. bohar* in the catch of age a.

A standard logistic function was then fitted to selectivity coefficients s_a at length, l (FL: mm):

for all $a \leq t_r$:
$$\hat{s}_a = \frac{1}{1 + e^{(a\_select \times l_{a,y}) + b\_select}} \qquad (7.5)$$

where;

a_select = model parameter;

b_select = model parameter;

$l_{a,y}$ = observed length group as it relates to each age group predicted by the length-age matrix in the model.

All fish older than t_r were assumed to be “fully selected” (Ricker 1969) to the fishery, and thus were assigned selectivity coefficients ($\hat{s}_a$) of 1. A FL corresponding to each catch-at-age group frequency was calculated using the von Bertalanffy function (Eqn 4.1) parameterised for recently sampled FL-at-age from the Mahe Plateau (Table 7.1). This selectivity sub-model was fitted to the assigned FL bins for each age group because hook and line fisheries are typically selective by fish size (Ralston 1982; 1990) rather than age. The fitted selectivity function was then incorporated into the CAGEAN model by referencing the FL-at-age by year matrix, $l_{a,y}$, to determine the appropriate selectivity coefficient for each age group ($\hat{s}_a$) in each year, y.

7.2.3. The Deterministic Model.

The CAGEAN model incorporates the catch equations of Baranov (1918) to predict the effects of fishing mortality on numbers-at-age in the population:

$$\hat{C}_{a,y} = \frac{\hat{F}_{a,y}}{\hat{Z}_{a,y}}\left[1 - e^{-\hat{Z}_{a,y}}\right]\hat{N}_{a,y}\,; \tag{7.6}$$

$$\hat{N}_{a+1,y+1} = \hat{N}_{a,y}e^{-\hat{Z}a,y} \quad \text{; and} \tag{7.7}$$

$$\hat{Z}_{a,y} = \hat{F}_{a,y} + M \tag{7.8}$$

where;

$\hat{C}_{a,y}$ = Predicted catch-at-age *a*, in year *y*;

$\hat{F}_{a,y}$ = Instantaneous rate of fishing mortality at age *a* in year *y*;

M = Instantaneous rate of natural mortality;

$\hat{Z}_{a,y}$ = Instantaneous rate of total mortality at age *a*, in year *y*; and

$\hat{N}_{a,y}$ = Predicted number of fish in the population at age *a*, in year *y*.

In this model, *M* was assumed to be constant for all age groups and years. Since only age groups up to and including 50 years (*Max age*) were explicitly modelled, mortality was applied to a “plus group” (Francis 1992) of *L. bohar* older than (and including) 50 years:

$$N_{50+,y} = (N_{50,y-1} + N_{49,y-1})e^{-(Z_{y-1}+Z_y)} \tag{7.9}$$

Numbers at age in the year prior to the commencement of fishing (i.e., the simulated “virgin state” population) were calculated using the formulae of Francis (1992):

$$N_{a,y} = R_0 e^{-M(a-1)} \quad \text{for } a < 50 \text{ years; and} \tag{7.10}$$

$$N_{50+,y} = \frac{R_0 e^{-M(49)}}{1-e^{-M}} \quad \text{for } a = 50+ \text{ years.} \qquad (7.11)$$

where; R_0 = the number of recruits (0+ individuals) in the virgin state.

Fishing mortality was assumed to be a separable product of age-specific selectivity, $\hat{s}_a$, and full-recruitment fishing mortality, $\hat{f}_y$:

$$\hat{F}_{a,y} = \hat{s}_a \hat{f}_y \qquad (7.12)$$

Observed annual effort (E_y) was used to predict full recruitment fishing mortality by estimating a catchability parameter for the fishery, q:

$$\hat{f}_y = qE_y \qquad (7.13)$$

and, for simplicity, q was assumed to be temporally invariant.

Observed E_y, recorded in units of "man days" (i.e., the average number of fishers fishing per day multiplied by the number of days fished per year; Government of Seychelles 2000), were available from 1989 to 2003. Years of missing data (1990, 1991, 1992, 1995, 1996, 1997) were interpolated using the mean of annual efforts for those years where data were available (Punt and Smith 2001). Annual efforts were also linearly extrapolated (Mapstone et al. 2004) from 1988 back to 1976, which was the year when larger vessels were introduced to the fishery to exploit offshore waters (Mees 1996) where *L. bohar* inhabit.

The finding that larger, older *L. bohar* were likely to reside in deeper waters (Wright et al. 1986; Chapter 4) indicated that this component of the population might be less available to a fishery that does not operate over the full depth range of the exploited population. To account for this, an availability parameter was fitted for those age groups that appeared to be less available in the catch according to the variant of the model proposed by Murphy (1965), and later modified by Megrey (1989):

$$\hat{C}_{a,y} = P\left(\frac{\hat{F}_{a,y}}{\hat{Z}_{a,y}}\left[1-e^{-\hat{Z}_{a,y}}\right]\right)\hat{N}_{a,y} \text{ ; and} \tag{7.14}$$

$$\hat{N}_{a+1,y+1} = \hat{N}_{a,y}Pe^{-\hat{Z}a,y} + N_{a,y}\left(1-P\right)e^{-M} \tag{7.15}$$

where;

$P =$ proportion of the population available to the fishery (0-1).

Age groups that appeared to be less available to harvest were identified visually by a consistent under-representation in the catch relative to the catch of other age groups and that expected from the application of *Z* to younger age groups. The effect of the *P* parameter on model fit was evaluated by comparing calculated Akaike’s Information Criterion (AIC$_C$; Burnham and Anderson 1998) between the fit of the model with and without *P*.

Annual age-specific biomass estimates were calculated by multiplying the expected biomass per recruit (using parameters of the weight-length and von Bertalanffy growth functions) by the expected numbers at age:

$$\hat{B}_{a,y} = \frac{\left[a\_wt\left(L_{\infty y}\left(1-e^{\left(-K_y\left(a-t_0\right)\right)}\right)^{b\_wt}\right)\right]}{1000000}\hat{N}_{a,y} \tag{7.16}$$

where;

$\hat{B}_{a,y}$ = expected biomass (tonnes) at age *a* in year *y*;

$\hat{N}_{a,y}$ = expected numbers at age *a* in year *y* in the population;

$L_{\infty y}$ = von Bertalanffy growth parameter (mean asymptotic length) for year *y*;

K_y = von Bertalanffy growth parameter (growth coefficient) for year *y*; and

t_0, *a_wt* and *b_wt* are from Table 7.1.

The denominator term (1,000,000) in Equation 7.16 was required to convert biomass estimates in grams to tonnes.

The Beverton-Holt (1957) function was used for the simulated stock-recruitment relationship:

$$\hat{N}_{0,y} = \frac{\hat{S}_{y-1}}{\alpha + \beta\left(\hat{S}_{y-1}\right)} \;; \qquad (7.17)$$

$$\alpha = \frac{\hat{A}_0(1-h)}{4hR_0} \; \text{; and} \qquad (7.18)$$

$$\beta = \frac{5h-1}{4hR_0} \;; \qquad (7.19)$$

after Francis (1992), which assumes a stable age distribution for the virgin population (B_0) where;

α = Beverton-Holt function model parameter;

β = Beverton-Holt function model parameter;

h = steepness;

$\hat{S}_{y-1}$ = expected spawning biomass in the year preceding year y;

$\hat{A}_0$ = expected spawning biomass per recruit in the virgin population;

R_0 = assumed number of recruits in the virgin state.

7.2.4. Adding a density-dependent increase in L_∞ to depletion.

The CAGEAN model was augmented with a hypothetical sub-model that made L_∞ density-dependent so that it would be responsive to fishing depletion as indicated in Chapter 5. A logistic model was used to simulate, each year, increases in L_∞ (L_{∞_y})

with decreases in population density caused by fishing, from the L_{∞_y} assumed for the virgin state (L_{∞_0} **:** observed estimate for Amirantes Plateau) to the current L_{∞_y} ($L_{\infty_{2000}}$ **:** observed estimate for Mahe Plateau; Table 7.1). A density-dependent increase in L_{∞_y} was assumed to be a positive logistic function of increasing depletion, and $L_{\infty_{2000}}$ had the potential to increase with further depletion to approach a hypothetical upper limit, *MaxFL*, when the population neared extirpation (Fig. 7.3). The converse of this assumption was that the L_∞ could also have decreased back to L_{∞_0} with an increase in population density up to the initial carrying capacity of the species' environment. For this sub-model, “depletion” was quantified as:

$$\text{Depletion} \qquad = 1 - \frac{N_y}{N_0} \tag{7.20}$$

and was scaled from 0 to 1.

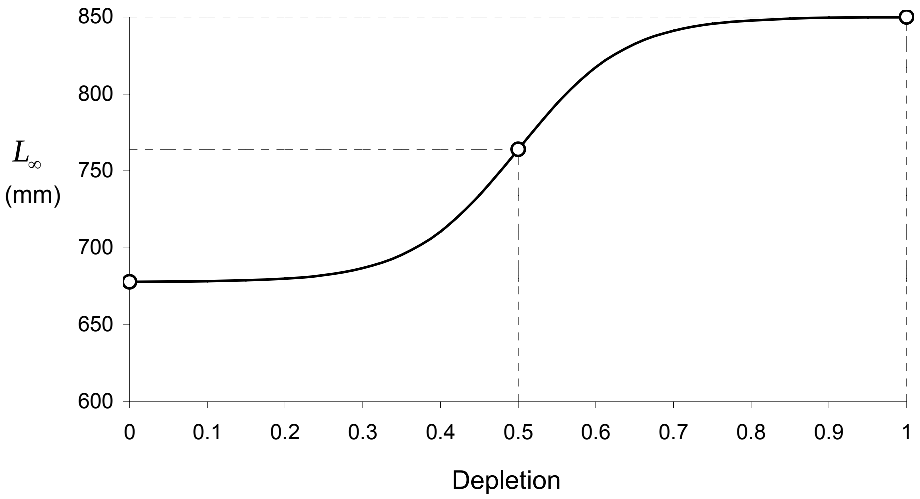


Figure 7.3 Assumed functional relationship between depletion in population density of *L. bohar* due to fishing and increase in L_∞ as a density-dependent growth response. The thick unbroken line was the expected trend (see Eqn 7.19 below) that must pass through 3 data pairs {*Depletion,* L_∞ }: {0, L_{∞_0} (677.88mm)}; {0.5, (*MaxFL* - L_{∞_0})/2}; and {1, *MaxFL*}. Positions of these data pairs relative to axes indicated by dashed lines. This relationship also assumed that there was no rapid "switch point" at any period from one state to the other; the increase in L_∞ with depletion was constantly changing and therefore symmetrical about the mid-way point (Depletion = 0.5) from harvest commencement (0) to extirpation (1), as dictated by the logistic function.

A logistic function seemed reasonable because it prevented the implausible scenario where L_{∞_y} continued to increase or decrease indefinitely in response to changes in population density. The "*MaxFL*" (Table 7.1) was assumed as an upper bound for subsequent increases in L_{∞_y} with depletion. The functional form of this sub-model was:

$$L_{\infty_y} = L_{\infty_0} + \frac{MaxFL - L_{\infty_0}}{1 + e^{(0.5r - (Depletion \times r))}} \tag{7.21}$$

where;

r	= parameter determining the slope of the logistic function;
MaxFL	= maximum observed length sampled from Mahe Plateau (Table 7.1);

L_{∞_0} = observed estimate for Amirantes Plateau (Table 7.1);

$Depletion$ = current depletion predicted from the numbers at age matrix ($N_{a,\mathrm{y}}$) within the model using Equation 7.20.

The estimate for the slope parameter, r, was calculated iteratively to be the value that maximised the increase in L_{∞_y} with depletion for the initial period of harvest (Depletion = 0.1 to 0.15) whilst subject to the constraint: $L_{\infty_0} \le 678\,\mathrm{mm}$ (i.e. Amirantes Plateau L_∞ rounded up to whole numbers). This constraint was required because as r increases the L_{∞_0} increases above 677.88 and the curve "flattens out," eventually resembling a linear relationship. Thus, this constraint on L_{∞_0} ensured the start and end values for L_{∞_y} were reasonable when r was estimated. r was maximised to ensure that the rate of transition from L_{∞_0} to $MaxFL$ would be the most gradual, which was considered the most biologically plausible scenario (i.e., no rapid “switch” from one state to another). The curve was symmetrical about the 0.5 depletion level, where L_{∞_y} was expected to be mid-way between the L_{∞_0} and $Max\ FL$, because the change in L_{∞_y} was also assumed to be continuous between these limits, from the commencement of fishing (Depletion = 0) to extirpation of the stock (Depletion = 1).

Since it is known that K is highly correlated with L_∞ (Bernard 1981), changes in K_y with L_{∞_y} were calculated using this formula:

$$K_y = -\ln\left(1 - \frac{66.3462}{L_{\infty_y}}\right) \tag{7.22}$$

where the value 66.3462 was the expected length when $a - t_0 = 1$. This value was an estimate of l_a which removes fish age, a, from the von Bertalanffy equation and was calculated by substituting parameter estimates for the Amirantes Plateau (Table 7.1) and $a = -1.6$ years into the von Bertalanffy equation. For simplicity, t_0 was assumed invariant with changing population size, N_y.

7.2.5. Fitting the model.

As in Deriso et al. (1985), observed catch-at-age data were assumed to differ from predicted values by a log-normal random variate, which can be minimised using non-linear least squares:

$$\text{min SSQ (catch)} = \sum_{a,y} \left(\ln\left(C_{a,y}\right) - \ln\left(\hat{C}_{a,y}\right)\right)^2 ; \qquad (7.23)$$

where;

SSQ = the residual sum of squares.

Model parameters which are not known or highly uncertain can be estimated to improve the fit of the model to observed data (Fournier and Archibald 1982; Deriso et al. 1985). It has been pointed out by Doubleday (1976), however, that fitting to catch-at-age data alone results in high correlations among model parameters, and, therefore, it is recommended to fit the model to an auxiliary set of observations from the fishery to “calibrate” predictions (Deriso et al. 1985; Megrey 1989; Quinn and Deriso 1999). Accordingly, I also fitted the model to observed sector and region-specific catch per unit effort (I_y) data that were collected by the SFA from 1994 to 2001 for whaler vessels from the Mahe Plateau, the sector that accounted for the majority of *L. bohar* annual catch:

$$\text{min SSQ (CPUE)} = \lambda_1 \sum_{a,y} \left(\ln\left(I_y\right) - \ln\left(q\hat{B}_y^E\right)\right)^2 ; \qquad (7.24)$$

where;

$\hat{B}_y^E$ = predicted exploitable biomass in year y;

q = catchability coefficient;

I_y = observed catch per unit effort data;

λ_1 = weighting term, which was the variance of observed logarithm catch from Equation 7.23 divided by the variance of observed auxiliary (CPUE) data (Deriso et al. 1985).

This assumed that catch per unit effort was a reliable index of abundance for this stock. Estimates for R_0, q, and P were then obtained by minimising the composite objective function:

$$\text{min SSQ (catch)} + \text{min SSQ (CPUE)} \qquad (7.25)$$

The bootstrap method (Efron 1982) was used to randomly resample, with replacement, 1000 times the lognormal residuals from this model fit. Sampled residuals were added to observed catch-at-age ($C_{a,y}$) and CPUE (I_y) data to create “bootstrapped” data sets, which had the same statistical properties as the original observed data. The CAGEAN model was refitted to bootstrapped data sets to produce bootstrapped estimates for R_0, q, P, and relative biomass depletion. The means and standard deviations of bootstrapped estimates were then used to assess bias and calculate standard errors of the original fitted estimates following Deriso et al. (1985). Estimated 95% confidence intervals were adjusted to account for bias following Haddon (2001).

7.2.6. Scenarios explored.

The deterministic model was fitted for three different growth scenarios to explore the effects of alternative hypotheses postulated for observed regional differences in growth in Chapter 5 on predictions of relative depletion (i.e., estimated population biomass in 2003 as a proportion of the estimated virgin state biomass: $\hat{B}_{2003}/\hat{B}_0$). The three growth scenarios were: (i) L_{∞_y} and K_y were current estimates for the Mahe Plateau (Table 7.1) and remained invariant with harvest; (ii) L_{∞_y} and K_y were current estimates for the Amirantes Plateau (Table 7.1) and remained invariant with harvest; and (iii) L_{∞_y} (and thus K_y) of *L. bohar* changed in response to depletions in density (approximated by $\hat{N}_y$) caused by fishing, from predicted virgin state values (assumed to approximate those observed for the Amirantes Plateau) to the current estimates observed for the Mahe Plateau (see Section 7.2.4.). Estimates of relative depletion were compared: (a) between scenarios (i) and (iii); (b) between scenarios (ii) and (iii); and (c) between scenarios (i) and (ii).

Comparison (a) was done to detect the overall influence of different growth assumptions for the exploited Mahe Plateau population on predicted relative depletion. A significant difference between estimates of relative depletion was detected when there was no overlap of bias-adjusted 95% confidence intervals from each scenario. Comparisons (b) and (c) were done to determine the significance of effects on predicted relative biomass depletion corresponding to alternative hypotheses that were postulated for observed differences in growth between the Amirantes and Mahe Plateaux in Chapter 5. The alternative hypotheses were that: a density-dependent change in L_∞ on the Mahe Plateau in response to fishing (b), and regional variation in (non-changing) growth (c), explained the observed differences in growth. The significance of an effect for each hypothesis was also tested by comparing the bias-adjusted 95% confidence intervals of relative biomass depletion predicted from the different model scenarios.

The credibility of the density-dependent L_∞ scenario was evaluated by comparing the current observed von Bertalanffy growth parameters for the Mahe Plateau and current catch to corresponding estimates predicted by the model. If this scenario was credible, then the current observed L_∞ and K from the Mahe Plateau would be within the combined range of 95% confidence bounds for $\hat{L}_{\infty 2000}$ and $\hat{L}_{\infty 2002}$ predicted by the model because observed FL-at-age data used to describe growth on the Mahe Plateau were collected from 2000 to 2002. Since the annual catch from 2003 was not used for the model fit it was also considered reasonable to use for this test of model accuracy. This observed catch was compared to the 95% confidence bounds of 2003 catch predicted by the model. Likelihood ratio tests (described in Chapter 4) were also done to determine if fits of the von Bertalanffy model to observed FL-at-age using deterministic estimates of $\{\hat{L}_{\infty 2000}, \hat{K}_{2000}\}$, $\{\hat{L}_{\infty 2001}, \hat{K}_{2001}\}$, and $\{\hat{L}_{\infty 2002}, \hat{K}_{2002}\}$ from the density-dependent L_∞ scenario were significantly different from the original fit of the von Bertalanffy model.

In addition to these scenarios on growth, I also explored whether effects of the P and/or maturity parameters were most likely to be dependent on age or length because there was no evidence to indicate which was more appropriate for predictions of relative depletion. Thus the scenarios explored were:

Scenario:	Growth parameters:	*P*:	Maturity:
1.	Mahe Plateau (static)	Relates to FL	Relates to FL
2.	Amirantes Plateau (static)	Relates to FL	Relates to FL
3.	Change (density-dependent)	Relates to FL	Relates to FL
4.	Mahe Plateau (static)	Relates to age	Relates to FL
5.	Amirantes Plateau (static)	Relates to age	Relates to FL
6.	Change (density-dependent)	Relates to age	Relates to FL
7.	Mahe Plateau (static)	Relates to FL	Relates to age
8.	Amirantes Plateau (static)	Relates to FL	Relates to age
9.	Change (density-dependent)	Relates to FL	Relates to age
10.	Mahe Plateau (static)	Relates to age	Relates to age
11.	Amirantes Plateau (static)	Relates to age	Relates to age
12.	Change (density-dependent)	Relates to age	Relates to age

In an effort to unravel the potential confounding influence of solving for *P* when fitting these different scenarios, additional fits were done where *P* was constrained among growth scenarios (for like scenarios of *P* and maturity) to the estimate predicted for Amirantes Plateau static growth. Bias adjusted 95% confidence intervals of the relative depletion estimates from different model scenarios were overlayed on plots to assess overlap and thus detect the significance of explored effects. The relative depletion of age frequencies from each scenario was also plotted to show depletion effects on population age structure.

7.2.6. Sensitivity analysis

A sensitivity analysis was done for two growth (Mahe Plateau static and density-dependent growth) and two availability (*P* relates to size and *P* relates to age) scenarios. For each model parameter, the deterministic estimate was perturbed by +5%, and then by -5%, whilst constraining all other parameters to their original fitted estimates. The percent change on resulting model outputs ($\hat{B}_0, \hat{B}_{2003}, \hat{C}_{2003}$) for each perturbation was then recorded. This was done to identify the relative importance of parameter uncertainty on model predictions.

7.2.7. Monte Carlo simulations.

Simulations of harvest, and recovery without harvest, were then done by running Monte Carlo simulations for various hypothetical harvest scenarios. First, the probability density function (PDF) of the normal distribution, which is:

$$\text{Normal distribution PDF} = \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{-(X-\mu)^2}{2\sigma^2}\right)} \qquad (7.26);$$

was used to describe the distribution of bootstrapped R_0 estimates ($\mu = \hat{R}_0, \sigma^2 =$ sample variance of the R_0 bootstrapped estimates) because the distribution of bootstrapped estimates was approximately normal (skewness = -0.14 ± 0.08 SE; kurtosis = -0.23 ± 0.16 SE). Since this PDF described the expected variability of annual recruitment prior to exploitation, it was also used as a proxy for the distribution of expected variations in annual recruitment for projected years. Random sampling from under this PDF was then done to generate stochastic variation to add to expected recruitments in projected years, $\hat{N}_{0,y}$, using the algorithm in Haddon (2001).

Simulations were done for projections where: fishing was stopped; fishing continued at the current level of effort, no harvest regulations; and fishing continued at the current level of effort with a minimum legal size (MLS) limit imposed. The current level of effort for projected harvest was calculated as the mean of observed E_y for the recent decade of harvest (1993 to 2003), excluding interpolated annual efforts (E_{1995}, E_{1996}). The MLS was based on the estimated average FL at which females were observed to achieve maturity in Chapter 6 (L_{50} = 428.96mm FL). For the purpose of simulating a MLS that was likely to be enforced but based solely on this biological criterion, the L_{50} was converted to total length (TL; length conversions from formulas in Wright et al. 1986) and then rounded to the nearest cm in TL (i.e., 45 cm TL). This was then converted back into units that were consistent with the model (mm FL) for simulations.

