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Spatial patterns in population biology of a large coral reef fish: What role can movement play?

Thesis submitted by
Ashley John Williams BSc(Hons)
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Abstract

Recent empirical studies have demonstrated significant spatial variation in the population biology of coral reef fish. The scales at which this variation occurs often depend on the species and processes that are examined. Most research on coral reef fish population biology has focussed on relatively small, site-attached species and results from such research often indicate variations in population biology at localised spatial scales, such as 10's to 100's or 1000's of meters. There have been fewer studies of large reef fish species and, consequently, little is known of the spatial patterns in population biology of large reef fish. Large reef fish are generally thought to be more mobile and have larger home ranges than small reef fish species. Therefore, the spatial scales that define intermixed populations of large reef fish may differ from those at which small reef fish vary. Furthermore, large reef fish species are often the targets for commercial and recreational fisheries. Information on the spatial patterns in population biology of harvested species will be of particular importance for fisheries management, as population responses to fishing pressure and different management strategies will vary among populations with different dynamics. Within this context, the broad objectives of this thesis were to:

1) Estimate a number of reproductive parameters, including spawning season, maturity schedules and size and age at sex change for the red throat emperor (*Lethrinus miniatus*) and compare the parameters between the northern and southern areas of the distribution of *L. miniatus* on the Great Barrier Reef (GBR);

2) Estimate rates of growth and mortality for *L. miniatus* and compare these parameters within and among three regions of the GBR over a temporal scale of five years; and

3) Explore the potential for large-scale movement of post-settlement *L. miniatus* to explain the observed spatial patterns in population age structures.

Estimates of population parameters for these objectives required reliable estimates of age. Accordingly, age estimates of *L. miniatus* were first validated using marginal increment analysis (MIA) and captive rearing of chemically tagged fish. The MIA was achieved by obtaining monthly samples of *L. miniatus* from commercial line fishing vessels from the northern and southern areas of the GBR. Fish that were chemically tagged and reared in an aquarium were also collected from a commercial fishing vessel. Opaque increments in the otoliths of *L. miniatus* were found to be deposited on an annual basis, but the timing of formation varied slightly between years and areas.

Reproductive parameters (Objective 1) were derived from the monthly samples collected from the commercial fleet. A peak spawning season was observed between July and October in both the northern and southern areas of the distribution of *L. miniatus* on the GBR. The proportion of spawning females, however, was greater in the northern area than in the southern area. The size at which *L. miniatus* changed sex from female to male was significantly larger in the southern area, but there were no spatial differences in the age at sex change. The size and age at maturity were estimated to be 180 mm FL and 1.2 years respectively, but data were insufficient to allow spatial comparisons of these parameters.

Spatial patterns in growth and mortality of *L. miniatus* (Objective 2) were estimated from annual samples of populations of *L. miniatus* from four reefs within three regions of the GBR (Townsville, Mackay and Storm Cay) over a period of five years. Growth rates were found to vary among years but this variation was consistent among regions and reefs. Mortality rates were consistent among cohorts within each region and reef. Rates of growth and mortality were relatively similar at the spatial scale of individual reefs within regions but differed significantly among regions. This regional variation was consistent over years. The Townsville (northern-most) region was characterised by the smallest maximum size, and lowest rates of mortality. In contrast, the Mackay region was characterised by the largest maximum size, and highest rates of mortality. Rates of growth and mortality for the Storm Cay (southern-most) region were intermediate between the other two regions.

The potential for migration of *L. miniatus* to contribute to the observed patterns in population parameters (Objective 3) was explored by developing an age structured model for *L. miniatus* populations from the Townsville, Mackay and Storm Cay regions of the GBR, using the empirical data collected from the annual regional samples. Model age structures were compared with observed age structures to determine the net movement that would be required to explain the significant regional variations in age structure. The model predicted significant immigration to the Townsville region of fish aged from three to 10 years and significant emigration of fish aged three and four years from the Mackay region. Predicted net movement in the

Storm Cay region was negligible, although immigration of a small number of seven year old fish was predicted under some model scenarios. A number of hypotheses that might explain the model results are discussed. The results from this thesis highlight the need to determine the spatial scales at which all demographic processes operate, including movement, to obtain reliable estimates of population structure and provide the most useful information with which to optimise harvest strategies for reef fish.

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Chapter 1. General Introduction

The world's human population continues to increase at an exponential rate, particularly in developing countries (United Nations 2001). Consequently, demands on renewable resources, including food, are also increasing (FAO 2003). For centuries humans have harvested the world's oceans for valuable food resources, using numerous methods of fishing. Increasing pressure on our ocean resources in more recent decades, however, has resulted in most fish stocks being declared fully exploited, over exploited, or depleted (FAO 2003). Consequently, now more than ever, it is critical that we improve our management of marine resources if they are to be sustained for future generations.

1.1. Coral reef fisheries

Coral reefs support many important commercial, recreational and subsistence fisheries, particularly around the large population centres of the islands of the Caribbean and south-east Asia. In these areas, rapidly expanding populations coupled with inadequate management have placed increasing pressure on reef fish populations, and many fisheries are now considered to be over-exploited (Russ 1991, Munro 1996, Sale 2002). Concerns of over-exploitation of coral reef fisheries are not limited to developing regions however. In the southern Atlantic Ocean, off the coast of south-eastern United States, fishing has reduced stocks of reef fish to very low levels of spawning stock biomass (e.g. 5-10% of original size, Plan Development Team 1990). Within the Great Barrier Reef (GBR) line fishery there is concern about the impact of present fishing levels on the sustainability of the fishery (Williams and Russ 1994, Mapstone et al. 1997, Williams 2002). Clearly, there is a need to implement more effective management strategies for the sustainability of coral reef fisheries worldwide.

The successful management of coral reef fisheries has been inhibited by several factors. Controls over catch and effort have been difficult to implement because most coral reef fisheries, particularly in developing countries, are dominated by subsistence or artisanal fishing in situations with few alternative employment opportunities or sources of protein (Russ 1991, Munro 1996). Fishing effort is usually unevenly distributed spatially, and often catches are landed across a large number of small sites spread across a wide area. This spatial complexity in fishing activity makes it difficult to obtain essential catch and effort data needed for basic stock assessments (Munro 1987) or to police fishing regulations. Most coral reef fisheries are multispecific and multigear, targeting very many species with gears including hook and line, spears, traps, nets, poisons and explosives (Dalzell 1996). Furthermore, the funding for research and management of coral reef fish has been relatively low compared with larger, more economically important fisheries (Russ 1991).

The complexity of managing coral reef fisheries is exacerbated by the diverse range of life histories of coral reef fish (Sale 1991), and their inter and intra-specific interactions. For example, relatively small species such as caesionids that have high natural mortality rates and a maximum longevity of only 2-3 years (Carpenter 1988) may be harvested in the same fishery as larger species such as epinepheline serranids and lutjanids that have relatively low natural mortality rates and potential longevities in excess of 30 years (Coleman et al. 1999, Huntsman et al. 1999). Sexual strategies may also vary among species harvested in the same fishery. For example, serranids are typically protogynous hermaphrodites, changing sex from female to male, while lutjanids are gonochoristic, remaining the same sex throughout life (Sadovy 1996). Clearly, population dynamics are likely to differ among target species, as is their response to varying fishing patterns (Dugan and Davis 1993). In order to improve management of coral reef fisheries it is important to understand the dynamics of reef fish populations, the processes that control them, and their likely responses to different levels of fishing pressure. Unfortunately, research on the ecology and population dynamics of reef fish in the past generally has been focussed on non-harvested rather than harvested species, and consequently our knowledge of the dynamics of exploited reef fish populations is relatively limited (Roberts 1996).

1.2. Population dynamics of coral reef fish

Research on coral reef fish during the past two decades has focussed on the relative importance of recruitment strength and post-settlement processes in structuring populations (see reviews by Doherty 1991, Hixon 1991, Jones 1991, Doherty 2002, Hixon and Webster 2002, Jones and McCormick 2002). Consequently, a large amount of research on coral reef fish has focussed on estimates of settlement to benthic populations and the abundance of newly settled post-recruits. There has been far less research on the structure of juvenile and adult populations, and the processes structuring these populations have usually been inferred from patterns of distribution and abundance, rather than estimated directly. In an attempt to redress this imbalance, Jones (1991) advocated a more comprehensive approach, encompassing the estimation of age, size and sex distributions, and the estimation of rates of demographic processes such as growth, mortality and movement that underlie these distributions.

Prior to the early 1980's it was generally considered difficult to determine the age of coral reef fish (Munro 1983), and consequently estimates of growth and mortality were often based on length frequency data (Munro 1983, Pauly 1984, 1987). More recently, the recognition that reliable age estimates of coral reef fish could be obtained from otoliths (Fowler 1995) has facilitated the estimation of age-based population parameters such as growth and mortality for a range of coral reef fish species (e.g. Ferreira and Russ 1992, 1994, Doherty and Fowler 1994, Choat and Axe 1996, Choat et al. 1996, Newman et al. 1996*a,b*, Choat and Robertson 2002, Kritzer 2002, Williams et al. 2003). Direct measurements of movement rates in reef fish are uncommon, although there is increasing evidence that post-settlement movement of reef fish can have a major influence on the size and structure of local populations (Robertson 1988, Warner 1995, Rakitin and Kramer 1996, Lewis 1997).

1.3. Spatial patterns in population biology of coral reef fish

There has been some convergence recently in the dichotomous hypotheses about the processes determining the size and structure of coral reef fish populations (Doherty 2002, Hixon and Webster 2002, Jones and McCormick 2002). This has occurred mainly due to greater appreciation of the importance of spatial scale in ecological processes (Sale 1998). The result has been a more pluralistic view that all processes are likely to be important at some spatial scale(s), and that the appropriate spatial scale(s) to study will depend on the questions being asked and the species being studied. For example, the factors important in determining the survival of a relatively sedentary species, such as predation and habitat availability, may operate on a relatively local spatial scale (e.g. small patch reefs). The important factors determining the survival of a more mobile species are likely to be operating on a much larger spatial scale (e.g. whole reefs). There is little evidence to suggest that any single process is entirely responsible for structuring a fish population, and in fact, such a scenario is highly unlikely (Jones 1991, Caley et al. 1996). The general consensus now is for a multi-scale approach to reef fish studies, in order to gain a holistic understanding of reef fish population dynamics (Jones 1991, Caley et al. 1996, Sale 1998, Sale 2002).

Recent empirical studies have demonstrated significant spatial variation in population biology of coral reef fish. For example, variation has been observed over spatial scales of more than 1000 km (e.g. Meekan et al. 2001) to 100's km (Adams et al. 2000, Williams et al. 2003), and even at localised scales of less than 10 km (e.g. Pitcher 1992, Choat and Axe 1996, Hart and Russ 1996). Most studies examining spatial variation in population biology of reef fish, however, have been limited to single spatial scales. Multi-scale studies of reef fish population biology have appeared in the literature only recently (e.g. Adams et al 2000, Gust et al. 2002, Kritzer 2002, Williams et al. 2003). These multi-scale studies have demonstrated how the relative importance of different population parameters varies at different spatial scales.

The significant spatial variation demonstrated for reef fish populations has important implications for fisheries management. Traditional fisheries management defines a fish stock as a homogeneous population of fish with uniform population parameters. Clearly, the inherent spatial complexity of coral reefs and the observed spatial patterns in population parameters at a range of spatial scales demonstrates that the traditional view of fisheries management may not always be applicable to coral reef fish. More recently, the improved knowledge of the spatial structure of several exploited temperate species has highlighted the importance of applying fisheries management at spatial scales relevant to the underlying spatial scale of population processes (Smedbol and Stephenson 2001). At face value, spatially explicit management strategies hold some appeal for coral reef fisheries. The success of such management strategies, however, is underpinned by the accuracy and detail of the spatial information gathered from the harvested population (Smedbol and Stephenson 2001) and the capacity to regulate fisheries in spatially structured ways. It is unlikely that sufficiently detailed information is available for exploited populations of coral reef fish at this stage to devise spatially varying harvest strategies. It will be important, therefore, to obtain more empirical information on the spatial patterns in coral reef fish population parameters to determine the spatial scales that are important in structuring populations of coral reef fish if spatially explicit management is to be considered seriously.

1.4. The red throat emperor

The focal species of this thesis is the red throat emperor *Lethrinus miniatus*. The distribution of *L. miniatus* is relatively restricted compared with other members of the family Lethrinidae. Populations of *L. miniatus* are found only in waters around Australia, New Caledonia, Norfolk Island and the Ryuku Islands of southern Japan (Carpenter and Allen 1989). *L. miniatus* is a generalist predator consuming a wide range of fishes and invertebrates (Walker 1978). *L. miniatus* generally inhabits coral reefs (Carpenter and Allen 1989), but is also commonly encountered on deeper shoal areas between reefs to depths of more than 100 m (Newman and Williams 1996). The most abundant populations of *L. miniatus* are found on the east coast of Australia, where they are restricted to the southern half of the GBR from approximately 18°S to

24.5°S. *L. miniatus* is an important commercial species in the line fisheries of the GBR (Mapstone et al. 1996), Norfolk Island (Church 1995) and New Caledonia (Carpenter and Allen 1989). In the GBR line fishery, *L. miniatus* contributes approximately 20% (~1000 t) to the combined annual commercial and recreational reef fish catch (Mapstone et al. 1996, Higgs 2001).

The movement patterns of *L. miniatus* are unknown, but lethrinids are generally considered to be one of the more mobile families of coral reef fish (Carpenter and Allen 1989, Jones 1991). Bean et al. (2003) described the reproductive development of *L. miniatus* from the GBR and demonstrated that protogyny (sex change from female to male) was a likely sexual pathway for at least a proportion of the population. The spawning season for *L. miniatus* has been reported to occur predominantly during July and August in the central GBR (Walker 1975) and September to November in the far southern GBR (Brown et al. 1994). Growth and longevity data for *L. miniatus* from the GBR suggest a maximum size of around 600 mm fork length (FL) and maximum age of at least 20 years (Brown and Sumpton 1998, Williams et al. 2003). Both these studies also indicated significant regional differences in age, growth and mortality of *L. miniatus* populations on the GBR, but both studies only provided spatial comparisons for a single point in time. If persistent, such patterns may reflect regional differences in productivity, responses to present or historical harvest patterns, or the existence of separate isolated populations (stocks) (Williams et al. 2003). Any of these alternative explanations has important implications for the assessment of the stock(s), the potential effects of fishing on the stock(s), management of the fishery and conservation of regional biodiversity on the GBR. It is unclear whether these spatial patterns are consistent over time scales relevant to management. Furthermore, there have been no detailed spatial comparisons of *L. miniatus* reproductive parameters, such as spawning season, size and age at maturity, and size and age at sex change. The central goal of this thesis was to examine the temporal consistency of spatial patterns in population biology of *L. miniatus* on the GBR and explore spatial patterns in the reproductive biology of *L. miniatus*.

1.5. Thesis objectives

This thesis has three primary objectives:

1) To estimate various reproductive parameters of *L. miniatus* and determine the variation in these parameters at a large (regional) spatial scale (Chapter 4).
2) To determine the variation in growth and mortality of *L. miniatus* populations at small (among individual reefs) and large (regional) spatial scales (Chapters 5 and 6).
3) To explore the potential of large-scale movement of *L. miniatus* for explaining the observed spatial patterns in population parameters (Chapter 7).

Demographic parameter estimates for fish populations must be based upon reliable estimates of age. Accordingly, in Chapter 3 I report validation of age estimates obtained from otoliths of *L. miniatus*, as a prerequisite to the work reported in subsequent chapters.

Chapter 2. General Methods.

2.1. Introduction

This thesis is based on two distinct data sets. The first data set was compiled from fishery *dependent* samples (fleet samples) of *L. miniatus* collected from commercial line fishing vessels operating within the GBR World Heritage Area (GBRWHA). These data form the basis of Chapters 3 and 4. The second data set was compiled from fishery *independent* surveys (catch surveys) which were part of the Cooperative Research Centre for the GBR World Heritage Area (CRC Reef) Effects of Line Fishing (ELF) Experiment (Mapstone et al. 1996, Davies et al. 1998, Mapstone et al. 1998, Campbell et al. 2001, Mapstone et al. 2003). These data underpin the work presented in Chapters 5, 6 and 7. This methods chapter describes in detail the collection of samples for each of these data sets and, where common to more than one chapter, the methods used to process samples. Additional chapter-specific methods and analytical procedures are provided in the relevant following chapters.

2.2. Field collection of samples

2.2.1. Fleet samples

A total of 1767 samples of *L. miniatus* were collected from the fishery dependent sampling program. Samples were collected in the form of frozen fish frames (head, skeleton and viscera) from 14 commercial line fishing vessels operating from approximately 18°S to 22.5°S within the Central and Mackay/Capricorn sections of the GBR (Figure 2.1). Samples were collected monthly from December 1998 to December 2000 from a total of 91 reefs.

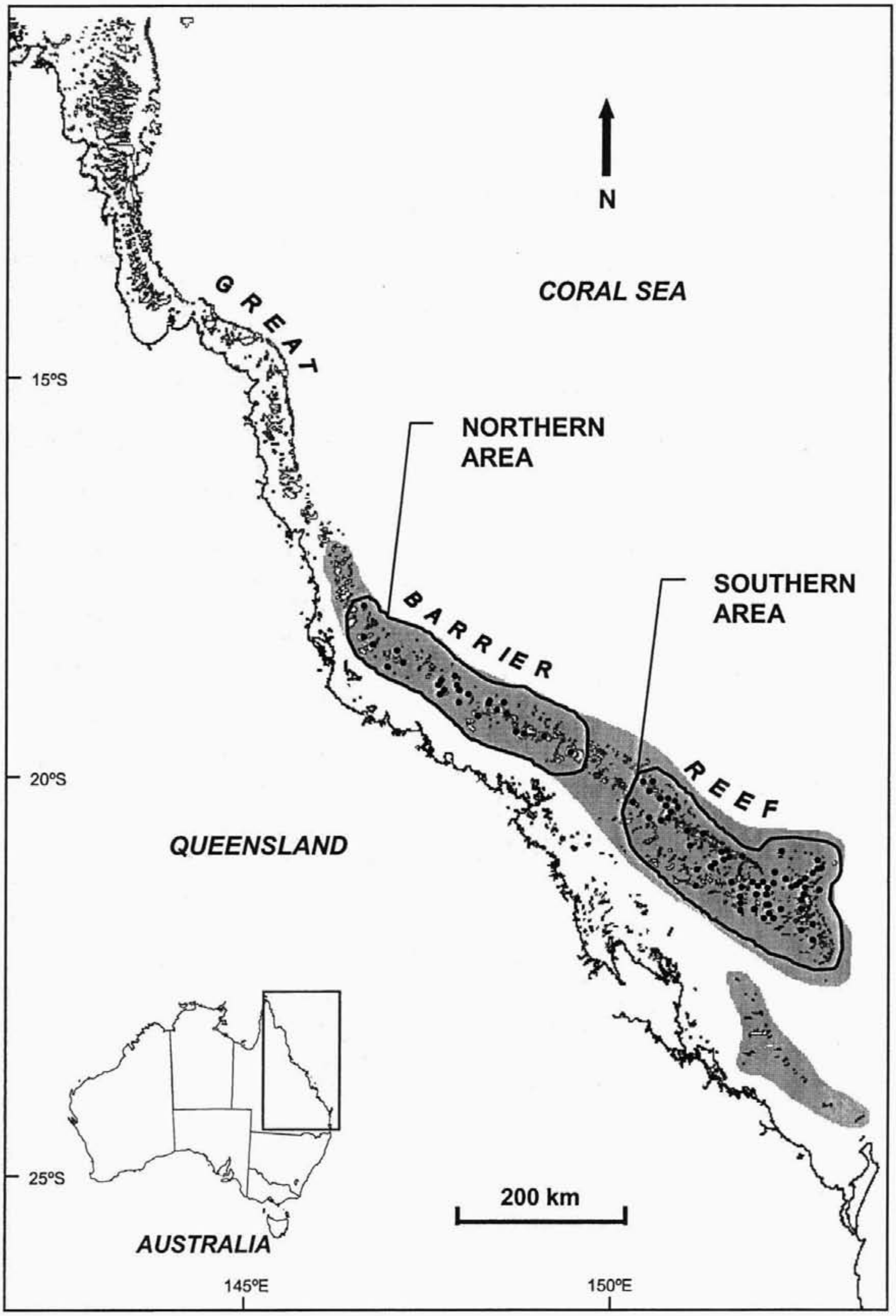

Figure 2.1. Distribution of *Lethrinus miniatus* on the Great Barrier Reef (shaded area) and the location of reefs sampled (•) within the northern and southern areas from which *L. miniatus* were collected by commercial line fishing vessels.

Samples collected north and south of 20°S latitude were divided into 'northern' and 'southern' areas respectively (Figure 2.1). These areas were treated as discrete for several reasons. First, there was a clear separation (of approximately 100km) between the two nearest reefs sampled on the north and south sides of 20°S latitude. Second, 20°S latitude marks a significant change in the structure of the reefs on the GBR[1], and third this latitude is approximately the midpoint of the distribution of *L. miniatus* on the GBR. A total of 726 fish from 27 reefs were sampled from the northern area and 1041 fish were taken from 64 reefs in the southern area. The large number of fish in each area enabled reliable spatial comparisons of various population parameters between *L. miniatus* from the northern and southern areas.

After thawing the fish frames, the fork length (FL) of all samples was measured to the nearest millimetre and sagittal otoliths were removed and cleaned of any residual material, then dried and weighed to the nearest 0.1mg. Gonads were removed and the sex determined for each sample macroscopically. Gonads were preserved in formaldehyde acetic acid calcium chloride (FAACC, Winsor 1984). After fixation, each ovary or testis was dried of residual FAACC and weighed to the nearest 0.01g.

2.2.2. Effects of Line Fishing (ELF) Experiment catch surveys

The experimental design of the CRC ELF Experiment consists of 24 reefs spread over 7° latitude from the Northern GBR (Cape Flattery) to the Southern GBR (Swain

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[1] South of 20°S the reefs on the GBR are typically located further from the Queensland coastline and consequently further from terrestrial influences than reefs north of 20°S (Figure 2.1). The reefs south of 20°S are also spread over a larger distance across the continental shelf than reefs north of 20°S (Figure 2.1). Finally, the outer-shelf reefs between 20°S and 21°S are located much closer together than outer-shelf reefs between 18°S and 20°S forming what is known as the 'hardline' of reefs.

Reefs). The 24 reefs are grouped into four clusters of six adjacent reefs, located in four different regions of the GBR: around Lizard Island (~15°S), off Townsville (~18.5°S), off Mackay (~20.5°S), and around Storm Cay (~21.5°S) (Figure 2.2). The research program was initiated in 1995 and will conclude in 2006. Prior to 1995, four reefs in each region had been zoned Marine National Park B by the Great Barrier Reef Marine Park Authority (GBRMPA) and closed to all forms of fishing for more than eight years (hereafter 'closed' reefs). The other two reefs in each region were zoned General Use B and had always been open to line and spear fishing (hereafter 'open' reefs). Two of the closed reefs in each region represented the 'closed control' reefs of the ELF Experiment and will remain closed for the duration of the research program. The other four reefs in each region (2 closed, 2 open) represented the 'treatment' reefs of the ELF Experiment. In March of 1997, one open and one closed treatment reef in each region were subjected to increased (manipulative) fishing pressure. These reefs were closed to fishing in March 1998 for a period of five years. This manipulation of fishing pressure was repeated for the remaining treatment reefs (1 open, 1 closed) in each region in March 1999 with previously open reefs being closed and previously closed reefs reclosed in March 2000 (Mapstone et al. 1998, Mapstone et al. 2003).

Samples of *L. miniatus* were collected from the three southern regions of the ELF Experiment (Townsville, Mackay and Storm Cay) (Figure 2.2). In relation to the areas defined for the commercial fleet samples, the Townsville region is located within the northern area whilst the Mackay and Storm Cay regions are located within the southern area (Figures 2.1 and 2.2). No samples were collected from the Lizard Island region of the ELF Experiment as *L. miniatus* is rarely encountered north of Cairns on the GBR (17°S). Samples of *L. miniatus* used for this thesis were collected during annual ELF catch surveys between September and November in each year from three (1997-1999) or four (1995-1996) closed reefs in each region.