Model development, bootstrap replications and Monte Carlo simulations were done in Microsoft Excel using “macros,” which facilitated programmable iterations using code that was compatible with Visual Basic. Macros were programmed to save forecasted N_y and B_y from each scenario for the analysis of recovery when fishing of *L. bohar* was stopped 50 years after the last sampled E_y (i.e., from 2004). Macros were also programmed to save estimated spawning stock biomass (SSB_y) for the projected 20 years to evaluate the potential effectiveness of the MLS for preventing recruitment overfishing. SSB_y was selected as the most relevant indicator to detect the likelihood of recruitment overfishing because it was directly relevant to the recruitment function and because the more a SSB is depleted, the more likely recruitment failure could result (King 1995).

7.3. Results.

7.3.1. The descriptive model.

A catch-curve analysis indicated the age at full recruitment to the fishery and a possible influence of depth-related availability on the catch of older age groups (Fig. 7.4). Age groups less than 5 years were not fully recruited and age groups older than 21years were suspected to be not fully available to the fishery because of their apparent under-representation in the catch. Unfortunately, both CAS catch-at-length samples and annual catch data were available for only one year (1994) for converting to an estimate of the annual catch-at-age of the fishery. The fit of the selectivity function (Eqn. 7.5) to selectivity data calculated from observed catch-at-age (Eqn. 7.3, 7.4) is shown in Figure 7.5.

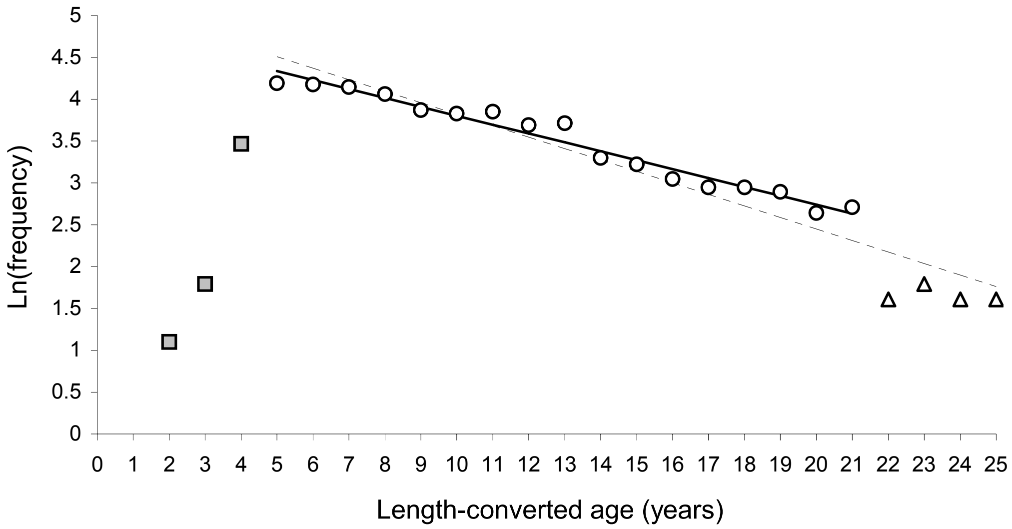


Figure 7.4 Catch-curve analysis of observed catch-at-age, 1994. Squares are log-transformed frequencies of age groups assumed to be not fully recruited to the fishery. Open triangles are log-transformed frequencies of age groups assumed not fully available to the fishery. Dashed line is the catch curve fitted in the conventional way (all age groups assumed fully available to fishery). Solid line is the catch curve fitted only to those age groups inferred to be fully available to the fishery (5 to 21 years).

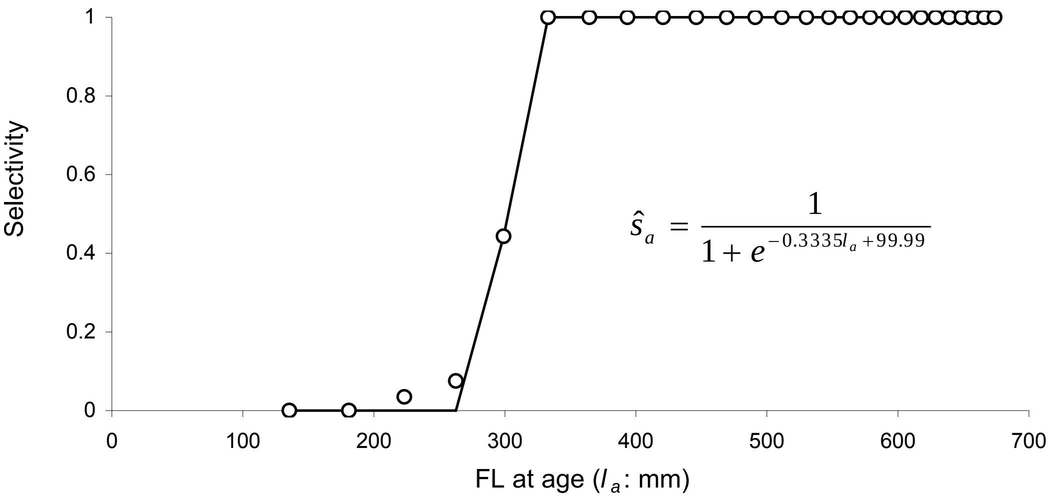


Figure 7.5. Selectivity function fitted to selectivity calculated from observed catch-at-age (1994). Open circles are calculated age-specific selectivity coefficients, s_a, (see Eqn. 7.3 for calculations) and solid line is the fitted selectivity function (Eqn. 7.4). Parameter estimates given in Table 7.1., and the equation for the fitted sub-model is given. l_a refers to the predicted length-at-age in 1994 according to the growth scenario that current Mahe Plateau estimates of von Bertalanffy parameters remain invariant with harvest.

A residual plot of the CAGEAN model fit to observed catch-at-age for the Mahe Plateau static growth, maturity-FL scenario (Fig. 7.6a) demonstrated an apparent biasing effect on model fit of observed frequencies for age groups older than 21years. As shown in Figure 7.6b, solving for *P* resulted in a more even distribution of residuals of $C_{a,1994}$ about the line of best fit. Although the incorporation of *P* did not result in a significant improvement in model fit (AIC_C difference < 2), retention of the availability parameter was considered valid on biological grounds (see Section 7.2.3.) and the benefit would seem to outweigh the cost to model parsimony by the addition of an extra parameter.

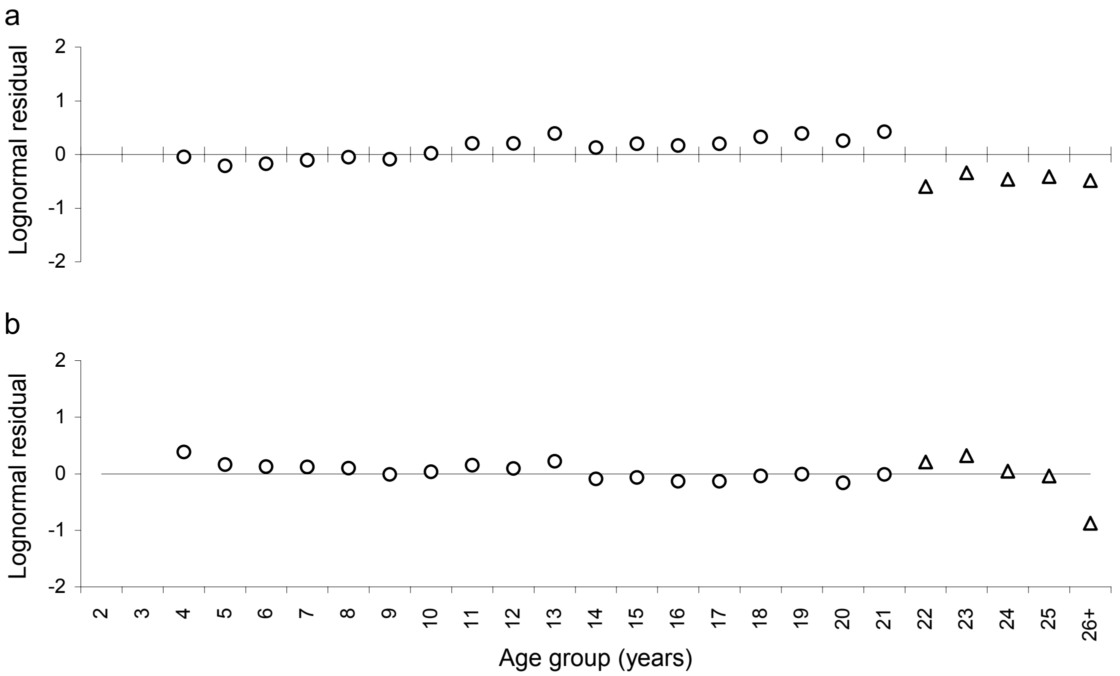


Figure 7.6 Residual plots of lognormal errors of catch-at-age ($C_{a,1994}$) from fit of the model (a) without and (b) with an availability parameter for age groups 22 to 25 years and the 26+ group. Age groups assumed not to be fully available to the fishery are represented by triangles on plots. Solving for an availability parameter for older age groups in (b) results in a more even distribution of residuals about the line of best fit.

7.3.2. Predictions of relative depletion from different model scenarios.

Fitted parameter estimates of R_0, q, and P and predicted relative depletion for each model scenario are given in Table 7.3. The bootstrap mean and standard deviation of estimates were also shown to provide an indication of bias and precision, respectively.

Table 7.3. Deterministic and bootstrap model estimates. For each parameter-scenario combination (from top to bottom) the original estimate, the bootstrap mean, and the bootstrap standard deviation are given. Relative Depletion is the estimated population biomass in 2003 as a proportion of the estimated virgin state biomass. R_0, P, and q are model parameters. See Section 7.2.6 for a description of scenarios. "AP" = Amirantes Plateau; "MP" = Mahe Plateau; "D-D" = density-dependent increase in L_∞.

Scenario			Parameter estimates			Relative Depletion
Growth	P	Maturity	$\hat{R}_0$	$\hat{P}$	$\hat{q}$	
AP static	size	size	110,619	0.237	4.06×10^{-6}	0.231
			111,930	0.353	4.07×10^{-6}	0.232
			12,254	0.277	5.03×10^{-7}	0.029
MP static	size	size	105,911	0.299	3.82×10^{-6}	0.245
			108,637	0.318	3.85×10^{-6}	0.244
			5,563	0.110	3.90×10^{-7}	0.030
D-D response	size	size	111,538	0.215	4.02×10^{-6}	0.255
			112,537	0.257	3.99×10^{-6}	0.255
			5,653	0.147	2.19×10^{-7}	0.014
AP static	age	size	110,470	0.657	3.84×10^{-6}	0.234
			113,646	0.686	3.82×10^{-6}	0.243
			10,440	0.208	5.59×10^{-7}	0.042
MP static	age	size	106,190	0.249	3.78×10^{-6}	0.256
			108,691	0.255	3.81×10^{-6}	0.255
			5,119	0.051	3.13×10^{-7}	0.025
D-D response	age	size	106,260	1	3.70×10^{-6}	0.240
			112,406	0.999	4.06×10^{-6}	0.223
			5,832	0.011	2.32×10^{-7}	0.011
AP static	size	age	110,619	0.237	4.06×10^{-6}	0.231
			111,717	0.358	4.05×10^{-6}	0.303
			11,986	0.279	5.11×10^{-7}	0.030
MP static	size	age	105,911	0.299	3.82×10^{-6}	0.245
			108,637	0.318	3.85×10^{-6}	0.238
			5,563	0.110	3.90×10^{-7}	0.029
D-D response	size	age	111,967	0.223	4.02×10^{-6}	0.254
			111,556	0.278	4.02×10^{-6}	0.234
			5,516	0.173	2.22×10^{-7}	0.015
AP static	age	age	110,471	0.657	3.84×10^{-6}	0.234
			114,534	0.683	3.84×10^{-6}	0.242
			11,098	0.211	5.76×10^{-7}	0.045
MP static	age	age	106,189	0.249	3.78×10^{-6}	0.256
			108,198	0.257	3.79×10^{-6}	0.256
			5,344	0.051	3.05×10^{-7}	0.025

Table 7.3. (Continued).

Scenario			Parameter estimates			Relative Depletion
Growth	*P*	Maturity	$\hat{R}_0$	$\hat{P}$	$\hat{q}$	
D-D response	age	age	109,259	1	3.93 x 10^{-6}	0.228
			112,709	0.992	4.06 x 10^{-6}	0.223
			6,275	0.039	2.43 x 10^{-7}	0.012
MP static (*P* constrained)	size	size	108,238	0.237*	3.60 x 10^{-6}	0.272
			110,300		3.60 x 10^{-6}	0.273
			5,808		2.75 x 10^{-7}	0.021
D-D response (*P* constrained)	size	size	111,468	0.237*	3.94 x 10^{-6}	0.257
			111,658		3.95 x 10^{-6}	0.257
			5,533		2.08 x 10^{-7}	0.011
MP static (*P* constrained)	age	size	107,514	0.657*	4.85 x 10^{-6}	0.159
			110,995		4.86 x 10^{-6}	0.160
			9,594		3.65 x 10^{-7}	0.013
D-D response (*P* constrained)	age	size	113,457	0.657*	3.90 x 10^{-6}	0.243
			112,380		3.70 x 10^{-6}	0.255
			6,757		3.03 x 10^{-7}	0.019
MP static (*P* constrained)	size	age	108,238	0.237*	3.60 x 10^{-6}	0.272
			110,328		3.59 x 10^{-6}	0.205
			5,690		2.70 x 10^{-7}	0.020
D-D response (*P* constrained)	size	age	111,204	0.237*	4.01 x 10^{-6}	0.253
			112,070		3.99 x 10^{-6}	0.338
			5,487		2.12 x 10^{-7}	0.012
MP static (*P* constrained)	age	age	107,514	0.657*	4.85 x 10^{-6}	0.159
			110,342		4.83 x 10^{-6}	0.160
			9,489		3.68 x 10^{-7}	0.013
D-D response (*P* constrained)	age	age	113,964	0.657*	4.02 x 10^{-6}	0.237
			111,848		3.72 x 10^{-6}	0.254
			6,693		3.03 x 10^{-7}	0.019

Estimates of relative depletion were similar for all scenarios and ranged from 0.228 to 0.256 (Table 7.3). Different maturity scenarios resulted in identical solutions and thus it was apparent that there was no effect of maturity (i.e., whether it was related to age or FL) on model predictions. Although $\hat{R}_0$ and $\hat{q}$ were similar among all scenarios, $\hat{P}$ varied markedly among scenarios when it was an age-based, rather than a size-based parameter. $\hat{P}$ was lowest for the Mahe Plateau static growth scenarios and highest for the density-dependent growth scenarios. This indicated a possible interaction effect of fitting age-based P for different growth scenarios.

Despite these differences in age-based $\hat{P}$, however, there was no overall effect of the different scenarios on estimates of relative depletion apparent from inspection of the bias-adjusted 95% confidence intervals (Fig. 7.7). Narrower confidence intervals apparent for the density-dependent L_∞ scenarios indicated that this scenario predicted relative depletion with higher precision. The off-set positioning of bias-adjusted 95% confidence intervals about some of the distributions of bootstrapped estimates (Figs. 7.7d and 7.7h) suggested, however, considerable bias in some of the estimates of relative depletion from the density-dependent model.

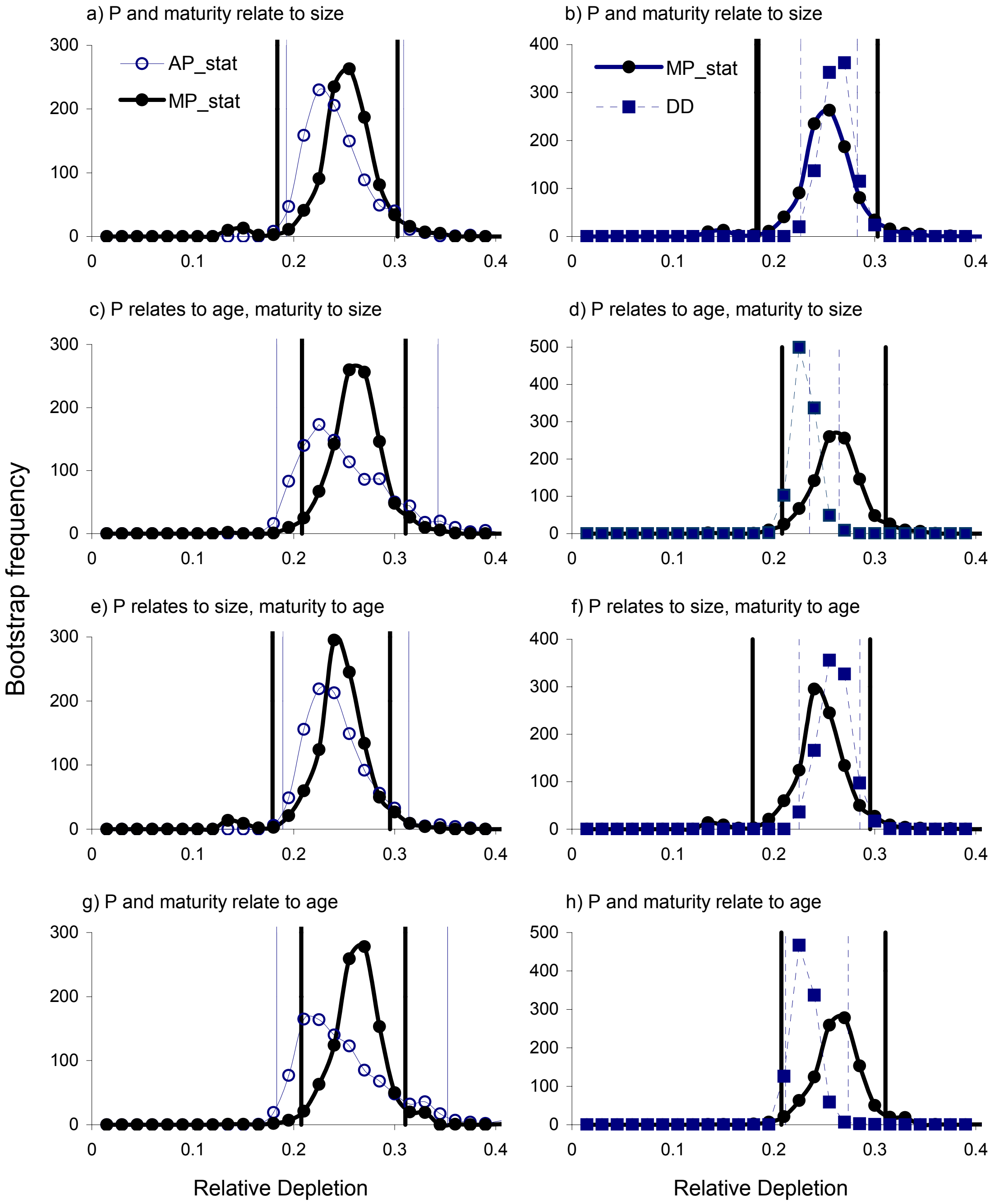


Figure 7.7. Frequency distribution of bootstrapped estimates of Relative Depletion for different model scenarios. Bias-adjusted 95% confidence intervals shown. “AP_stat” = Amirantes Plateau static growth; “MP_stat” = Mahe Plateau static growth; “DD = density-dependent increase in L_∞ ; *P* = availability of larger or older *L. bohar* to harvest. See Section 7.2.6 for details of scenarios.

The failure to detect significant differences among predictions of relative biomass depletion from all (unconstrained) scenarios has led to two conclusions. Firstly, the different growth assumptions for *L. bohar* on the Mahe Plateau did not significantly affect the prediction of relative biomass depletion (Comparison (a): Mahe Plateau static growth v density-dependent L_∞). Secondly, there was no significant effect on predictions of biomass depletion for either of the hypotheses explored for observed regional differences in growth (Comparison (b) Amirantes Plateau static (assumed virgin state) growth v density-dependent L_∞ and (c) Amirantes Plateau static growth v Mahe Plateau static growth).

The significance of differences in age-based $\hat{P}$ among growth scenarios on estimates of relative depletion was indicated when this parameter was constrained among growth scenarios. Significant differences in predictions of relative depletion were apparent from the non-overlap of 95% confidence intervals in Figures 7.8e and 7.8i between Mahe Plateau static and density-dependent L_∞ growth scenarios when age-based P was constrained. A marked reduction in relative depletion predicted by the Mahe Plateau static growth scenario was attributed to a higher constrained age-based $\hat{P}$ than was estimated for the unconstrained fit.

This influence of differences in age-based $\hat{P}$ among results of the different growth scenarios was further apparent when plots of the relative depletion of age structures were compared (Fig. 7.9). The lower age-based $\hat{P}$ fitted for the Mahe Plateau static growth scenarios resulted in the noticeably lower depletion (higher “percent depletion” on plots) predicted for older age groups. Depletion of older age groups was predicted to be higher for Amirantes Plateau static and density-dependent L_∞ growth scenarios because of a higher age-based $\hat{P}$. Plots of different maturity (but same growth and availability) scenarios were identical, further demonstrating that there was no effect of maturity scenario on model predictions.

The significant effect of differences in age-based $\hat{P}$ among growth scenarios on predictions of the relative depletion of age groups was also indicated when this parameter was constrained. A marked difference between age structure depletions when age-based P was unconstrained (Figs. 7.9b,c) and constrained (Figs. 7.10b,c) partly revealed the nature of effects on overall depletion estimates detected in Figures 7.7 and 7.8. This effect, however, was not so apparent when size-based P was constrained (compare Figs. 7.9a,d with 7.10a,d), which reflected the less variable (similar) size-based $\hat{P}$ among unconstrained scenarios.

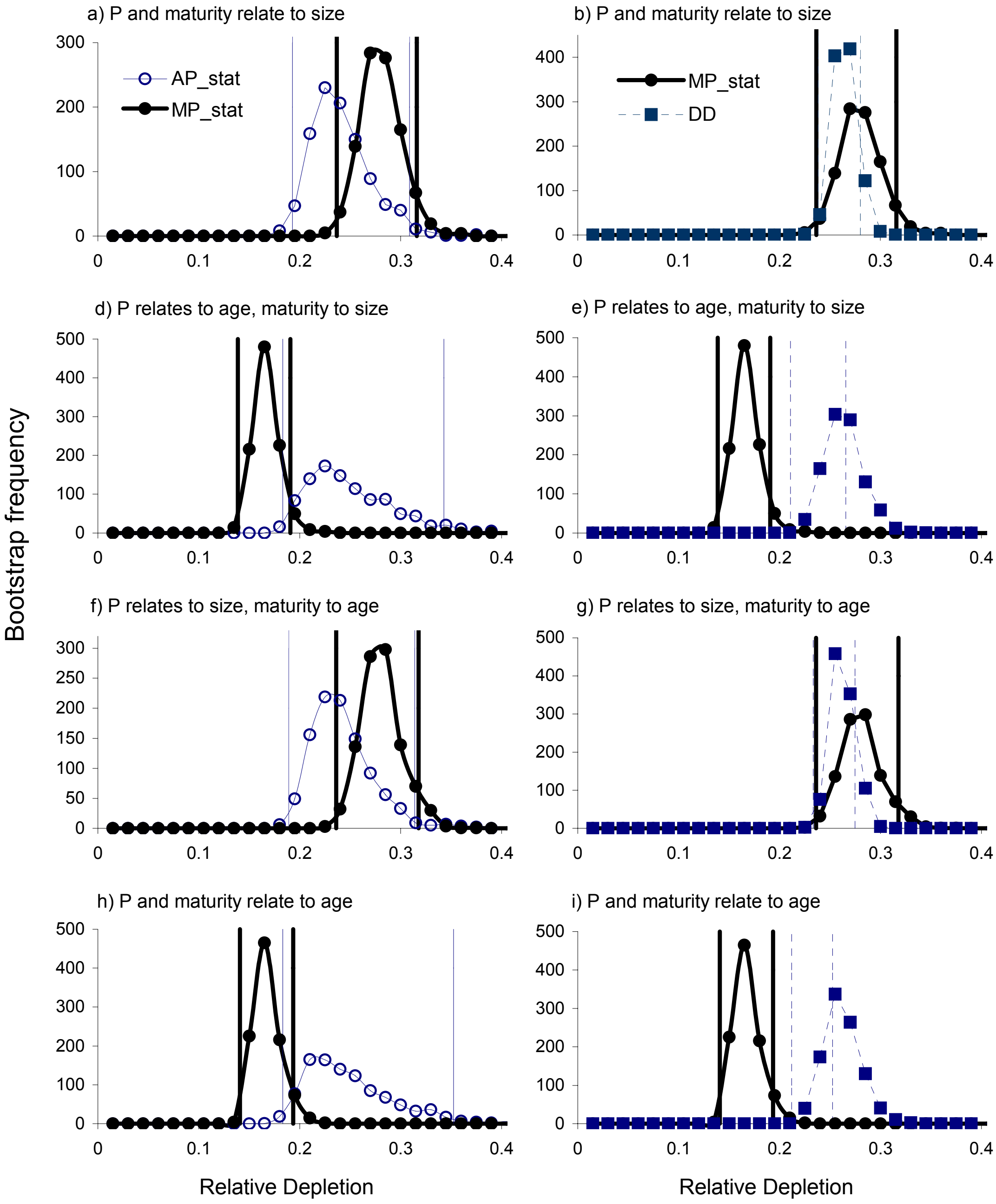


Figure 7.8. Frequency distribution of bootstrapped estimates of Relative Depletion for different model scenarios, *P* constrained. Bias-adjusted 95% confidence intervals shown. "AP_stat" = Amirantes Plateau static growth; "MP_stat" = Mahe Plateau static growth; "DD = density-dependent increase in L_∞ ; *P* = availability of larger or older *L. bohar* to harvest. *P* constrained for growth scenarios to the $\hat{P}$ for the corresponding AP_stat scenario.

Comparison of relative depletion at age among size-based *P* scenarios was therefore instructive for unravelling the effects of different growth scenarios because $\hat{P}$ was relatively constant among growth scenarios and therefore was not likely to confound results. Although the different growth scenarios did not result in different estimates of relative depletion in terms of population biomass (Fig. 7.7), an effect of growth on the depletion of older age groups was detected (Figs. 7.9a,c). Older age groups were depleted least under the Mahe Plateau static growth scenario and most under the Amirantes Plateau static growth scenario.

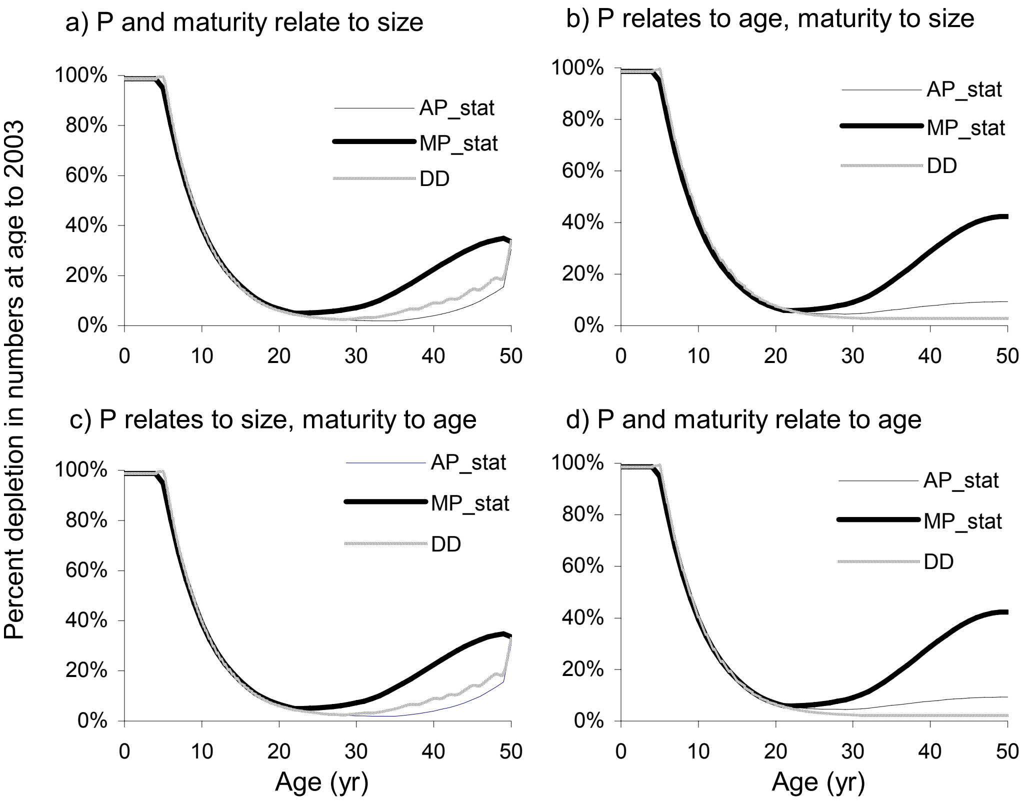


Figure 7.9. Percent depletion in numbers at age to 2003. Percent depletion quantified as the predicted number of *L. bohar* per age group in the population in 2003 as a proportion of the predicted number per age group in the virgin state. “AP_stat” = Amirantes Plateau static growth; “MP_stat” = Mahe Plateau static growth; “DD = density-dependent increase in L_∞ ; *P* = availability of larger or older *L. bohar* to harvest.

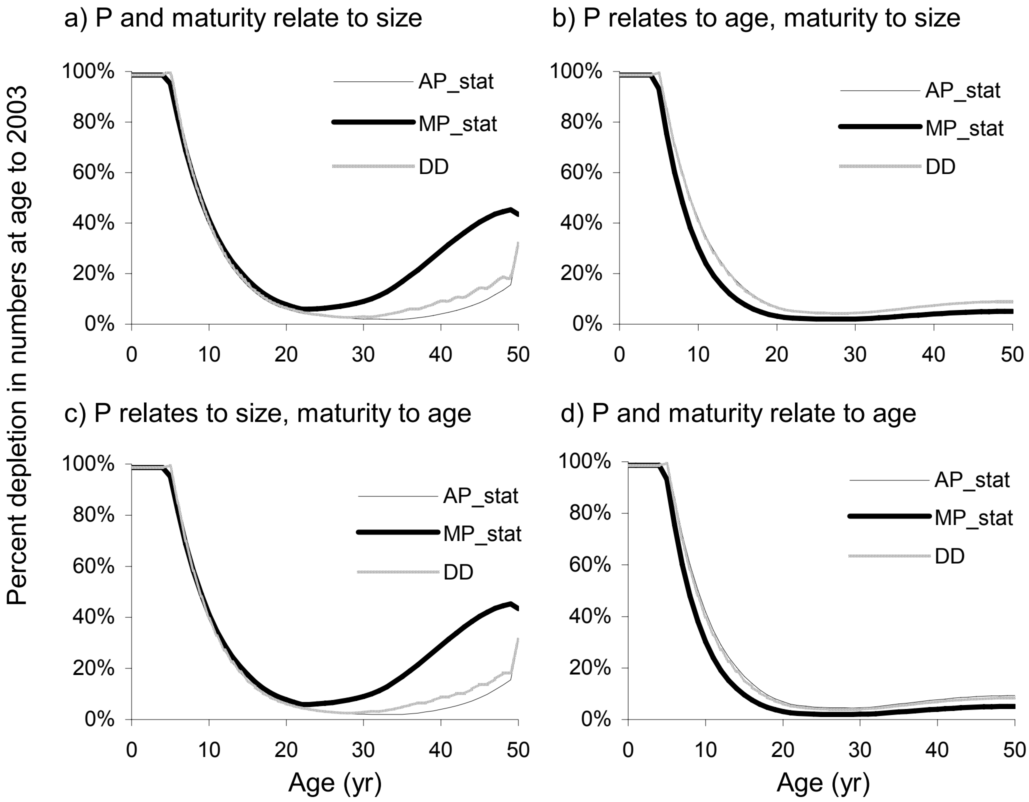


Figure 7.10. Percent depletion in numbers at age in 2003; *P* constrained. Percent depletion quantified as the predicted number of *L. bohar* per age group in the population in 2003 as a proportion of the predicted number per age group in the virgin state. “AP_stat” = Amirantes Plateau static growth; “MP_stat” = Mahe Plateau static growth; “DD = density-dependent increase in L_∞ ; *P* = availability of larger or older *L. bohar* to harvest. *P* constrained for growth scenarios to the $\hat{P}$ for the corresponding AP_stat scenario.

7.3.3. Credibility of the density-dependent L_∞ hypothesis for explaining observed regional differences in growth.

The observed catch of *L. bohar* in 2003 was within bias-adjusted 95% confidence limits of model predictions from all density-dependent L_∞ scenarios, demonstrating satisfactory predictions of catch (Table 7.4). However, observed catch was also within bias-adjusted 95% confidence bounds of catch predicted by all other growth scenarios explored, so this was not a reliable criterion for distinguishing between the credibility of the competing growth hypotheses.

Table 7.4. Estimates of growth parameters and catch for the density-dependent L_∞ growth scenarios to evaluate the plausibility of this hypothesis. Model predictions done for period of observed effort. Model predictions tabulated for comparison with observed $\hat{L}_\infty$ (774.19 ± 26.03), $\hat{K}$ (0.074 ± 0.008), and C_{2003} (44.95 T) for the exploited *L. bohar* population (see text). Bias adjusted 95% "Lower" and "Upper" confidence bounds on deterministic "Original" estimates are given.

Scenario			Model Predictions				
P	Maturity		$\hat{L}_{\infty 2000}$	$\hat{L}_{\infty 2002}$	$\hat{K}_{2000}$	$\hat{K}_{2002}$	$\hat{C}_{2003}$
size	size	Lower	701.97	702.74	0.080	0.080	43.60
		Original	708.54	709.28	0.081	0.081	48.31
		Upper	715.92	716.35	0.082	0.082	53.30
age	size	Lower	700.83	706.31	0.081	0.081	41.62
		Original	707.00	707.41	0.081	0.081	46.29
		Upper	708.34	719.82	0.082	0.082	48.44
size	age	Lower	701.51	702.35	0.080	0.080	44.38
		Original	708.54	709.28	0.081	0.081	48.53
		Upper	715.16	715.86	0.082	0.082	53.90
age	age	Lower	700.17	700.86	0.080	0.080	41.78
		Original	710.58	710.92	0.081	0.081	47.47
		Upper	716.21	716.44	0.082	0.082	51.04

The observed L_∞ for the Mahe Plateau was higher, and the observed *K* was lower, than bias-adjusted 95% confidence intervals of model predictions (Table 7.4). Further, fits of the von Bertalanffy model to observed length-at-age using predicted parameters from the density-dependent L_∞ scenario were significantly worse than the original fit to observations (i.e., Coincident and L_∞ tests, Table 7.5). Both results provide evidence to indicate that the simulated density-dependent increase in L_∞ to harvest depletion was not a credible model for explaining the observed differences in growth between Seychelles' regions, given assumptions of the CAGEAN model. This evidence against the density-dependent L_∞ hypothesis therefore goes some way to indicate that observed differences in growth between Seychelles' regions were not likely due to fishing effects but were due to the effect(s) of other factors: that is, intrinsic regional variation.

Table 7.5. Results of likelihood ratio tests comparing the fit of predicted growth in 2000 to 2002 to the original fit of the von Bertalanffy model. All models were fitted to original FL-at-age data sampled from Mahe Plateau. Von Bertalanffy parameters for 2000 to 2002 predicted from the density-dependent L_∞ scenario. "Coincident" tests compared overall fit; "L_∞" and "*K*" tests compared the fit of the von Bertalanffy model with these predicted values to the original fit. Significant differences (at $\alpha = 0.05$) in **bold**.

Scenario			Coincident		L_∞		*K*	
P	Maturity	Year	χ^2	p	χ^2	p	χ^2	p
size	size	2000	19.43	**<0.001**	9.76	**0.002**	0.91	0.339
		2001	18.79	**<0.001**	9.53	**0.002**	0.91	0.339
		2002	18.76	**<0.001**	9.52	**0.002**	0.91	0.339
age	size	2000	20.85	**<0.001**	10.27	**0.001**	0.91	0.339
		2001	20.36	**<0.001**	10.10	**0.002**	0.91	0.339
		2002	20.47	**<0.001**	10.13	**0.002**	0.91	0.339
size	age	2000	19.43	**<0.001**	9.76	**0.002**	0.91	0.339
		2001	18.79	**<0.001**	9.53	**0.002**	0.91	0.339
		2002	18.79	**<0.001**	9.52	**0.002**	0.91	0.339
age	age	2000	17.62	**<0.001**	9.11	**0.003**	0.91	0.339
		2001	17.18	**0.001**	8.95	**0.003**	0.91	0.339
		2002	17.33	**0.001**	9.00	**0.003**	0.91	0.339

7.3.4. Sensitivity analysis.

Changes in the *b_wt* parameter resulted in the greatest changes in $\hat{B}_0$, $\hat{B}_{2003}$, and $\hat{C}_{2003}$ for all model scenarios (Fig. 7.11). Since it was difficult to discern the sensitivity of other model parameters on this scale, the weight-FL parameters were excluded from these plots for further analysis (Fig. 7.12). Apart from the weight-FL parameters, model predictions of the virgin state biomass were most sensitive to perturbations of L_∞, and then of M, K, and R_0 (Fig. 7.12a). This demonstrates the importance of the described FL of older fish (i.e., those nearing or at average asymptotic FL) to predicted virgin state biomass, and thus to estimates of relative depletion presented in Table 7.3 and in Figures 7.7 and 7.8.

Although perturbations of L_∞ continued to have a large influence on $\hat{B}_{2003}$, the sensitivity to perturbations of L_∞ were somewhat diminished and the perturbations of harvest parameters *a*-select, *b*-select, and q, had a noticeably larger effect on $\hat{B}_{2003}$ (Fig. 7.12b). Perturbations of M resulted in the greatest proportional changes in $\hat{B}_{2003}$ and $\hat{C}_{2003}$, further demonstrated the importance of estimates for this parameter on model predictions. The $\hat{B}_{2003}$ and $\hat{C}_{2003}$ were also relatively sensitive to perturbations of R_0 and L_∞ but, surprisingly, perturbations by the harvest parameters q and P had little effect on $\hat{C}_{2003}$.

Most of these parameters, however, had relatively low coefficients of variation (CV), which indicates a relatively low uncertainty in the initial estimates (Tables 7.1, 7.3; mean CV for R_0 = 6.8%; mean CV for q = 9.5%), in terms of precision. No estimate of the variability of M was available, however, which highlights a potentially important source of uncertainty in the model. Conversely, the CV was relatively high for P when related to size (mean CV = 57.5%) and age (mean CV = 17.7%) in all model scenarios (26.4-27.3%) but changes in this parameter were observed to have a relatively minor impact on $\hat{B}_0$, $\hat{B}_{2003}$, and $\hat{C}_{2003}$.

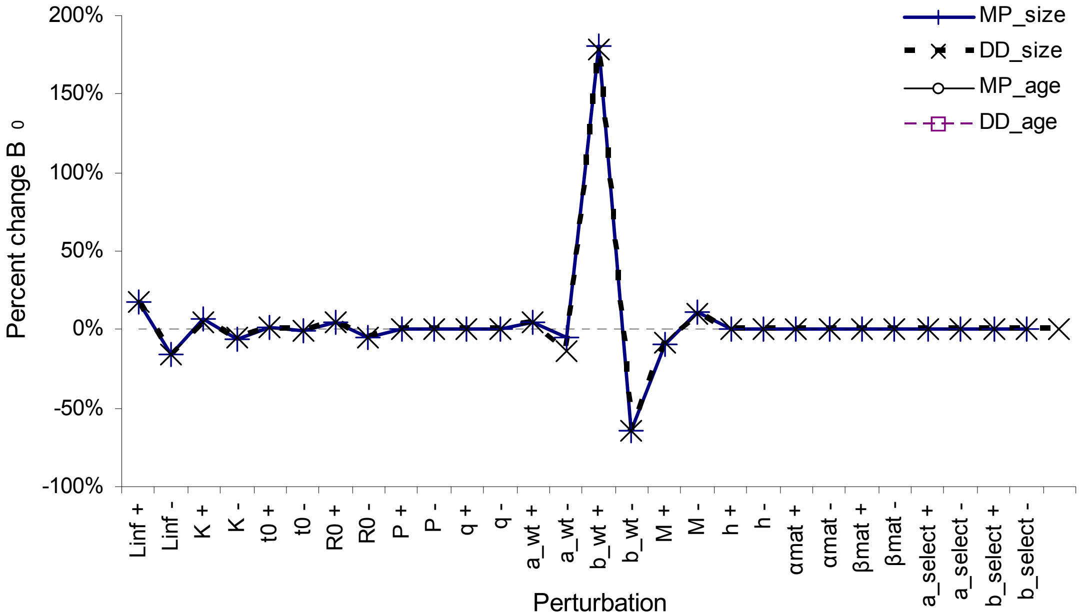


Figure 7.11. Sensitivity analysis: effects of perturbations of all parameters on B_0. "Linf" = $\hat{L}_\infty$ in virgin state; other parameters defined in Section 7.2.2. Perturbations were "+" and "-" 5% of original estimates (see Tables 7.1; 7.3). Scenarios: "MP_size" = Mahe Plateau static growth, *P* related to FL; "DD_size" = density-dependent L_∞, *P* related to FL; "MP_age" = Mahe Plateau static growth, *P* related to age; "DD_age" = density-dependent L_∞, *P* related to age.

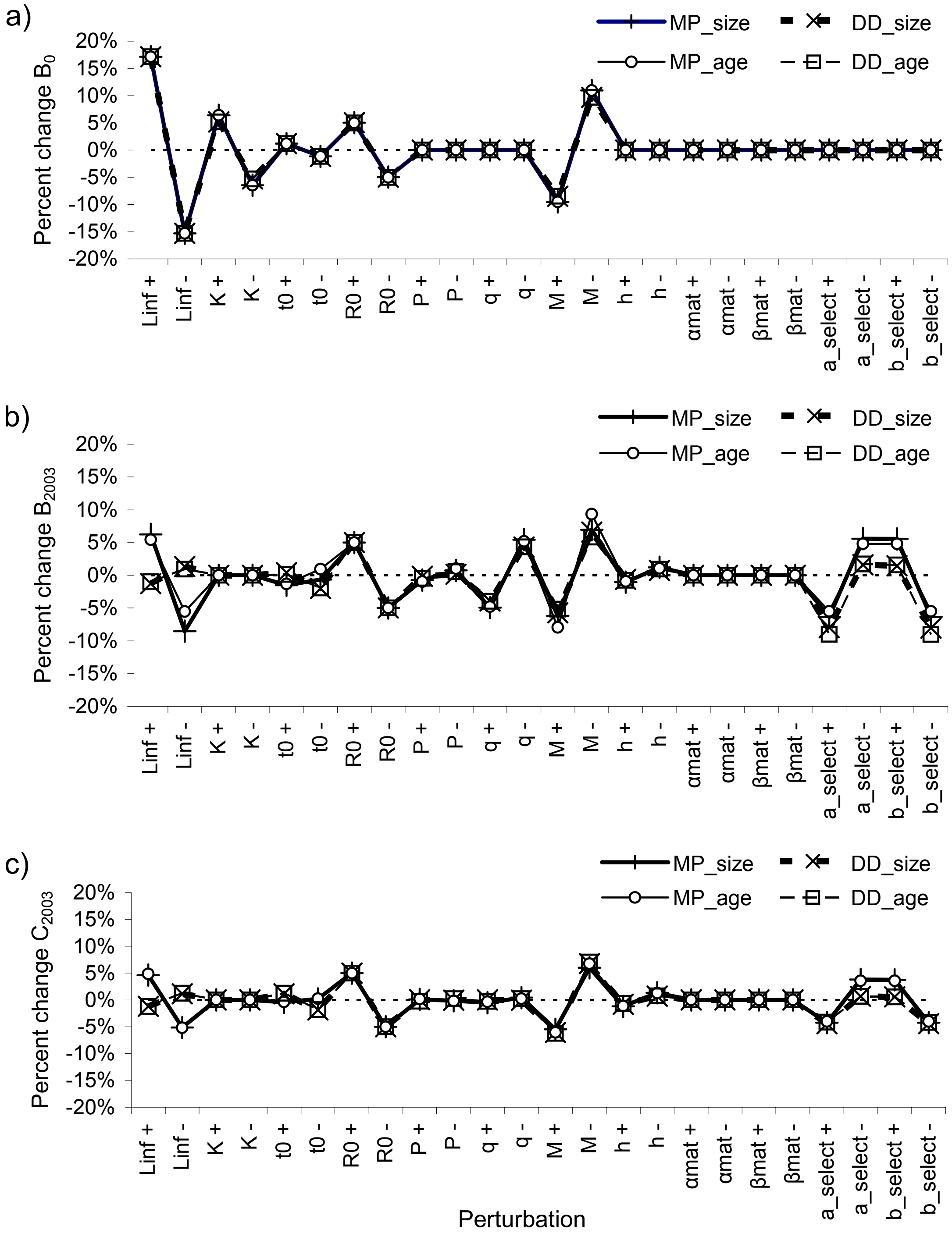


Figure 7.12. Sensitivity analysis: effects of parameter perturbations, excluding *b_wt*. Effects of perturbations of deterministic parameter estimates of 5% on (a) initial biomass in virgin state, $\hat{B}_0$, (b) population biomass in 2003, $\hat{B}_{2003}$, and (c) annual catch of *L. bohar* in 2003, $\hat{C}_{2003}$. "Linf" = $\hat{L}_\infty$ in virgin state; other parameters defined in Section 7.2.2. Perturbations were "+" and "-" 5% of original estimates (see Tables 7.1; 7.3). Scenarios: "MP_size" = Mahe Plateau static growth, *P* related to FL; "DD_size" = density-dependent L_∞, *P* related to FL; "MP_age" = Mahe Plateau static growth, *P* related to age; "DD_age" = density-dependent L_∞, *P* related to age.