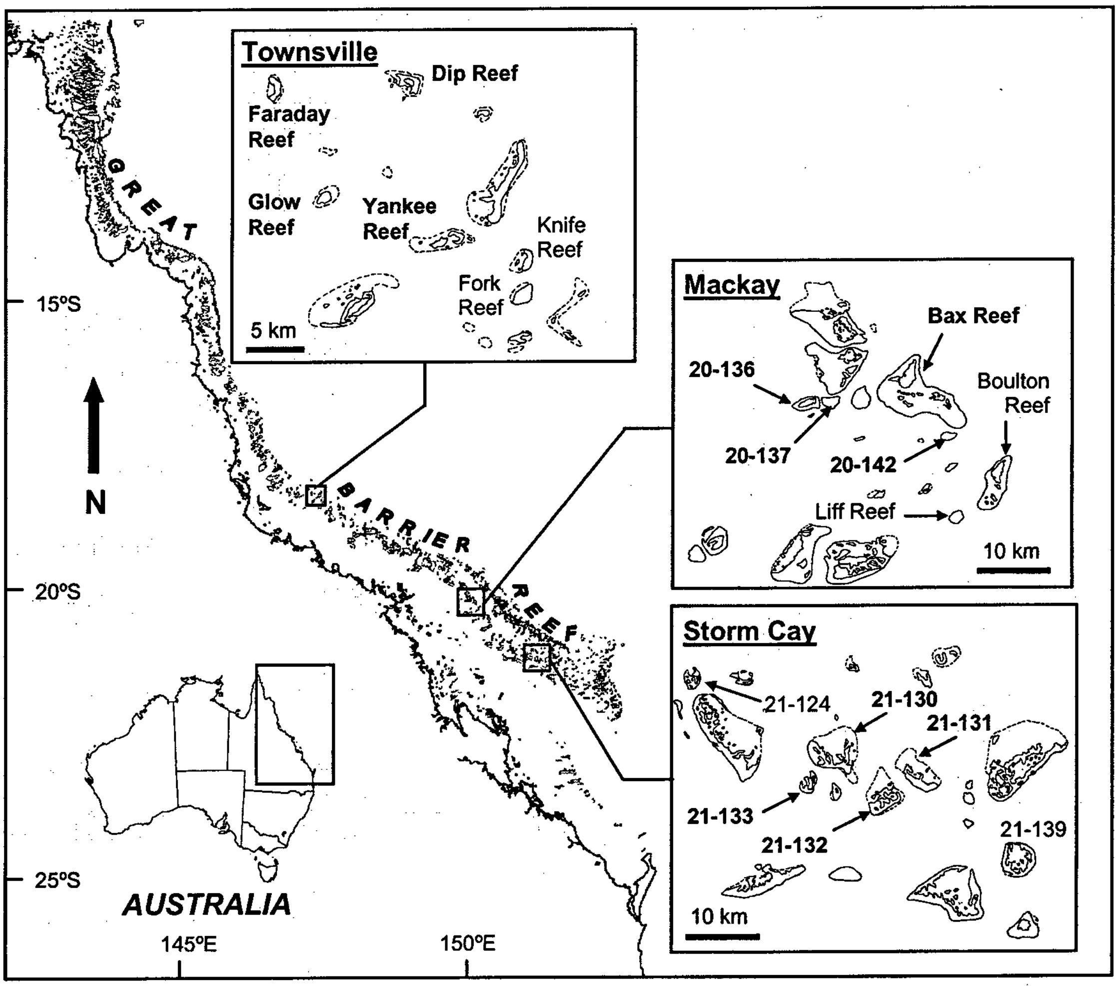

Figure 2.2. Location of reefs sampled for *Lethrinus miniatus* within three regions of the Great Barrier Reef as part of the Effects of Line Fishing Experiment. Maps of reefs indicate the relative position and size of the six reefs in the experiment in each region. Reefs named in bold are those from which samples of *L. miniatus* were used for this thesis.

Each reef was sampled for one day in each annual survey by four commercial line fishers using standardised line fishing gear consisting of size 8/0 hooks, 36kg breaking strain monofilament line, and pilchard baits (Davies et al. 1998, Mapstone et al. 2003). Each fisher operated under the supervision of a researcher and sampling effort was kept consistent among reefs by dividing the perimeter of each reef into 6 approximately equal size 'blocks' and distributing fishing effort evenly among blocks and across two depth strata (<12m, 12-40m) within each block. Fork length (FL) of all fish was measured to the nearest millimetre immediately upon capture and whole body weight was weighed to the nearest 10g on the day of capture. Sagittal otoliths were removed on return of fish to the laboratory, cleaned of any residual material, dried and weighed to the nearest 0.1mg.

2.3. Sample processing

2.3.1. Otolith processing and age determination

The right otolith was chosen to estimate the age of all fish unless it was missing or damaged, in which case the left one was used. Otoliths from fleet samples of *L. miniatus* were used to validate the periodicity and timing of increment formation using marginal increment analysis (Chapter 3). Consequently it was necessary to section these otoliths to provide a consistent flat horizontal plane for increment measurements. Otoliths to be sectioned were embedded in epoxy resin and cut transversely, adjacent to the anterior side of the nucleus, using a Buehler Isomet low-speed saw. The posterior portion of the otolith was retained and mounted on a glass microscope slide with Crystal Bond 509 adhesive. A second transverse cut adjacent to the posterior side of the nucleus resulted in a thin section, incorporating the otolith nucleus, remaining on the slide. Otolith sections were then ground on 800- and 1200-grade sandpaper to remove saw marks and a single drop of immersion oil was placed on sections to fill surface irregularities. Otolith sections were examined under a stereo dissecting microscope with reflected light and a black background. Counts of opaque increments were made from the nucleus to the proximal surface, along the dorsal margin of the sulcus acousticus (Figure 2.3). The opaque increment closest to the margin of the otolith was only included in the count when the reader interpreted the increment as completely formed and with discernible translucent material between that opaque increment and the otolith margin.

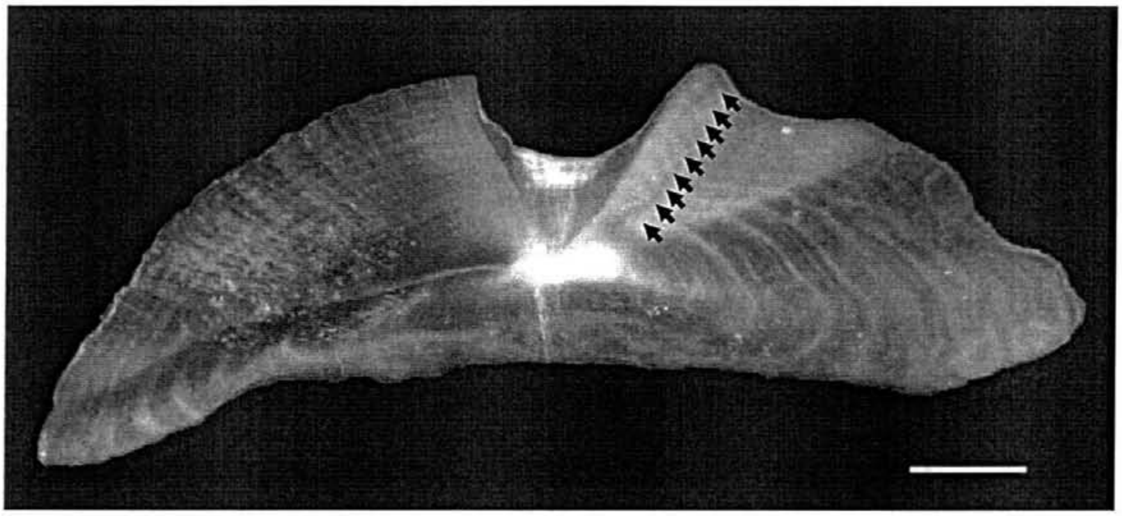

Figure 2.3. Section of a sagittal otolith of *Lethrinus miniatus* estimated to have been nine years old from Glow Reef in the Townsville region of the Great Barrier Reef. Arrowheads indicate annual opaque increments and the path along which they were counted. Scale bar = 1mm.

Williams et al. (2003) demonstrated that age estimates from whole otoliths of *L. miniatus* on the GBR did not differ significantly from age estimates from sectioned otoliths. The estimation of age from whole otoliths also requires significantly less time and expense than using sectioned otoliths. Accordingly, whole otoliths were used to estimate ages of *L. miniatus* collected from ELF catch surveys, as only estimates of age were required from these otoliths. These age estimates were used to estimate rates of growth (Chapter 5) and mortality (Chapter 6) and provided age frequency data for an age-structured population model (Chapter 7). Otoliths to be read whole were placed in a small black dish of immersion oil and examined under reflected light using a stereo dissecting microscope. Counts of opaque increments were made from the nucleus to the dorso-posterior edge, on the convex face of the otolith (Figure 2.4). Similar to counts from sectioned otoliths, the opaque increment closest to the margin of whole otoliths was only counted if completely formed.

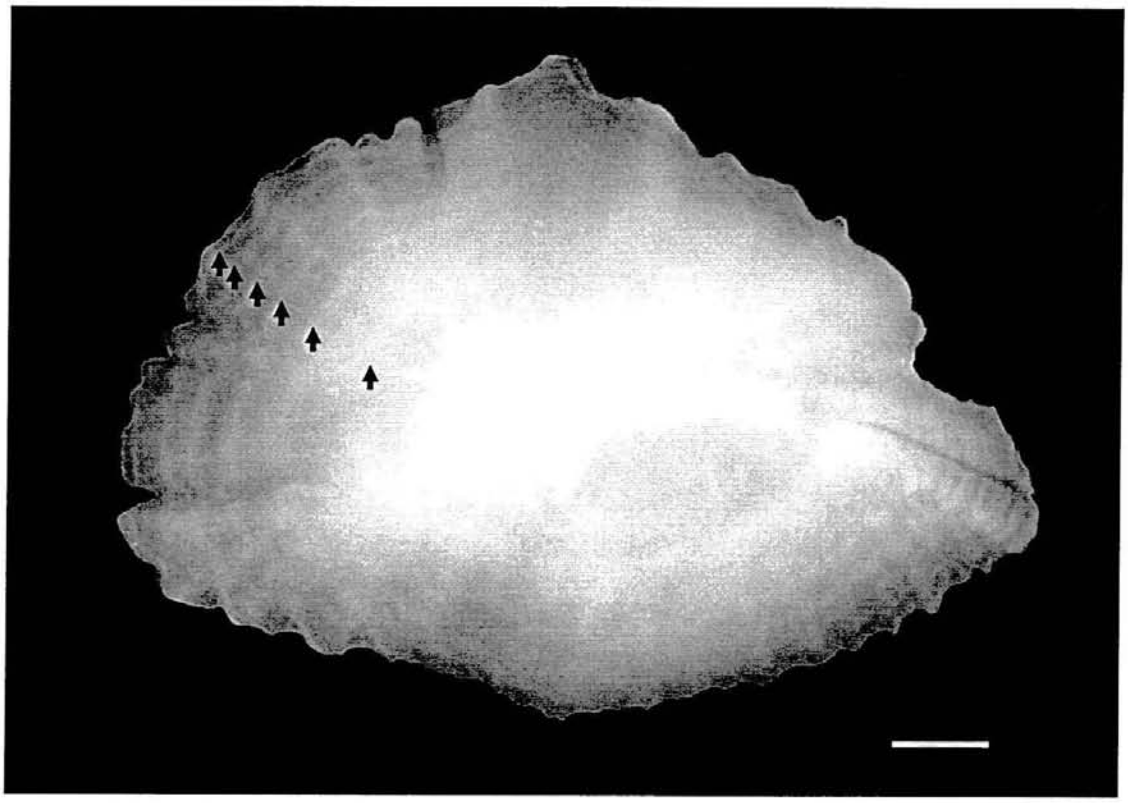

Figure 2.4. Whole sagittal otolith of *Lethrinus miniatus* estimated to have been six years old from Reef 21-133 in the Storm Cay region of the Great Barrier Reef. Arrows indicate annual opaque increments and the path along which they were counted. Scale bar = 1mm.

The precision of age estimates was calculated using the index of average percent error (IAPE, Beamish and Fournier 1981) for three readings of each otolith from a random sub-sample ($n = 355$) of whole and sectioned otoliths. The IAPE is defined as:

$$IAPE = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{\left|X_{ij}-X_{j}\right|}{X_{j}}\right]\times 100 \qquad (2.1)$$

where:

N is the total number of fish for which ages were estimated;

R is the number of times the age of each fish is estimated;

X_{ij} is the ith age estimate of the jth fish; and

X_j is the average age estimate for the jth fish.

The IAPE was very low for whole (1.6%) and sectioned (1.4%) otolith readings, indicating that otolith readings for both methods were highly repeatable. Accordingly, thereafter all whole and sectioned otoliths were read in random order only once by a single reader (AW) with no prior knowledge of collection date, location or size of fish.

2.3.2. Gonad histology

Histological sections of gonads were used to assign sex and reproductive stage of *L. miniatus* samples collected from the commercial fleet. This information, together with gonad weight, was used to estimate the spawning season, size and age at maturity, size and age at sex change and sex ratio (Chapter 4). Medial samples from all gonads were used for histological examination, as development along the length of *L. miniatus* gonads is consistent (Bean et al. 2003). Transverse sections were taken from the medial sample of one gonad lobe and placed in histological cassettes and stored in 70% alcohol for 2 hours prior to transferring to an automatic tissue processor. Cassettes were then placed in a Labec Vacuum Setup for 30 minutes to completely remove all water from the tissue and infiltrate with paraffin wax (Winsor 1994). Tissue sections were embedded in paraffin and sectioned at 5μm thickness. All sections were stained using Myer's Haematoxylin and Young's Eosin-Erythrosin and mounted with DPX resin (Winsor 1994). Sections were read in random order without prior knowledge of the location of capture or the size or age of the fish.

2.4. Data storage and analysis

Data collected from the fleet samples were entered into an MS EXCEL spread sheet and compared with original data sheets to check for errors in data entry. Data collected from catch surveys were entered independently on two occasions into an MS ACCESS database and then compared to locate errors in data entry as part of quality control procedures for the ELF Project (Mapstone et al. 2003). All data were imported into SPSS for statistical analysis and all figures were produced in MS EXCEL.

Chapter 3. Validation of the periodicity and timing of opaque increment formation in the otoliths of *Lethrinus miniatus* from the Great Barrier Reef.

3.1. Introduction

Information on the age composition of fish populations forms the basis for understanding population biology, assessing stocks and developing management strategies for exploited stocks (Gulland 1988, Hilborn and Walters 1992). Techniques for age estimation usually are based on counts of periodic growth increments in calcified structures such as scales, vertebrae and otoliths. It is essential, however, that the period of increment formation in such structures is validated in order to verify the accuracy of age estimates from them (Beamish and McFarlane 1983, Campana 2001). Inaccurate age estimates may result in biased stock assessments and, possibly, overexploitation of stocks or potential forgone yield (Beamish and McFarlane 1983, Lai and Gunderson 1987, Campana 2001).

There are many techniques available for the validation of age periodicity in age-related structures, each with relative advantages and disadvantages (see review by Campana 2001). A frequently employed and rigorous technique is the mark-release-recapture of chemically tagged wild fish. This method results in a precise temporal reference mark in otoliths (and other calcified structures) that can be related to naturally formed increments in the otolith and used to determine the periodicity of increment formation. This method is typically cost and labour intensive, however, and often suffers from low recapture rates, particularly for highly mobile species. Edge type analysis (ETA) and marginal increment analysis (MIA) (Panfili and Morales-Nin 2002) are perhaps the most widely used techniques, particularly for determining the timing of otolith increment formation, since they are relatively inexpensive to implement and there is not the necessity to recapture individuals from the field (Campana 2001). ETA requires classifying the otolith margin (edge) as either opaque or translucent and examining temporal trends in the proportion of each edge type to determine the time of opaque increment formation. However, ETA provides only ordinal data on the population and does not provide a measure of variability in growth of the otolith margin among individual fish. MIA, on the other hand, requires direct measurements of otolith increments and the spacing between them from individual fish. This provides data for estimates of individual variability in the position and timing of increment formation within and between populations. MIA involves an examination of the seasonal variation in the distance between the most recent complete increment and the otolith margin, with changes in that distance providing an estimate of the timing and periodicity of increment formation.

The mechanism regulating cyclic deposition of increments in the form of opaque and translucent increments in otoliths is not well understood (Beckman and Wilson 1995). It is commonly assumed to be related to seasonal variation in somatic growth and environmental factors (Campana 1999). The formation of otolith increments has been correlated with a number of factors, however, including water temperature (Thomas 1983, Schramm 1989, Pearson 1996), food availability (Schramm 1989, Fowler 1990), photoperiod (Morales-Nin and Ralston 1990) and reproductive activity (Morales-Nin and Ralston 1990, Hostetter and Munroe 1993). A number of studies have demonstrated significant variation in the timing of otolith increment formation among ages (Hyndes et al. 1992, Fletcher and Blight 1996, Fowler and Short 1998, Vilizzi and Walker 1999, Pilling et al. 2000), years (Fletcher and Blight 1996, Pearson

1996, Cappo et al. 2000), and locations (Pearson 1996, Smith and Deguara 2003). Such variation in the timing of increment formation is likely to obscure annual trends in increment formation when pooling samples among ages, years and locations (Hyndes et al. 1992, Campana 2001). It is important, therefore, to explicitly examine such variability when validating the periodicity and timing of increment formation in otoliths by dividing the sample by age, year and location where possible. Failure to account for this variability in otolith increment formation may lead to biased estimates of the timing of increment formation.

The apparent lack of seasonal variation in environmental cues that might cause periodic changes in otolith structure at tropical latitudes led to the widespread opinion that it was difficult, if not impossible, to determine the age of tropical fish on the basis of annual increments in otoliths (Munro 1983, Campana and Neilson 1985, Longhurst and Pauly 1987, Gulland 1988). Many recent studies, however, have used either MIA or mark-release-recapture of chemically tagged wild fish to successfully validate both daily and annual increments in otoliths of a number of species of tropical reef fish from a range of families, including serranids (Ferreira and Russ 1992, 1994, Mosse 2001), lutjanids (Newman et al. 1996b, Cappo et al. 2000, Burton 2001, 2002), haemulids (Al-Husaini et al. 2001), lethrinids (Hilomen 1997, Pilling et al. 2000, Grandcourt 2002), pomacentrids (Fowler 1990, Fowler and Doherty 1992), scarids (Lou and Moltschaniwskyj 1992, Choat et al. 1996), gobies (Hernaman et al. 2000), and acanthurids (Lou and Moltschaniwskyj 1992, Choat and Axe 1996, Hart and Russ 1996).

There have been two previous attempts to validate the periodicity of increments in *L. miniatus* otoliths using the technique of mark-release-recapture of chemically tagged wild fish. Both have proven to be unsuccessful. Only a single fish was recaptured by Brown et al. (1994), after less than 12 months at liberty. The recapture of tagged fish in the wild is likely to be a difficult validation technique for *L. miniatus* due to the remarkably low recapture rates for the species from previous tagging studies (Brown et al. 1994) and the potential dispersive movements of the species (Brown et al. 1994, Chapter 7). Consequently, Brown and Sumpton (1998) used ETA to determine the timing of increment formation in the otoliths of *L. miniatus* from the far southern region of the GBR. The results from their work can not be applied to *L. miniatus* of all ages in all locations, however, as their data were pooled across age classes and locations. Furthermore their data were limited to only 10 months within a single year from the southern region of the GBR. A minimum of two years of data is considered necessary to detect annual periodicity in otolith increments using either ETA or MIA (Campana 2001).

To convincingly validate the relationship between the periodicity of increments in otoliths and fish age, three criteria must be fulfilled: 1) otoliths must continue to grow throughout the lifespan of individual fish; 2) otoliths must have an internal structure of discernible growth increments that can be interpreted consistently and unambiguously; and 3) this internal structure must correspond to a regular time scale (Beamish and McFarlane 1983, Fowler 1990). Williams et al. (2003) have shown that *L. miniatus* otoliths fulfil the first two of these criteria by demonstrating a positive linear relationship between number of distinct opaque increments in otoliths and otolith weight, and a high level of precision of counts of opaque increments from readings of both whole and sectioned otoliths. The aim of this chapter was to address the third criterion by validating the periodicity and timing of opaque increment formation in *L. miniatus* otoliths, using MIA and captive rearing of chemically tagged fish. The effects of location, year and age on the periodicity and timing of opaque increment formation also were examined with the MIA.

3.2. Methods

3.2.1. Marginal increment analysis

Samples for marginal increment analysis (MIA) were collected from two areas representing the northern and southern distribution of *L. miniatus* on the GBR by the commercial line fishing fleet as described in Chapter 2 (See Figure 2.1). While whole *L. miniatus* otoliths are reliable structures for total counts of opaque increments (Williams et al. 2003), increment measurements from whole *L. miniatus* otoliths would not be practical nor accurate due to the irregular surface of whole otoliths (Hyndes et al. 1992). Accordingly, sagittal otoliths from all fleet samples were sectioned and age estimates obtained using the methods described in Chapter 2.

Measurements for MIA were made along the same axis in which counts of opaque increments were made (Figure 3.1) using the image analysis software package ImageTool (University of Texas Health Science Center, San Antonio, Texas, USA). Otoliths were measured in random order with no prior knowledge of collection date, location or fish age to eliminate potential bias in increment measurements (Fletcher and Blight 1996). The marginal increment (MI) and previous increment (PI) were measured for each sectioned otolith. The MI is defined here as the distance between the margin of the otolith and the distal edge of the last-completed opaque increment, and the PI is the distance between the distal edges of the outermost two opaque increments (Figure 3.1). The distal edge of opaque increments was chosen as a reference point for increment measurements to allow the timing of opaque increment completion to be determined, as only completed opaque increments were included in counts for age estimation. Marginal increment ratio analysis (MIRA) (e.g. Vilizzi and Walker 1999) was used to express the MI of each otolith as a percentage of the PI by calculating the marginal increment ratio (MIR) using: MIR = MI/PI * 100. The MIR is therefore a measure of the proportion of otolith growth since the last increment was formed relative to the previous year of otolith growth. An assumption of the method is that the widths of outermost two increments are relatively similar, such that when the forming increment is complete, the MIR will be ~100%.

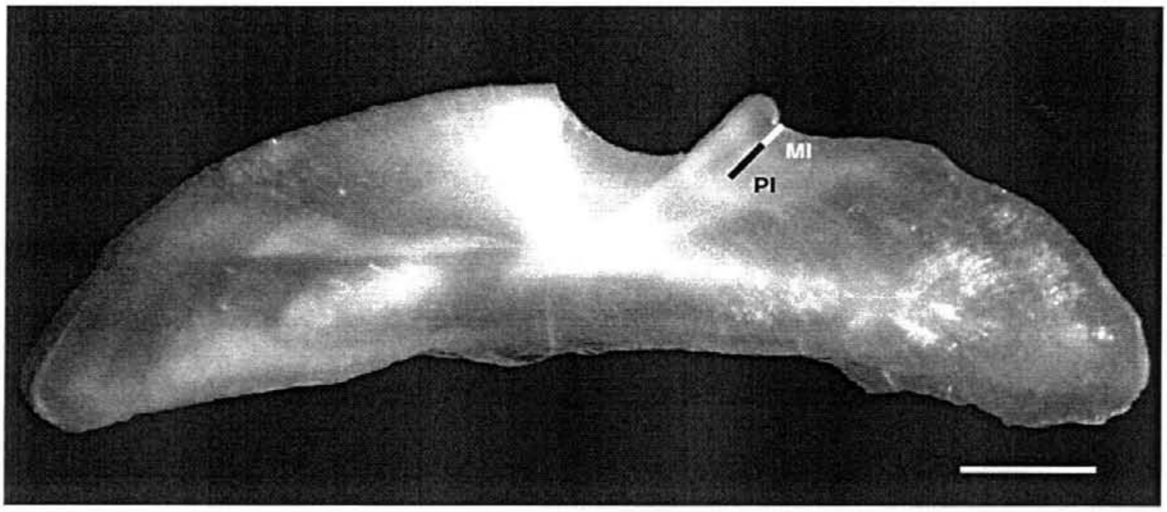

Figure 3.1. Transverse section of a sagittal otolith from a two year old *Lethrinus miniatus* indicating the marginal increment (MI) and previous increment (PI) measurements used for marginal increment analysis (MIA). Scale bar = 1mm.