7.3.5. Monte Carlo simulations.

Recovery of the population to estimated pre-exploitation levels when fishing of *L. bohar* was stopped was predicted to take decades, from 22 years for population numbers and from 35 years for population biomass, respectively (i.e., the upper confidence limits of combined forecasted trends in Fig. 7.13). Further, the lower 95% confidence limits of simulated recovery had not reached the estimated virgin state levels after a projected 50 years of no fishing, predicting that at least 97.3% of virgin population numbers and at least 98.1% of virgin biomass would have recovered after 50 years of ceased fishing.

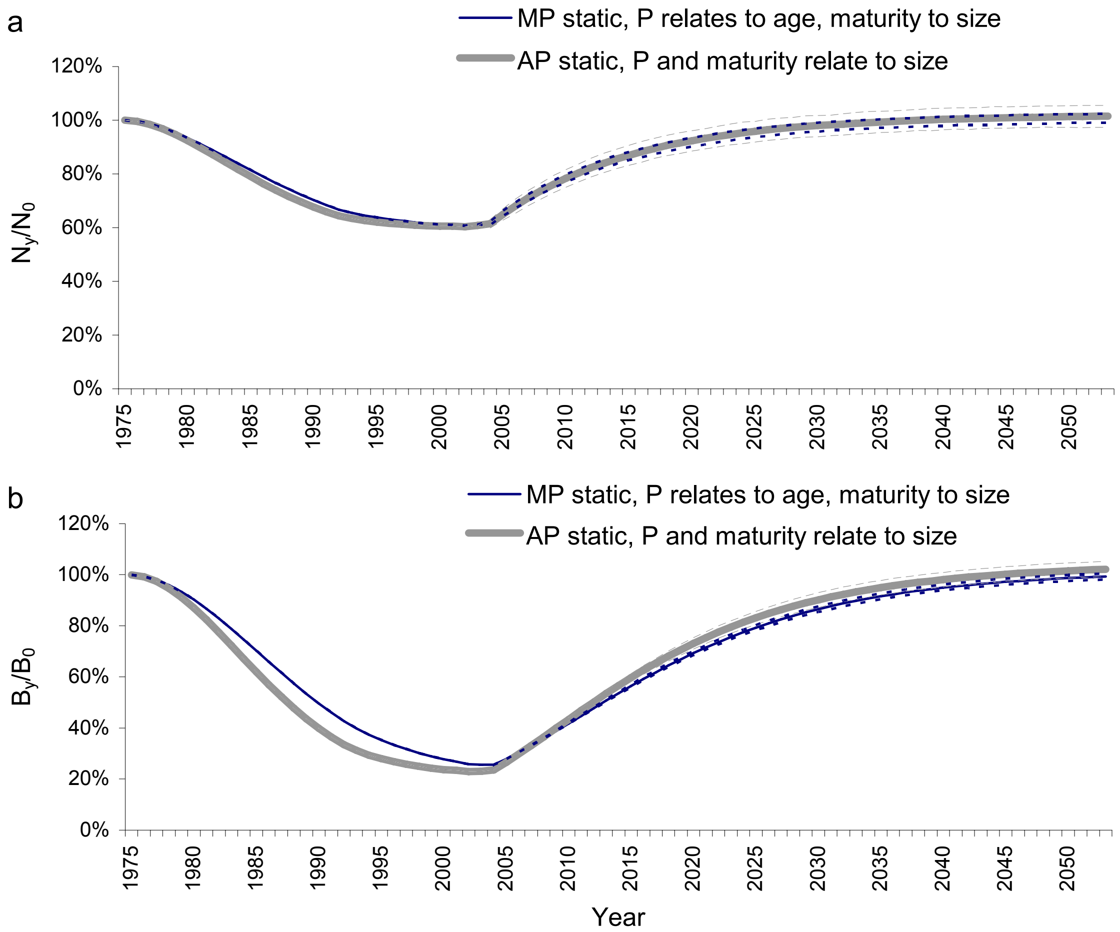
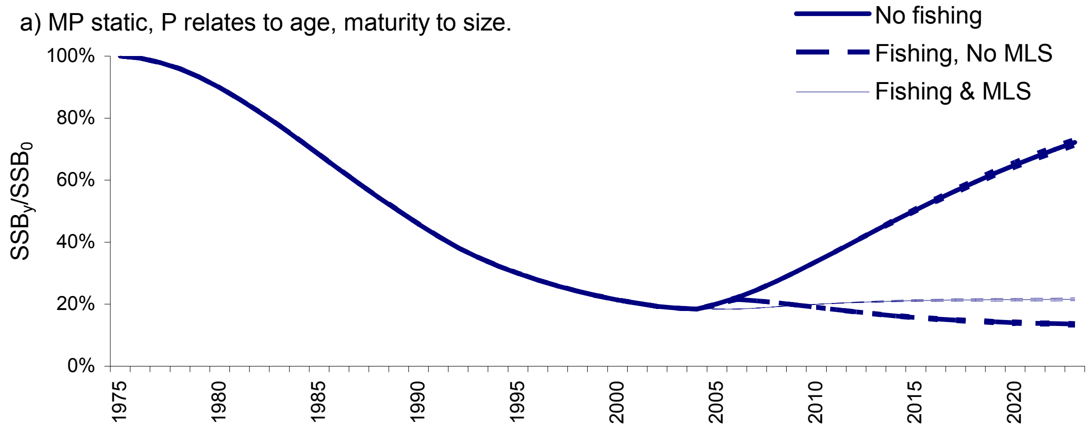


Figure 7.13. Projected recovery of *L. bohar* population if fishing were stopped for different model scenarios of (a) population numbers each year (N_y) and (b) population biomass each year (B_y), from 2004 to 2053. Dotted lines are 95% confidence intervals about extrapolated estimates. Thin horizontal reference line indicates population size prior to fishing.

Model predictions of spawning stock biomass (SSB) from the different simulated harvest scenarios (for a projected 20 years) are presented in Figure 7.14. This figure shows that the MLS could result in estimated SSB_y remaining relatively constant at ~18 to 22% of the SSB_0, or recovering to ~22% of the SSB_0, for the Mahe Plateau static (Fig. 7.14a) and Amirantes Plateau static (Fig. 7.14b) growth scenarios, respectively. Recovery of SSB_y under MLS is predicted to be slight, relative to that expected under no fishing, but prevents the SSB_y decreasing further down to ~12% (Mahe Plateau static scenario) and ~10% (Amirantes Plateau static scenario) of the SSB_0 under continued harvest with no MLS.


a) MP static, P relates to age, maturity to size.

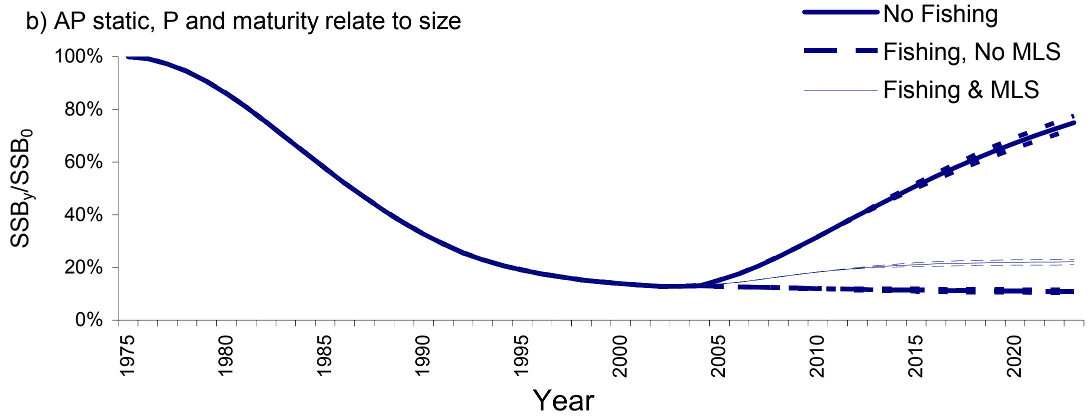

b) AP static, P and maturity relate to size

Figure 7.14. Projected Spawning Stock Biomass each year (SSB_y) with different management strategies. Dotted lines represent 95% confidence limits about extrapolated trends, from 2004 to 2023. “MP” = Mahe Plateau; “AP” = Amirantes Plateau; “MLS” = implementation of minimum legal size limit management strategy.

7.4. Discussion.

The use of the CAGEAN stock assessment model for an exploration of factors affecting predictions of the vulnerability of a fished *L. bohar* population to overfishing has also elucidated those factors most important to consider for stock assessment. For instance, although the effect of different growth scenarios did not have any apparent effect on estimates of overall depletion, the interaction of growth, with an inferred size-dependent availability of older age groups to harvest, was potentially important to predictions of depletion impacts on population age structure. Thus, this modelling approach was useful for facilitating the exploration of the interaction effects of biological and harvest parameters on predicted consequences of overfishing.

7.4.1. Effects of Growth Scenarios.

I suspect the variability in age-based $\hat{P}$ among unconstrained growth scenarios was largely the result of converting the catch-at-length to catch-at-age data using different, scenario-specific von Bertalanffy growth parameters (i.e. different L_{∞_y}, K_y in Eqn. 7.1). For instance, the conversion of catch-at-length to catch-at-age using the shorter L_∞ for the Amirantes Plateau static growth scenario would have resulted in a higher frequency of older *L. bohar* in the observed catch-at-age than was fitted for the Mahe Plateau static growth scenario. This phenomenon would have led to a higher $\hat{P}$ for the Amirantes Plateau than for the Mahe Plateau under static growth scenarios. This effect was not observed for size-based *P* scenarios because *P* related back to a critical FL, and thus to catch-at-length frequencies, which were consistent among scenarios.

For the un-confounded size-based *P* scenarios, there was no difference in the predicted relative depletion of population biomass, although there appeared to be a difference in depletion effects on population age structure. Older age groups were depleted least under the Mahe Plateau static growth scenario and most under the Amirantes Plateau static growth scenario. A longer L_∞ for the Mahe Plateau static growth scenario meant that older fish were predicted to be longer, and thus were more likely to be above the critical size at which *L. bohar* were inferred to be less available to harvest. A greater number of older *L. bohar* for the Mahe Plateau static scenario were thus less available to harvest and depleted less because of the longer L_∞, given a similar $\hat{P}$, and given that all other aspects of the model, including observed catch-at-length, were consistent among the growth scenarios.

Other length-based parameters that were permitted to vary with growth scenario appeared to have a negligible effect on model predictions. For instance, a growth scenario describing a steeper curvature, and thus a faster increase in FL-at-age would be expected to result in an earlier average age at maturity and a younger t_r because maturity (in some scenarios) and selectivity (in all scenarios) were related to FL. However, there was no difference in estimates of relative depletion of biomass or population age structure for different maturity scenarios and an effect of selectivity, which would be expected to be detected for younger age groups, was not detected on plots of relative depletions of population age structure (Fig. 7.9).

It should be noted, however, that the *Max FL* used as an upper bound for the density-dependent L_∞ sub-model had a considerable bearing on the L_{∞_y} at 0.5 Depletion and the steepness parameter, *r,* and therefore, on the resulting prediction of current *L. bohar* growth on the Mahe Plateau. A longer *Max FL* would have resulted in predictions closer to observations by increasing *r* and thus lengthening $L_{\infty_{2000}}, L_{\infty_{2002}}$, but this would have required using an extrapolated upper bound of maximum FL for *L. bohar*. There is, however, no current evidence to suggest how much longer than the *Max FL L. bohar* could grow because the corresponding total length (TL) for the *Max FL* specimen was equivalent to the maximum reported TL for this species (90 cm TL; Frimodt 1995).

Nevertheless, given the assumptions of the model, evidence was presented against the "density-dependent increase in L_{∞} with fishing" hypothesis being a plausible explanation for observed differences in growth between these Seychelles' regions with different historical levels of fishing (Table 7.4, 7.5). Accordingly, this indicated that the observed differences in growth between the Amirantes and Mahe Plateaux were not likely due to fishing but rather were due to effect(s) of other region-specific factors. The implications of the favoured "intrinsic regional variation in growth" hypothesis were: (i) no significant effect on predicted relative biomass depletion; but (ii) a considerable effect on the predicted depletion of older age groups through an interaction with apparent size-based availability.

7.4.2. Predicted vulnerability to overfishing and recovery if harvest were stopped.

The estimated level of depletion of the Mahe Plateau population ranged from *c.* 20 to 30% of its estimated virgin biomass, with deterministic estimates of Spawning Potential Ratio (SPR: calculated as the SSB_{2003} / SSB_0, given that $\hat{N}_{0,y}$ were observed not to vary over the harvest period) ranging from 12.8 to 18.7%. This SPR predicted severe depletion of the stock, given that a SPR of less than 20% is considered to indicate a high probability of stock collapse (Goodyear 1989). There was high uncertainty in these predictions though, considering the relatively few data to number of parameters estimated (Burnham and Anderson 1998; Haddon 2001) and the many assumptions made in the analysis. For instance, only one year of catch-at-length data was available for converting to catch-at-age input data for the model and no knowledge of the stock-recruitment relationship or recruitment variability is available for this species. Nevertheless, in the absence of such information, results suggest that a precautionary approach (FAO 1995) should be adopted for the management of this species' harvest.

The relatively long time predicted for the stock to recover to an estimated virgin state when harvest was stopped was consistent with a low predicted resilience of this species to harvest impacts. Other studies that have predicted recovery times for lutjanids have found similar results and no study has hitherto documented a clear return to asymptotic abundance or biomass (Russ 2002). McClanahan et al. (2002) speculated, assuming a nominal average maximum age of 25 years for reef fish, that it would take approximately 12 to 20 years for a reef fish community to recover from fishing. Arreguin-Sanchez and Manickchand-Heileman (1998) used the "Ecosim" model (Walters et al. 1997) with estimates of rates of biomass production and ecosystem connectance (Krebs 1994) to predict recovery times for *Lutjanus campechanus* populations to be 11 and 14 years from a simulated overfishing perturbation. The predicted recovery of *L. bohar* was at least twice this duration.

From long term monitoring of the recovery rates of "large predators" (i.e., Lutjanidae, Serranidae, Lethrinidae, Carangidae) in the Sumilon and Apo reserves in the Philippines, Russ and Alcala (2004) extrapolated the observed exponential increase in biomass to asymptote at 15 and 40 years after the cessation of fishing, respectively.

These estimates bracket the minimum forecasted durations for recovery of *L. bohar* numbers and biomass and are probably the best estimates available, given the relatively long time series of data analysed. From the same study, Russ and Alcala (1996; 1998) also observed that large predators decreased significantly in density when fished and recovered slowly relative to other species when protected from fishing.

Vulnerability to overfishing and recovery times, however, are not entirely dependent on life history characteristics. Jennings (2001) listed the main factors likely to influence recovery rates as: initial population size, the intrinsic rate of population increase, the nature of the stock-recruitment relationship, meta-population structure, the success of individual recruitment events, and the extent of reductions in fishing mortality. The simulations of *L. bohar* harvest depletion have facilitated the exploration of some such factors, and their interactions, on the likely vulnerability of this stock to overfishing.

One important consideration for the stock assessment and future harvest of *L. bohar* elucidated in this study was the interaction of growth with a size-dependent reduction in the availability of older age groups. This was relevant for *L. bohar* because it was consistent with evidence that suggested a trend of increasing average size with depth (Wright et al. 1986; Chapter 4) overlaid by a diminishing proclivity for fishers to use manually operated hook and line gears in deeper habitats. Regional differences in $\hat{L}_\infty$ appeared to have considerable effects on the predicted depletion of older age groups because a longer L_∞ predicted that older *L. bohar* were longer and therefore more likely to reside in deeper, less-fished waters. Although it was unclear whether this interaction was or was not a real phenomenon, it highlighted the potential importance of depth-related availability for the persistence of older age groups in harvested *L. bohar* populations.

7.4.3. Predicted effectiveness of a MLS management strategy.

Simulations predicted that the implementation of a MLS strategy could be effective for increasing the SPR above the critical limit of 20% (Goodyear 1989). A MLS was also predicted to be effective for preventing further declines in SPR with continued fishing. Accordingly, it can be concluded that the model predicted the MLS to be an effective strategy for reducing the probability of stock collapse, although this conclusion rests on several assumptions (discussed below).

The effectiveness of a MLS is dependent upon many assumptions, including that the ability of all *L. bohar* shorter than the MLS continue to grow and reproduce at the same capacity as if not affected by fishing. Unfortunately this was not an accurate assumption because many *L. bohar* shorter than the MLS were partially or fully selected to fishing and those fish caught and released are typically subject to higher rates of mortality (Coleman et al. 2000). Another assumption likely to have had a considerable bearing on the predicted chance of recruitment failure was the form of the stock-recruitment relationship. Predicted recruitments from the stock-recruitment function in this model appeared fairly robust to harvest depletion. Although this function was used because it was described for two other closely-related species, we still do not know empirically what this relationship is for *L. bohar*.

It is plausible to assume, however, that recruitment is relatively robust for *L. bohar* because the inferred less available and numerous older age groups could collectively function to store reproductive potential (Warner and Chesson 1985) and thus act to buffer periods of poor recruitment (Kirkwood et al. 1993; Secor 2000). It also should be noted that these older age groups are likely to contribute significantly to the volume and quality of recruits (Chambers and Leggett 1996; Kjesbu et al. 1996; Trippel et al. 1997; Marteinsdottir and Steinarsson 1998; Heyer et al. 2001; Palumbi 2004) which could compensate, to some extent, for the depletion of younger mature age groups, at least in the short term. The greater harvest of fully selected and fully available age groups, older than t_r but younger than those assumed less available, was essentially a "Gauntlet" fishery though and eventually, when the less available age groups succumb to mortality, the stock could demonstrate rapid recruitment failure (Mortimer 1995).

7.4.4. Conclusion.

This applied modelling approach provided scope for objectively incorporating the best available information and concepts of the current understanding of fishery and population dynamics to explore questions pertaining to the vulnerability of *L. bohar* populations to overfishing. The explored growth scenarios appeared to have no significant effect on predictions of relative depletion of population biomass by the CAGEAN model. Also, the density-dependent increase in L_∞ with fishing postulated as an explanation for observed regional differences in growth in Chapter 5 was not supported by model simulations. Accordingly, this indicated that the differences in growth observed between the Amirantes and Mahe Plateaux were not likely due to historical differences in fishing between regions but rather were due to effect(s) of other region-specific factors.

The approach facilitated the exploration of interactions among biological and harvest parameters when predicting vulnerability to overfishing, and, in this regard, identified a potentially important effect of regional variation in growth on predictions of the depletion of older, apparently less-available age groups. Deterministic estimates, although highly uncertain, predicted relatively high depletion of the stock and relatively slow recovery if harvest were stopped. Given the uncertainty of predictions and the predicted deleterious harvest impacts in the study, *L. bohar* is a suitable candidate species for adopting precautionary approaches to management. A MLS was identified as a potentially effective strategy for reducing the probability of recruitment failure, but given the aforementioned concerns, would be a high risk strategy on its own for ensuring the sustainable harvest of *L. bohar*.

Chapter 8: General Discussion.

This thesis provides an examination of the hypothesis that large, long-lived, slow-growing species are likely to be more vulnerable to fishing impacts and overfishing, based on *L. bohar* as a case study. The population biology of *L. bohar* was thoroughly described, and supported preliminary indications that *L. bohar* was a relatively slow-growing, long-lived, and late-maturing tropical reef fish. Spatial and temporal variation was investigated to assess the generality and robustness of results and to make inferences about biological processes that may operate on different spatial and temporal scales. Spatial comparisons were also done to infer the significance of fishing effects on *L. bohar* populations by comparing results between management zones, regions, and areas where *L. bohar* had been fished to different extents. Described aspects of population biology and collected data on historical harvest were then used to explore, in simulation space, the credibility of a hypothesis for an inferred effect of fishing on growth and the likely vulnerability of an exploited *L. bohar* population to overfishing.

In this chapter, I discuss the extent to which evidence from this thesis indicated vulnerability to overfishing by: (i) relating described body size, longevity, growth, and age at maturity to those for other closely-related species under the generalised model; and (ii) discussing how other described aspects of biology might influence or complicate this prediction. Given this knowledge of the species' biology, likely harvest, and the likely interaction among biological and harvest parameters, I then (iii) discuss management options to prevent the overfishing of this species.

8.1. The generalised model: body size, longevity, growth, and age at maturity.

L. bohar was demonstrated to be long-lived, slow-growing, and late-maturing relative to other closely related species. It has been argued that these features indicate a high potential vulnerability to overfishing and fishing impacts (Parent and Schriml 1995; Jennings et al. 1998; Crouse 1999; Musick 1999). Results for age-based demographic parameters indicated a different life history than would have been expected from some previous studies that used more rudimentary methods of age estimation (Wheeler 1953; Talbot 1960; Wright et al. 1986). Further, evidence for the accuracy of these results was presented, which has not previously been assessed for this species.

Results from studies of age, growth, and reproductive biology of lutjanids published since the previous reviews done by Manooch (1987) and Grimes (1987) (i.e., post 1986) were collated to put the results for *L. bohar* into a context relevant for predicting vulnerability to overfishing under the generalized model, relative to other species. Recent studies have adopted techniques that are widely considered to be more accurate, reliable, and precise for age estimation (Fowler 1995; Cappo et al. 2000) and reproductive assessment (West 1990; Sadovy 1996) of tropical reef fish populations. My collation, therefore, also provided scope for assessing, to some extent, whether these methodological developments were likely to have made a difference to our perception of lutjanid biology (and hence predicted vulnerability to overfishing) via a comparison with the earlier reviews.

Parameter estimates from the collated studies are presented for (i) age estimation and growth, and (ii) reproductive biology in Tables 8.1 and 8.2, respectively. Plots of maximum age (t_{max}) against L_∞ (Fig. 8.1) and K (Fig. 8.2) demonstrated differences between results from Manooch's (1987) earlier review and my recent collation, which revealed trends consistent with theoretical life history expectations (Stearns 1992). The recent data more clearly indicated a positive-sloping relationship that larger lutjanids were longer lived. This is a general trend of organisms (Partridge and Harvey 1988). A negative-sloping relationship was also more apparent between t_{max} and K for the recent data. This was consistent with other comparative studies of fish that previously demonstrated a negative correlation between t_{max} and the instantaneous rate of natural mortality (M; Hoenig 1983), which, in turn, was demonstrated to be positively correlated with K (Pauly 1980).

Table 8.1. Studies of age and growth of tropical snappers (Lutjanidae) since the review by Manooch (1987). Parameter estimates gleaned from literature. ‘Method’ = age estimation method: ‘LF’ = length frequency; ‘SO’ = sectioned otolith; ‘SC’ = scales; ‘V’ = vertebrae; ‘WO’ = whole otolith; ‘UR’ = urohyal bone. ‘Type’ = length measurement type: ‘TL’ = total length; ‘FL’ = fork length.

Genus	Species	Method	tmax	L_∞ (mm)	K	t_0	Type	Area / Region	Author(s)	Year
Lutjanus	*adetii*	SO	24	265.2	0.145	-8.08	FL	GBR	Newman et al.	1996
Lutjanus	*analis*	SO	29	869	0.16	-0.94	TL	Florida	Burton	2002
Lutjanus	*argentimaculatus*	SO	37	681.2	0.126	2.893	FL	Qld	Russell et al.	2003
Lutjanus	*bohar*	SO	53.5	650.8	0.095	-2.869	FL	GBR	This study	2005
Lutjanus	*buccanella*	LF	7	620	0.32	-0.04		Caribbean	Tabash & Sierra	1996
Lutjanus	*campechanus*	SO	52.6	977	0.19	-0.48	TL	Gulf of Mexico	Wilson & Nieland	2001
Lutjanus	*campechanus*	SO	34	969	0.192	0.02	TL	USA	Patterson et al.	2001
Lutjanus	*carponotatus*	SO	20	313	0.449	-0.016	FL	GBR	Newman et al.	2000
Lutjanus	*carponotatus*	SO	18	263.5	0.56	-0.049	FL	GBR	Kritzer	2002
Lutjanus	*erythropterus*	SO	32	584.5	0.392	0.177	FL	GBR	Newman et al.	2000
Lutjanus	*griseus*	SO	24	717	0.17	-0.025	TL	N Florida	Burton	2001
Lutjanus	*griseus*	SO	24	625	0.13	-1.33	TL	S Florida	Burton	2001
Lutjanus	*kasmira*	SO	6	340	0.29	-1.37	TL	Hawaii	Morales-Nin & Ralston	1990
Lutjanus	*malabaricus*	SO	31	565.8	0.262	-0.09	FL	NW Australia	Newman	2002
Lutjanus	*malabaricus*	SO	20	727.6	0.287	0.24	FL	GBR	Newman et al.	2000
Lutjanus	*peru*	SO	31	973.2	0.11	-0.316	TL	Mexico	Rocha Olivares	1998
Lutjanus	*quinquelineatus*	SO	31	206.9	0.31	-2.59	FL	GBR	Newman et al.	1996
Lutjanus	*russelli*	SC	?	468	0.243	-0.376	?	China	Fuliang & Zhong Sheng	1996
Lutjanus	*sebae*	V	?	841.2	0.166	-0.378	?	Arafura Sea	Liu & Yeh	1991
Lutjanus	*sebae*	SO	22	792.1	0.14	-0.92	FL	GBR	Newman et al.	2000
Lutjanus	*sebae*	SO	34	482.6	0.271	0.065	FL	NW Australia	Newman & Dunk	2002
Lutjanus	*synagris*	WO	4	603	0.2	-0.68	TL	West Indes	Manickchand-Dass	1987
Lutjanus	*synagris*	SO	19	330.9	0.395	-1.95	FL	Bermuda	Luckhurst et al.	2000
Lutjanus	*synagris*	LF	11	450	0.23	-0.459	FL	Puerto Rico	Acosta & Appledoorn	1992
Lutjanus	*vitta*	SO	12	245.3	0.853	-0.179	FL	GBR	Newman et al.	2000
Lutjanus	*vitta*	UR	8	325	0.37	-0.23	FL	NW Australia	Davis & West	1992
Lutjanus	*vivanus*	LF	7	620	0.32	-0.04	?	Caribbean	Tobash and Sierra	1996

Table 8.1. (Continued).

Genus	Species	Method	tmax	L_∞ (mm)	*K*	t_0	Type	Area / Region	Author(s)	Year
Ocyrus	*chrysurus*	SO	17	502.5	0.139	-0.955	TL	US Virgin Islands	Manooch & Drennon	1987
Pristipomoides	*multidens*	SO	30	598	0.187	-0.173	FL	NW Australia	Newman & Dunk	2003
Rhomboplites	*aurorubens*	SO	13	298	0.25	-3.9	TL	Gulf of Mexico	Hood and Johnson	1998

Table 8.2. Reproductive studies of tropical snappers (Lutjanidae) since the review by Grimes (1987). Parameter estimates gleaned from literature. 'Sex Ratio Bias': 'M' = male-biased; 'F' = female-biased; 'N' = no bias (1:1). 'L_{50}F' = L_{50} for females; 'L_{max}' = maximum observed length 't_{mat}' = age at maturity; 'type' = length type measured. $\uparrow L_{50}$ = a higher L_{50} reported ?; $\uparrow L_\infty$ = a higher L_∞ reported?; $\uparrow K$ = a higher *K* reported?. 'N' = no difference; 'F' = higher for females; 'M' = higher for males.

Genus	Species	Sex Ratio Bias	L_{50}F (mm)	L_{max} (mm)	L_{50} / L_{max}	type	t_{mat}	$\uparrow L_{50}$	$\uparrow L_\infty$	$\uparrow K$	Area	Authors	Year
Aprion	*viriscens*	N	449	1028.7	0.44	FL	-	-	-	-	Hawaii	Everson et al.	1989
Etelis	*coruscans*	M	663	968.5	0.68	FL	-	-	-	-	Hawaii	Everson et al.	1989
Lutjanus	*adetii*	-	-	301	-	FL	-	-	M	F	GBR	Newman et al.	1996
Lutjanus	*analis*	-	-	880	-	TL	-	-	N	N	Florida	Burton	2002
Lutjanus	*argentimaculatus*	N	-	890	-	FL	-	-	-	-	Qld, Australia	Sheaves	1995
Lutjanus	*argentimaculatus*	N	512	854	0.60	FL	8	F	F	-	Qld, Australia	Russell et al.	2003
Lutjanus	*bohar*	N	429	760	0.56	FL	9.4	F	N	N	GBR	This study	2005
Lutjanus	*campechanus*	F	-	1000	-	TL	-	-	N	N	USA	Patterson et al.	2001
Lutjanus	*campechanus*	N	-	601	-	TL	-	-	-	-	Gulf of Mexico	Collins et al.	2001
Lutjanus	*campechanus*	N	-	1039	-	TL	-	-	F	M	Gulf of Mexico	Wilson & Nieland	2001
Lutjanus	*campechanus*	-	-	-	-	-	8	-	-	-	Gulf of Mexico	Goodyear	1995
Lutjanus	*carponotatus*	N	-	-	-	FL	-	-	M	-	GBR	Kritzer	2002
Lutjanus	*carponotatus*	-	-	385	-	FL	-		M	F	GBR	Newman et al.	2000
Lutjanus	*carponotatus*	-	190	330	0.58	FL	2		-	-	GBR	Kritzer	2004

Table 8.2. (Continued).

Genus	Species	Sex Ratio Bias	$L_{50}F$ (mm)	L_{max} (mm)	L_{50} / L_{max}	type	t_{mat}	$\uparrow L_{50}$	$\uparrow L_{\infty}$	$\uparrow K$	Area	Authors	Year
Lutjanus	*erythropterus*	-	486	-	-	FL	-		-	-	GBR	McPherson et al.	1992
Lutjanus	*erythropterus*	-	-	-	-	-	-	-	-	M	GBR	McPherson and Squire	1992
Lutjanus	*fulviflamma*	N	243	300	0.81	TL	-	F	-	-	Kenya	Kaunda-Arara & Ntiba	1997
Lutjanus	*griseus*	-	-	760	-	TL	-	-	M	-	Florida	Burton	2001
Lutjanus	*jocu*	-	-	-	-	-	-	-	M	-	Cuban Shelf	Claro et al.	1999
Lutjanus	*johnii*	F	630	780	0.81	FL	-	F	-	-	NT	Hay et al.	1996
Lutjanus	*malabaricus*	-	-	802	-	FL	8	-	M	F	NW Australia	Newman	2002
Lutjanus	*malabaricus*	-	576	-	-	FL	-	-	-	-	GBR	McPherson et al.	1992
Lutjanus	*malabaricus*	-	-	-	-	-	-	-	-	M	GBR	McPherson & Squire	1992
Lutjanus	*peru*	F	-	992	-	TL	-	N	M	F		Rocha Olivares	1998
Lutjanus	*quinquelineatus*	-	-	233	-	FL	-	-	M	M	GBR	Newman et al.	1996
Lutjanus	*russelli*	N	-	410	-	FL	-	-	-	-	Qld, Australia	Sheaves	1995
Lutjanus	*sebae*	-	-	728	-	FL	-	-	M	F	NW Australia	Newman & Dunk	2002
Lutjanus	*sebae*	-	542	-	-	FL	-	-	-	-	GBR	McPherson et al.	1992
Lutjanus	*sebae*	-	-	-	-	-	-	-	-	M	GBR	McPherson & Squire	1992
Lutjanus	*synagris*	F	221	430	0.51	FL	-	M	-	-	Jamaica	Aiken	2001
Lutjanus	*synagris*	M	245	370	0.66	FL	1	F	N	N	Bermuda	Luckhurst et al.	2000
Lutjanus	*synagris*	N	310	485	0.64	TL	2	F	M	-	West Indes	Manickchand-Dass	1987
Lutjanus	*vitta*	M	-	274	-	FL	-	-	N	N	GBR	Newman et al.	2000
Lutjanus	*vittus*	M	154	350	0.44	FL	-	N	M	F	NW Australia	Davis & West	1992
Pristipomoides	*multidens*	-	-	701	-	FL	-	-	N	N	NW Australia	Newman & Dunk	2003
Rhomboplites	*aurorubens*	F	160	-	-	TL	-	F	-	-	South Carolina	Zhao & McGovern	1997
Rhomboplites	*aurorubens*	N	-	585	-	TL	-	F	N	N	Gulf of Mexico	Hood & Johnson	1998
Rhomboplites	*aurorubens*	F	160	-	-	TL	-	F	-	-	South Carolina	Zhao & McGovern	1997

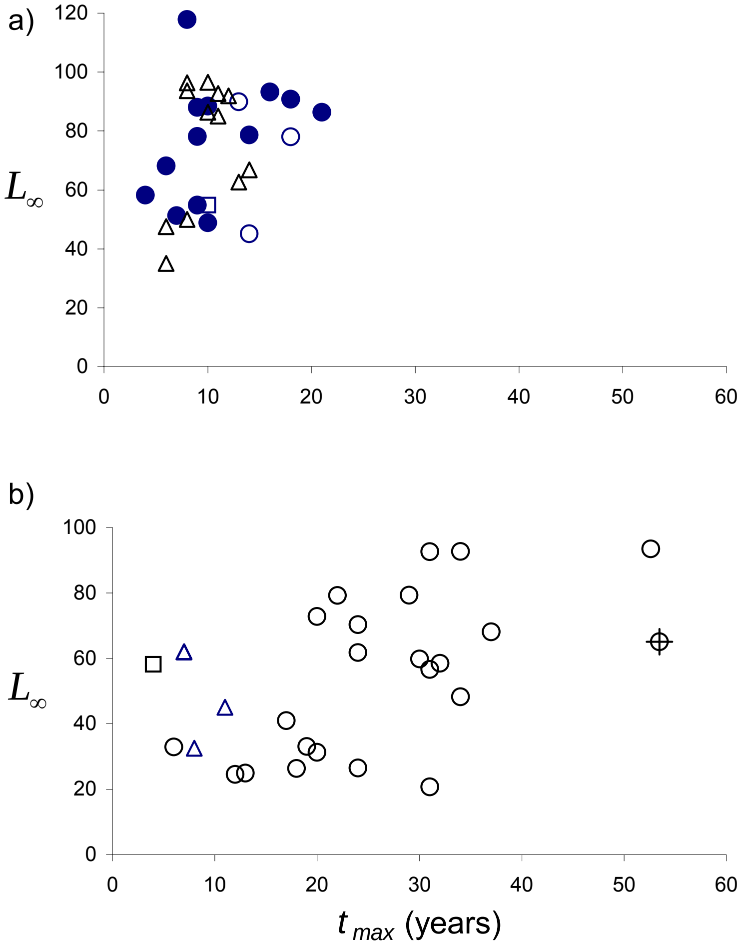


Figure 8.1. Relationship of maximum asymptotic length (L_∞) with maximum estimated age (t_{max}) from (a) previously reviewed studies by Manooch (1987) and (b) recent studies (i.e. post 1986). Results marked by age estimation method used: filled circles = otoliths, unspecified; open circles = sectioned otoliths; squares = whole otoliths; triangles = other. The result from this study is marked by a cross. L_∞ estimates from recent studies standardised to FL and cm measurement units using conversion formulas in Fishbase (Froese and Pauly 2004).

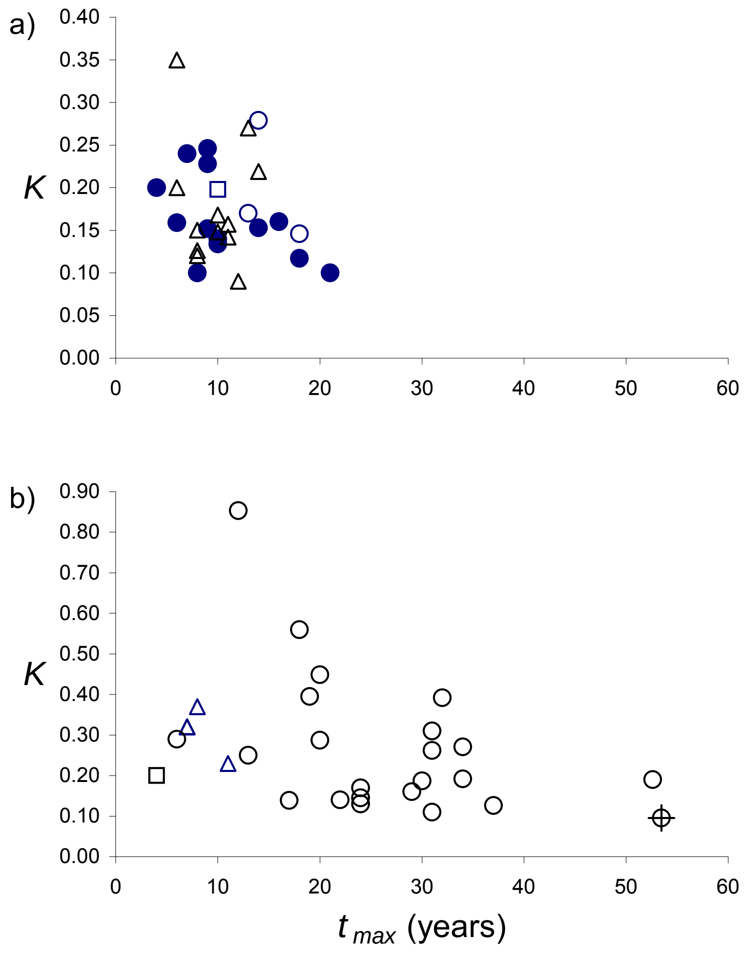


Figure 8.2. Relationship of von Bertalanffy growth coefficient (*K*) with maximum estimated age (t_{max}) from (a) previously reviewed studies by Manooch (1987) and (b) recent studies (i.e. post 1986). Results marked by age estimation method used: filled circles = otoliths, unspecified; open circles = sectioned otoliths; squares = whole otoliths; triangles = other. The result from this study is marked by a cross.

A lower percentage of results from the previous review (69.8%) were derived from reading otoliths, the most reliable age estimation method (Secor et al. 1995), compared to recently collated results (79.3%). The oldest maximum ages in both periods were estimated from otoliths, and much older maximum ages were reported for lutjanids during the recent period. These patterns could reflect the more frequent use of other less reliable methods of age estimation in the previously reviewed studies.

Correlation analyses were done to test the significance of the relationships suggested from Figures 8.1 and 8.2. For the recent data, only results from studies that estimated age from sectioned otoliths were analysed (n = 23), as estimates from sections were more likely to be accurate than those from whole otoliths (e.g., Rocha-Olivares 1998; Newman et al. 2000; Chapter 3). This is because sectioning makes the latter growth additions in otoliths of older fish more clearly visible (Brothers 1987). For the previously reviewed studies, however, there were insufficient results available for the correlation analysis that could be verified as having been estimated from whole or sectioned otoliths. Accordingly, those results that could not be verified to have been derived from whole or sectioned otoliths (i.e., within the group “unspecified” otolith method; n = 13; Figs. 8.1a, 8.2a) were combined with those that had been verified as derived from otolith sections (n = 3) for correlations of the previously reviewed data. Therefore, an effect of method could have confounded correlations done for the previously reviewed data.

A significant positive correlation between t_{max} and L_∞ (r = 0.582; p = 0.004) and a significant negative correlation between t_{max} and K (r = -0.448; p = 0.032) was detected for the recent collation but not for the previously reviewed data (r = 0.287; p = 0.281 and r = -0.362; p = 0.169, respectively). It was suspected that the inclusion of studies that used whole otoliths to estimate age affected correlations of previously reviewed data, although it was uncertain by how much. The most likely effect of including whole otolith results was to underestimate t_{max} and bias estimates of L_∞ and K. For this reason only recently reviewed results derived from sectioned otolith age estimates were analysed hereafter.

A positive correlation (r = 0.790; p = 0.004) observed between age at maturity and L_∞ (Fig. 8.3) was consistent with theoretical expectations (Stearns 1992). Average maturity also demonstrated a strong negative correlation with K (Fig. 8.4) (r = -0.866; p = 0.001), as was observed in general for fish by Ni (1978 *in* Roff 1984). These results, and those from previous plots, demonstrated that the results for *L. bohar* were at one end of a range of results reported for lutjanids and were thus consistent with a *K*-selected life history strategy (Pianka 1970).

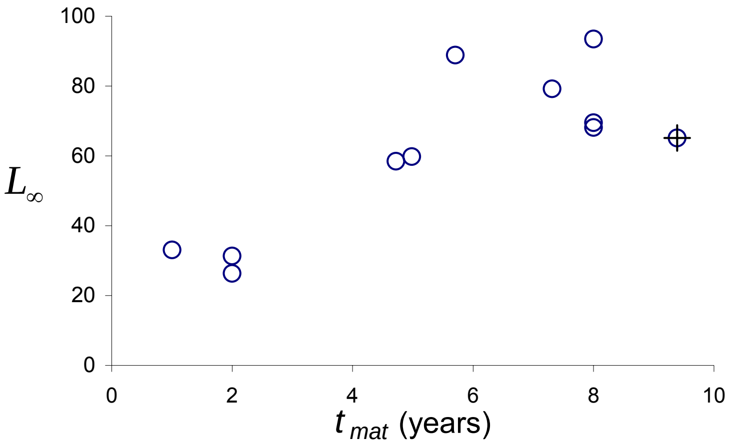


Figure 8.3. Relationship of maximum asymptotic length (L_∞) with estimated age at maturity (t_{mat}) from post-1986 studies of lutjanids. Results shown for studies that used otolith sections to estimate age only. The result from this study is marked by a cross.

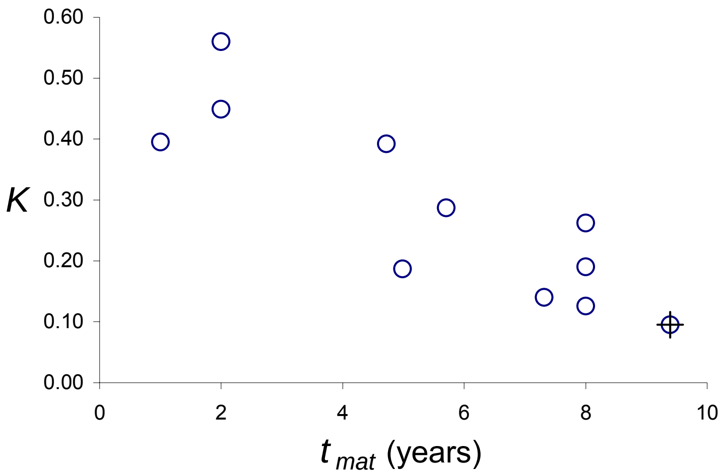


Figure 8.4. Relationship of von Bertalanffy growth coefficient (*K*) with estimated age at maturity (t_{mat}) from post-1986 studies of lutjanids. Results shown for studies that used otolith sections to estimate age only. The result from this study is marked by a cross.