Mean MIRs for each area and age class were plotted against month of capture to examine annual, spatial and age specific patterns in opaque increment formation. Age classes <4 years and age classes >7 years were pooled for these plots, due to lower sample sizes of both younger and older fish in both areas. There were also several months in both years when sample sizes were low or when no samples were collected at all, particularly in the northern area. A single, fully balanced analysis of Area*Month*Age was not possible due to this uneven distribution of the data across areas, months and age classes. Accordingly, four separate fixed factor analyses of variance (ANOVA) were used to test for the effects of Year, Area and Age on MIRs, and their interaction with Month. The first ANOVA tested for the effect of Year and Age for age classes 4 and 5 years in the southern area to determine whether the timing of opaque increment formation varied between years and age classes. The second ANOVA tested for the effects of Year for all age classes combined in the southern area to determine whether the timing of opaque increment formation varied between years for all age classes combined. The final two ANOVAs tested for the effects of Area for each Year separately, with all age groups combined, to determine whether the timing of opaque increment formation varied between Areas of the GBR in 1999 and 2000. Significant interactions between any factor and month were explored further using Bonferroni adjusted pairwise comparisons to determine in which months differences in MIRs occurred. Residual plots and normal probability plots were used to examine the assumptions of homogeneous variances and normality for all data prior to analysis. Since all data conformed to these assumptions, no transformations were necessary.

3.2.2. Captive rearing of chemically tagged fish

Five *L. miniatus* ranging in size from 300 mm to 510 mm fork length (FL) were collected in April 1998 from reefs in the central GBR by a commercial line fishing vessel and transported live to a 150,000L outdoor aquarium at James Cook

University. Upon arrival, fish were anaesthetised with benzocaine, weighed, measured and given an intraperitoneal injection of oxytetracycline (OTC) in a saline solution at a dose of approximately 50 mg kg^{-1} body weight (McFarlane and Beamish 1987). The aquarium was kept at ambient temperature with a relatively constant salinity (35ppt) and pH (8.2) and fish were fed a diet of scrap fish 3 times per week for the duration of the experiment. Unfortunately only two fish survived until the end of the validation experiment. Three other fish were consumed by larger predators in the aquarium, and their otoliths could not be recovered. The larger of the two surviving fish received a second OTC injection in mid April 1999, 12 months after the first injection. The sagittal otoliths were removed from the two surviving fish in September 1999. These otoliths were sectioned following the procedures described in Chapter 2 and viewed, firstly under reflected light to examine the position of opaque increments, and then under ultra-violet light to examine the relative positions of the OTC marks.

3.3. Results

3.3.1. Marginal increment analysis

Mean MIRs generally showed a seasonal pattern for the southern area for all age classes examined (Figure 3.2) but showed more ambiguous results for the northern area (Figure 3.3). If opaque increments in otoliths form on an annual basis, and the time of formation is strongly seasonal, MIRs will reach a maximum immediately prior to the completion of opaque increment formation and a minimum at the time shortly after opaque increments are completed and translucent material appears at the otolith margin. In the southern area, MIRs were generally at a maximum between October and December and were followed by a minimum between January and April (Figure

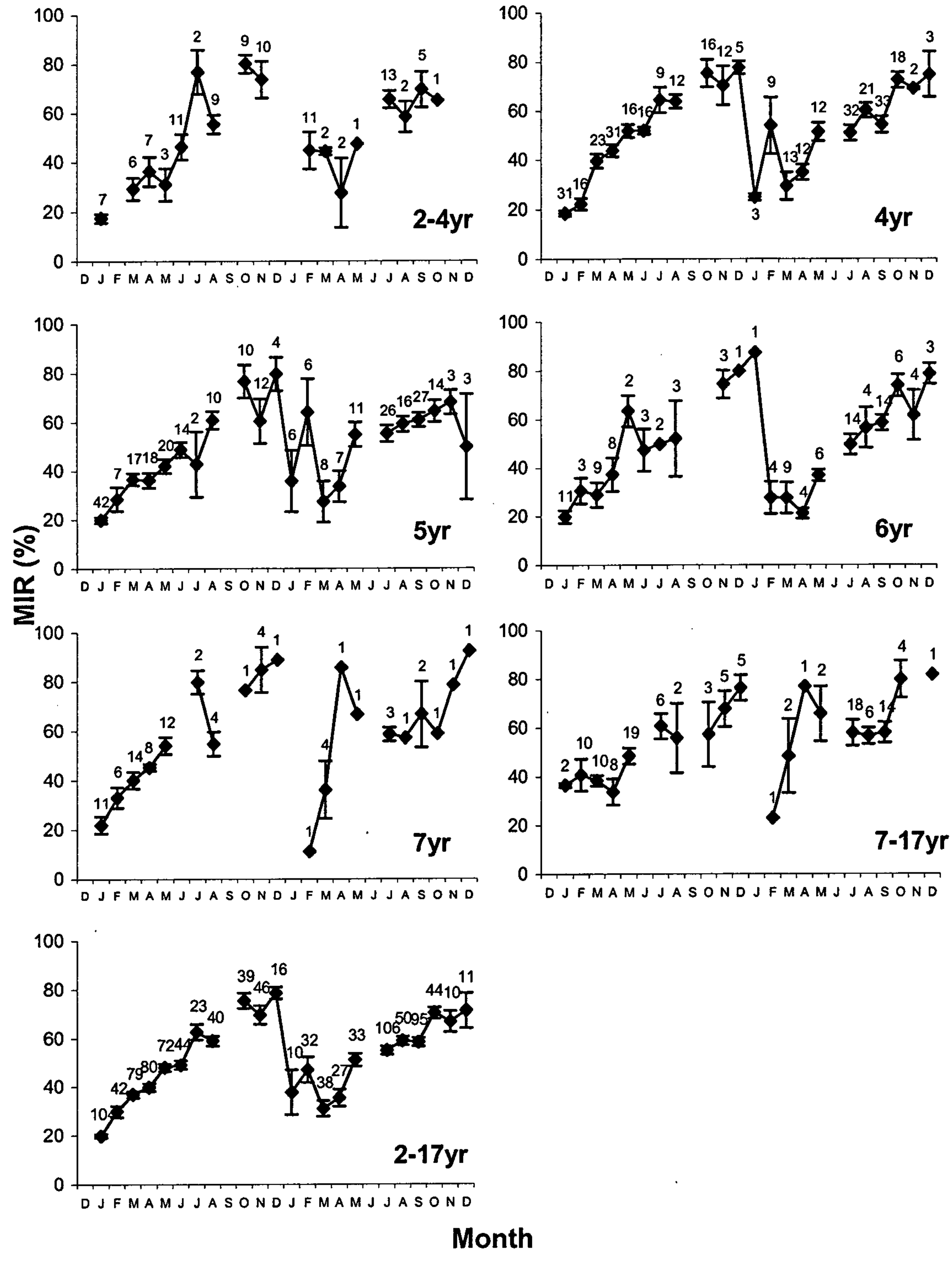

Figure 3.2. Mean monthly values of the marginal increment ratio (MIR) for *Lethrinus miniatus otoliths* collected from December 1998 to December 2000 from the southern area of *L. miniatus* distribution on the Great Barrier Reef. Data shown are for each age class between 4 to 7 years, and pooled age classes 2-4, 7-17 and 2-17 years. Sample sizes for each month are given above each point. Error bars are standard errors.

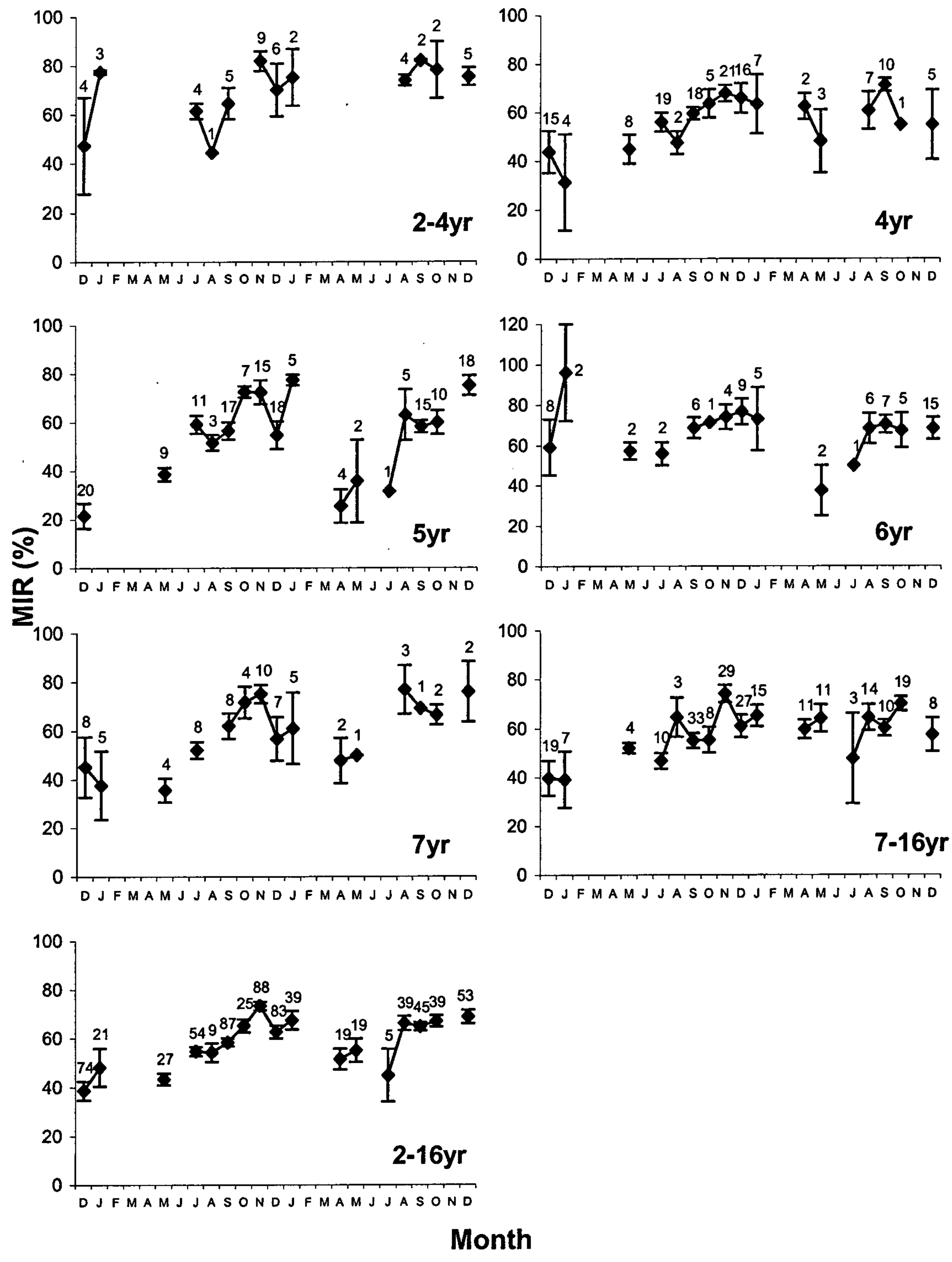

Figure 3.3. Mean monthly values of the marginal increment ratio (MIR) for *Lethrinus miniatus* otoliths collected from December 1998 to December 2000 from the northern area of *L. miniatus* distribution on the Great Barrier Reef. Data shown are for each age class between 4 to 7 years, and pooled age classes 2-4, 7-16 and 2-16 years. Sample sizes for each month are given above each point. Error bars are standard errors.

3.2) suggesting that opaque increments are completely formed by April in all age classes in this area.

Maximum and minimum MIRs were more difficult to distinguish in the northern area, in part due to missing data from some months. In particular there were no data for the months between February and April in 1999 and February and March in 2000 for the northern area. These months were typically the months of minimum MIRs in the southern area. For the months where data were available for the northern area, minimum MIRs were generally observed in April and May, but these minima were not as low as minimum MIRs for the southern area between January and April (Figure 3.3). Maximum MIRs in the northern area generally occurred between October and January and were similar in magnitude to maximum MIRs in the southern area (Figure 3.3).

Statistical analyses indicated significant differences in monthly MIRs between years and areas. Monthly MIRs for age classes 4 and 5 years from the southern area differed significantly between 1999 and 2000 (Year*Month interaction) but did not differ significantly between age classes (Table 3.1). Age classes were therefore pooled within the southern area based on the assumption that MIRs did not differ significantly among other age classes. Analysis of variance for these pooled data indicated that MIRs differed significantly between 1999 and 2000 for at least some months (Year*Month interaction) for all age classes combined (Table 3.2). Pairwise comparisons revealed that this difference was due to higher MIRs in 2000 during January ($t_{882} = 3.31$, $p = 0.010$) and February ($t_{882} = 4.50$, $p < 0.001$) compared with the same months in 1999 (Figure 3.4). Maximum MIRs occurred during December in both 1999 and 2000, but the minimum MIRs occurred during January in 1999 and March in 2000 (Figure 3.4).

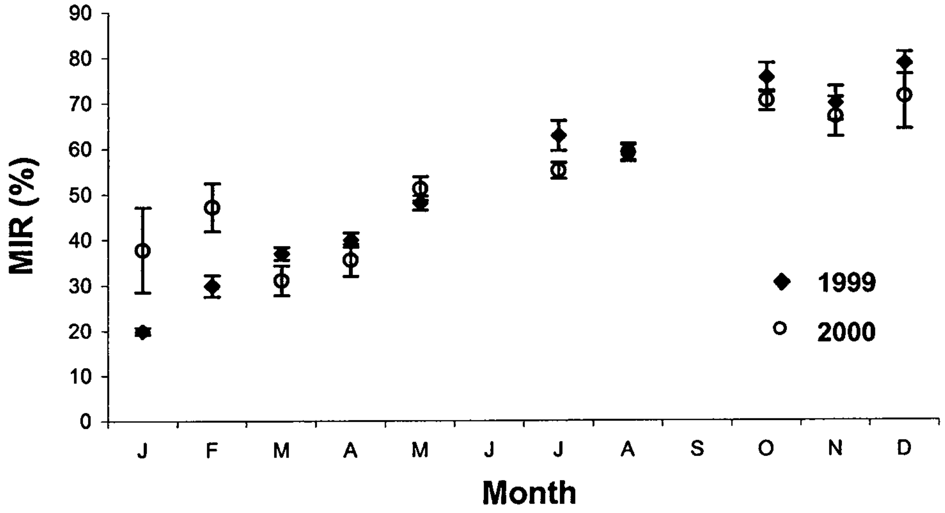

Figure 3.4. Comparison of mean monthly values of the marginal increment ratio (MIR) for *Lethrinus miniatus* otoliths collected in 1999 and 2000 from the southern area of *L. miniatus* distribution on the Great Barrier Reef. Data shown are for pooled age classes 2-17 years. Error bars are standard errors.

Table 3.1. Analysis of variance comparing monthly otolith marginal increment ratios (MIR) between the 4 and 5 year age classes, and between 1999 and 2000 for *Lethrinus miniatus* from the southern area of the Great Barrier Reef.

Source of variation	df	MS	*F*	*p*
Year	1	105.324	0.400	0.527
Month	9	9800.520	37.243	**<0.001**
Age	1	518.758	1.971	0.161
Year*Month	9	1594.115	6.058	**<0.001**
Year*Age	1	227.214	0.863	0.353
Month*Age	9	231.714	0.881	0.542
Year*Month*Age	9	293.746	1.116	0.349
Residual (error)	498	263.152		

Table 3.2. Analysis of variance comparing monthly otolith marginal increment ratios (MIR) between 1999 and 2000 for all age classes of *Lethrinus miniatus* from the southern area of the Great Barrier Reef.

Source of variation	df	MS	F	p
Year	1	130.404	0.498	0.480
Month	8	9399.465	35.930	**<0.001**
Year*Month	8	1808.203	6.912	**<0.001**
Residual (error)	553	261.606		

To examine the effects of area on MIRs it was necessary to pool age classes within each area under the assumption that MIRs did not differ significantly among age classes in either area. Analyses of variance for these pooled data indicated that MIRs differed significantly between areas in some months (Area*Month interaction) in both 1999 (Table 3.3) and 2000 (Table 3.4). Pairwise comparisons revealed that these differences were due to higher MIRs in the northern area during January in 1999 ($t_{633} = 6.82, p < 0.001$) and 2000 ($t_{618} = 4.77, p < 0.001$) and April in 2000 ($t_{618} = 3.05, p = 0.02$) compared with the same months and years in the southern area (Figure 3.5). In the northern area, maximum MIRs occurred during November in 1999 and December in 2000, which was similar to the southern area, where maximum MIRs always occurred during December (Figures 3.4 & 3.5). It was not clear exactly when minimum MIRs would have occurred in the northern region due to missing data from a number of months in both 1999 and 2000. Minimum MIRs in the available data occurred during May in 1999 and July in 2000 in the northern region, which is considerably later than minimum MIRs in the southern region (Figures 3.4 & 3.5), but the magnitude of these MIRs suggests those from earlier months were likely to have been smaller (closer to the zero value expected immediately after completion of a new opaque increment).

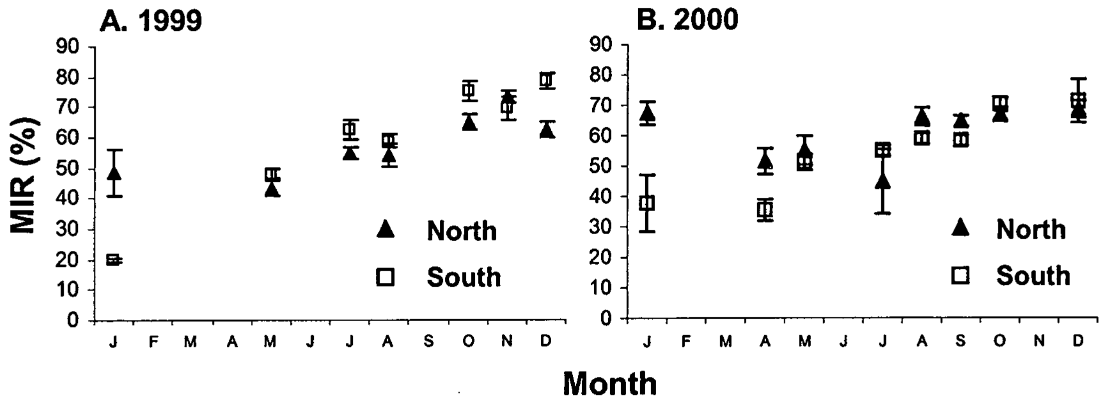

Figure 3.5. Comparison of mean monthly values of the marginal increment ratio (MIR) for *Lethrinus miniatus* otoliths collected from the northern and southern area of *L. miniatus* distribution on the Great Barrier Reef in 1999 (A) and 2000 (B). Data shown are for pooled age classes 2-17 years. Error bars are standard errors.

Table 3.3. Analysis of variance comparing monthly otolith marginal increment ratios (MIR) between the northern and southern areas of the Great Barrier Reef in 1999 for all age classes of *Lethrinus miniatus*.

Source of variation	df	MS	*F*	*p*
Area	1	295.778	0.979	0.323
Month	6	15232.052	50.420	**<0.001**
Area*Month	6	3517.277	11.643	**<0.001**
Residual (error)	633	302.105		

Table 3.4. Analysis of variance comparing monthly otolith marginal increment ratios (MIR) between the northern and southern areas of the Great Barrier Reef in 2000 for all age classes of *Lethrinus miniatus*.

Source of variation	df	MS	*F*	*p*
Area	1	2978.849	9.670	**0.002**
Month	7	4115.362	13.359	**<0.001**
Area*Month	7	1340.181	4.350	**<0.001**
Residual (error)	618	308.059		

3.3.2. Captive rearing of chemically tagged fish

An OTC mark was observed in the sectioned otolith from only one of the two captive *L. miniatus* that survived the duration of the experiment. This fish was injected with OTC in April 1998 and the resulting OTC mark was clearly visible under ultra-violet light, adjacent to the outer margin of the second last opaque increment (Figure 3.6). The position of the OTC mark relative to second last opaque increment indicated that this opaque increment was completely formed by April. The amount of growth in the otolith in the 17 months subsequent to the OTC injection was consistent with expected otolith growth if opaque increments are deposited annually. That is, in this period, the formation a complete translucent increment followed by a single opaque increment and then a partially complete translucent increment was observed between the OTC mark and the otolith margin (Figure 3.6). No OTC marks were visible in the sectioned otolith of the other fish that survived, even though it was injected with OTC on two occasions.

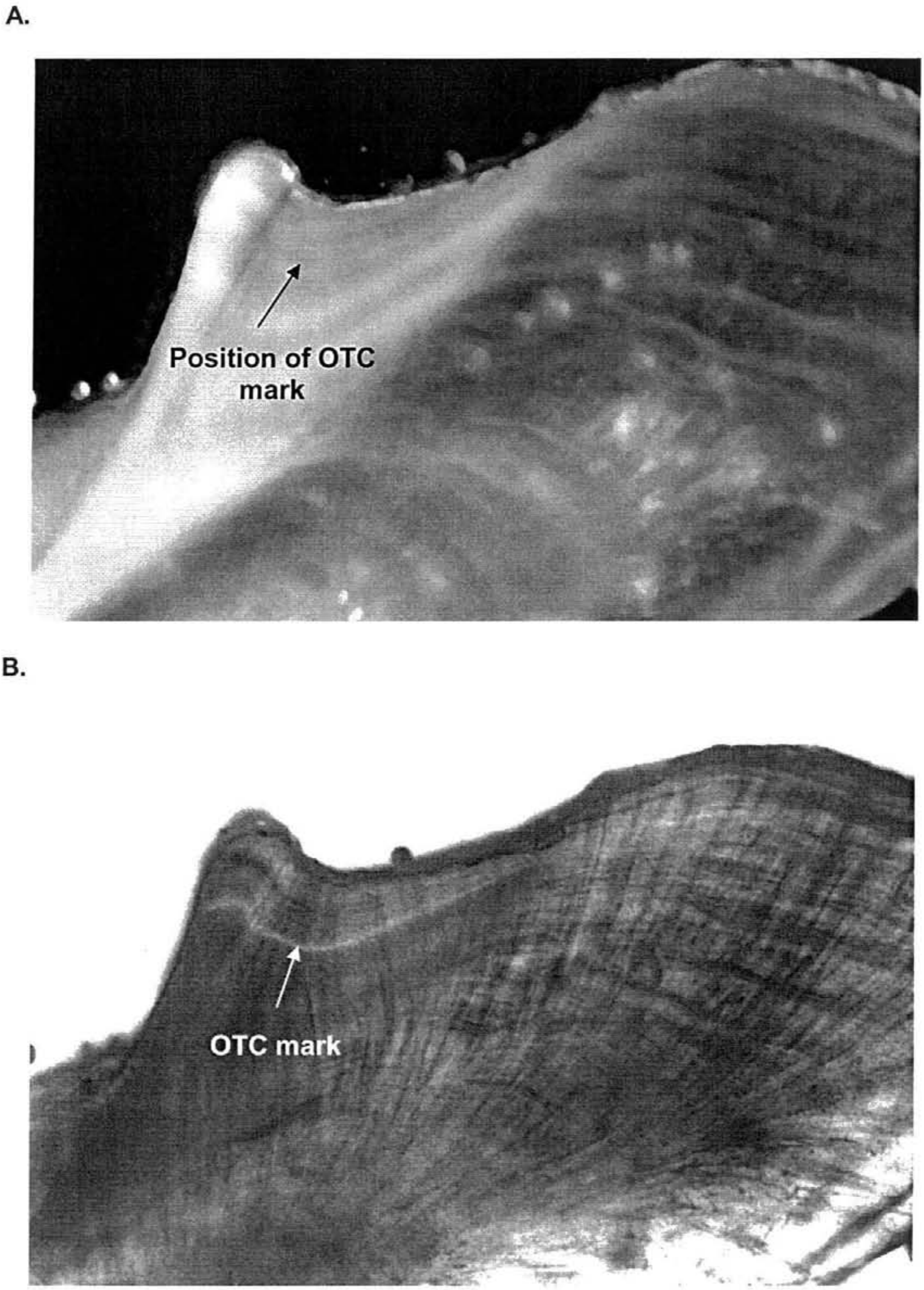

Figure 3.6. Transverse section of a sagittal otolith from a captive *Lethrinus miniatus* injected with oxytetracycline (OTC) in April 1998 and recaptured in September 1999. Images were taken under reflected light (A) and transmitted ultraviolet light (B). The fluorescent band from the OTC (OTC mark) is located adjacent to the second most distal opaque increment.

3.4. Discussion

Analyses of both MIA and chemical tagging successfully validated the annual periodicity in the formation of opaque increments of *L. miniatus* otoliths. In addition, MIA indicated that the months in which opaque increments are formed varied slightly between years and areas.