8.2. Other factors affecting predictions of vulnerability to overfishing.

Evidence of a spatially complex population structure on the GBR was demonstrated for *L. bohar*. Observed differences in sampled size structure from different cross-shelf positions between samples from different depth ranges in the Lizard Island region (Chapter 4) and between ELF reefs in different regions (Chapter 5) were consistent with cross-shelf or depth related clines in size, or both. This was consistent with trends observed for other lutjanids (Newman and Williams 1996), where juveniles were suspected to move further offshore across the GBR shelf as they grow. Regional variation in population structure could result in disproportionate harvest impacts on particular life stages if harvest effort is spatially heterogeneous, such as is the case for some gauntlet fisheries (e.g., Reddin and Friedland 1999).

A spatially-complex population structure could also potentially enhance the resilience of *L. bohar* populations to harvest. For instance, the inferred reduced availability of older age groups to harvest was predicted to explain the apparent persistence of a heavily-exploited *L. bohar* population in the Seychelles (Chapter 7). This was because a reduced availability of older age groups was inferred to enhance the "storage effect" of older reproducing age groups and thus act as a buffer to harvest impacts and periods of poor recruitment (Warner and Chesson 1985; Kirkwood et al. 1993; Secor 2000). It is important to note, however, that this might only mitigate deleterious harvest impacts in the short term because the greater harvest of younger, fully available age groups could eventually result in rapid recruitment failure when the less available older age groups succumb to natural mortality and are not adequately replenished from the younger cohorts (Mortimer 1995).

The importance of larger, older *L. bohar* to reproductive output and vulnerability to overfishing was also indicated by the high estimate of batch fecundity for the oldest, largest female and from trends of increasing ovarian and testis weight with fish size (Chapter 6). The Plan Development Team (1990) for the South Atlantic Fishery Management Council demonstrated, using data for *L. campechanus*, that fishing impacts on population fecundity were likely to be much higher if larger individuals produced the bulk of gametes. There is also an increasing amount of literature suggesting that larger, older fish also produce better quality, more viable offspring (Chambers and Leggett 1996; Kjesbu et al. 1996; Trippel et al. 1997; Marteinsdottir and Steinarsson 1998; Heyer et al. 2001; Palumbi 2004). This result therefore indicates a further potential enhancement to the resilience of *L. bohar* populations to harvest due to the likely reduced availability of older age groups, provided such 'refuge' populations are sustained.

Evidence for a prolonged spawning period (Chapter 6) was consistent with a “bet-hedging” reproductive strategy (Stearns 1992). Although no aggregative spawning was observed in this study, *L. bohar* have been indicated to form spawning aggregations in other areas (Johannes 1978; Johannes and Hviding 2000; L. Squire *pers. comm.*). This suggests that spawning aggregations of *L. bohar* could be available to harvest for a long period each year. Recruitment overfishing is therefore increasingly probable if this species aggregates to spawn at predictable sites and times (Coleman et al. 2000) outside of restricted seasonal fishing closures, such as those currently enforced to protect spawning reef fish on the GBR.

Regional variation in growth that was observed for *L. bohar* on the GBR and in the Seychelles was demonstrated to have potentially significant effects on predictions of relative depletion, and thus of vulnerability to overfishing. Regional differences in growth parameters were shown to potentially affect predictions from the CAGEAN model of the relative depletion of the important older age groups through an interaction with assumed size-based availability (Chapter 7). Regional differences in growth were also demonstrated to affect catch-at-age groups used for the fit of the CAGEAN model when they were converted from observed catch-at-length groups using the inverse of the von Bertalanffy growth function. Although characteristics of biology for a species seem to provide a general indication of vulnerability to overfishing, less productive components could be overfished (Ricker 1975; Pella and Robertson 1979) if the management of *L. bohar* populations and meta-populations does not account for regional variation in demographics.

Similarly, temporal variation in described aspects of biology can affect predicted vulnerability to overfishing. For instance, regional and/or temporal variability in growth, size, and age of *L. bohar* on the GBR demonstrated the potential for making inappropriate inferences about relative harvest impacts from spatial comparisons without replication in both space and time. Thus, caution is warranted in the interpretation of the (un-replicated) comparisons between fully fished and lightly fished regions in the Seychelles (Chapter 5). The use of imprecise or biased estimates for developing management strategies could subsequently result in an elevated depletion of stocks though overfishing because of the erroneous prediction of sustainable harvest capacity (e.g., Beamish and McFarlane 1983; Hilborn and Walters 1992; Begg et al. 1999).

8.3. Management options.

Deterministic estimates from the CAGEAN model of a fully fished *L. bohar* population in the Seychelles, albeit given the model and data uncertainty, predicted relatively high depletion of the stock and slow recovery if harvest were stopped. Given this predicted vulnerability to overfishing, observed spatially-complex population biology, and uncertainty, it is advised that a precautionary approach (FAO 1995) be adopted for the management of this species' harvest. Since there are many potential management regulations that could be implemented for this species, the trade-offs of two commonly-used management strategies for reef fish harvest were discussed as they pertain to *L. bohar*: (i) minimum legal size (MLS) and (ii) marine reserves.

A MLS was predicted by the CAGEAN model to effectively reduce the risk of recruitment overfishing of *L. bohar* with respect to predicted trends in the spawning potential ratio, SPR (Chapter 7; Goodyear 1989). This prediction was contingent on the many assumptions of the model, however, including that the catch of *L. bohar* would remain constant. Thus, a MLS on its own would be a high risk strategy to prevent overfishing. A single-species strategy is also less likely to be effective because reef fish are part of a species-rich complex and therefore the catch of protected individuals (including those smaller than the MLS) with other species targeted by fishers is likely (Medley et al. 1993) and released fish are believed to be subject to high mortality rates (Coleman et al. 2000).

Marine reserves are widely advocated as a fisheries management tool for coral reefs (Russ 2002). Reserves or no-take areas would circumvent some of the problems associated with regulating single-species strategies for tropical reef fish, particularly for conserving those species more vulnerable to overfishing (Coleman et al. 2000), such as *L. bohar*. Reserves or no-take areas would need to be appropriately implemented and monitored, though, and the indication of cross-shelf ontogenetic migrations in many longer-lived lutjanids highlights the need for corresponding cross-shelf management protection (Newman and Williams 1996) to ensure all life stages are afforded some protection from overfishing and facilitate adequate replenishment of the ‘unavailable’ populations of larger fish in deeper habitats. Further, the likely slow recovery of these long-lived species indicates that inter-generational management (Russ and Alcala 2004) would be required to ensure the protected components of depleted stocks have the opportunity to recover to acceptable levels.

8.4. Conclusions.

The generality that large, long-lived, slow-growing species are more vulnerable to overfishing was supported for this case study of *L. bohar* in most respects. Age-based parameters demonstrated relatively slow growth, late maturity, and a long reproductive life, indicating slow rates of population turnover and a reduced potential to withstand to the size-selective mortality imposed by harvest. The adoption of the most advanced and reliable methods for quantifying aspects of biology were demonstrated to have a significant bearing on results and to indicate significantly different rates of biological processes and inferred life history strategies for populations of this (and other) lutjanid species. These revised estimates of population biology, increasing global demand for tropical reef fish, and corresponding increases in fishing pressure highlight the need to revise perceptions of the likely vulnerability of lutjanids to overfishing and subsequently, to revise management approaches for harvested stocks.

In this study of *L. bohar* a high predicted reproductive output, regional variations in population biology, a high predicted population biomass, and a suspected reduced availability of older age groups complicated predictions of vulnerability to overfishing and thus refine the above generalisations made for *L. bohar*. Although generalised predictions of vulnerability to overfishing seem appropriate, the importance of collecting additional biological and harvest information for a better insight into likely actual (as opposed to theoretical) harvest effects was also demonstrated. Given the uncertainties, the precautionary approach should be adhered to when developing and implementing fisheries management strategies for this species. This thesis has demonstrated, though, that an understanding of the fundamental biological parameters of a harvested stock could be very useful for providing an initial indication of the vulnerability of a stock to overfishing and devising relevant management strategies.

List of References.

Acosta, A. and Appledoorn, R.S. 1992. Estimation of growth, mortality and Yield Per Recruit for *Lutjanus synagris* (Linnaeus) in Puerto Rico. *Bull. Mar. Sci.* **50**: 282-291.

Adams, P.B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fish. Bull.* **78**: 1-12.

Aiken, K.A. 2001. Aspects of reproduction, age and growth of the Lane Snapper, *Lutjanus synagris* (Linnaeus, 1758) in Jamaican waters. *Proc. Gulf. Carib. Fish. Inst.* **52**: 116-134.

Aldenhoven, J.M. 1986. Local variation in mortality rates and life-expectancy estimates of the coral-reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). *Mar. Biol.* **92**: 237-244.

Allen, G.R. 1985. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. Rome, FAO.

Andrews, A.H., Burton, E.J., Coale, K.H., Cailliet, G.M. and Crabtree, R.E. 2001. Radiometric age validation of Atlantic tarpon, *Megalops atalanticus. Fish. Bull.* **99**: 389-398.

Archibald, C.P., Shaw, W. and Leaman, B.M. 1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters. 1977-1979. *Can. Tech. Rep. Fish. Aquat. Sci.* **1048**: 61.

Arreguin-Sanchez, F. and Manickchand-Heileman, S. 1998. The trophic role of lutjanid fish and impacts of their fisheries in tow ecosystems in the Gulf of Mexico. *J. Fish Biol.* **53A**: 143-153.

Atkinson, D. 1994. Temperature and organism size - a biological law for ectotherms? *Adv. Ecol. Res.* **25**: 1-58.

Ault, J.S., Bohnsack, J.A. and Meester, G.A. 1998. A retrospective (1979-1996) multispecies assessment of coral reef fish stocks in the Florida Keys. *Fish. Bull.* **96**: 395-414.

Baker, M.S.J. and Wilson, C.A. 2001. Use of bomb radiocarbon to validate otolith section ages of red snapper *Lutjanus campechanus* from the northern Gulf of Mexico. *Limnol. Oceanogr.* **46**: 1819-1824.

Baranov, T.I. 1918. On the question of the biological basis of fisheries. *Naunchn issledov. Ikhtiologicheskii Inst. Izv.* **1**: 81-128.

Barlow, J. 1984. Mortality estimation: biased results from unbiased ages. *Can. J. Fish. Aquat. Sci.* **41**: 1843-1847.

Beacham, T.D. 1983. Variability in median size and age at sexual maturity of Atlantic cod, *Gadus morhua*, on the Scotian Shelf in the northwest Atlantic Ocean. *Fish. Bull.* **81**: 303-321.

Beamish, R.J. and Fournier, D.A. 1981. A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.* **38**: 982-983.

Beamish, R.J. and Chilton, D.E. 1982. Preliminary evaluation of a method to determine the age of sablefish, *Anoploma fimbria*. *Can. J. Fish. Aquat. Sci.* **39**: 277-287.

Beamish, R.J. and McFarlane, G.A. 1983. The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fis. Soc.* **112**: 735-743.

Begg, G.A., Hare, J.A. and Sheehan, D.D. 1999. The role of life history parameters as indicators of stock structure. *Fish. Res.* **43**: 141-163.

Bell, G. 1980. The costs of reproduction and their consequences. *Am. Nat.* **116**: 45-76.

Bell, J.D., Lyle, J.M., Bulman, C.M., Graham, K.J., Newton, G.M. and Smith, D.C. 1992. Spatial variation in reproduction, and occurrence of non-reproductive adults, in orange roughy, *Hoplostethus atlanticus* Collett (Trachichthyidae), from south-eastern Australia. *J. Fish. Biol.* **40**: 107-122.

Bellwood, D.R., Hughes, T.P., Folke, C. and Nystrom, M. 2004. Confronting the coral reef crisis. *Nature* **429**: 827-833.

Bernard, D.R. 1981. Multivariate analysis as a means of comparing growth in fish. *Can. J. Fish. Aquat. Sci.* **38**: 233-236.

Beverton, R.J.H. and Holt, S.J. 1957. On the dynamics of exploited fish populations. *U.K. Ministry of Agriculture and Fisheries, Fisheries Investigations (Series 2).* **19**: 1-533.

Blindloss, J., Singh, S., Swaney, D. and Strauss, R. 2001. Mauritius, Reunion and Seychelles. (4th ed.) Footscray, Australia., Lonely Planet Publications.

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genetics* **13**: 115-155.

Brothers, E.B. 1987. Methodological approaches to the examination of otoliths in aging studies. *In*: The Age and Growth of Fish. Summerfelt, R.C. and Hall, G.E. Ames, Iowa, The Iowa State University Press**:** 319-330.

Brown, I.W. and Sumpton, W.D. 1998. Age, growth and mortality of redthroat emperor *Lethrinus miniatus* (Pisces: Lethrinidae) from the southern Great Barrier Reef, Queensland, Australia. *Bull. Mar. Sci.* **62**: 905-917.

Burgmeier, J.W., Boisen, M.B.J. and Larsen, M.D. 1990. Brief Calculus with Applications. New York, McGraw-Hill Inc.

Burnham, K.P. and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. New York, Springer-Verlag.

Burton, M.P.M., Penney, R.M. and Biddiscombe, S. 1997. Time course of gametogenesis in Northwest Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **54 (Suppl. 1)**: 122-131.

Burton, M.L. 2001. Age, growth, and mortlaity of gray snapper, *Lutjanus griseus*, from the east coast of Florida. *Fish. Bull.* **99**: 254-265.

Burton, M.L. 2002. Age, growth and mortality of mutton snapper, *Lutjanus analis*, from the east coast of Florida, with a brief discussion of management implications. *Fish. Res.* **59**: 31-41.

Caley, M., Carr, M., Hixon, M., Hughes, T., Jones, G. and Menge, B. 1996. Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.* **27**: 477-500.

Caley, M.J. 1998. Reef fish, mortality curves and life-history consequences. *In*.Jones, G.P., Doherty, P.J., Mapstone, B.D. and Howlett, L. (eds.) ReeFish '95: Recruitment and Population Dynamics of Coral Reef Fishes. pp. 151-154. Kuranda Rainforest Resort, Queensland, Australia,10-16 December 1995.

Campana, S.E., Annand, M.C. and McMillan, J.I. 1995. Graphical and statistical methods for determining the consistency of age determinations. *Trans. Am. Fis. Soc.* **124**: 131-138.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.* **59**: 197-242.

Campbell, R.A., Mapstone, B.D. and Smith, A.D.M. 2001. Evaluating large-scale experimental designs for management of Coral Trout on the Great Barrier Reef. *Ecol. App.* **11**: 1763-1777.

Cappo, M., Eden, P., Newman, S.J. and Robertson, S. 2000. A new approach to validation of periodicity and timing of opaque zone formation in the otoliths of eleven species of *Lutjanus* from the central Great Barrier Reef. *Fish. Bull.* **98**: 474-488.

Carter, J. and Perrine, D. 1994. A spawning aggregation of dog snapper, *Lutjanus jocu* (Pisces: Lutjanidae) in Belize, Central America. *Bull. Mar. Sci.* **55**: 228-234.

Cech, J.J. 1992. White Sturgeon. *In*: Leet, W.S., Dewees, C.M. and Haugen, C.W. (eds.) California's living marine resources and their utilisation. pp. 70-71, California Sea Grant, Davis.

Chambers, R.C. and Leggett, W.C. 1996. Maternal influences on variation in eff sizes in temperate marine fishes. *Amer. Zool.* **36**: 180-196.

Chapman, D.G. and Robson, D.S. 1960. The analysis of a catch curve. *Biometrics* **16**: 354-368.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge, Cambridge University Press.

Choat, J.H. and Robertson, D.R. 2002. Age based studies. *In* Sale, P.F. (ed.). Coral Reef Fishes. Academic Press. pp57-80.

Choat, J.H., Robertson, D.R., Ackerman, J.L. and Posada, J.M. 2003. An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride. Mar. Ecol. Prog. Ser.* **246**: 265-277.

Clark, M.R. and Tracey, D.M. 1994. Changes in a population of orange roughy, *Hoplostethus atlanticus,* with commercial exploitation on the Challenger Plateau, New Zealand. *Fish. Bull.* **92**: 236-253.

Claro, R., Sierra Sierra, L.M. and Garcia Arteaga, J.P. 1999. Biology of the dog snapper *Lutjanus jocu* in the NE and SW zones of Cuban Shelf, II. Feeding, age and growth. *Revista de investigaciones marinas.* Mexico City. **20**: 30-38.

Coleman, F.C., Koenig, C.C., Huntsman, G.R., Musick, J.A., Eklund, A.M., McGovern, J.C., Chapman, R.W., Sedberry, G.R. and Grimes, C.B. 2000. Long-lived reef fishes: The grouper-snapper complex. *Fisheries* **25**: 14-21.

Collins, L.A., Fitzhugh, G.R., Mourand, L., Lombardi, L.A., Walling, W.T.J., Fable, W.A.J., Burnett, M.R. and Allman, R.J. 2001. Preliminary results from a continuing study of spawning and fecundity in the Red Snapper (Lutjanidae: *Lutjanus campechanus*) from the Gulf of Mexico, 1998-1999. *Proc. Gulf. Carib. Fish. Inst.* **52**: 34-47.

Conover, D.O. and Munch, S.B. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* **297**: 94-96.

Crabtree, R.E., Cyr, E.C. and Dean, J.M. 1995. Age and growth of tarpon, *Megalops atlanticus,* from South Florida waters. *Fish. Bull.* **93**: 619-628.

Craig, M.T., Pondella, D.J.I. and Hafner, J.C. 1999. Analysis of age and growth in two Eastern Pacific groupers (Serranidae: Epinephelinae). *Bull. Mar. Sci.* **65**: 807-814.

Crouse, D.T. 1999. The consequences of delayed maturity in a human-dominated world. *In*: Musick, J.A. (ed.) Life in the Slow Lane. Ecology and Conservation of Long-lived Marine Animals. pp. 195-202. American Fisheries Society Symposium, Monterey, USA.

Cuellar, N., Sedberry, G.R. and Wyanski, D.M. 1996. Reproductive seasonality, maturation, fecundity, and spawning frequency of the vermilion snapper, *Rhomboplites aurorubens,* off the southeastern United States. *Fish. Bull.* **94**: 635-653.

Cury, P. and Pauly, D. 2000. Patterns and propensities in reproduction and growth of marine fishes. *Ecol. Res.* **15**: 101-106.

Cushing, D.H. 1968. Fisheries Biology, a Study in Population Dynamics. Madison, University of Wisconsin Press.

Davis, T.L.O. and West, G. 1992. Growth and mortality of *Lutjanus vittus* (Quoy and Galmard) from the North West Shelf of Australia. *Fish. Bull.* **90**: 395-404.

Davis, T.L.O. and West, G.J. 1993. Maturation, reproductive seasonality, fecundity, and spawning frequency in *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia. *Fish. Bull.* **91**: 224-236.

de Moussac, G. 1988. Summary of data on the artisanal fishery of the Seychelles. Biology, resources and exploitation. Seychelles Fishing Authority, Victoria, Seychelles. 64pp.

Deriso, R.B., Quinn, T.J.I. and Neal, P.R. 1985. Catch-age analysis with auxillary information. *Can. J. Fish. Aquat. Sci.* **42**: 815-824.

deVlaming, V., Grossman, G. and Chapman, F. 1982. On the use of the gonosomatic index. *Comp. Biochem. Physiol.* **73A**: 31-39.

Doubleday, W.G. 1976. A least-squares approach to analysing catch at age data. *Research Bulletin of the International Commission for Northwest Atlantic Fisheries.* **12**: 69-81.

Druzhinin, A.D. 1970. The range and biology of snappers (fam. Lutjanidae). *J. Ichthyol.* **10**: 717-736.

Echeverria Wyllie, T.1987. Thiry-four species of California rockfishes: maturity and seasonality of reproduction. Fishery Bulletin 85: 229-250.

Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. *CBMS-NSF Reg. Comb. Ser. Appl. Math. SIAM* **38**: 92.

Ehrhardt, N.M. and Legault, C.M. 1996. Impact of the variability in numbers and size at first recruitment on the $F_{0.1}$ reference point in the U.S. red snapper fisheries of the Gulf of Mexico. *In*: Biology, fisheries, and culture of tropical groupers and snappers. ICLARM Conference Proceedings. **48:** 337-349.

Eklund, J., Parmanne, R. and Aneer, G. 2000. Between-reader variation in herring otolith ages and effects on estimated population parameters. *Fish. Res.* **46**: 147-154.

Eschenroder, R.L. 1977. Effects of intensified fishing, species changes, and spring water temperatures on Yellow Perch, *Perca flavescens*, in Saginaw Bay. *J. Fish. Res. Bd. Can.* **34**: 1830-1838.

Everson, A.R., Williams, H.A. and Ito, B.M. 1989. Maturation and reproduction in two Hawaiian Eteline snappers, Uku, *Aprion viriscens,* and Onaga, *Etelis coruscans*. *Fish. Bull.* **87**: 877-888.

FAO 1995. Precautionary approach to fisheries. Part 1: Guidelines on the precautionary approach to capture fisheries and species introductions. FAO Technical Paper.

Ferreira, B.P. 1993. Reproduction of the inshore coral trout *Plectropomus maculatus* (Perciformes: Serranidae) from the Central Great Barrier Reef, Australia. *J. Fish Biol.* **42**: 831-844.

Ferreira, B.P. and Russ, G.R. 1992. Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces: Serranidae) from the Central Great Barrier Reef, Australia. *Aust. J. Mar. Freshwater Res.* **43**:1301-1312.

Ferreira, B.P. and Russ, G.R. 1994. Age validation and estimation of growth rate of coral trout, *Plectropomus leopardus* (Lacepede 1802) from Lizard Island, Northern Great Barrier Reef. *Fish. Bull.* **92**: 46-57.

Ferreira, B.P. 1995. Reproduction of the common coral trout *Plectropomus leopardus* (Serranidae: Epinepelinae) from the central and northern Great Barrier Reef, Australia. *Bull. Mar. Sci.* **56**: 653-669.

Ferry, R.E. and Kohler, C.C. 1987. Effects of trap fishing on fish populations inhabiting a fringing coral reef. *N. Amer. J. Fish. Manag.* **7**: 580-588.