3.4.1. Marginal increment analysis

Observation of the monthly trends in MIRs suggested formation of opaque increments in *L. miniatus* otoliths from the northern and southern areas of the GBR followed an annual periodicity across the years 1999 and 2000 and for all age classes (2-17 years) examined. The seasonal periodicity in monthly MIRs was less pronounced in the northern area, but this was likely to be due primarily to missing data from a number of key months in each year. Notably, for the available data, any significant variation in MIRs between years and areas occurred only for the months during which opaque increments were deposited (January – April). This variation may reflect differences in the timing of opaque increment formation between years and areas. For example, the higher MIR during January and February 2000 in the southern area relative to these months in 1999 suggests the completion of opaque increments may have occurred up to two months later in 2000 than in 1999. Similarly, higher MIRs in the northern (relative to southern) area for January 1999 and 2000 suggests that the completion of opaque increments may have occurred a month later in this area over both years. Missing data in some months for the northern area make it difficult to determine precisely when spatial differences in the timing of opaque increment formation may have occurred, if at all. Importantly, however, MIRs were similar among most months during both years in both areas. Thus, if annual and spatial differences in the timing of opaque increment formation do exist, they are not likely to differ by more than one to two months, based on these observations over two years, and so not significantly undermine annual age estimation for *L. miniatus*.

It is unclear whether variation in water temperature is the dominant cause of the observed variation in the timing of opaque increment formation in *L. miniatus* otoliths between years and locations. Water temperature has often been correlated with the formation of annual increments in fish otoliths (e.g. Panella 1980, Schramm 1989), and variation in water temperature is commonly offered as an explanation for annual and spatial variations in timing of increment formation (e.g. Pearson 1996). However, the variation in water temperature between the two areas in this study rarely exceeds 1°C and maximum and minimum sea surface temperatures occurred during January and August respectively in both 1999 and 2000 in each area (GBRMPA 2003). More detailed temperature measurements, particularly closer to the sea floor where *L. miniatus* usually occur, are required to fully assess the correlation between water temperature and increment formation.

It is unlikely that opaque increment formation in *L. miniatus* otoliths is a consequence of spawning activity. Other authors have correlated the formation of either opaque or translucent increments to reproductive development or spawning season (e.g. Morales-Nin and Ralston 1990, Hostetter and Munroe 1993). The spawning season for *L. miniatus* occurs between July and October (Chapter 4) and all individuals in the samples were mature (Chapter 4). Although the formation of translucent increments in *L. miniatus* otoliths occurs during the months of the spawning season, their formation was unlikely to be directly caused by spawning activity as translucent increments were also deposited over several months either side of the spawning season.

Several studies have suggested that error in the measurement of otolith increments may contribute to apparent variation in the timing of otolith increment formation (e.g. Smith and Deguara 2003). During the months in which opaque increments are deposited, many otoliths have either a very wide or very narrow translucent increment at the margin. Error in the measurement of marginal increments is likely to be greatest during these months as it is often difficult to discern a completed opaque increment at the otolith margin due to the light refractive properties at the otolith margin. Measurement error in this study is likely to have been partitioned evenly between areas and years, however, as samples were completely randomised prior to measuring increments and there were no apparent differences in the readability of otoliths between years or areas. Thus, the observed variation in timing of opaque increment formation between areas and years is unlikely to have been biased by measurement error.

In contrast, variability in the timing of opaque increment formation among reefs within each area may have contributed to the significant annual and spatial variation in monthly MIRs. There were 27 reefs sampled in the northern area and 64 reefs sampled in the southern area (Chapter 2). These reefs were spread over several hundred kilometres within each area and a different set of reefs were sampled in each month. If the timing of opaque increment formation varied significantly but non-randomly among reefs within each area, and sampling selected disproportionately from reefs with similar timing of opaque increment formation, then annual and spatial variation in MIRs would be confounded with reefs and months of collection. Unfortunately sample sizes from individual reefs in any area or year were not large enough to test this hypothesis.

There was no significant variation in monthly MIRs among age classes. It was only possible to examine the effect of age for the four and five year old age classes in a single area due to the distribution of the samples among age classes. Variation in the timing of otolith increment formation among age classes has been reported for several other fish species (e.g. Hyndes et al. 1992, Vilizzi and Walker 1999) and some authors suggest that increments are deposited later in older fish (Brown and Sumpton 1998, Smith and Deguara 2003) due to slower rates of somatic growth (Smith and Deguara 2003). It is possible that the timing of opaque increment formation in *L. miniatus* otoliths varied among other age classes that were not examined individually. This variation is unlikely to have been large, however, as the pattern of monthly MIRs for all ages pooled up to 17 years showed a very similar annual cycle to that for monthly MIRs for individual age classes. The timing of opaque increment formation in *L. miniatus* otoliths for age classes younger than two years was not examined in this study. It will be necessary to identify and locate the juvenile habitat of *L. miniatus* before adequate samples of younger fish (<2yo) can be collected, and the patterns of formation of the first opaque increment can be examined. By determining the time at which the first opaque increment is deposited it will be possible to validate absolute ages (Campana 2001).

3.4.2. Captive rearing of chemically tagged fish

Results from the captive rearing of chemically tagged fish were consistent with the results from the MIA, suggesting opaque increments in *L. miniatus* otoliths were completely formed by April and deposited annually. It is unclear why fluorescent marks from the OTC injections were not visible in sectioned otoliths from one of the fish that survived beyond one year in the captive validation experiment. It is possible that the fish with no visible OTC mark required a higher concentration of OTC, since this fish was more than twice the weight of the fish that showed a clear OTC mark. An increase in OTC concentration usually increases the probability of OTC marks being formed in otoliths, but also increases the likelihood of mortality (McFarlane and Beamish 1987).

3.4.3. Applications for knowledge of the timing of increment formation

The timing of opaque increment completion in *L. miniatus* otoliths coincided with the end of the austral summer, which is consistent with the pattern observed in a number of other coral reef fishes (e.g. Fowler 1990, Fowler and Doherty 1992, Beckman and Wilson 1995, Fowler 1995, Choat and Axe 1996, Choat et al. 1996, Hart and Russ 1996) and for *L. miniatus* from the far southern region of the GBR (Brown and Sumpton 1998). Knowledge of the timing of opaque increment formation in *L. miniatus* otoliths can be used when designing sampling programs to minimise potential biases in age estimates. The most appropriate period of the year to sample populations of *L. miniatus* to obtain reliable age estimates would be between April and December, when translucent increments are being deposited and the distal opaque increment is completely formed and clear. A sample of *L. miniatus* otoliths collected from a single occasion during this period would most likely yield reliable estimates of age. In addition, samples of *L. miniatus* collected from multiple occasions throughout this period could still be used to estimate age reliably by using marginal increment measurements to assign estimates of fractional ages (e.g. 6.5 years) as opposed to whole year ages (e.g. 6 years), if necessary. It would be comparatively difficult to assign unbiased age estimates for *L. miniatus* collected between January and April, since a large proportion of otoliths are likely to have incomplete opaque increments at the margins.

The validation of the periodicity and timing of opaque increment formation in *L. miniatus* otoliths established in this study is particularly important for providing confidence in estimates of a range of age-based population parameters including growth, mortality and recruitment history. Recruitment histories and estimates of mortality for populations of fish are usually derived from age frequency data. Therefore unreliable age estimates are likely to result in inaccurate or imprecise estimates of recruitment history and mortality. Further, since samples used to compare growth and mortality of *L. miniatus* (Chapters 5 and 6) were collected between September and December of each year, slight variations in the timing of increment completion (Jan-Mar) would not have confounded spatial comparisons of these population parameters.

Information on the timing of increment formation in *L. miniatus* otoliths has particular implications for the estimation of growth, especially when samples are collected throughout the year. Often it is not possible to collect a large enough sample of fish to obtain reliable parameter estimates from a single sampling occasion. Samples are often collected from multiple occasions throughout the year to obtain a larger sample.

Estimates of growth are usually derived by fitting specific growth models to size-at-age data. As fish continue to grow throughout the year, estimates of growth obtained from fish collected at different times of the year will be biased if estimates of age are expressed in whole years. However, knowledge of the timing of increment formation and measurements of marginal increment widths will allow the back-calculation of age to within fractions of a year for samples collected at different times of the year. Incorporating these more precise estimates of age into estimates of growth may reduce the variability in size-at-age when samples are pooled over time. Specifically, information on the timing of increment formation in *L. miniatus* otoliths may now enable individual variability in growth to be incorporated explicitly into assessment and evaluation models.

3.4.4. Summary and conclusions

This chapter adds to the growing list of tropical species for which age estimates have been successfully validated. Using a systematic sampling program and MIA, I validated the annual periodicity of opaque increments in *L. miniatus* otoliths for a number of age classes from two areas covering the majority of the species' distribution on the GBR. MIA was critically reviewed by Campana (2001) as a highly subjective technique for validation of age estimates unless four important criteria were fulfilled: 1) Samples are examined in random order, with no knowledge of when the samples were collected; 2) a minimum of two complete cycles are examined; 3) results are interpreted statistically, and; 4) MIA is analysed age-specifically. The MIA procedure I used in this chapter adhered to all four of these criteria, indicating the results can be applied with some confidence.

Chapter 4. Spatial patterns in spawning activity and reproductive biology of *Lethrinus miniatus* on the Great Barrier Reef.

4.1. Introduction

The reproductive biology of lethrinids has received comparably less attention than other commercial reef fish families, such as lutjanids (Grimes 1987) and serranids (Shapiro 1987), despite their importance to many coastal reef fisheries around the world. The few available studies indicate that lethrinids are protogynous hermaphrodites, changing sex from females to males at some stage during their life (Young and Martin 1982, Ebisawa 1997, 1999, Bean et al. 2003). It is generally considered that protogynous species are more vulnerable to increased fishing pressure than gonochoristic species for which sexes are separate throughout life (Huntsman and Schaaf 1994), as fishing often impacts disproportionately on larger and older fish, which in protogynous populations are predominantly male (Bannerot et al. 1987).

Where sex change is flexible and under social control, larger females may change sex to compensate for the removal of males (compensated response: Vincent and Sadovy 1998). As a consequence, sex ratios are maintained, but the average size and age of males and females is reduced. All else being equal, this will result in a reduction in the reproductive output of the population (Sadovy 1996). Where sex change is not flexible and occurs at a fixed size or age, or the rate of removal of males from the population exceeds the rate at which they can be replaced by females via the compensatory response, sex ratios are likely to become female biased (uncompensated response: Coleman et al. 1996, Vincent and Sadovy 1998). As a result, the number of males in the population may be reduced to a level where sperm limitation occurs

(Coleman et al. 1996, Vincent and Sadovy 1998). These alternative mechanisms of sex change, and their different implications for the nature of impacts of fishing on populations of protogynous species, places considerable importance on increasing our knowledge of the reproductive biology of lethrinids in order to implement the most appropriate management responses.

Studies to date indicate that *Lethrinus miniatus* is a protogynous hermaphrodite (Young and Martin 1982, Brown et al. 1994, Bean et al. 2003). Estimates for some reproductive parameters of *L. miniatus* populations from the Great Barrier Reef (GBR) are available, but only from the far southern region (Brown et al. 1994). Williams et al. (2003) found significant differences in age, growth and mortality of *L. miniatus* populations among three regions within the GBR. This variation in age, growth and mortality may also be evident in reproductive parameters, resulting in regional differences in reproductive potential. Regional patterns in the reproductive biology of *L. miniatus* on the GBR, however, have yet to be examined.

Spatial variation in reproductive biology is a relatively common feature of reef fish populations. A number of authors have reported significant variation among locations in maturity schedules (Cowen 1990, Ebisawa 1999), spawning season (Ebisawa 1997, 1999), sex ratios (Buxton 1993, Adams et al. 2000), size or age at sex change (Cowen 1990, Buxton 1993, Ebisawa 1999, Adams et al. 2000, Platten et al. 2002) and fecundity (Ebisawa 1999). Significant spatial variation in maturity and sex change schedules has been suggested to be facilitated by the relative plasticity in sex determination in hermaphroditic fish (Hovey and Allen 2000). Variations in the stage at which individuals mature or change sex may occur in response to either variations in local environmental conditions such as water temperature (e.g. Conover and Heins 1987) or in response to changes in sex ratios of the population or local sub-population (Shapiro 1984).

Spatial variation in reproductive biology has important implications for fisheries management. For example, minimum legal sizes are often implemented in a fishery based on size at maturity information (Hill 1990). In a fishery with a single minimum size limit, variations in maturity schedules between locations within the fishery may result in recruitment overfishing of populations that reach maturity at a larger size than that of the average for the whole population. Similarly, spawning closures implemented across a fishery at the one time will not protect all components of the stock if there are significant differences in the timing of the spawning season among geographic locations within the fishery.

The objective of this chapter was to increase our knowledge of lethrinid reproductive biology by estimating and comparing various reproductive parameters of *L. miniatus* among areas of the GBR. More specifically, the aims were: i) to estimate seasonality of spawning; ii) document sex ratios, size and age at maturity and size and age at sex change; iii) compare these parameters between the northern and southern areas of the GBR; and iv) use the estimates of these reproductive parameters to develop hypotheses about the mating patterns and sexual strategies of *L. miniatus* relative to other studies of *L. miniatus* and other reef fish species.

4.2. Methods

4.2.1. Sample collection

Samples of *L. miniatus* were collected from the GBR commercial line fishing fleet as described in Chapter 2. During the collection of samples there was a legal minimum size limit for *L. miniatus* of 350 mm total length (TL, = 320 mm fork length) for all commercial and recreational fishers. As a result, individuals less than 320 mm fork length (FL) were rare in the samples collected, and no immature individuals were identified. An additional sample of 92 *L. miniatus* containing smaller (<300 mm FL) individuals was collected from reefs within the Capricorn Group in the far southern region of the GBR to provide an estimate of size and age at maturity (Figure 4.1). These fish were collected in September 2002, which coincided with the peak spawning period in this region (Brown et al. 1994) and therefore maximised the contrast between mature and immature individuals. Samples were collected using hook and line (size 6 hooks) and were used only in the analysis of maturity schedules. Gonads from these samples were removed within one hour of capture and preserved in 4% Formaldehyde. Gonads from samples collected from the commercial fleet were removed and preserved as described in Chapter 2. Otoliths from all fish were sectioned and ages determined using the methods described in Chapter 2.

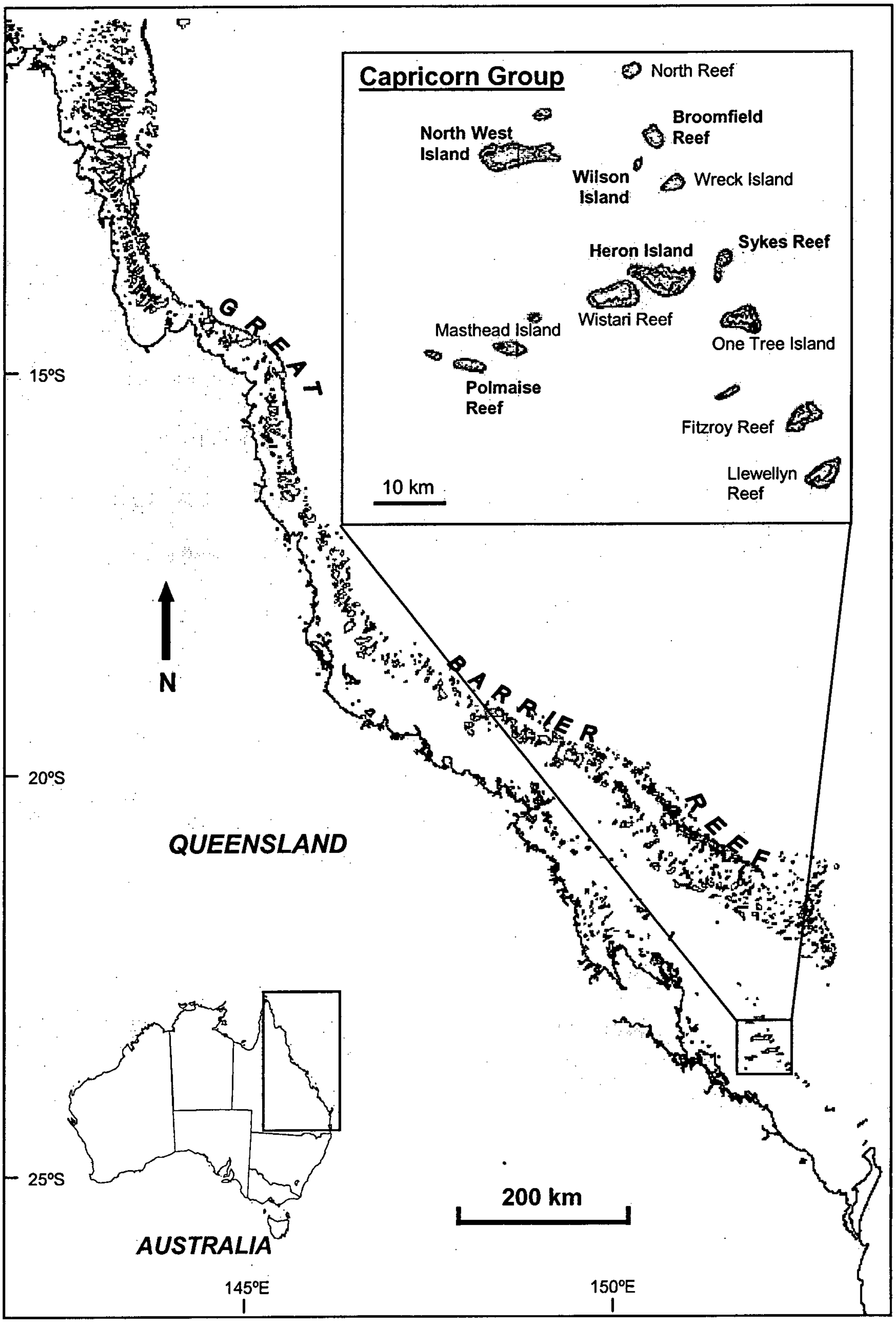

Figure 4.1. Location of reefs sampled for 'small' *Lethrinus miniatus* in the Capricorn Group within the Great Barrier Reef. Specific reefs sampled (in bold) were North West Island, Broomfield Reef, Wilson Island, Heron Island, Sykes Reef and Polmaise Reef.

4.2.2. Gonosomatic indices

Each pair of ovaries or testes was dried of excess fixative and weighed to the nearest 0.01g after fixation. A gonosomatic index (GSI: gonad weight / whole body weight * 100) was calculated for each sample collected from commercial vessels. Whole body weights of these samples were not available directly, as commercial fishers provided only filleted 'frames'. Consequently, whole body weights were estimated using the relationship between fork length and total weight obtained from fish collected during structured research surveys (the length-weight relationship from these samples is analysed in detail in Chapter 5). It was assumed that estimates of total weights would suffice for estimates of GSI because only the temporal patterns in GSI, rather than the absolute values of GSI, were required to determine the spawning season. Where only one gonad lobe was available, due to damage during processing, gonad weight was estimated by multiplying the weight of the single lobe by two. It was assumed that this provided a reasonably accurate measure of gonad weight, as the two gonad lobes are generally equal in size for *L. miniatus* (Bean et al. 2003).

4.2.3. Histology and reproductive staging

Histological sections were taken from all gonads following the procedures outlined in Chapter 2. Ovaries were staged based on the most advanced non-atretic cell type present (West 1990). Additional features used in histological staging included the presence of brown bodies, atretic oocytes, vascularisation, and the relative thickness of the gonad wall, all of which may indicate prior spawning (Sadovy and Shapiro 1987). Ovaries and testes were classified into developmental stages adapted from Adams et al. (2000) and Bean et al. (2003). Five female and four male stages were identified through histology (Table 4.1 & 4.2). For analyses, female stages IVa and

Table 4.1. Description of histological features of ovarian developmental stages of *Lethrinus miniatus* (based on Bean et al. 2003).

	Developmental Stage	**Histological description**
Inactive	I. Immature	Ovary dominated by pre-vitellogenic oocytes (gonia, chromatin nucleolus, early peri-nucleolus and late peri-nucleolus stages). Inter-lamellar mesenteries are filamentous or absent. No evidence of prior spawning in the form of brown bodies, atretic vitellogenic oocytes, or intra-lamellar muscle bundles.
	II. Resting	Ovary dominated by pre-vitellogenic oocytes. Evidence of prior spawning indicated by the presence of brown bodies, atretic vitellogenic oocytes, post-ovulatory follicles and intra-lamellar muscle bundles.
Active	III. Ripening	The most advanced oocytes present are at yolk vesicle stage. Atretic oocytes and/or brown bodies may be present.
	IVa. Ripe	Ovary is in active vitellogenesis with yolk globule and migratory nucleolus stage oocytes present. Atretic oocytes and brown bodies are rare and inter-lamellar mesenteries thin.
	IVb. Hydrated	Ovary contains hydrated oocytes as well as some yolk globule and migratory nucleolus stage oocytes. Post-ovulatory follicles may be present and atretic oocytes and brown bodies are rare.

Table 4.2. Description of histological features of testicular developmental stages of *Lethrinus miniatus* (based on Bean et al. 2003).

	Developmental Stage	**Histological description**
Inactive	I. Spent	Testis is loose and disrupted containing few spermatocysts of any sperm stage. Sperm sinuses are empty or collapsed.
	IIa. Post-spawn resting	Spermatocysts no longer loose or disrupted and are separated by scar tissue. Earlier sperm stages are common.
	IIb. Pre-spawn resting	Testis contains densely packed spermatocysts of spermatogonia, spermatocytes and spermatids. Spermatozoa occurred most frequently in spermatocysts alongside inter-lamellar mesenteries. Sperm has not filled the sperm sinuses.
Active	III. Ripe	Testis dominated by spermatozoa both within spermatocysts and filling all sperm sinuses. Early stages of sperm development are rare and occur along the peripheral margins of the gonad lamellae.

IVb were treated as a single 'ripe' stage, due to the relatively low number of stage IVb females. Similarly, male stages IIa and IIb also were treated as a single stage in analyses, as both are resting stages.

4.2.4. Reproductive biology

Mean monthly GSI values for mature fish were plotted separately for males and females from each area (north and south, Chapter 2) to determine the peak spawning period for *L. miniatus*. The proportion of samples in each mature female and male reproductive stage in each month were also plotted for each area to examine the ovarian and testicular development patterns throughout the year, and the degree of spawning activity occurring in each month in each area.

A spatial comparison of the size and age at maturity was not possible due to the lack of small individuals collected from commercial fishers in the northern and southern areas. Therefore, the sample collected from the Capricorn Group that included smaller *L. miniatus* was used to estimate the size and age at maturity using the logistic equation,

$$P_m = (1 + e^{-\ln 19(m-m_{50})/(m_{95}-m_{50})})^{-1} \tag{4.1}$$

where:

P_m is the proportion of mature fish in age or 10 mm length class m;

m_{50} is the age or length at 50% maturity; and

m_{95} is the age or length at 95% maturity.

Similarly, the size at sex change was estimated by regression for each area using the logistic equation,

$$P_s = (1 + e^{-\ln 19(s - s_{50}^k)/(s_{95}^k - s_{50}^k)})^{-1} \tag{4.2}$$

where:

P_s is the proportion of males in each 10 mm length class s;

s_{50}^k is the length at which 50% of the population are males in area k; and

s_{95}^k is the length at which 95% of the population are males in area k.

The logistic function did not provide a good fit to the pattern of age at sex change. Accordingly, a second order polynomial function was used to describe the pattern of age at sex change for each area, as it provided the best fit to the data. The form of the polynomial function was,

$$P_x = a^k x^2 + b^k x + c^k \tag{4.3}$$

where:

P_x is the proportion of males in each age class x; and

a^k, b^k and c^k are coefficients of the polynomial function in each area k.

Likelihood ratio tests (Haddon 2001) were used to test for differences in the size and age at sex change between the northern and southern areas.

The sex assigned from histology was used to calculate the sex ratios for each area, which were compared between areas using a chi-square contingency test and compared with an expected ratio of 1:1 by chi-square goodness of fit tests.

4.3. Results

4.3.1. Spawning season

Mean monthly GSI values for mature females were highest in July to October in the northern area and July to September in the southern area (Figure 4.2). The mean monthly GSI values for males were highest in July to October in both areas (Figure 4.2). Missing data in June 1999 in the northern area and June 2000 in both areas precluded the specific verification of whether spawning commenced in July or June in either area. Based on GSI, however, it appears that the spawning season for *L. miniatus* is similar in both areas of the GBR and spans at least 3 to 4 months. Average GSIs for both females and males were higher in the northern area than in the southern area during the spawning season (Figure 4.2).