Fienberg, S.E. 1970. The analysis of multidimensional contingency tables. *Ecol.* **51**: 419-433.

Forrester, G.E. 1990. Factors influencing the juvenile demography of a coral reef fish. *Ecol.* **71**: 1666-1681.

Fournier, D. and Archibald, C.P. 1982. A general theory for analyzing catch at age data. *Can. J. Fish. Aquat. Sci.* **39**: 1195-1207.

Fowler, A.J. and Doherty, P.J. 1992. Validation of annual growth increments in the otoliths of two species of damselfish from the southern Great Barrier Reef. *Aust. J. Mar. Freshwat. Res.* **43**: 1057-68.

Fowler, A.J. 1995. Annulus formation in coral reef fish - a review. *In*: Secor, D.H., Dean, J.M. and Campana, S.E. (eds.) Recent Developments in fish otolith research. pp. 45-64. Univ. of South Carolina Press, Columbia**.**

Fowler, A.J. and Short, D.A. 1998. Validation of age determination from otoliths of the King George whiting *Sillaginodes punctata* (Perciformes). *Mar. Biol.* **130**: 577-587.

Francis, M.P., Mulligan, K.P., Davies, N.M. and Beentjes, M.P. 1998. Age and growth estimates for New Zealand hapuku, *Polyprion oxygeneios*. *Fish. Bull*. **97**: 227-242.

Francis, R.I.C.C. 1988. Are growth parameters estimated from tagging and age-length data comparable? *Can. J. Fish. Aquat. Sci.* **45**: 936-942.

Francis, R.I.C.C., Paul, L.J. and Mulligan, K.P. 1992. Ageing of adult snapper (Pagrus auratus) from otolith annual ring counts: validation by tagging and oxytetracycline injection. *Aust. J. Mar. Freshwat. Res.* **43**: 1069-89.

Francis, R.I.C.C. 1992. Use of risk analysis to assess fishery management strategies: A case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. *Can. J. Fish. Aquat. Sci.* **49**: 922-930.

Frimodt, C. 1995. Multilingual illustrated guide to the world's commercial warmwater fish. Fishing News Books, Oxford, England.

Froese, R. and Pauly, D. 2004. FishBase. World Wide Web electronic publication. www.fishbase.org. version (06/2004).

Fuliang, Y. and Zongsheng, T. 1996. Study on age and growth of *Lutjanus russelli.* Bleeker. *J. Zhanjiang Fish. Coll./Zhangjiang Shuichan Xuenyuan Xuebao* **16**: 15-18.

Gauldie, R.W. 1988. Similarities in fine structure of annual, and non-annual, check rings in the otolith of the New Zealand snapper *(Chrysophyrus auratus). NZ. J. Mar. Freshwat. Res.* **22**: 273-278.

Gilbert, G.C. 1981. Modelling Society. An introduction to Loglinear Analysis for Social Researchers. London, U.K., George Allen & Unwin Ltd.

Gillespie, C., Lewis, R.J., Pearn, J.H. and Bourke, A.T.C. 1986. Ciguatera in Australia: occurrence, clinical features, pathophysiology and management. *Med. J. Aust.* **145**: 584-590.

Gladstone, W. and Westoby, M. 1988. Growth and reproduction in *Canthigaster valentini* (Pisces, Tetraodontidae): a comparison of a toxic reef fish with other reef fishes. *Env. Biol. Fish.* **21**: 207-221.

Glantz, M.H. 1979. Science, politics and economics of the Peruvian anchoveta fishery. *Mar. Policy* **3**: 201-210.

Goodyear, C.P. 1989. Spawning stock biomass per recruit: The biological basis for a fisheries management tool. ICCAT Working Document SCRS/89/82.

Goodyear, C.P. 1995. Mean size at age: An evaluation of sampling strategies with simulated red grouper data. *Trans. Am. Fis. Soc.* **124**: 746-755.

Grandcourt, E.M. 1999. The population biology of exploited reef fish from the Seychelles and Great Barrier Reef. Masters Thesis. James Cook University, Townsville. 106pp.

Grier, H.J. and Taylor, R.G. 1998. Testicular maturation and regression in common snook. *J. Fish Biol.* **53**: 521-542.

Grimes, C.B. and Huntsman, G.R. 1980. Reproductive biology of the Vermilion Snapper, *Rhomboplites aurorubens* from North Carolina and South Carolina. *Fish. Bull.* **78**: 137-146.

Grimes, C.B. 1987. Reproductive Biology of the Lutjanidae: a review . *In*: Polovina, J.J. and Ralston, S. (eds.) Tropical snappers and groupers: biology and fisheries management. pp. 238-294. Westview Press, U. S. A.

Grimes, C.B., Johnson, A.G. and Fable, W.A.J. 1987. Delineation of king mackerel (*Scomberomorus cavalla*) stock along the U.S. East Coast and in the Gulf of Mexico. *In*: Kumpf, H.E., Vaught, R.N., Grimes, C.B, Johnson, A.G., Nakamura, E.L. (eds.). Proceedings of The Stock Identification Workshop 5-7 November 1985, Panama City Beach, Florida. pp: 186-187. NOAA Technical Memorandum NMFS-SEFC-199. United States Government Printing Office.

Gulland, J.A. 1983. Fish Stock Assessment. A manual of basic methods. Chichester, John Wiley and Sons.

Gust, N., Choat, J.H. and Ackerman, J.L. 2002. Demographic plasticity in tropical reef fishes. *Mar. Biol.* **140**: 1039-1051.

Haddon, M. 2001. Modelling and Quantitative Methods in Fisheries. Chapman & Hall/CRC, Boca Raton.

Hanson, A.J. and Smith, H.D. 1967. Mate selection in a population of sockeye salmon (*Oncohynchus nerka*) of mixed age-groups. *J. Fish. Res. Board Can.* **24**: 1955-1977.

Hart, A.M. and Russ, G.R. 1996. Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofuscus. Mar. Ecol. Prog. Ser.* **136**: 25-35.

Hay, T., Knuckley, I. and Calogeras, C. 1996. Population biology of the golden snapper *Lutjanus johnii*. *Fishnote* **21**: 3.

Hesp, S.A., Potter, I.C. and Hall, N.G. 2002. Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (*Glaucosoma hebraicum*) and their relevance to the management of this species. *Fish. Bull.* **100**: 214-227.

Heyer, C.J., Miller, T.J., Binkowski, F.P., Caldarone, E.M. and Rice, J.A. 2001. Maternal effects as a recruitment mechanism in Lack Michigan yellow perch (*Perca flavescens*). *Can. J. Fish. Aquat. Sci.* **58**: 1477-1487.

Heyman, W.D., Graham, R.T., Kjerive, B. and Johannes, R.E. 2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Mar. Ecol. Prog. Ser.* **215**: 275-282.

Hilborne, R. and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, Great Britain.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.* **82**: 898-902.

Hoenig, J.M., Morgan, M.J. and Brown, C.A. 1995. Analysing differences between age determination methods by tests of symmetry. *Can. J. Fish. Aquat. Sci.* **52**: 364-368.

Hood, P.B. and Johnson, A.K. 1998. Age, growth, mortality, and reproduction of vermilion snapper, *Rhomboplites aurorubens,* from the eastern Gulf of Mexico. *Fish. Bull.* **97**: 828-841.

Hunter, J.R. and Goldberg, S.R. 1980.Spawning incidence and batch fecundity in Northern Anchovy, *Engraulis mordax. Fish. Bull.* **77**: 641-652.

Hunter, J.R. and Macewicz, B.J. 1980. Sexual maturity, batch fecundity, spawning frequency, and temporal pattern of spawning for the northern anchovy, *Engraulis mordax,* during the 1979 spawning season. Calif. Coop. Oceanic Fish. Invest. Rep. 21: 139-149.

Hunter, J.R. and Macewicz, B.J. 1985. Measurement of spawning frequency in multiple spawning fishes. *In* Lasker, R. (ed.) An egg production method for estimating spawning biomass of pelagic fish: Application to the Northern Anchovy, *Engraulis mordax.* NOAA Tech. Rep. NMFS **36**: 79-94.

Hunter, J.R., Lo, N.C.H. and Leong, R.J.H. 1985. Batch fecundity of multiple spawning fishes., NOAA**:** 67-77.

Hunter, J.R., Macewicz, B.J., Chyan-huei Lo, N. and Kimbrell, C.A. 1992. Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus,* with an evaluation of assumptions and precision. *Fish. Bull.* **90**: 101-128.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**: 187-211.

Hutchings, J.A. and Myers, R.A. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua,* in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **50**: 2468-2474.

Hutchings, J.A. and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua,* of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* **51**: 2126-2146.

Jennings, S., Grandcourt, E. and Polunin, N. 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* **14**: 225-235.

Jennings, S. and Marshall, S. 1995. Seeking sustainability in the Seychelles. *Biologist* **42**: 197-202.

Jennings, S. and Lock, J.M. 1996. Population and ecosystem effects of fishing. *In*: Polunin, N.V.C. and Roberts, C.M. (eds.) Reef Fisheries. pp. 193-218. Chapman & Hall, London.

Jennings, S., Reynolds, J.D. and Mills, S.C. 1998. Life history correlates of repsonses to fisheries exploitation. *Proc. R. Soc. Lond. B* **265**: 333-339.

Jennings, S. and Kaiser, M.J. 1998. The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* **34**: 201-303.

Jennings, S., Reynolds, J.D. and Polunin, N.V.C. 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conserv. Biol.* **13**: 1466-1475.

Jennings, S., Marshall, S.S., Cuet, P. and Naim, O. 2000. The Seychelles. *In*: McClanahan, T.R., Sheppard, C.R.C. and Obura, D.O. (eds.) Coral reefs of the Indian Ocean: their ecology and conservation. pp. 383-410. Oxfork University Press, New York.

Jennings, S. 2001. Patterns and prediction of population recovery in marine reserves. *Rev. Fish Biol.Fish.* **10**: 209-231.

Johannes, R.E. 1978. Reproductive strategies of coastal marine fishes in the tropics. *Env. Biol. Fish.* **3**(1): 65-84.

Johannes, R.E. 1981. Words of the Lagoon. University of California Press, Berkeley.

Johannes, R.E. and Hviding, E. 2000. Traditional knowledge possessed by the fishers of Marovo Lagoon, Solomon Islands, concerning fish aggregating behaviour. *SPC Traditional Marine Resource Management and Knowledge Information Bulletin.***12**.

Jones, G.P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. *In*: Sale, P.F. (ed.) The Ecology of Fishes on Coral Reefs. pp. 294-328. Academic Press, San Diego.

Jones, B.C. and Green, G.H. 1997. Age and growth of spiny dogfish (*Squalus acanthias* L.) in the strait of Georgia. *British Columbia. Fish. Mar. Serv. Research Dev. Tech. Rep.* **669**.

Kaunda-Arara, B. and Ntiba, M.J. 1997. The reproductive biology of *Lutjanus fulviflamma* (Forskal, 1775) (Pisces: Lutjanidae) in Kenyan inshore marine waters. *Hydrobiol.* **353**: 153-160.

Kimura, D.K. 1980. Likelihood methods for the von Bertalanffy growth curve. *Fish. Bull.* **77**: 765-776.

Kimura, D.K. and Lyons, J.L. 1991. Between-reader bias and variability in the age determination process. *Fish. Bull.* **89**: 53-90.

King, M. 1995. Fisheries biology: assessment and management. Blackwell Science Ltd., Great Britain.

Kingsford, M.J. 1992. Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs* **11**: 193-198.

Kirkpatrick, M. 1993. The evolution of size and growth in harvested natural populations. *In*: Stokes, K., McGlade, J.M. and Law, R. (eds.) The exploitation of evolving resources. Lecture Notes in Biomathematics 99. Proceedings of an International Conference held at Julich, Germany. 3-5 September, 1991. pp. 145-154. Springer-Verlag, Berlin.

Kirkwood, G.P., Beddington, J.R. and Rossouw, J.A. 1993. Harvesting species of different lifespans. In: *Large-Scale Ecology and Conservation Biology.* Edwards, P.J., May, R.M. and Webb, N.R. Oxford, Blackwell Scientific Publications**:** 199-227.

Kjesbu, O.S., Kryvi, H. and Norberg, B. 1996. Oocyte size and structure in relation to blood plasma steriod hormones in individually monitored, spawning Atlantic cod. *J. Fish. Biol.* **49**: 1197-1215.

Kloser, R.J., Koslow, J.A. and Williams, A. 1996. Acoustic assessment of the biomass of a spawning aggregation of orange roughy (*Hoplostethus atlanticus*, Collett) off south-eastern Australia, 1990-1993. *Mar. Freshwat. Res.* **47**: 1015-1024.

Knight, W. 1968. Asymptotic growth: An example of nonsense disguised as mathematics. *J. Fish.Res. Bd. Can.* **25**: 1303-1307.

Krebs, C.J. 1994. Ecology: The Experimental Analysis of Distribution and Abundance, Fourth Edition. HarperCollins, New York.

Kritzer, J.P. 2002. Variation in the population biology of stripey bass *Lutjanus carponotatus* within and between two island groups on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **243**: 191-207.

Kritzer, J.P. 2004. Sex-specific growth and mortality, spawning season, and female maturation of the stripey bass (*Lutjanus carponotatus*) on the Great Barrier Reef. *Fish. Bull.* **102**: 94-107.

Lai, H.L. and Gunderson, D.R. 1987. Effects of ageing errors on estimates of growth, mortality and Yield Per Recruit for Walleye Pollock (*Theragra chalcogramma*). *Fish. Res.* **5**: 287-302.

Law, R. and Grey, D.R. 1989. Evolution of yields from populations with age-specific cropping. *Evol. Ecol.* **3**: 343-359.

Law, R. 1991. On the quantitative genetics of correlated characters under directional selection in age-structured populations. *Phil. Trans. R. Soc. Lond. B* **331**: 213-223.

Law, R. and Rowell, C.A. 1993. Cohort-structured populations, selection responses, and exploitation of the North Sea Cod. *In*: Stokes, K., McGlade, J.M. and Law, R. (eds.) The exploitation of evolving resources. Lecture Notes in Biomathematics 99. Proceedings of an International Conference held at Julich, Germany. 3-5 September, 1991. pp. 155-173. Springer-Verlag, Berlin.

Laws, E.A. and Archie, J.W. 1981. Appropriate use of regression analysis in marine biology. *Mar. Biol.* **65**: 13-16.

Laws, E.A. 1997. El Nino and the Peruvian Anchovy Fishery. Sausalito, California, University Science Books.

Lewis, R.J. 2001(a). The changing face of ciguatera. *Toxicon* **39**: 97-106.

Lewis, A. 2001(b). Great Barrier Reef Depth and Elevation Model: GBRDEM. CRC Reef Res. Cent. Tech. Rep. Townsville, Australia. 58pp.

Lewis, P.D. and Mackie, M. 2002. Methods used in the collection, preparation, and interpretation of narrow-barred Spanish mackerel (*Scomberomorus commerson*) otoliths for a study of age and growth in Western Australia. Fisheries Research Report for the Department of Fisheries. Perth, Western Australia. No. **143**.

Liu, C.C. and Yeh, S.Y. 1991. Age determination and growth of red emperor (*Lutjanus sebae*) in the Arafura Sea off north Australia. *Act. Ocean. Taiwan.* **26**: 36-52.

Longhurst, A.R. and Pauly, D. 1987. Ecology of Tropical Oceans. Academic Press Inc., California.

Lou, D.C. and Moltschaniwskyj, N.A. 1992. Daily otolith increments in juvenile tropical parrotfishes and surgeonfishes. *Aust. J. Mar. Freshwater Res.* **43**: 973-81.

Loubens, G. 1980. Biologie de quelques especes de poiison du lagon Neo Caledonien III. *Croissance Cahiers de I'Indo Pacifique* **2**: 101-153.

Luckhurst, B.E., Barnes, J.A. and Sadovy, Y. 1992. Record of an unusually large red hind, *Epinephelus guttatus* (Pisces: Serranidae) form Bermuda with comments on its age. *Bull. Mar. Sci.* **51**: 267-270.

Luckhurst, B.E., Dean, J.M. and Reichert, M. 2000. Age. growth and reproduction of the lane sanpper *Lutjanus synagris* (Pisces: Lutjanidae) at Bermuda. *Mar. Ecol. Prog. Ser.* **203**: 255-261.

MacArthur, R.H. and Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton.

Mace, P.M. and Doonan, I.J. 1988. A generalised bioeconomic model for fish population dynamics. *N.Z. Fish. Assess. Res. Doc.* **88/4**.

Manickchand-Dass, S. 1987. Reproduction, age and growth of the Lane snapper, *Lutjanus synagris* (Linnaeus) in Trinidad, West Indes. *Bull. Mar. Sci.* **40**: 22-28.

Manickchand-Heileman, S.C. and Phillip, D.A.T. 2000. Age and growth of the yellowedge grouper, *Epinephelus falvolimbatus,* and the yellowmouth grouper, *Mycteroperca interstitialis*, off Trinidad and Tobago. *Fish. Bull.* **98**: 290-298.

Maniwavie, T., Sweatman, H., Marshall, P., Munday, P. and Rei, V. 2002. Status of coral reefs of Australasia: Australia and Papua New Guinea. *In*: Wilkinson, C.R. (ed.). Status of coral reefs of the world: 2002. pp. 141-157. Australian Institute of Marine Science, Townsville.

Mann, R.H.K. and Mills, C.A. 1979. Demographic aspects of fish fecundity. *Symp. zool. Soc. Lond.* **44**: 161-177.

Manooch, C.S.I. and Matheson, R.H.I. 1981. Age, growth and mortality of gray snapper collected from Florida waters. *Proc. Ann. Conf. Southeastern Assoc. Fish. Wild. Agencies* **35**: 331-344.

Manooch, C.S. 1987. Age and growth of snappers and groupers. *In*: Polovina, J.J. and Ralston, S. (eds.) Tropical snappers and groupers: biology and fisheries management. pp. 329-373. Westview Press, U. S. A.

Manooch III, C.S. and Drennon, C.L. 1987. Age and growth of Yellowtail Snapper and Queen Triggerfish collected from the U.S. Virgin Islands and Puerto Rico. *Fish. Res.* **6**: 53-68.

Mapstone, B.D., McKinlay, J.P. and Davies, C.R. 1996. A description of the commercial reef line fishery logbook data held by the Queensland Fisheries Management Authority. Report to the Queensland Fisheries Management Authority. 480pp.

Mapstone, B.D., Davies, C. and Robertson, J. 1997. The effects of fishing on the Great Barrier Reef: available evidence and future directions. Proceedings of the Great Barrier Reef science, use and management conference. **1**: 178-192.

Mapstone, B.D., Jones, A., Davies, C.R., Slade, S.J. and Williams, A.J. 2001. The live fish trade on Queensland's Great Barrier Reef: changes to historical fishing practices. *SPC Live Reef Fish Information Bulletin* **9**: 10-13.

Mapstone, B.D., Davies, C.R., Little, L.R., Punt, A.E., Smith, A.D.M., Pantus, F., Lou, D.C., Williams, A.J., Jones, A., Ayling, A.M., Russ, G.R. and McDonald, A.D. 2004. The effects of line fishing on the Great Barrier Reef and evaluations of alternative potential management strategies. CRC Reef Res. Cent. Tech. Rep. **52**. 205pp.

Marriott, R.J. and Cappo, M. 2000. Comparative precision and bias of five different ageing methods for the large tropical snapper *Lutjanus johnii*. *As. Fish. Sci.* **13**: 149-160.

Marriott, R.J. 2002. Age, growth and sex structure of red bass populations on the Great Barrier Reef. *In*: Williams, A.J., Welch, D.J., Muldoon, G., Marriott, R.J., Kritzer, J.P. and Adams, S. (eds.) Bridging the gap: a workshop linking student research with fisheries stakeholders. CRC Reef Res. Cent. Tech. Rep. **48.:** 81-86.

Marshall, C.T., Yaragina, N.A., Lambert, Y. and Kjesbu, O.S. 1999. Total lipid energy as a proxy for total egg production by fish stocks. *Nature* **402**: 288-290.

Marteinsdottir, G. and Steinarsson, A. 1998. Maternal influence on the size and viability of Iceland cod (*Gadus morhua* L.) eggs and larvae. *J. Fish. Biol.* **52**: 1241-1258.

McClanahan, T.R., Polunin, N.V.C. and Done, T.J. 2002. Resilience of Coral Reefs. *In*: Gunderson, L.H. and Pritchard, L.J. (eds.) Resilience and the Behaviour of Large-Scale Systems. pp. 111-163. Island Press, Washington, USA.

McMillan, W.O. and Palumbi, S.R. 1995. Concordant evolutionary patterns among Indo-West Pacific Butterflyfishes. *Proc. R. Soc. Lond. B.* **260**: 229-236.

McPherson, G.R., Squire, L. and O'Brien, J. 1992. Reproduction of three dominant *Lutjanus* species of the Great Barrier Reef inter-reef fishery. *As. Fish. Sci.* **5**: 15-24.

McPherson, G.R. and Squire, L. 1992. Age and growth of three dominant *Lutjanus* species of the Great Barrier Reef Inter-Reef Fishery. *As. Fish. Sci.* **5**: 25-36.

Medley, P.A., Gaudian, G. and Wells, S. 1993. Coral reef fisheries stock assessment. *Rev. Fish Biol. Fish.* **3**: 242-285.

Meekan, M.G., Ackerman, J.L. and Wellington, G.M. 2001. Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. *Mar. Ecol. Prog. Ser.* **212**: 223-232.

Mees, C.C. 1989. Biological and stock assessment studies relating principally to the demersal fisheries of the Seychelles. A brief review of past activities and future requirements. Seychelles Fishing Authority, Victoria, Seychelles. 15pp.

Mees, C.C. 1992. A summary of the trends observed in the artisanal fishery from 1985 to 1992. Seychelles Fishing Authority, Victoria, Seychelles. 9pp.

Mees, C.C. 1996. Management of Multi-species Tropical Fisheries: Final Report. MRAG Ltd., London. 194pp.

Megrey, B.A. 1989. Review and comparison of age-structured stock assessment models from theoretical and applied points of view. *American Fisheries Society Symposium* **6**: 8-48.