The monthly trend in the frequency of mature ovarian stages suggested a similar temporal pattern in spawning activity to the monthly GSI values for both areas (Figure 4.3). There was some evidence of spawning in the months of January, April, May, and November in the northern area, but the majority of spawning activity occurred in the months of July to October (Figure 4.3). In the southern area, a relatively large proportion of ripe females were present in the months of May and November suggesting a slightly protracted spawning season in this area, although again the majority of spawning-ready individuals occurred between July and September (Figure 4.3).

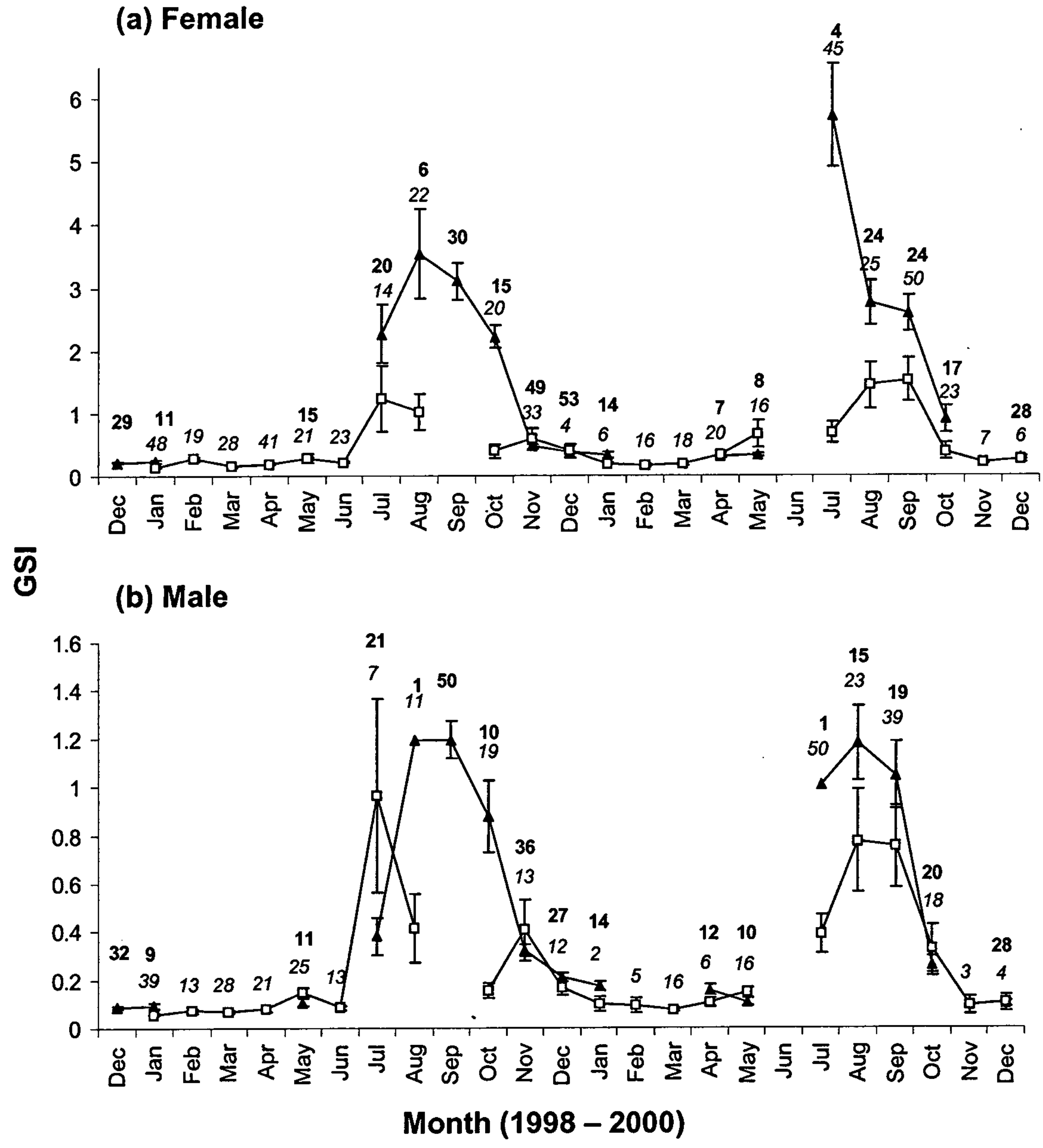

Figure 4.2. Mean monthly gonosomatic index (GSI) values for mature female (a) and all male (b) *Lethrinus miniatus* within two areas of the Great Barrier Reef representing the north (▲) and south (□) of *L. miniatus* distribution. Error bars are standard errors. Sample sizes for the northern (bold) and southern (italics) areas are indicated above data points for each month.

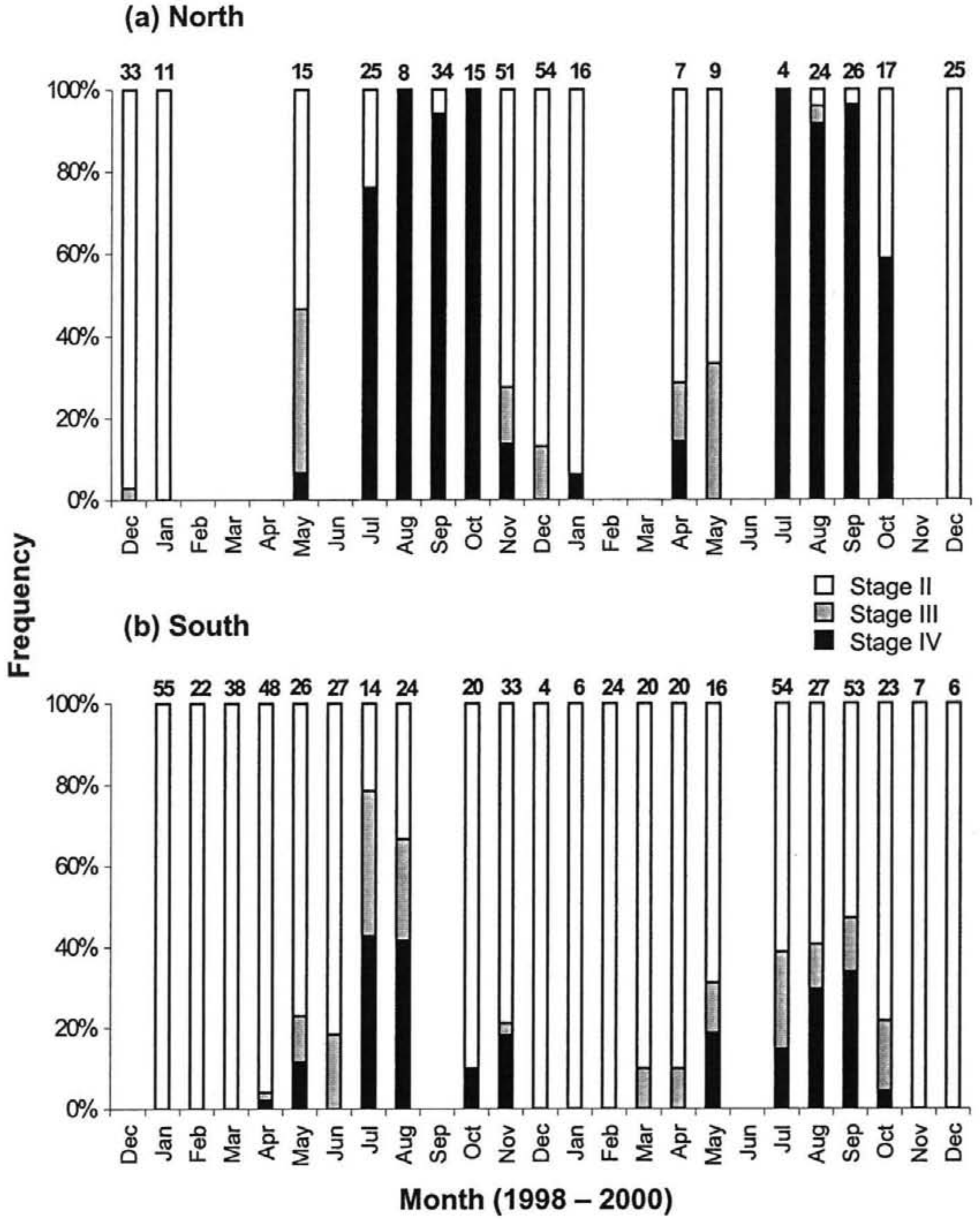

Figure 4.3. Monthly frequencies of mature ovarian stages of *Lethrinus miniatus* within two areas of the Great Barrier Reef representing the north (a) and south (b) of the *L. miniatus* distribution. Stage descriptions are provided in Table 4.1. Sample sizes for each month are indicated above each bar.

There was a large difference between areas in the proportion of ripe females during the peak spawning months (Figure 4.3). Between 59% and 100% of females were ripe during the peak spawning months in the northern area whereas no more than 43% of females were ripe in any month in the southern area (Figure 4.3). This large difference between areas was not an expected result. The relationship between size and reproductive stage was examined to determine if the low number of ripe females in the southern area was related to the size of ripe females. The proportion of ripe (stage IVa & b) ovaries during the spawning season was relatively consistent among size classes in the northern area and exceeded 70% of all ovaries in all but one size class (Figure 4.4). In contrast, the proportion of ripe ovaries during the spawning season in the southern area generally increased with size, and ripe ovaries did not exceed 50% of all ovaries until the 450 mm FL size class (Figure 4.4). Ripe females were observed at a much smaller size in the northern area (280 mm FL) compared with the southern area (350 mm FL).

Males appeared to be capable of spawning over an extended period of time either side of the spawning season (as defined by the presence of active females) in both areas, as indicated by the monthly trend in the frequency of testicular stages (Figure 4.5). Greater than 50% of males had mature sperm present in all months except December and January in the northern area and December through March in the southern area (Figure 4.5).

4.3.2. Size and age at maturity

Samples collected from reefs in the Capricorn Group ranged in size from 179 mm to 460 mm FL and from 0^+ to 6 years of age (Figure 4.6). The smallest and youngest

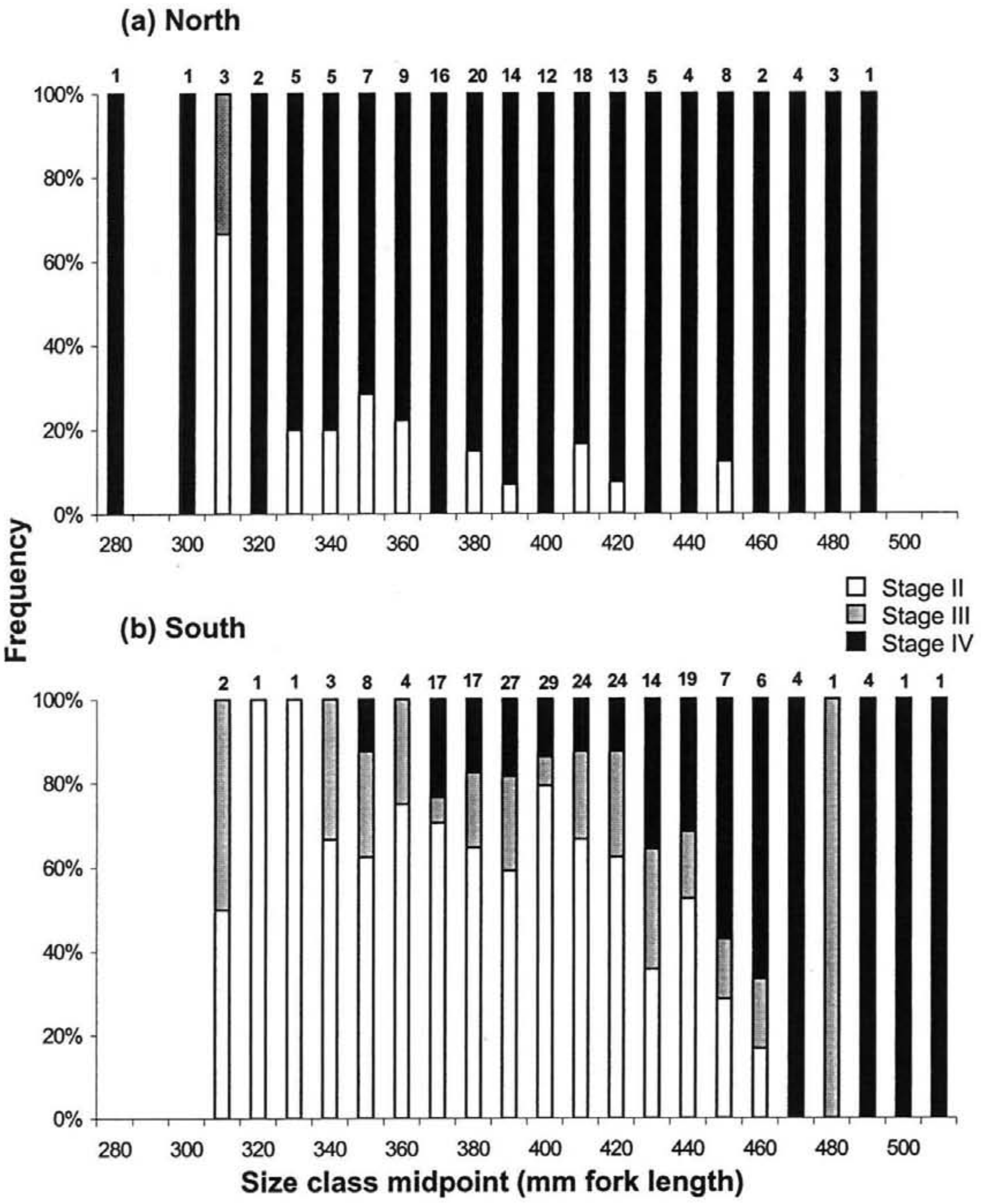

Figure 4.4. Proportion of each developmental stage for *Lethrinus miniatus* ovaries collected during the peak spawning months (Jul. – Oct.) in 10mm size classes within two areas of the Great Barrier Reef representing the north (a) and south (b) of *L. miniatus* distribution. Sample sizes for each size class are indicated above each bar.

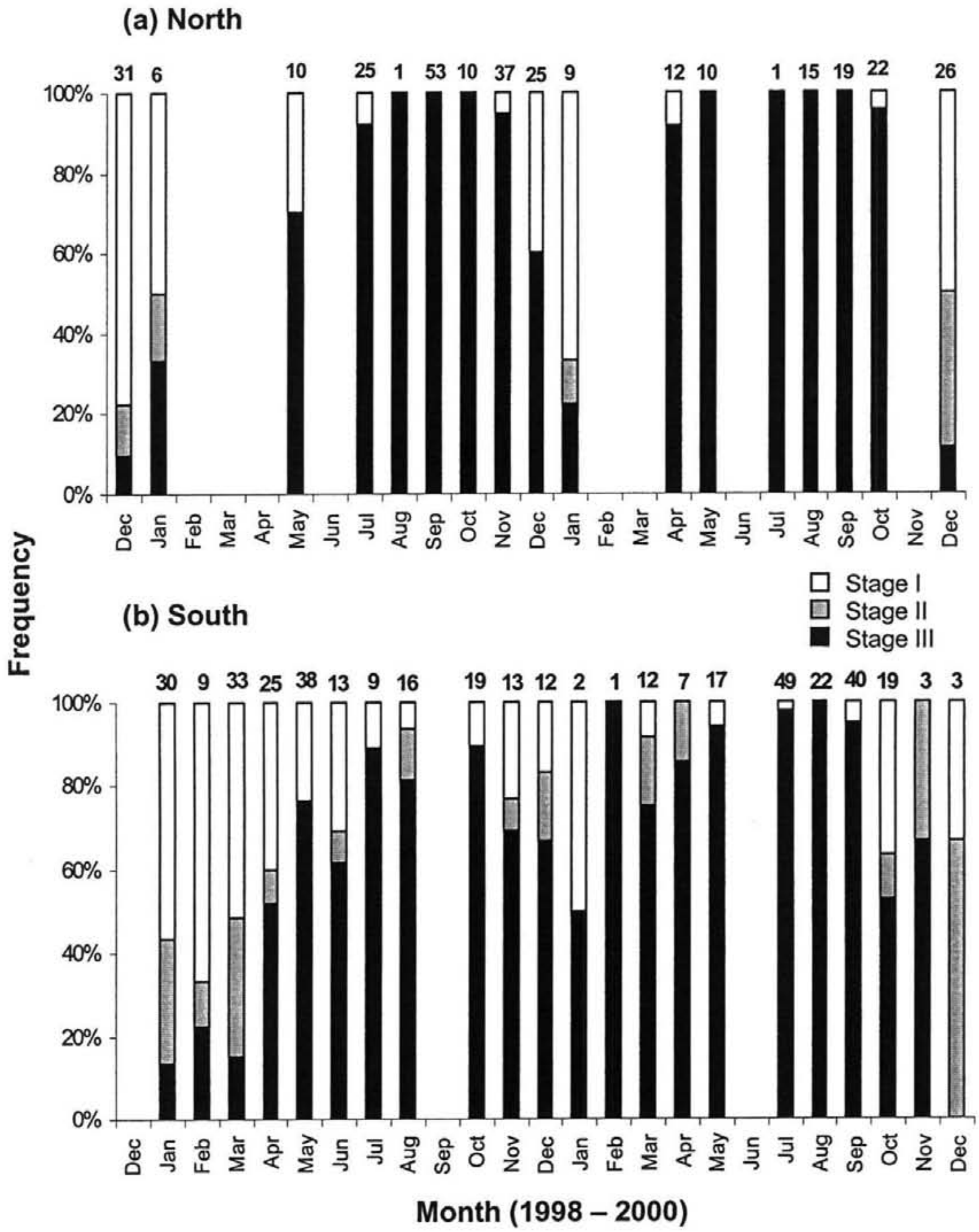

Figure 4.5. Monthly frequencies of testicular stages of *Lethrinus miniatus* within two areas of the Great Barrier Reef representing the north (a) and south (b) of the *L. miniatus* distribution. Stage descriptions are provided in Table 4.2. Sample sizes for each month are indicated above each bar.

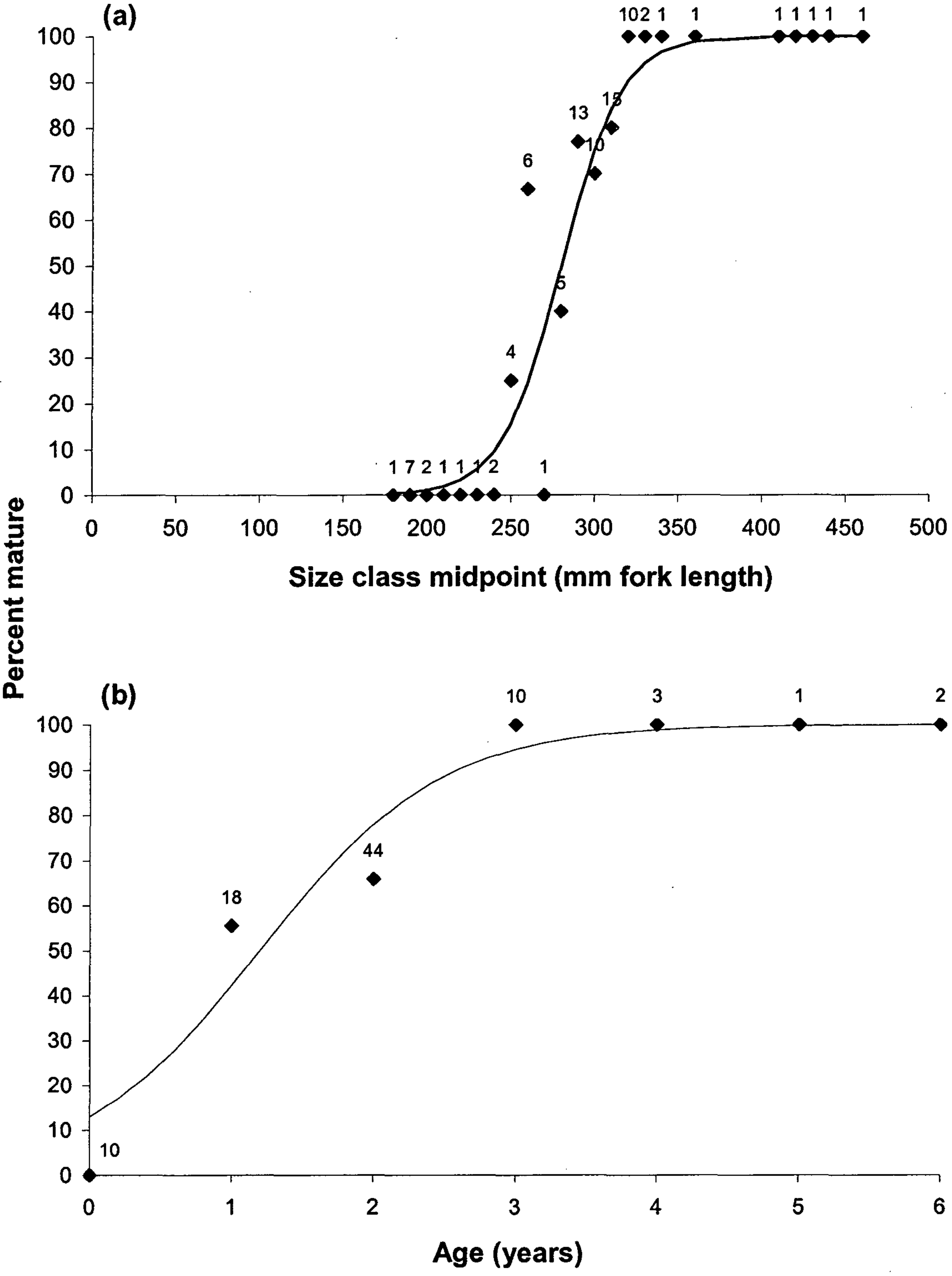

Figure 4.6. Percentage of mature female *Lethrinus miniatus* and estimated logistic maturation schedules for the Capricorn Group region of the Great Barrier Reef related to size (a) and age (b). Parameters of the maturation functions are provided in Table 4.3. Sample sizes are indicated above each data point.

mature female in the sample was 250 mm FL and 1 year of age, while the largest and oldest immature female was 313 mm FL and 2 years old (Figure 4.6). The size and age at which 50% of the sample was mature, estimated from the logistic function, was 280 mm FL and 1.2 years of age (Figure 4.6; Table 4.3), and 95% of individuals would be expected to be mature at 333 mm FL and 3.1 years of age (Table 4.3).

Table 4.3. Parameters of age and size-specific maturity schedules for *Lethrinus miniatus* populations in the Capricorn Group region of the GBR estimated by logistic regression. (m_{50} and m_{95} are the age or length at 50% and 95% maturity respectively).

	m_{50}	m_{95}	R^2
Age-specific	1.2 years	3.1 years	0.94
Size-specific	280 mm	333 mm	0.92

4.3.3. Size and age at sex change

There was a large overlap in the size distributions of males and females in both areas, although females dominated the smaller size classes and males dominated the larger size classes (Figure 4.7). Likelihood ratio tests indicated the pattern in the size at sex change differed significantly between the northern and southern areas ($\chi^2 = 7.80$, df = 2, $p = 0.02$), which was attributed to a difference in the size at which 50% of the population had changed sex from female to male (size at 50% sex change) ($\chi^2 = 7.35$, df = 1, $p < 0.01$). The size at 50% sex change was 13 mm greater in the southern area compared with the northern area (Figure 4.8, Table 4.4). Furthermore, the size at which males first appeared in the population was slightly smaller in the northern area (325-334 mm FL size class) compared with the southern area (335-344 mm FL size class) (Figure 4.8). There was also a greater proportion of females in some larger size classes in the southern area compared with the northern area (Figure 4.8).

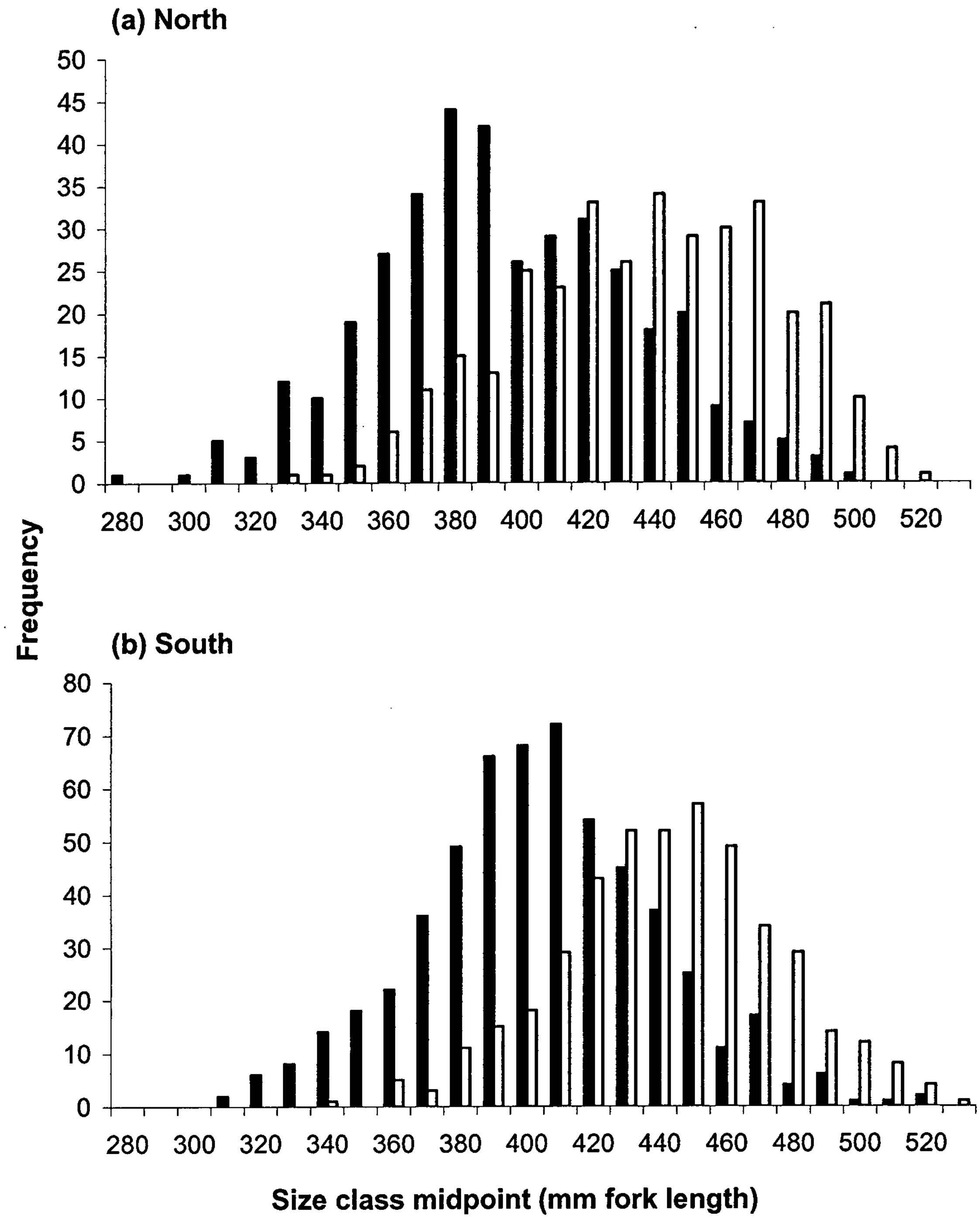

Figure 4.7. Size frequency distributions for female (solid bars) and male (open bars) *Lethrinus miniatus* from two areas of the Great Barrier Reef representing the north (a) and south (b) of *L. miniatus* distribution. Note the difference in y-axis scales.

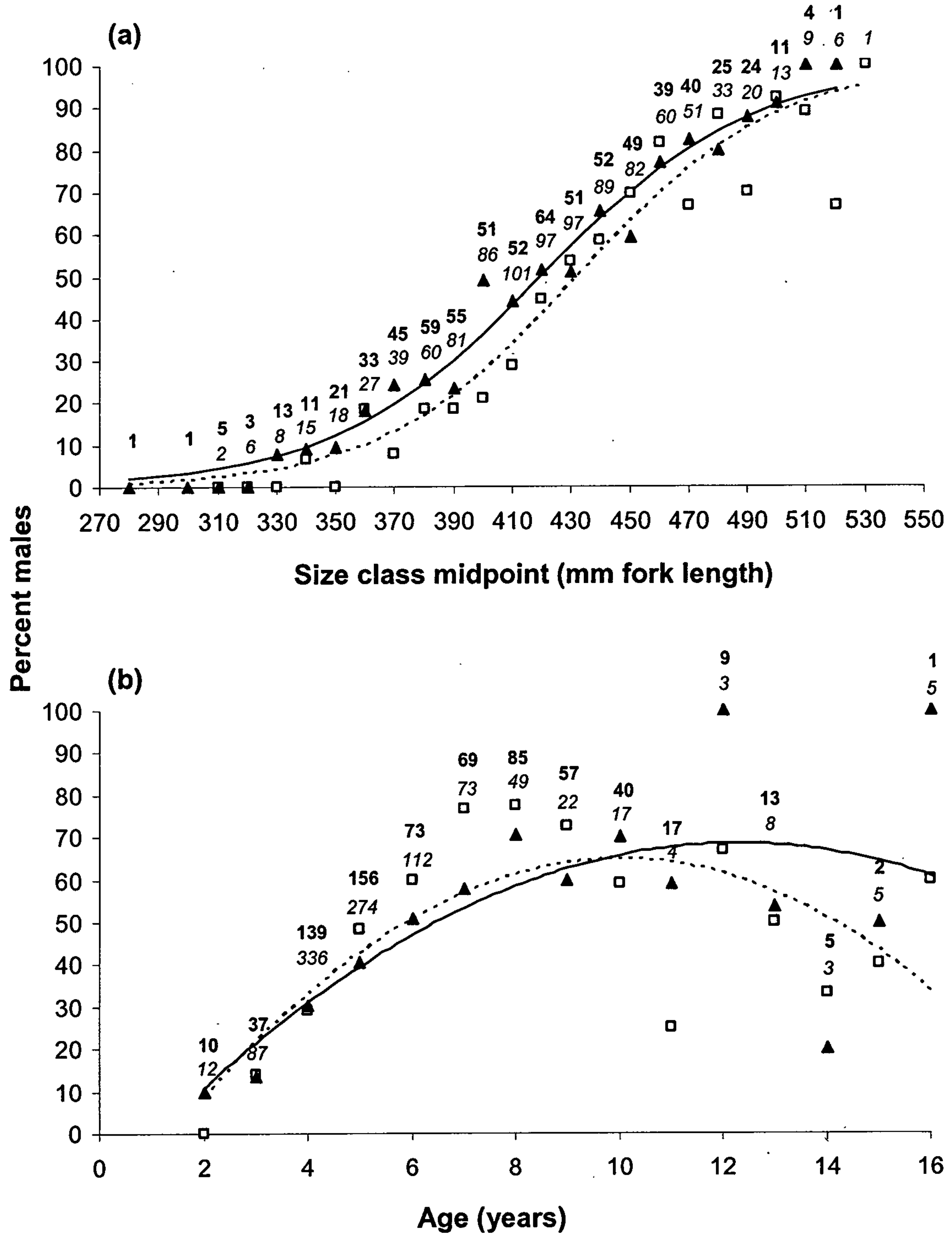

Figure 4.8. Percentage of male *Lethrinus miniatus* and estimated sex change schedules from two areas of the Great Barrier Reef representing the north (▲, solid lines) and south (□, dashed lines) of *L. miniatus* distribution. A logistic function was used to describe the size at sex change (a) and a second order polynomial function used to describe the age at sex change (b). Parameters of the sex change functions are provided in Table 4.4. Sample sizes for northern (**bold**) and southern (*italics*) areas are indicated above each data point.

Table 4.4. Parameters of age and size-specific sex change for *Lethrinus miniatus* within the northern and southern areas of the Great Barrier Reef (GBR) (s_{50} and s_{95} are the length at which 50% and 95% of the population are males respectively, *a*, *b*, and *c* are coefficients of the second order polynomial function used to describe the pattern of age at sex change in each area, and age_{50} is the earliest age at which 50% of individuals were male).

	Size-specific sex change			**Age-specific sex change**				
Location	s_{50}	s_{95}	R^2	*a*	*b*	*c*	R^2	age_{50}
Northern area	420 mm	525 mm	0.98	-0.55	13.45	-13.97	0.47	6.46 y
Southern area	433 mm	530 mm	0.94	-0.87	17.48	-23.00	0.52	5.93 y

The pattern of age at sex change differed from the pattern of size at sex change in both areas (Figure 4.8). The proportion of males in each age class increased from 10% or less at 2 years to over 70% at 8 years for both areas. Although the proportion of males fluctuated greatly in the following age classes, there was a general trend for the proportion of males to decrease after 8 years of age (Figure 4.8), which was not expected for a protogynous species or for a gonochore. Likelihood ratio tests indicated that the pattern of age at sex change was not significantly different between the northern and southern areas ($\chi^2 = 2.63$, df = 2, $p = 0.45$). A single estimate of the age at 50% sex change was not possible for either area as the fitted polynomial functions suggested that after the initial increase in the proportion of males to over 50%, the proportion of males then decreased below 50% in older age classes. The earliest age at which 50% of individuals changed sex, however, was 6.46 and 5.93 years for the northern and southern areas respectively (Table 4.4).

4.3.4. Sex ratio

The female:male sex ratio was 1.10:1 in the northern area and 1.28:1 in the southern area. A chi-square contingency test indicated that the sex ratios were not significantly different between areas ($\chi^2 = 2.22$, df = 1, $p = 0.14$). Consequently, data were pooled across areas to compare the overall sex ratio to a 1:1 sex ratio. Chi-square goodness of fit tests suggested that the sex ratio for the data pooled across areas (1.20:1) was significantly different from 1:1 ($\chi^2 = 14.48$, df = 1, $p = 0.0001$).

4.4. Discussion

4.4.1. Spawning season

A peak spawning period for *L. miniatus* was identified between July and October using monthly trends in both GSI and frequency of ovarian stages. The months of peak spawning were similar in both the northern (Jul-Oct) and southern (Jul-Sep) areas, although the monthly trend in the frequency of mature ovarian stages suggested some spawning may have occurred outside this period in the southern area. The peak spawning period is consistent with previous observations from the northern (Walker 1975) and southern (Brown et al. 1994) extremes of the species distribution on the GBR, suggesting a common spawning period throughout the species range on the GBR. The similarity in spawning season between areas and the consistency in observations between this chapter and previous studies contradict the suggestion by Brown et al. (1994) that *L. miniatus* populations spawn earlier at lower latitudes on the GBR.

From the limited evidence available, the period from late winter through early summer appears to be the most common spawning period for lethrinids (Loubens

1980*a*, Sadovy 1996). The spawning period identified here for *L. miniatus* on the GBR fits within this general period, even though it is somewhat shorter in duration than that reported for most other lethrinids (Sadovy 1996). Data for populations of *L. miniatus* in other geographic regions, however, suggest the spawning season differs from *L. miniatus* populations on the GBR. Loubens (1980*a*) observed ripe females during the months of October through December in New Caledonia, but there were no data available for the months of June through September. It is possible, therefore, that the spawning season for *L. miniatus* is initiated earlier than October in New Caledonia, given that other congeners in the region, such as *L. nebulosus* and *L. genivittatus* (*L. nematacanthus*), begin spawning as early as July (Loubens 1980*a*). Church (1995) found the peak spawning period for *L. miniatus* to be in the warmer months of January through March at Norfolk Island, at the southern extreme of the distribution of the species. Similarly, the spawning season for *L. miniatus* at the Ryukyu Islands off Japan occurs predominantly during the months of northern spring through early summer (March-July, A. Ebisawa, Okinawa Prefectural Fisheries Experiment Station, Okinawa, Japan pers. comm.). The spawning of *L. miniatus* during the warmer months at Norfolk and the Ryukyu Islands may be a result of the higher latitude, and consequently cooler water temperatures, in these regions.

Seasonality in spawning of reef fishes often has been linked to environmental variables, most commonly water temperature (Sadovy 1996). Although the water temperature range differs considerably among locations where *L. miniatus* have been studied, the peak spawning period in all locations appears to coincide with a common water temperature range of 21 to 25°C. This temperature range is consistent with the spawning season of other coral reef fish, for which a general range in water temperature of 19 to 29°C has been observed (Sadovy 1996).

4.4.2. Spawning omission

Although the spawning season for *L. miniatus* is similar throughout the GBR, the proportion of ripe females collected during the spawning season was significantly lower in the southern area than in the northern area. Similarly, the data from Brown et al. (1994) showed that the proportion of ripe females rarely exceeded 25% of all females during the spawning season in the southern extreme of the GBR, although the authors did not comment on this feature. Notably, this observation is inconsistent with results for most other coral reef fish populations, including other lethrinids, in which more than 50% of females have been found to be ripe for at least one month of the spawning season (Sadovy 1996).

My data indicate that the low proportion of ripe females in the southern area is due to a relatively large proportion of smaller females (<450 mm FL) persisting in the resting stage during the spawning season. Brown et al. (1994) found a similar pattern in the far southern region of the GBR, but assumed that the majority of these 'inactive' females were immature, since they were collected during the spawning season. Consequently, Brown et al. (1994) estimated the size at first reproduction to be 350 to 400 mm FL and estimated that 50% of *L. miniatus* females did not mature until 400 to 450 mm FL. Similarly, in the present study, if the majority of resting females identified as mature in the southern area were assumed to be immature, the estimate of size at first reproduction would be approximately 350 mm FL and the size at 50% maturity around 450 mm FL. Given an approximate mean asymptotic size of

500 mm FL (Brown et al. 1994, Williams et al. 2003, Chapter 5), these maturity estimates would suggest that *L. miniatus* reaches maturity at greater than 70% of its maximum size and 50% maturity at greater than 85% of its maximum size. The relative size at 50% maturation for most reef fish is much lower than this (Sadovy 1996), suggesting the maturity estimate from Brown et al. (1994) for *L. miniatus* may be an overestimate. The independent estimate of 50% maturity obtained from the far southern region of the GBR (Capricorn Group) in this study, in which immature individuals were identified histologically, indicated 50% maturity at 280 mm FL, further supporting my argument that the estimate of Brown et al. (1994) may be in error. The large proportion of ripe females in nearly all size classes in the northern area also suggests maturity in that area occurs at a smaller size than estimated by Brown et al. (1994).

It is possible that the large number of small mature resting females in the southern area spawned outside the times and/or locations sampled in this study. This would suggest, however, a very restricted spawning season of less than one month for the smaller females. Given that the few small females that were ripe during the spawning season were sampled in all months from July through October, a restricted spawning season for only some small females seems unlikely.

It is more likely that the resting females sampled in the southern area during the spawning season were mature, but a large proportion of females in the smaller size classes did not spawn in the spawning seasons sampled. This explanation is supported, at least to some degree, by the presence of a small number of ripe and ripening females less than 450 mm FL during the spawning season in the southern area. Why most smaller females do not spawn during some years, prior to reaching a certain size, is unclear, but for other species spawning omission has been linked to low food availability (Pollock 1984, Burton 1994, Burton et al. 1997), reduced water temperature (Chauvet 1991) and geographic position at the edge of the species distribution (Fennessy and Sadovy 2002). For *L. miniatus*, spawning has been observed at cooler water temperatures and at much higher latitudes than the southern area sampled in this study (Church 1995), suggesting latitude and temperature may not be limiting factors for reproductive activity in the southern area of the GBR. It is unclear whether food limitation contributes to spawning omission in the southern area, as there are no data available on the distribution of prey species of *L. miniatus* on the GBR, or elsewhere, or on their variation over time.

4.4.3. Mating pattern and sexual strategy

Populations of *L. miniatus* were found to be significantly female biased in both areas, but the bias was small. Studies that have incorporated a broader size range of samples found that populations of *L. miniatus* on the GBR typically have a much larger female bias (Brown et al. 1994, Bean et al. 2003) than the results here indicate. This difference is most likely due to the selectivity of the sampling gear used in the present study. For example, size classes less than 320 mm FL, in which females predominate, were poorly represented in the present study as the sample collection from the commercial fleet was restricted by a minimum size. Brown et al. (1994) observed a female biased sex ratio of 4.45:1 for *L. miniatus* populations in the Swains and Capricorn Bunker regions of the GBR, based on a broader size range. Sex ratios for *L. miniatus* estimated from the Effects of Line Fishing (ELF) catch surveys (Chapter 2), where all fish selected by the gear were kept, ranged from 1.40:1 to 2.53:1 (C. Davies et al., CRC Reef Research Centre, Townsville, Australia unpublished data).

A female biased population is typical for protogynous reef fish (Sadovy and Shapiro 1987) and suggests a polygynous mating pattern for *L. miniatus*, whereby a single male pair-spawns consecutively with a number of females. Such a mating system is further supported by the difference in size between testes (around 1% body weight) and ovaries (up to 5% body weight) during the spawning season. The unrealised potential for an increase in the size of testes suggests a mating system for *L. miniatus* with little or no sperm competition (Sadovy et al. 1994, Sadovy 1996) and is consistent with other pair-spawning reef fish (Sadovy 1996). Unfortunately there have been no direct observations of wild spawning events to confirm this type of mating system for *L. miniatus*, or for any other lethrinid, although Suzuki and Hioki (1978) observed pair-spawning for *Gymnocranius griseus*, a coastal lethrinid of the Indo-Pacific, in a controlled aquarium environment.

Brown et al. (1994) and Young and Martin (1982) have suggested protogyny is the predominant sexual strategy for *L. miniatus*. The presence of transitional individuals is considered a necessary condition from which to infer protogyny in fish populations (Sadovy and Shapiro 1987). No transitional gonads were observed histologically in this study, although transitional individuals have been found to comprise only between 0.05% (Brown et al. 1994) and 0.6% (Bean et al. 2003) of *L. miniatus* populations on the GBR, and are often found in very low frequencies in other reef fish populations (Sadovy and Shapiro 1987, Munday et al. 1998, Adams et al. 2000, Adams 2002). The absence of transitional individuals from monthly samples in this study suggests that either sex transition in *L. miniatus* is very rapid, or that protogyny is not the only, nor even the dominant, sexual strategy in the species. Bean et al. (2003) argued in favour of rapid sexual transition based on the complete absence of any female tissue in *L. miniatus* testes. The duration of sex transition in a number of other reef fish has been found to be less than one month (Sadovy and Shapiro 1987). It is also possible that only a proportion of females change sex (Sadovy and Shapiro 1987, Warner 1982), resulting in a reduced probability of sampling transitional individuals. The presence of a small number of females in some of the largest size classes, particularly in the southern area, and the tendency for the proportion of males to decrease after eight years of age is evidence in support of a proportion of female *L. miniatus* not changing sex. For the proportion of males to decrease in older age classes, however, there would also need to be diminished survival of males, or net emigration of older males from the population, or both.

Sex change in *L. miniatus* appears to be a function of size rather than age, given the poor relationship between age and the proportion of males in the population. The size at sex change in *L. miniatus* is also very flexible, as indicated by the large overlap in the size distributions of males and females observed for populations in both areas of the GBR. Such a large overlap is indicative of a social control of sex change, whereby females are able to change sex to male to maintain some threshold sex ratio (Shapiro 1981, Ross et al. 1983, Sadovy and Shapiro 1987, Cowen 1990, Vincent and Sadovy 1998) rather than changing sex at a predetermined size or age. The controlling mechanism for sex change remains unclear for the majority of protogynous fish, including *L. miniatus*. More accurate information on sex ratios over the full size range of the population in each area and detailed behavioural studies or manipulative experiments would be necessary to test the hypothesis that sex change in *L. miniatus* is under social control. For example, experimentally manipulating the sex ratio by removing a proportion of males from subsets of the population and monitoring the size or age at sex change of the remaining fish in the population may help clarify the mechanisms of sex change. If the sex ratio became increasingly female biased after the removal of males, and the size or age at sex change remained the same, it would be likely that sex change was controlled endogenously and occurred at a pre-determined size or age. If the sex ratio remained relatively constant after the removal of males, however, and there was a reduction in the size or age at sex change, sex change would be likely to be under social control.

Marine protected areas (MPAs) and the adjacent areas open to fishing may provide the ideal setting for testing the alternative hypotheses of sex change, as fishing may have already reduced the number of males in populations outside MPAs (e.g. Buxton 1993, Adams et al. 2000). However, experiments that use MPAs to attempt to distinguish between the different hypotheses of sex change will need to be carefully designed if they are to be successful. For example, it would be advantageous to have size, age and sex-specific data prior to populations being exposed to fishing, so the effects of fishing on the population can be separated from natural differences in populations between areas included or excluded from MPAs. Such a scenario may be achieved by temporarily opening areas to fishing that have been previously closed to fishing for a significant period of time (e.g. Adams 2002, Mapstone et al. 2003). Furthermore, information on the relationship between the minimum size limit, the sex of fish and the targeting selectivity behaviour of the fishery would also be needed so the effects of fishing on the sex ratio and size or age at sex change could be quantified.

The size at 50% sex change for *L. miniatus* was significantly larger in the southern area compared with the northern area of the GBR, although the difference was only 13 mm in length. If sex change in *L. miniatus* is under social control, an increase in fishing pressure may reduce the size at sex change as females change sex at a smaller size to compensate for the removal of larger males (e.g. Buxton 1993, Platten et al. 2002). It is unlikely, however, that the smaller size at sex change in the northern area is a result of fishing pressure alone, as historic fishing effort has been greater in the southern area of the GBR (Mapstone et al. 1996), where the size at 50% sex change was larger. Spatial variation in growth appears a likely explanation for the difference in the size at sex change, given that the average maximum size of *L. miniatus* is larger in the southern area of the GBR (see Mackay and Storm Cay regions, Chapter 5) than in the northern area (see Townsville region, Chapter 5). A larger size at 50% sex change may be a mechanism to maintain a constant sex ratio for a population reaching a larger maximum size, assuming sex change is under social control. Sex ratios in this study showed no significant spatial variation, but as discussed earlier these sex ratios are inevitably biased due to selective sampling.

4.4.4. Implications for fisheries management

There is currently a proposal for a closure of the GBR line fishery for nine-day periods around the new moon in October and November in northern areas and in November and December in southern areas of the GBR (QFMA 1999). These proposed closures are intended to protect the spawning activity of reef fish, particularly spawning aggregations (QFMA 1999), but would not coincide with the peak spawning period for *L. miniatus*. It can therefore be assumed that the spawning stock of *L. miniatus* will gain little, if any, protection of spawning activity from the proposed spawning closures. The proposed spawning closures are based on the spawning activity of common coral trout, *Plectropomus leopardus*, as it is the main target species of the GBR line fishery (Mapstone et al. 1996). A paucity of information existed on the spawning activity of other targeted reef fish at the time these closures were proposed, although recent information for several serranids indicates spawning times similar to *P. leopardus* (R. Pears and B. Mapstone, CRC Reef Research Centre, Townsville, Australia unpublished data). The results from this study highlight the importance of gathering information on the spawning activity of other target and non-target species before implementing spawning closures. Without such information, the intended objectives of proposed spawning closures might not be achieved for these other reef fish species.

The minimum size limit for *L. miniatus* currently is 350mm TL (approximately 320mm FL) for all commercial and recreational fishers in all regions of the GBR. The stated objective of minimum legal sizes is to allow at least 50% of fish to reach maturity and spawn before being vulnerable to the fishery (QFMA 1999). Given the size at maturity estimate of 280 mm FL for *L. miniatus* in the Capricorn group, this size limit appears to be meeting the stated objective. In addition, data from the northern area also indicate that more than 50% of females are mature at a size smaller than the minimum size limit. However, the estimate of size at maturity was obtained from a single region of the GBR. It will be important to estimate maturity from other regions of the GBR, as the single minimum size limit for *L. miniatus* is based on the assumption that the size at maturity is relatively uniform across all regions. Furthermore, the low proportion of ripe females observed during the spawning season from the southern area, particularly in the smaller size classes, indicates that 50% of females do not spawn in all seasons until they reach 450 mm FL. From a management perspective, the large proportion of resting females are effectively 'immature' for the years they do not contribute to egg production in each year. Accordingly, the larger females are likely to be very important to the spawning stock, as their relative contribution to egg production is disproportionately greater than would be expected if the majority of mature females in all size classes were spawning every year. Consequently, there is the potential for fishing to greatly reduce the reproductive output of *L. miniatus* in the southern area by more than might be suggested by the relationship between maturity schedules and the minimum legal size limit, assuming that fishing diminishes the abundance of larger females in the population. Clearly it will be important to determine the causal factor(s) for spawning omission in order to predict the potential effects of fishing on the reproductive potential of *L. miniatus* in the medium to long term.