Menenzes, M.F.d. and Gesteira, T.C.V. 1974. Age and growth of the paro, *Lutjanus purpureus* Poey, of the north and northeast of Brazil. *Arq. Cienc. Mar.* **14**: 81-85.

Morales-Nin, B. and Ralston, S. 1990. Age and growth of Lutjanus kasmira (Forskal) in Hawaiian waters. *J. Fish. Biol.* **36**: 191-203.

Morison, A.K., Robertson, S.G. and Smith, D.C. 1998. An integrated system from production fish ageing: image analysis and quality assurance. *N. Amer. J. Fish. Manag.* **18**: 587-598.

Mortimer 1995. Teaching critical concepts for the conservation of sea turtles. *Marine Turtle Newsletter* **71**: 1-4.

Moulton, P.L., Walker, T.I. and Saddlier, S.R. 1992. Age and growth studies of gummy shark, *Mustelus antarcticus* Gunther, and school shark, *Galeorhinus galeus* (Linnaeus), from southern Australian waters. *Aust. J. Mar. Freshwat. Res.* **43**: 1241-1267.

Munro, J.L. 1983. Caribbean Coral Reef Fishery Resources. ICLARM, Manilla, Philippines.

Murphy, G.I. 1965. A solution of the catch equation. *J. Fish. Res. Bd. Can.* **22**: 191-202.

Murphy, G.I. 1968. Pattern in life history and the environment. *Am. Nat.* **102**: 391-403.

Murphy, M.D. and Taylor, R.G. 1990. Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. *Fish. Bull.* **88**: 531-542.

Musick, J.A. 1999. Ecology and conservation of long-lived marine animals. *In*: Musick, J.A. (ed.). Life in the Slow Lane. Ecology and conservation of long-lived marine animals. pp. 1-10. American Fisheries Society, Monterey, USA.

Musick, J.A., Harbin, M.M., Berkeley, S.A., Burgess, G.J., Eklund, A.M., Findley, L., Gilmore, R.G., Golden, J.T., Ha, D.S., Huntsman, G.R., McGovern, J.C., Parker, S.J., Poss, S.G., Sala, E., Schmidt, T.W., Sedberry, G.R., Weeks, H. and Wright, S.G. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific Salmonids). *Fisheries* **25**: 6-30.

Myers, R.A. and Mertz, G. 1998. The limits of exploitation: A precautionary approach. *Ecol. Appl.* **8**: 5165-5169.

Myers, R.A., Bowen, K.G. and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* **56**: 2404-2419.

Nagahama, Y. 1983. The functional morphology of teleost gonads. *In*: Hoar, W.S., Randall, D.J. and Donaldson, E.M. (eds.). Fish Physiology. pp. 223-275. Academic Press, Sydney.

Newman, S.J., Williams, D.M. and Russ, G.R. 1996(a). Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetti* (Castelnau, 1873) and *L. quinqelineatus* (Bloch, 1790) from the cental Great Barrier Reef, Australia. *Mar. Freshwat. Res.* **47**: 575-584.

Newman, S.J. and Williams, D.M. 1996. Variation in reef associated assemblages of the Lutjanidae and Lethrinidae at different distances offshore in the central Great Barrier Reef. *Env. Biol. Fish.* **46**: 123-138.

Newman, S.J., Williams, D.M. and Russ, G.R. 1996(b). Variability in the population structure of *Lutjanus adetii* (Catelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) among reefs in the central Great Barrier Reef, Australia. *Fish. Bull.* **94**: 313-329.

Newman, S.J., Cappo, M. and Williams, D.M. 2000. Age, growth, mortality rates and corresponding yield estimates using otoliths of the tropical red snappers, *Lutjanus erythropterus*, *L. malabaricus*, and *L. sebae*, from the Central Great Barrier Reef. *Fish. Res.* **48**: 1-14.

Newman, S.J. 2002. Growth rate, age determination, natural mortality and production potential of the scarlet seaperch, *Lutjanus malabaricus* Schneider 1801, off the Pilbara coast of north-western Australia. *Fish. Res.* **58**: 215-225.

Newman, S.J. and Dunk, I.J. 2002. Growth, age validation, mortality, and other population characteristics of the Red Emperor Snapper, *Lutjanus sebae* (Cuvier, 1828), off the Kimberley Coast of North-Western Australia. *Estuarine, Coastal and Shelf Science* **55**: 67-80.

Newman, S.J. and Dunk, I.J. 2003. Age validation, growth, mortality, and additional population parameters of the goldband snapper (*Pristipomoides multidens*) off the Kimberley coast of northwestern Australia. *Fish. Bull.* **101**: 116-128.

Nzoika, R.M. 1979. Observations on the spawning seasons of East African reef fishes. *J. Fish. Biol.* **14**: 329-342.

Palumbi, S.R. 2004. Why mothers matter. *Nature* **430**: 621-622.

Panfili, J., Pontual, H., Troadec, H. and Wright, P.J. 2002. Manual of Fish Sclerochronology. Ifremer-IRD coedition.

Parent, S. and Schriml, L.M. 1995. A model for the determination of fish species at risk based upon life-history traits and ecological data. *Can. J. Fish. Aquat. Sci.* **52**: 1768-1781.

Partridge, L. and Harvey, P.H. 1988. The ecological context of life history evolution. *Science* **241**: 1449-1455.

Patterson, W.F.I., Cowan, J.H.J., Wilson, C.A. and Shipp, R.L. 2001. Age and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area off Alabama in the northern Gulf of Mexico. *Fish. Bull.* **99**: 617-627.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil. Conseil International pour l'Exploration de la Mer.* **39**: 175-192.

Pauly, D. and Tsukayama, L. 1987. The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change. ICLARM, Manila.

Payet, R. 1996. Artisanal fishing boats in Seychelles. Seychelles Fishing Authority. Victoria, Seychelles. 25pp.

Pella, J.J. and Robertson, T.L. 1979. Assessment of composition of stock mixtures. *Fish. Bull.* **77**: 387-398.

Peres, M.B. and Haimovici, M. 2004. Age and growth of southwestern Atlantic wreckfish *Polyprion americanus*. *Fish. Res.* **66**: 157-169.

Perrone, M.Jr. 1978. Mate size and breeding success in a monogamous cichlid fish. *Environ. Biol. Fishes.* **3**: 193-201.

Pianka, E.R. 1970. On r- and K-selection. *Am. Nat.* **109**: 592-593.

Pilling, G.M. 1999. The effects of fishing on the growth and assessment of snappers and emperors. Ph.D. Thesis. University of London, Great Britain.

Pimm, S.L. 1984. The complexity and stability of ecosystems. *Nature* **307**: 321-326.

Pitcher, C.R. 1992. Growth of juvenile coral reef Damselfish: Spatial and temporal variability, and the effect of population density. *Aust. J. Mar. Freshwat. Res.* **43**: 1129-1149.

Plan Development Team, 1990. The Potential of Marine Fishery Reserves for Reef Fish Management in the U.S. Reef Fish Management Plan, Southern Atlantic Fishery Management Council. Miami, Florida. 45pp.

Policansky, D. 1993. Fishing as a cause of evolution in fishes. *In*: Stokes, K., McGlade, J.M. and Law, R. (eds.) The exploitation of evolving resources. Lecture Notes in Biomathematics 99. Proceedings of an International Conference held at Julich, Germany. 3-5 September, 1991. pp. 2-18. Springer-Verlag, Berlin.

Porter, S.C. 1989. Some geological implications of average quaternary glacial conditions. *Quat. Res.* **32**: 245-261.

Powers, J.E. 1983. Some statistical characteristics of ageing data and their ramifications in population analysis of oceanic pelagic fishes. *In*: Prince, E.D. and Pulos, L.M. (eds.) Proceedings of the internationsal workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. NOAA Tech. Rep., U.S. Dep. Comm. NMFS **8**: 19-24.

Punt, A.E. and Smith, D.C. 2001. Assessments of species in the Australian South East Fishery can be sensitive to the method used to convert size- to age-composition data. *Mar. Freshwat. Res.* **52**: 683-690.

QFS 2002. Combined regulatory impact statement and public benefit test report. Draft Fisheries (Coral Reef Fin Fish) Management Plan 2002. Queensland Fisheries Service, Brisbane.

Quinn, T.J.I. and Deriso, R.B. 1999. Quantitative Fish Dynamics. Oxford University Press, Oxford.

Ralston, S. 1982. Influence of hook size in the Hawaiian deep-sea handline fishery. *Can. J. Fish. Aquat. Sci.* **39**: 1297-1302.

Ralston, S. 1990. Size selection of snappers (*Lutjanidae*) by hook and line gear. *Can. J. Fish. Aquat. Sci.* **47**: 696-700.

Randall, J.E. 1980. A survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes. *Fish. Bull.* **78**: 201-249.

Rangarajan, K. 1971. Maturity and spawning of the snapper, Lutjanus kasmira (Forskal) from the Andaman Sea. *Indian J. Fish.* **18**: 114-125.

Reddin, D.G. and Friedland, K.D. 1999. A history of identification to continent of origin of Atlantic salmon (*Salmo salar* L.) at west Greenland, 1969-1997. *Fish. Res.* **43**: 221-235.

Rein, T.A. and Beamesderfer, R.C. 1994. Accuracy and precision of White Sturgeon age estimates from pectoral fin rays. *Trans. Am. Fis. Soc.* **123**: 255-265.

Reynaldo, P. and Fumio, T. 1995. Gonads. *In*: Takashima, F. and Hibiya, T. (eds.) An Atlas of Fish Histology. pp. 128-153. Kodansha Ltd., Tokyo.

Reznick, D.A., Bryga, H. and Endler, J.A. 1990. Experimentally induced life-history evolution in a natural population. *Nature* **346**: 357-359.

Richards, L.J., Schnute, J.T., Kronlund, A.R. and Beamish, R.J. 1992. Statistical models for the analysis of ageing error. *Can. J. Fish. Aquat. Sci.* **49**: 1801-1815.

Ricker, W.E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. *J. Fish. Res. Bd. Can.* **26**: 479-541.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin.* **191**.

Ricker, W.E. 1981. Changes in the average size and average age of Pacific Salmon. *Can. J. Fish. Aquat. Sci.* **38**: 1636-1656.

Ricker, W.E. 1984. Computation and uses of central trend lines. *Can. J. Zool.* **62**: 1897-1905.

Rocha-Olivares, A. 1998. Age, growth, mortality, and population characteristics of the Pacific red snapper, Lutjanus peru, off the southeast coast of Baja California, Mexico. *Fish. Bull.* **96**: 562-574.

Rochet, M., Cornillon, P., Sabatier, R. and Pontier, D. 2000. Comparative analysis of phylogenetic and fishing effects in life history patterns of teleost fishes. *OIKOS* **91**: 255-270.

Roff, D.A. 1981. Reproductive uncertainty and the evolution of iteroparity: Why dont' flatfish put all their eggs in one basket? *Can. J. Fish. Aquat. Sci.* **38**: 968-977.

Roff, D.A. 1983. An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.* **40**: 1395-1404.

Roff, D.A. 1984. The evolution of life history parameters in teleosts. *Canadian Journal of Can. J. Fish. Aquat. Sci.* **41**: 989-1000.

Rojas, M.J.R. 1997. Fecundity and reproductive seasons of *Lutjanus guttatus* (Pisces: Lutjanidae) in Golfo de Nicoya, Costa Rica. *Revista de Biologia Tropical* **44**: 477-487.

Roscoe, J.T. and Byars, J.A. 1971. Sample size restraints commonly imposed on the use of the chi-square statistic. *J. Amer. Statist. Assoc.* **66**: 755-759.

Russ, G. 1991. Coral reef fisheries: effects and yields. *In*: Sale, P.F. (ed.) The ecology of fishes on coral reefs. pp. 601-635. Academic Press, San Diego.

Russ, G.R. and Alcala, A.C. 1996. Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol. Appl.* **63**: 947-961.

Russ, G.R. and Alcala, A.C. 1998. Natural fishing experiments in marine reserves 1983-1993: roles of life history and fishing intensity in family responses. *Coral Reefs* **17**: 399-416.

Russ, G.R. 2002. Marine reserves as reef fisheries management tools: Yet another review. *In*: Sale, P.F. (ed.). Coral Reef Fishes. Academic Press.

Russ, G.R. and Alcala, A.C. 2003. Marine reserves: rates a patterns of recovery and decline of predatory fish, 1983-2000. *Ecol. Appl.* **13**: 1553-1565.

Russ, G.R. and Alcala, A.C. 2004. Marine reserves: long-term protection is required for full recover of predatory fish populations. *Oecologia* **138**: 622-627.

Russell, D.J., McDougall, A.J., Fletcher, A.S., Ovenden, J.R. and Street, R. 2003. Biology, management and genetic stock structure of mangrove jack (*Lutjanus argentimaculatus*) in Australia. The State of Queensland, Department of Primary Industries and the Fisheries Research Development Corporation. 189pp.

Sadovy, Y. and Shapiro, D.Y. 1987. Criteria for the diagnosis of hermaphroditism in fishes. *Copeia* **1987**: 136-156.

Sadovy, Y.J. 1996. Reproduction of reef fishery species. *In*: Polunin, N.V.C. and Roberts, C.M. (eds.) Reef Fisheries. pp. 15-59. Chapman & Hall, London.

Saetersdal, G. 1980. A review of past management of some pelagic stocks and its effectiveness. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* **177**: 505-512.

Sala, E., Aburto-Oropeza, O., Paredes, G. and Thompson, G. 2003. Spawning aggregations and reproductive behaviour of reef fishes in the Gulf of California. *Bull. Mar. Sci.* **72**: 103-121.

Sale, P.F. 1998. Appropriate spatial scales for studies of reef fish ecology. *Aust. J. Ecol.* **23**: 202-208.

Samoilys, M.A. 1997. Periodicity of spawning aggregations of coral trout *Plectropomus leopardus* (Pisces: Serranidae) on the northern Great Barrier Reef. *Mar. Ecol. Prog. Ser.* **160**: 149-159.

Samoilys, M.A. and Roelofs, A. 2000. Defining the reproductive biology of a large serranid, *Plectropomus leopardus.* CRC Reef Res. Cent. Tech. Rep. **31**. 36pp.

Saville, A. and Bailey, R.S. 1980. The assessment and management of the herring stocks in the North Sea and to the west of Scotland. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer.* **177**: 112-142.

Scott-Denton, E. and Nance, J. 1996. Shrimp trawl bycatch research in the U.S. Gulf of Mexico and Southeastern Atlantic. *In*: Arreguin-Sanchez, F., Munro, J.L., Balgos, M.C. and Pauly, D. (eds.). Biology, fisheries and culture of tropical groupers and snappers. *ICLARM Conference Proceedings* **48:** 360-363.

Secor, D.H. and Dean, J.M. 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., Dean, J.M. and Campana, S.E. 1995. *Recent developments in fish otolith research.* University of South Carolina Press, Columbia.

Secor, D.H. 2000. Longevity and resilience of Chesapeake Bay striped bass. *ICES J. Mar. Sci.* **57**: 808-815.

Sedberry, GR; Andrade, CAP; Carlin, JL; Chapman, RW; Luckhurst, BE; Manooch, CS III; Menezes, G; Thomsen, B; Ulrich, GF. 1999. Wreckfish Polyprion americanus in the North Atlantic: Fisheries, Biology, and Management of a Widely Distributed and Long-Lived Fish. *In In*: Musick, J.A. (ed.). Life in the Slow Lane. Ecology and conservation of long-lived marine animals. pp. 27-50. American Fisheries Society, Monterey, USA.

SFA 2001. Annual Report 2001. Seychelles Fishing Authority. Victoria, Seychelles. 64pp.

Sheaves, M. 1995. Large lutjanid and serranid fishes in tropical estuarines: Are they adults or juveniles? *Mar. Ecol. Prog. Ser.* **129**: 31-40.

Smith, D.C., Fenton, G.E., Robertson, S.G. and Short, S.A. 1995. Age determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annulus counts with radiometric aging. *Can. J. Fish. Aquat. Sci.* **52**: 391-401.

Smith, P.J. 1999. Genetic resources and fisheries: Policy aspects. *ICLARM Conference Proceedings* **59**: 43-62.

Smith, K.A. and Deguara, K. 2003. Formation and annual periodicity of opaque zones in sagittal otoliths of *Mugil cephalus* (Pisces: Mugilidae). *Mar. Freshwat. Res.* **54**: 57-67.

Sokal, R.R. and Rohlf, F.J. 1995. Biometry. The principles and practice of statistics in biological research. (3^{rd} ed.). W. H. Freeman and Co., New York.

Sparre, P. and Venema, S.C. 1992. Introduction to tropical fish stock assessment. *FAO Fisheries Technical Paper* **306/1**. FAO, Rome. 375pp.

Stearns, S.C. 1976. Life history tactics: a review of the ideas. *Q. Rev. Biol.* **51**: 3-47.

Stearns, S.C. and Koella, J.C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40**: 893-913.

Stearns, S.C. 1989. Trade-offs in life-history evolution. *Funct. Ecol.* **3**: 259-268.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, New York. 249pp.

Steinberg, C.R. and Burrage, D.M. 2001. Transports of the East Australian Current System: Volume II - Sea levels 1988-1999. AIMS Data Report.

Stevenson, J.T. and Secor, D.H. 1999. Age determination and growth of Hudson River Atlantic sturgeon, *Acipenser oxyrinchus. Fish. Bull.* **97**: 153-166.

Sutherland, W.J. 1990. Evolution and fisheries. *Nature* **344**: 814-815.

Swain, D.P. and Foote, C.J. 1999. Stocks and chameleons: the use of phenotypic variation in stock identification. *Fish. Res.* **43**: 113-128.

Tabash, B.F.A. and Sierra, S.L.M. 1996. Assessment of *Lutjanus vivanus* and *Lutjanus buccanella* in the North Caribbean Coast of Costa Rica. *Naga* **Oct. 1996**: 48-51.

Talbot, F.H. 1960. Notes on the biology of the Lutjanidae (Pisces) of the east African coast with special reference to Lutjanus bohar (Forsskal). *Annals. S. Afr. Mus.* **XLV**(1): 549-579.

Tarbit, J. 1980. Demersal Trawling in Seychelles Waters. Victoria, Seychelles., Fisheries Division, Seychelles Government: 84pp.

Thresher, R.E. and Brothers, E.B. 1985. Reproductive ecology and biogeography of Indo-West Pacific angelfishes (Pisces; Pomacanthidae). *Evolution* **39**: 878-887.

Thresher, R.E. Colin, P.L., Bell, L.J. 1989. Planktonic duration, distribution and population structure of western and central Pacific damselfishes (Pomacentridae). *Copeia* **1989**: 420-434.

Trippel, E.A. 1995. Age at maturity as a stress indicator in fisheries. *BioScience* **45**: 759-771.

Trippel, E.A., Kjesbu, O.S. and Solemdal, P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. *In*: Chambers, R.C. and Trippel, E.A. (eds.). Early life history and recruitment in fish populations. pp. 31-62. Chapman and Hall, New York.

Underwood, A.J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.* **19**: 513-605.

van Rooij, J.M., Bruggemann, J.H., Videler, J.J. and Breeman, A.M. 1995. Plastic growth of the herbivorous reef fish *Sparisoma viride:* field evidence for a trade-off between growth and reproduction. *Mar. Ecol. Prog. Ser.* **122**: 93-105.

Victor, B.C. 1982. Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus. Mar. Biol.* **71**: 203-208.

Victor, B.C. 1983. Recruitment and population dynamics of a coral reef fish. *Science.* **219**: 419-420.

Wallace, R.A. and Selman, K. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. *Amer. Zool*. **21**: 325-343.

Walters, C., Christensen, V. and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balanced assessments. *Rev. Fish Biol. Fish.* **7**: 139-172.

Warner, R.R. and Chesson, P.L. 1985. Coexistence mediated by recruitment fluctuations: A field guide to the Storage Effect. *Am. Nat.* **125**: 769-787.

Weatherley, A.H. and Gill, H.S. 1987. The study of fish growth. *In*: Weatherley, A.H. and Gill, H.S. (eds.) The Biology of Fish Growth. pp. 1-21. Academic Press, London.

Weber, D.D. and Ridgway, G.J. 1962. The deposition of tetracycline drugs in bones and scales of fish and its possiible use for marking. *The Progressive Fish-Culturist* **Oct 1962**: 150-155.

West, G. 1990. Methods of assessing ovarian development in fishes: a review. *Aust. J. Mar. Freshwat. Res.* **41**: 199-222.

Wheeler, J.F.G. 1953. Part I: The Bottom Fishes of Economic Importance. *In*: Wheeler, J.F.G. and Ommaney, F.D. (eds.) Report on the Mauritius-Seychelles Fisheries survey 1948-1949. Colonial Office Fishery Publications. **1:** 1-49.

Wicklund, R. 1969. Observations on spawning of the lane snapper. *Underwater Naturalist* **6**: 40.

Williams, A.J., Davies, C.R., Mapstone, B.D. and Russ, G.R. 2003. Scales of spatial variation in demography of a large coral-reef fish - an exception to the typical model? *Fish. Bull.* **101**: 673-683.

Wilson, C.A. and Nieland, D.L. 2001. Age and growth of red snapper, *Lutjanus campechanus,* from the northern Gulf of Mexico off Louisiana. *Fish. Bull.* **99**: 653-664.

Wootton, R.J. 1985. Energetics of reproduction. *In*: Tyler, P. and Calow, P. (eds.). Fish Energetics: new perspectives. Croom Helm, London.

Wright, A., Dalzell, P.J. and Richards, A.H. 1986. Some aspects of the biology of the red bass, *Lutjanus bohar* (Frosskal), from the Tigak Islands, Papua New Guinea. *J. Fish. Biol.* **28**: 533-544.
Yamamoto, K., Oota, I., Takano, K. and Ishikawa, T. 1965. Studies on the maturing process of the Rainbow Trout, Salmo gairdnerii irideus- I. Maturation of the ovary of a one-year old fish. *Bull. Jap. Soc. Sci. Fish.* **31**: 123-132.

Zar, J.H. 1999. Biostatistical Analysis. (4th ed.). Prentice-Hall Inc., New Jersey. 929pp.

Zhao, B. and McGovern, J.C. 1997. Temporal variation in sexual maturity in size at age of the vermillion snapper from the South Atlantic Bight. *Trans. Am. Fis. Soc.* **126**: 181-193.