The minimum size limit for *L. miniatus* on the GBR is considerably smaller than the size at 50% sex change in both areas of the GBR. Furthermore, the presence of male *L. miniatus* smaller than the minimum size limit is extremely rare on the GBR (Brown et al. 1994, Bean et al. 2003). Therefore *L. miniatus* may be particularly vulnerable to sperm limitation arising from overfishing of males, as the entire male population is vulnerable to the commercial fishing gear and there are no restrictions in place that prevent the capture of males. An increase in the current minimum size limit, or the introduction of a maximum size limit, are two mechanisms that may offer some protection from harvest to a proportion of the male *L. miniatus* population.

4.4.5. Summary and conclusions

Variation in reproductive biology of *L. miniatus* between the northern and southern areas of the GBR was observed in some reproductive parameters, but not others. In the northern area, the size at sex change was significantly larger and the proportion of spawning females greater than in the southern area. The spawning season and sex ratios, however, did not differ significantly between the northern and southern areas. It will be important to be cognisant of these spatial patterns in reproductive biology when managing populations of *L. miniatus* on the GBR. For example, if seasonal closures were chosen as a management strategy to protect spawning populations of *L. miniatus*, it would be appropriate to implement a synchronised closure across all areas of the GBR given the common spawning season of *L. miniatus* in all areas. A uniform minimum size limit, however, may not be appropriate in all areas, as a large proportion of females in the southern area do not spawn in all years and therefore are effectively 'immature' in the years when they do not spawn.

This chapter has also highlighted important areas for future research. These include, but are not limited to, resolving the causal factors of spawning omission, observing spawning behaviour to verify whether *L. miniatus* has a polygynous pair-spawning mating pattern, and elucidating the mechanisms of sex change. Only from this information can we predict with more certainty the potential effects that fishing may have on the reproductive output of *L. miniatus* populations across the GBR.

Chapter 5. Regional and inter-annual patterns in growth of *Lethrinus miniatus* populations on the Great Barrier Reef.

5.1. Introduction

Knowledge of growth rates, along with other life history traits, is essential for understanding the processes shaping populations and managing exploited species (Gulland 1988). For coral reef fish, reliable age-based estimates of growth have begun to emerge only in the past decade or so. The paucity of growth estimates for coral reef fish prior to the 1990's is primarily due to the once widely held perception that otoliths could not be used to determine the age of coral reef fish due to the apparent lack of seasonal variation at tropical latitudes (Munro 1983, Campana and Neilson 1985, Longhurst and Pauly 1987). Many studies have since validated the annual periodicity of increments in otoliths of reef fish (e.g. Manooch and Drennon 1987, Fowler 1990, Ferreira and Russ 1992, Lou 1992, Choat and Axe 1996, Choat et al. 1996, Cappo et al. 2000, Pilling et al. 2000, Chapter 3). These studies have provided a foundation for age-based estimates of population parameters, such as rates of growth, for coral reef fish.

Despite the recent increase in the number of age and growth studies of reef fish, there have been relatively few attempts to examine temporal and spatial variation in growth. Given the spatial complexity of coral reefs, and the sensitivity of fish growth to the local environment (Conover 1992, Shultz and Conover 1997, Yamahira and Conover 2002), considerable temporal and spatial variations in growth seem likely for reef fish populations, particularly at scales where differences in environmental conditions, recruitment and/or post-settlement processes are pronounced. Most studies of reef fish that have examined spatial variation in growth have focussed on small, site-attached species (e.g. Hart and Russ 1996, Meekan et al. 2001). Research on larger predatory reef fish species, which are often the target species of coral reef fisheries, usually report aggregated growth estimates based on pooled samples from several locations (e.g. Potts and Manooch 1995, Craig et al. 1997, Potts et al. 1998).

Spatial variation in growth has been shown to play an important role in maintaining population size under certain recruitment patterns (Kritzer 2001). Furthermore, the presence of temporal and/or spatial variations in growth is likely to have significant implications for fisheries management. Most stock assessment models explicitly depend on estimates of growth, and generally assume uniform parameters among populations within the stock (Beverton and Holt 1957, Gulland 1988, Hilborn and Walters 1992). Accordingly, management measures are often implemented uniformly across the stock as a whole. Variations in growth among populations within a stock, however, may indicate that productivity varies within the stock. Consequently, applying uniform fishing pressure to a stock with inherent spatial variation in growth may result in less productive components of the stock being overfished, failure to realise potential yields from more productive components of the stock, or both. Clearly, it is important to determine whether growth varies among populations within a managed stock.

In a recent multi-spatial scale study of *L. miniatus* Williams et al. (2003) demonstrated significant differences in growth among regions of the GBR, and to a lesser extent among reefs within regions. The temporal stability of these spatial patterns in growth was not resolved however, as Williams et al. (2003) analysed data collected from a single year only. This chapter substantially extends the work of Williams et al. (2003) by examining both the spatial and temporal patterns in growth of *L. miniatus* from the same 12 reefs and three regions over the period from 1995 to 1999. The specific aims of this chapter were to: i) verify the spatial patterns in growth of *L. miniatus* among reefs within regions and among regions on the GBR identified by Williams et al. (2003); and ii) examine the annual variation in growth to determine whether those spatial patterns in growth were consistent through time.

5.2. Methods

5.2.1. Sample collection

Samples of *L. miniatus* were collected annually from 1995 to 1999 inclusive from six reefs within three regions of the GBR using fishery independent catch surveys described in Chapter 2. Only samples collected from reefs closed to fishing were used, in order to obtain estimates of growth from relatively unexploited populations. Data collected from a total of 12 reefs (four closed reefs within each of three regions) were used in the analyses. One of these reefs in each region was opened to fishing for one year in 1997 with a second reef in each region opened to fishing for one year in 1999 (Mapstone et al. 1996, 1998, 2003, Chapter 2). Data collected from these two reefs during and following the years they were opened to fishing were not used in the analyses. Fork length, whole body weight and age estimates for *L. miniatus* were obtained as described in Chapter 2.

5.2.2. Temporal patterns in growth

Temporal patterns in growth were examined first to assess the variation in growth of *L. miniatus* among years. To determine whether growth varied among years, the mean annual growth increment of individual cohorts was estimated in each year from 1995 to 1999 using the equation,

$$\bar{i}_{c,n,r} = \bar{L}_{c,n(y),r} - \bar{L}_{c,n-1(y-1),r} \qquad (5.1)$$

where:

$\bar{i}_{c,n,r}$ is the mean annual growth increment for cohort c, of age n years, in region r;

$\bar{L}_{c,n(y),r}$ is the mean fork length of cohort c, of age n years, in year y, in region r; and

$\bar{L}_{c,n-1(y-1),r}$ is the mean fork length of cohort c, of age n-1 years in year y-1, in region r.

Mean annual growth increments are likely to decrease with an increase in age due to the asymptotic pattern of growth for *L. miniatus* (Williams et al. 2003). Consequently, it was not appropriate to analyse mean annual growth increments directly. To standardise for the age of fish and analyse the annual growth increment data, an overall mean annual growth increment for each age class was estimated by pooling length-at-age data across regions, cohorts and years using the equation,

$$\bar{I}_n = \bar{L}_{n(y)} - \bar{L}_{n-1(y-1)} \qquad (5.2)$$

where:

$\bar{I}_n$ is the overall mean annual growth increment for fish of age n;

$\bar{L}_{n(y)}$ is the mean fork length of fish of age *n* in year *y*; and

$\bar{L}_{n-1(y-1)}$ is the mean fork length of fish of age *n*-1 in year *y*-1.

These age-specific overall mean annual growth increments ($\bar{I}_n$) provided a baseline against which mean annual growth increments of each cohort within each region ($\bar{i}_{c,n,r}$) were compared. Deviations between the mean annual growth increments of each cohort within each region and the age-specific overall mean annual growth increments, $D_{c,n,r}$, were estimated and expressed as a percentage using the equation,

$$D_{c,n,r} = \frac{\left(\bar{i}_{c,n,r} - \bar{I}_n\right)}{\bar{I}_n} \times 100 \tag{5.3}$$

Estimates of $D_{c,n,r}$ were compared among Years, Regions and Ages using a three factor fixed effects analysis of variance (ANOVA), where an Age*Year interaction signified cohort-specific effects on growth. Sources of any suggested differences were identified by Least Significant Difference (LSD) adjusted multiple comparisons (Milliken and Johnson 2001). Residual plots and normal probability plots were used to examine the assumptions of homogeneous variances and normality for all data prior to analysis. All data conformed to these assumptions and accordingly no transformations were necessary.

Age classes older than six years were excluded from the analysis as annual variations in growth were likely to be more pronounced in the younger age classes, when more than 80% of growth for *L. miniatus* occurs (Brown and Sumpton 1998, Williams et al.

2003). Age classes younger than three years were also excluded because there were insufficient sample sizes for calculations in most years, presumably as a result of gear selectivity. Furthermore, only fish from the Mackay and Storm Cay regions were used in this analysis, as there were some years in which there were no young fish (3-5 years) collected from the Townsville region. Similarly there were some years in which there were no young fish collected from some reefs within the Mackay and Storm Cay regions. Accordingly, size-at-age data were pooled across reefs within the Mackay and Storm Cay regions to provide adequate sample sizes ($n \geq 5$) for both regions in all years. The pooling of data across reefs within regions assumes that temporal patterns in growth were similar among reefs in close proximity within regions. This appeared to be a reasonable assumption given the relative consistency of growth of *L. miniatus* among reefs within regions relative to large regional differences in growth demonstrated by Williams et al. (2003).

5.2.3. Spatial patterns in growth

Three aspects of growth were compared among reefs and regions: i) the relationship between fork length and whole body weight; ii) the relationship between fork length and age; and iii) the relationship between whole body weight and age. Comparisons of these aspects of growth among both reefs and regions were possible only after pooling size-at-age data over all years for each of the 12 reefs. These comparisons were based on the assumption that growth was similar among years for each reef (nested within region), and that any differences among years were the same for all reefs in all years. The interaction between region and year from the temporal comparison of growth (above) was used to test indirectly the validity of this assumption.

5.2.3.1. Length weight relationship

The relationship between fork length (*L*) and whole body weight (*W*) was described for each reef by a power function of the form,

$$W_{L,r} = a_r * L^{b_r} \tag{5.4}$$

where:

a_r is the coefficient of the power function for reef *r*; and

b_r is the exponent of the power function for reef *r*.

This relationship was compared among reefs and regions using a 2 factor nested analysis of covariance (ANCOVA) with Reefs (random factor) nested in Regions (fixed factor) and Fork Length the covariate of weight. Body weight data were transformed ($\log_e y$) for the analysis to satisfy the assumption of linearity. Sources of any suggested differences were identified by Least Significant Difference (LSD) adjusted multiple comparisons (Milliken and Johnson 2001). Reef-specific relationships between fork length and whole body weight were used to estimate the whole body weight for a small number of fish for which weight was not measured.

5.2.3.2. Length and weight at age

According to the parameter estimates from the Schnute (1981) growth function, the von Bertalanffy growth function (VBGF) provided the best fit to length and weight at age data for most reefs. Accordingly, the VBGF was used to model growth for all reefs and regions for consistency, and to enable spatial comparisons of growth parameters. The VBGF was fitted to length-at-age and weight-at-age data by nonlinear least-squares regression. The form of the VBGF used to model length-at-age data was,

$$L_{t,r} = L_{\infty,r}\left(1 - e^{-K_r^l\left(t - t_{0,r}^l\right)}\right) \tag{5.5}$$

where:

$L_{t,r}$ is the length at age *t* on reef or region r;

$L_{\infty,r}$ is the mean asymptotic fork length on reef or region *r*;

K_r^l is the rate at which L_∞ is approached on reef or region *r*; and

$t_{0,r}^l$ is the age at which the sampled fish have a theoretical length of zero on reef or region *r*.

The form of the VBGF used to model weight-at-age data was,

$$W_{t,r} = W_{\infty,r}\left(1 - e^{-K_r^w\left(t - t_{0,r}^w\right)}\right)^3 \tag{5.6}$$

where:

$W_{t,r}$ is the weight at age *t* on reef or region r;

$W_{\infty,r}$ is the mean asymptotic weight on reef or region *r*;

K_r^w is the rate at which W_∞ is approached on reef or region *r*; and

$t_{0,r}^w$ is the age at which the sampled fish have a theoretical weight of zero on reef or region *r*.

VBGF's were compared among reefs within each region and among regions using likelihood ratio tests (Kimura 1980), which are considered the most reliable procedure for such comparisons (Cerrato 1990). A common range of age classes was used in each analysis to assure validity of the comparisons (Haddon 2001).

Spatial patterns in growth were further examined by comparing the approximate 95% confidence ellipses for the VBGF parameter estimates of L_∞ (W_∞) and K^l (K^w) among reefs and regions (Draper and Smith 1966, Kimura 1980). Using this technique to compare growth parameters requires the VBGF parameter t_0^l (t_0^w) to be constrained to the same value for all growth curves. A common value for t_0 was obtained for reefs within each region by fitting an unconstrained VBGF to all size-at-age data from that region. Similarly a common value for t_0 for regions was obtained by fitting an unconstrained VBGF to the size-at-age data from all regions. The constraining of t_0 usually alters estimates of L_∞ (W_∞) and K^l (K^w) due to the correlation among VBGF parameters. Consequently, the results from this technique for growth comparison are not always consistent with results from the likelihood ratio tests. Furthermore, estimates of the differences among growth curves will be more conservative (i.e. less likely to be different) when t_0 is constrained to the same value for all curves due to the correlation among VBGF parameters.

5.3. Results

5.3.1. Temporal patterns in growth

Annual growth increments appeared variable among years, regions and age classes (Figure 5.1). Results from the ANOVA, however, indicated that there were no significant effects of the interactions between year, region and age or the main effects

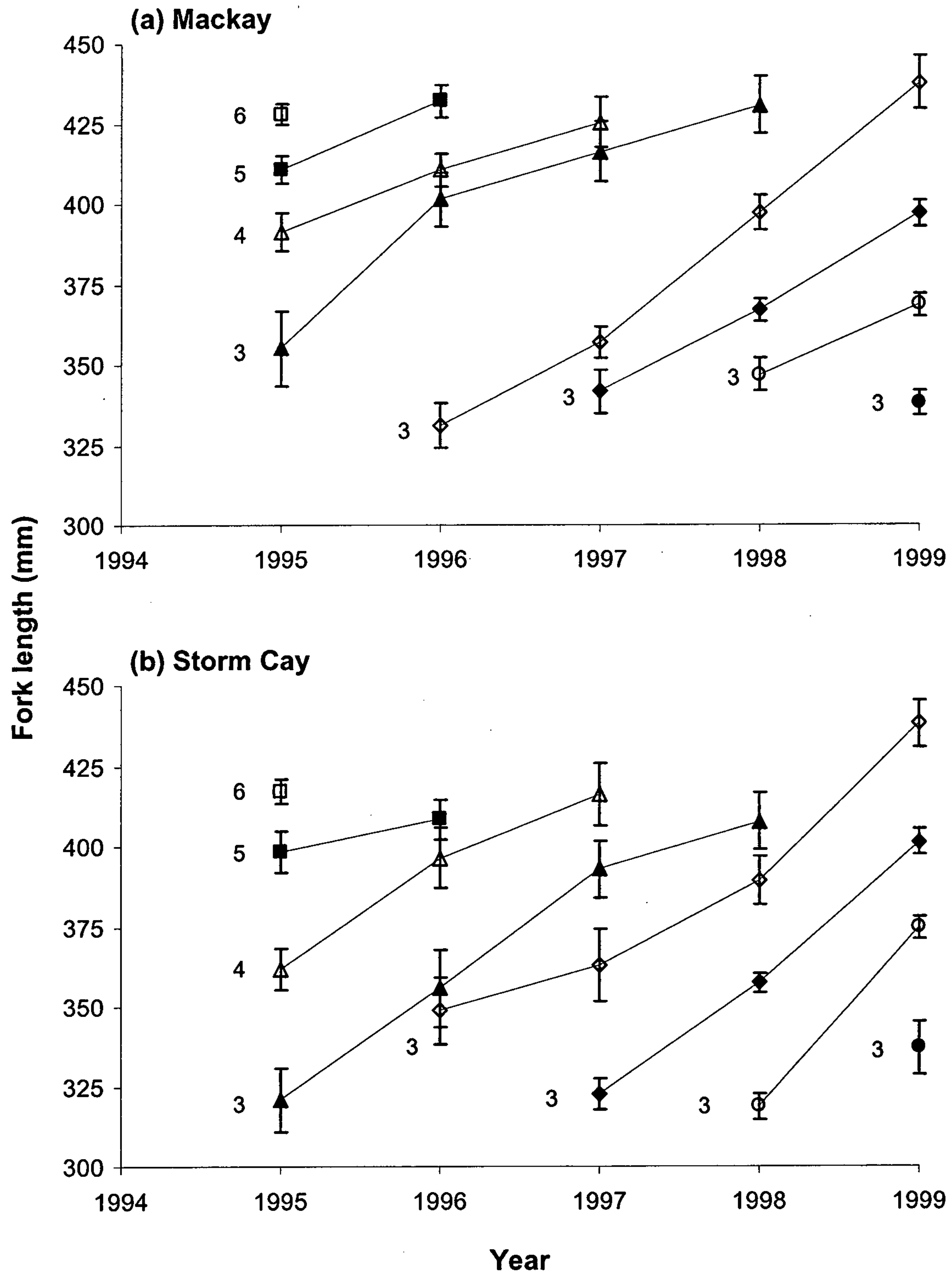

Figure 5.1. Mean fork length-at-age for *Lethrinus miniatus* cohorts aged 3 to 6 years from 1995 to 1999 from the Mackay (a) and Storm Cay (b) regions of the Great Barrier Reef. Numbers indicate age of cohort in relevant year. Joining lines represent growth trajectories of a single cohort, and a line joining two adjacent years (ages) represents an annual growth increment.

of region and age on the percentage deviation from the mean annual growth increments (Table 5.1). However, annual growth increments varied significantly among years, by up to 40% from the average for the five-year period (Figure 5.2). Mean annual growth was significantly higher in 1998-99 than in any other year (Table 5.1, Figure 5.2), but did not differ significantly among any other years. The non-significant interactions between year, region and age indicated that this temporal difference in growth increments was consistent among regions and age classes. Consequently it was assumed also that temporal patterns in growth were similar among reefs within regions and so annual effects would not confound spatial patterns among reefs. Accordingly size-at-age data were pooled over years to examine spatial patterns in growth.

Table 5.1. Analysis of variance comparing the percentage deviation of annual growth increments from average annual growth increments for *Lethrinus miniatus* between 1995 and 1999. Year (1995-96, 1996-97, 1997-98, 1998-99), Region (Mackay, Storm Cay), and Age (4, 5, & 6 years) were all fixed factors. Results of LSD multiple comparisons among years are also presented. df = degrees of freedom, MS = mean square, F = F-ratio, p = probability of the data if no difference existed.

Source of variation	df	MS	*F*	*p*
Year	3	0.585	4.985	**0.045**
Region	1	0.140	1.197	0.316
Age	2	0.034	0.290	0.758
Year*Region	3	0.153	1.301	0.357
Year*Age	6	0.242	2.059	0.200
Region*Age	2	0.037	0.311	0.744
Residual (error)	6	0.117		
LSD tests for differences among years:	1995-96	1996-97	1997-98	1998-99

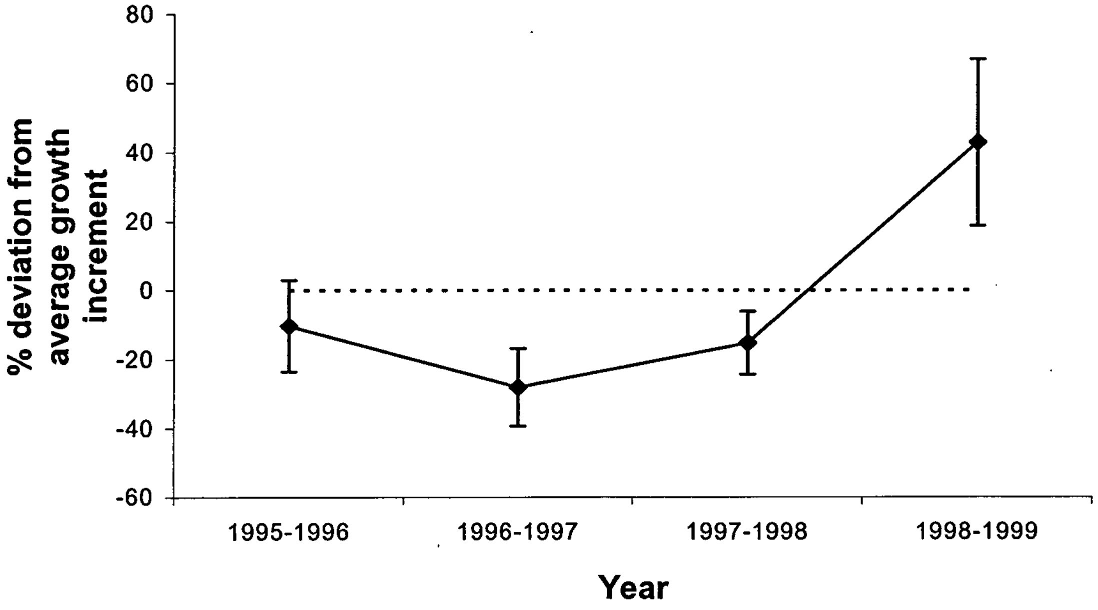

Figure 5.2. Percent deviation of annual growth increments of *Lethrinus miniatus* from the overall mean annual growth increments (represented by dashed line) for cohorts aged 3 to 6 years from the Mackay and Storm Cay regions of the Great Barrier Reef from 1995 to 1999. Error bars are standard errors.

5.3.2. Spatial patterns in growth

5.3.2.1. Length-weight relationship

The relationship between fork length and total weight was approximately cubic for all reefs and regions, as expected (Table 5.2). This relationship differed significantly among some reefs within each region (Table 5.3). In the Townsville region, the length-weight relationship at Glow Reef differed from those of Yankee and Faraday Reefs, and was similar to that of Dip Reef. The relationship was similar between two reefs within the Mackay (20-142 and Bax) and Storm Cay (21-132 and 21-133) regions and differed significantly among all other reefs within each of these regions (Table 5.3). Further, the overall length-weight relationships were significantly different among all three regions (Table 5.3). Generally, the larger value of the parameter *b* in the length-weight relationship for the Mackay and Storm Cay regions meant that fish were a greater mass for a given length in these more southern regions.

Table 5.2. Growth parameter estimates for *Lethrinus miniatus* from four reefs within three regions of the Great Barrier Reef. a and b are parameters of the cubic relationship ($W_L = a{\cdot}L^b$) between fork length (L) and whole body weight (W). L_∞ = mean asymptotic fork length, W_∞ = mean asymptotic whole body weight, K^l and K^w = von Bertalanffy growth coefficients for length and weight, t_0^l and t_0^w = theoretical age at length and weight zero. Data were pooled over 5 years between 1995 and 1999.

Region	Reef	Length-weight relationship			Growth in length				Growth in weight			
		$a(\times10^{-5})$	b	R^2	L_∞ (mm)	K^l	t_0^l	R^2	W_∞ (g)	K^w	t_0^w	R^2
Townsville	Glow	5.67	2.80	0.90	460.54	0.43	-0.24	0.40	1600.49	0.49	0.07	0.32
	Dip	7.21	2.76	0.89	449.72	0.61	0.61	0.24	1506.67	0.77	1.23	0.20
	Yankee	2.12	2.97	0.88	458.52	0.56	1.18	0.49	1790.79	0.36	-0.62	0.35
	Faraday	1.13	3.07	0.82	440.68	0.55	0.07	0.36	1566.19	0.52	0.04	0.25
	Pooled	***4.50***	***2.84***	***0.87***	***454.68***	***0.47***	***-0.06***	***0.36***	***1580.60***	***0.53***	***0.30***	***0.28***
Mackay	20-142	0.32	3.29	0.97	517.90	0.20	-2.00	0.65	2575.81	0.22	-1.46	0.58
	20-137	0.38	3.25	0.96	500.90	0.27	-1.43	0.70	2273.01	0.29	-0.94	0.66
	20-136	5.58	2.82	0.94	527.17	0.22	-2.45	0.67	2616.97	0.22	-2.62	0.66
	Bax	0.59	3.18	0.95	585.55	0.12	-4.46	0.55	4359.90	0.11	-4.47	0.55
	Pooled	***0.43***	***3.24***	***0.97***	***526.52***	***0.21***	***-2.07***	***0.67***	***2635.03***	***0.22***	***-1.56***	***0.63***
Storm Cay	21-132	0.48	3.21	0.94	475.88	0.27	-1.18	0.68	1836.19	0.32	-0.47	0.63
	21-131	0.40	3.24	0.96	489.15	0.30	-0.90	0.68	1996.65	0.36	-0.15	0.65
	21-130	2.06	2.98	0.94	476.05	0.33	-0.60	0.62	1924.78	0.38	-0.33	0.52
	21-133	0.17	3.39	0.94	483.79	0.26	-1.24	0.74	1952.59	0.33	-0.27	0.69
	Pooled	***0.42***	***3.24***	***0.95***	***483.18***	***0.28***	***-1.12***	***0.68***	***1938.40***	***0.33***	***-0.39***	***0.63***

Table 5.3. Analysis of Covariance comparing the slopes of the regression of whole body weight ($\log_e$ transformed) on fork length (covariate). Only results for interactions with the covariate are shown as these test for homogeneity of slopes. Region (Townsville, Mackay, and Storm Cay) is a fixed factor and Reef (with 12 levels, four nested within each region) is a random factor. Results of Least Significant Difference (LSD) multiple comparisons among regions and reefs are also presented. df = degrees of freedom, MS = mean square, F = F-ratio, p = probability of the data if no difference existed.

Source of variation	df	MS	F	p
Region*Fork length	2	0.247	26.682	**<0.001**
Reef*Fork length (Region)	9	0.111	11.926	**<0.001**

LSD tests for differences among reefs and regions:

Townsville:

Glow Dip Yankee Faraday

Mackay:

Bax 20-142 20-137 20-136

Storm Cay:

21-133 21-132 21-131 21-130

All regions:

Townsville Mackay Storm Cay

5.3.2.2. Length and weight-at-age

The growth patterns for *L. miniatus* in terms of length and weight were generally of asymptotic form for all reefs except for 20-142 and Bax reefs in the Mackay region (Figures 5.3 and 5.4). The less asymptotic growth at these reefs was most likely due to the relatively small number of fish over 10 years of age sampled from these reefs. Likelihood ratio tests indicated that patterns of growth, in terms of length and weight, differed among reefs within the Mackay and Storm Cay regions only (Table 5.4). Growth patterns were similar among all reefs in the Townsville region. In the Mackay

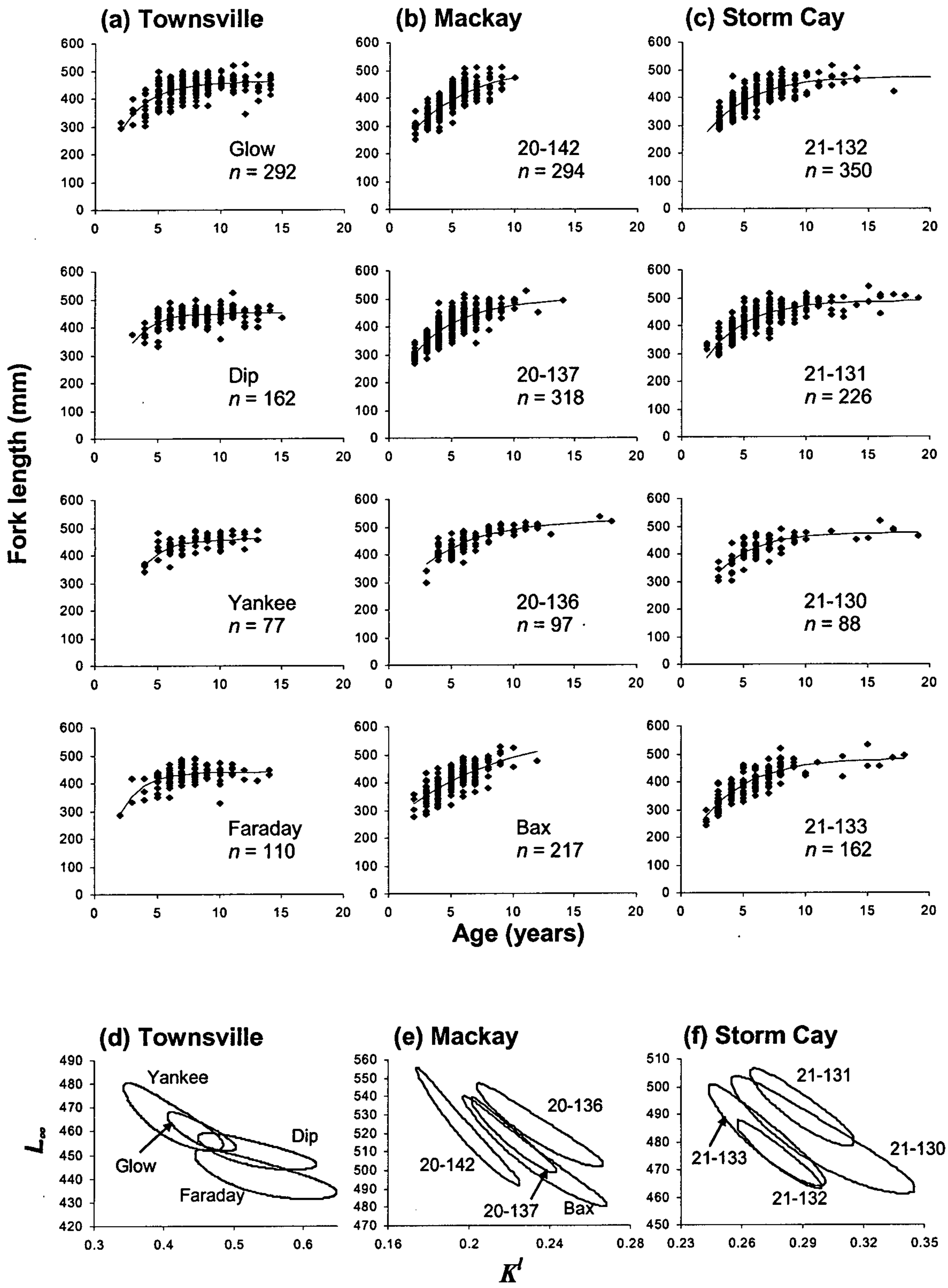

Figure 5.3. Length-at-age data and estimated von Bertalanffy growth curves (a-c) and approximate 95% confidence ellipses (d-f) of the parameters L_∞ and K^l for *Lethrinus miniatus* from four reefs within each of three regions of the Great Barrier Reef. Common values of the VBGF parameter t_0^l were used to estimate confidence regions (see text for details). Data were pooled over the years 1995 to 1999 excluding data from reefs opened to fishing in 1997 and 1999. *n* = sample size.

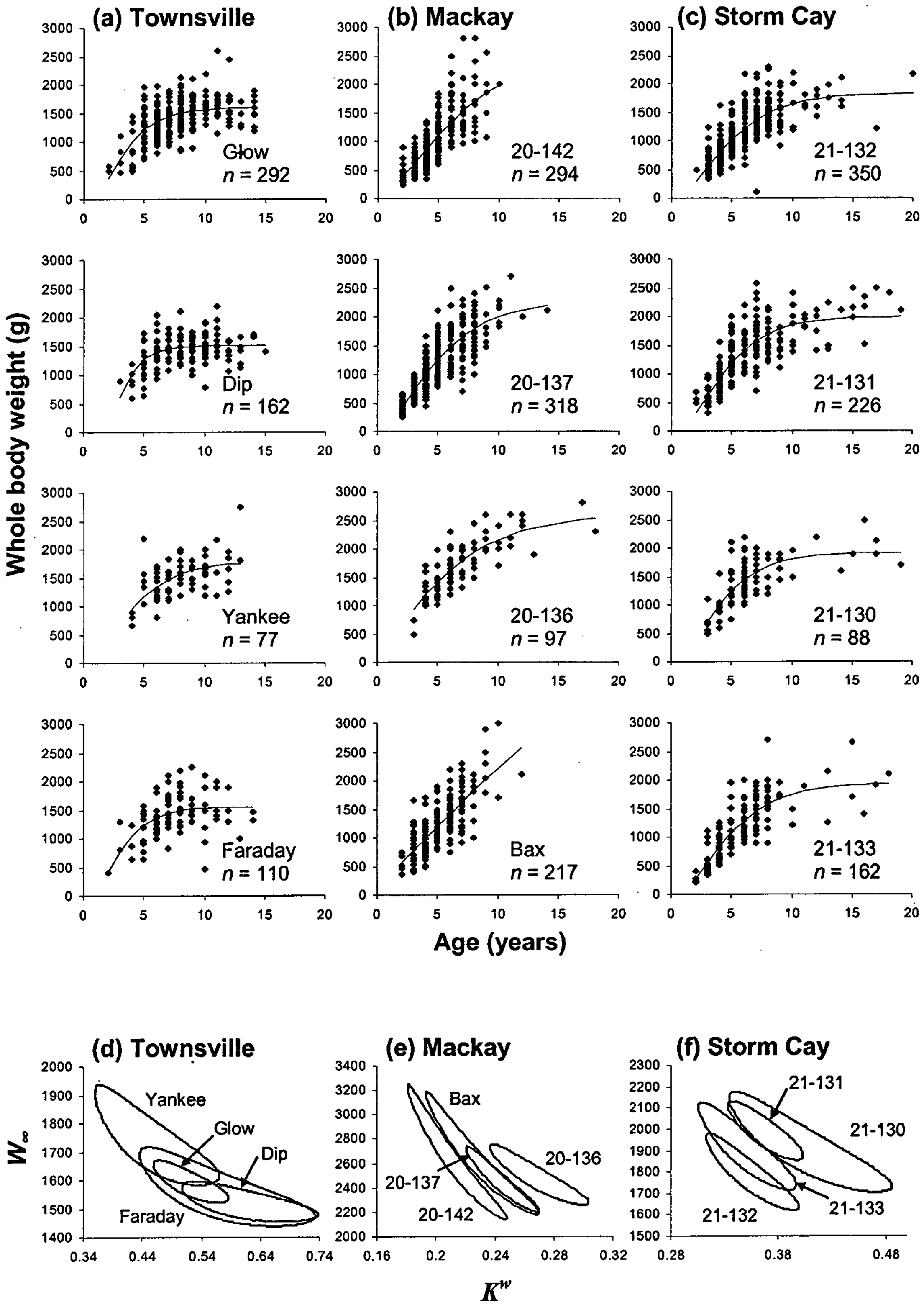

Figure 5.4. Weight at age data and estimated von Bertalanffy growth curves (a-c) and approximate 95% confidence ellipses (d-f) of the parameters W_∞ and K^w for *Lethrinus miniatus* from four reefs within three regions of the Great Barrier Reef. Common values of the VBGF parameter t_0^w were used to estimate confidence regions (see text for details). Data were pooled over the years 1995 to 1999 excluding data from reefs opened to fishing in 1997 and 1999. *n* = sample size.

Table 5.4. Results of likelihood ratio tests comparing estimates of von Bertalanffy growth (VBGF) parameters for *Lethrinus miniatus* from four reefs within each of three regions of the Great Barrier Reef (Townsville, Mackay, and Storm Cay). χ^2 = likelihood ratio Chi-squared statistic for length (L) and weight (W) based comparisons of growth. Each comparison tests the hypothesis that the three VBGF parameters L_∞, K^l, and t_0^l (or W_∞, K^w, and t_0^w) are from the same population.

Region	Age classes (years)	Comparison	df	$\chi^2(L)$	$p(L)$	$\chi^2(W)$	$p(W)$
Townsville	4 - 13	All reefs	9	16.20	0.063	11.42	0.248
Mackay	3 - 10	All reefs	9	79.98	**<0.001**	73.25	**<0.001**
		20-142 vs 20-137	3	42.18	**<0.001**	26.27	**<0.001**
		20-142 vs 20-136	3	48.67	**<0.001**	51.70	**<0.001**
		20-142 vs Bax	3	29.09	**<0.001**	22.56	**<0.001**
		20-137 vs 20-136	3	9.89	**0.020**	16.87	**0.001**
		20-137 vs Bax	3	7.05	0.070	11.64	**0.009**
		20-136 vs Bax	3	15.32	**0.002**	23.79	**<0.001**
Storm Cay	3 - 17	All reefs	9	67.50	**<0.001**	66.45	**<0.001**
		21-132 vs 21-131	3	59.73	**<0.001**	48.13	**<0.001**
		21-132 vs 21-130	3	15.65	**0.001**	40.92	**<0.001**
		21-132 vs 21-133	3	0.95	0.813	6.87	0.076
		21-131 vs 21-130	3	3.85	0.278	1.89	0.596
		21-131 vs 21-133	3	29.32	**<0.001**	10.73	**0.013**
		21-130 vs 21-133	3	8.19	**0.042**	13.22	**0.004**
All regions	2 - 14	All regions	6	139.75	**<0.001**	244.16	**<0.001**
		Townsville vs Mackay	3	77.98	**<0.001**	188.33	**<0.001**
		Townsville vs Storm Cay	3	53.56	**<0.001**	45.35	**<0.001**
		Mackay vs Storm Cay	3	75.28	**<0.001**	123.98	**<0.001**

region, growth patterns were similar only in terms of length, and only between 20-137 and Bax reefs. Growth patterns in terms of both length and weight in the Storm Cay region were similar only between 21-130 and 21-131, and between 21-132 and 21-133. Estimates of the 95% confidence regions for reef specific VBGF parameters L_∞ (W_∞) and K^l (K^w) support the results of the likelihood ratio tests (Figures 5.3 and 5.4). That is, there was more overlap in the 95% confidence regions for the reefs that were statistically indistinguishable than for reefs that differed significantly according to the likelihood ratio tests.

If regional variation in growth is to be inferred, it must be evident in spite of variation within regions. Region-specific growth was best estimated by pooling size-at-age data across reefs within regions. Thus, to examine regional patterns in growth, size-at-age data were pooled among reefs within each region to examine whether differences in growth existed among regions in spite of (ie. in addition to) variation in growth among reefs nested within regions. Although growth differences were present within regions, there was no overlap in the reef specific estimates of L_∞ or W_∞ among regions, and only minimal overlap in the estimates of K^l and K^w (Table 5.2).

Likelihood ratio tests indicated that growth patterns in terms of length and weight differed significantly among all regions (Table 5.4). While the differences in L_∞ among regions were significant, they were also relatively small. The estimate of L_∞ for the Mackay region was only 15.8% greater than for the Townsville region and represented the largest difference in the estimate of L_∞ among regions (Figure 5.5, Table 5.2). The difference in W_∞ between the Townsville and Mackay regions, however, was much greater (66.7%) due to both the cubic relationship between length

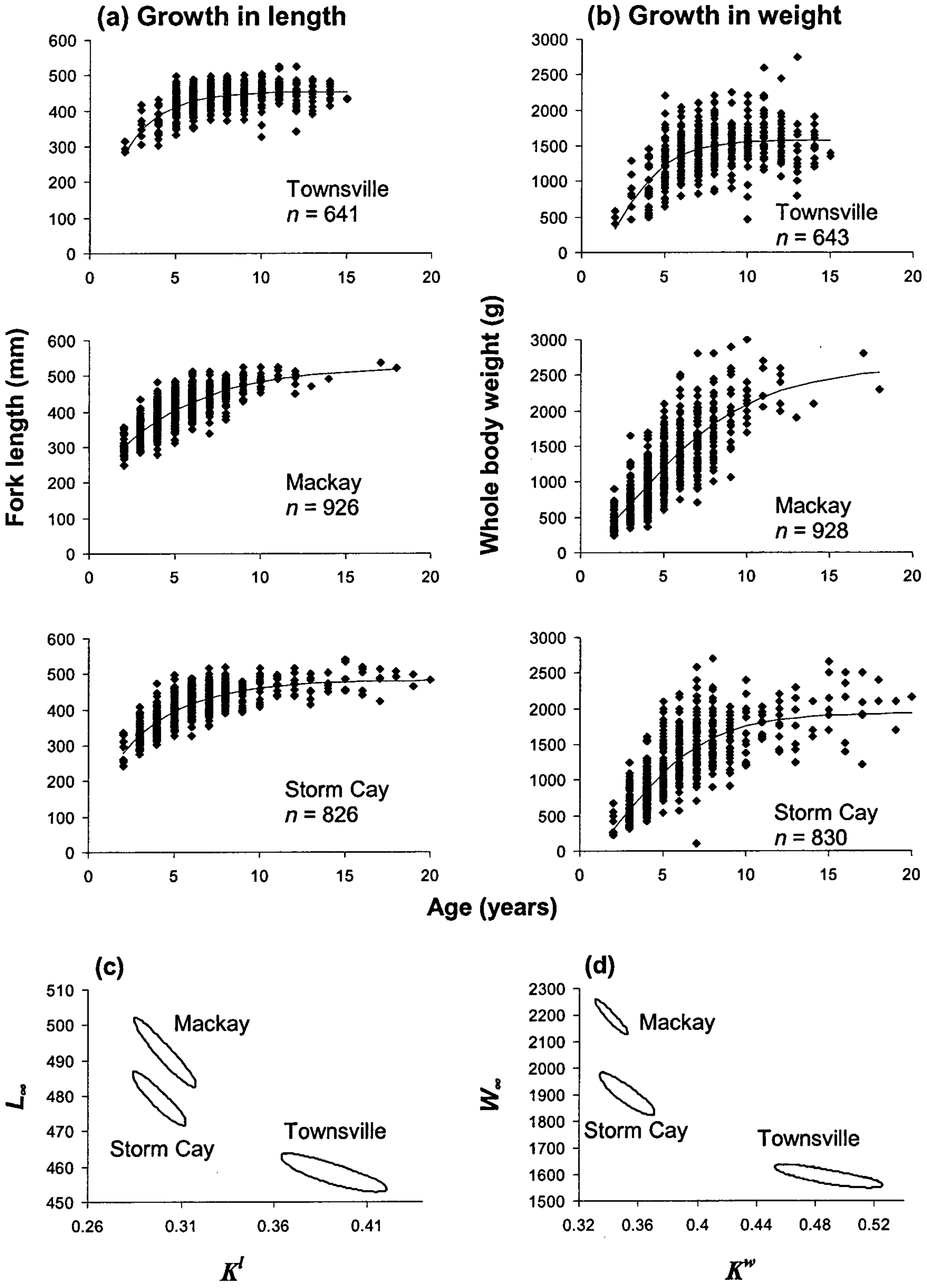

Figure 5.5. Length (a) and weight (b) at age data and estimated von Bertalanffy growth curves and approximate 95% confidence ellipses of the parameters L_∞ (W_∞) and K^l (K^w) (c-d) for *Lethrinus miniatus* from three regions of the Great Barrier Reef. Common values of the VBGF parameter t_0 were used to estimate confidence regions (see text for details). Data were pooled for four reefs within each region over the years 1995 to 1999. n = sample size.

and weight and regional differences in the length-weight relationship (Figure 5.5, Table 5.2). There was no overlap in estimates of the 95% confidence regions for region-specific VBGF parameters L_∞ (W_∞) and K^l (K^w) (Figure 5.5), which is consistent with the results of the likelihood ratio tests.

5.4. Discussion

Both temporal and spatial variation appear to be important in structuring patterns of growth in *L. miniatus* populations on the GBR. The observed inter-annual differences in growth suggest that conditions for growth in 1998-99 were more favourable than in other years. The consistency of these temporal patterns in growth among the age classes and regions examined indicate that the factors influencing temporal patterns in growth of *L. miniatus* are not age-specific, and operate at relatively large spatial scales, in this case over several degrees of latitude. Furthermore, the consistent temporal patterns in growth indicate that although growth may vary annually, the spatial patterns in growth observed by Williams et al. (2003) and in the present study were consistent over a period of 5 years.

The growth pattern of *L. miniatus* was found to vary at spatial scales of 10's of kilometres (among reefs within regions), and 100's of kilometres (among regions) on the GBR. However, the size of the variations in growth were most pronounced among regions, particularly with respect to weight. Spatial variation in growth of coral reef fish has been observed previously at relatively small scales such as within individual reefs (Gladstone and Westoby 1988, Pitcher 1992) and among reefs (Hart and Russ 1996, Newman et al. 1996*a*, Gust et al. 2002) within a region of the GBR. This is perhaps a reflection of both the size of the fish being studied (typically small), and the necessity for the selection of small spatial scales that were appropriate to the questions being addressed.

The variability in growth at these smaller spatial scales is not surprising given that growth is one of the traits most likely to respond to variations in the local environment (Yamahira and Conover 2002). More recently, however, differences in growth at large spatial scales have been observed for lethrinids (Williams et al. 2003), lutjanids (Kritzer 2002) and pomacentrids (Meekan et al. 2001). Typically, these larger spatial scale variations in growth are greater than small-scale variations, suggesting that variations in growth of reef fish may increase with spatial scale. The results of the present study support this hypothesis by demonstrating from a multi-scale approach that differences in growth are greater among regions than among reefs within regions for a large wide-ranging coral reef fish.

The possibility that the regional patterns in growth of *L. miniatus* may be confounded with cross-shelf variation needs to be considered. The reefs in the Townsville region are located closer to the outer edge of the continental shelf than reefs within the Mackay and Storm Cay regions, which are located in a mid-shelf position. Significant variation in the distribution and abundance of a number of species of lutjanids, lethrinids and serranids has been observed across the continental shelf on the central GBR (Williams 1991, Newman and Williams 1996, Newman et al. 1997). Gust et al. (2002) observed significant cross-shelf variation in growth, mortality and longevity of three species of scarid and one species of acanthurid in the northern GBR. The maximum size of fish was found to be significantly larger for mid-shelf reefs than for outer-shelf reefs. Cross-shelf variation in abundance of these species was proposed as the most likely causal mechanism for the observed differences in growth (Gust et al. 2001, 2002). The abundance of *L. miniatus* does not vary significantly between mid-shelf and outer-shelf reefs in the Townsville region (Newman and Williams 1996), which suggests that if cross-shelf variation in growth of *L. miniatus* exists, it is not likely to vary in response to abundance. Furthermore, there is more than 15 km in shelf position separating the reefs sampled within the Townsville region, amongst which growth did not differ in any respect. Thus, the similar estimates of growth among reefs within the Townsville region provide evidence that cross-shelf variation in *L. miniatus* growth is negligible and suggests that regional variation in growth arises from causes unrelated to shelf position.

The causal factors of the observed spatial patterns in *L. miniatus* growth remain unclear. A number of factors have been shown to affect growth of fish, including environmental factors, most notably temperature, density dependent effects, and food availability (Weatherley and Gill 1987). Water temperature has been shown to be an important factor in controlling rates of growth in many temperate fish populations (e.g. Brander 1995), but the shape of the relationship between growth rate and water temperature usually varies among species, and depends on the temperature range studied (Yamahira and Conover 2002). Often populations of a species with a wide latitudinal distribution exhibit faster growth rates and reach larger maximum sizes at higher latitudes, where water temperatures are cooler (Boehlert and Kappenman 1980, Parrish et al. 1985, Conover and Present 1990, Conover et al. 1997, Yamahira and Conover 2002). This seems somewhat counter-intuitive to the general perception that, as poikilotherms, fish grow faster at higher temperatures (Atkinson 1994). For many species of temperate fish, however, latitudinal compensation in growth has been demonstrated to occur via genetic variations in response to either temperature or the duration of peak water temperatures, or both (Yamahira and Conover 2002). For coral reef fish, Choat and Robertson (2002) demonstrated a negative correlation between water temperature and the average maximum size for *Ctenochaetus striatus* and *Acanthurus bahianus* across latitudinal gradients of 14° and 16° respectively, with mean annual sea temperature range of 4°C and 6°C, respectively. Water temperatures are relatively homogeneous among the regions examined in this study, with a difference of less than 1°C in the monthly average sea surface temperature between the Townsville and Storm Cay regions (Lough 1994). It appears unlikely, therefore, that temperature alone is driving the variations in growth of *L. miniatus* populations on the GBR. Similarly, water temperature was dismissed as a causal factor maintaining spatial patterns in growth of three scarid species and one acanthurid species from the northern GBR (Gust et al. 2002) and of pomacentrids in the tropical eastern Pacific Ocean (Meekan et al. 2001), as water temperature ranges were very similar among those localities.

Density effects are also unlikely to be the dominant cause of the spatial variation in *L. miniatus* growth. Growth of fish is generally considered to be inhibited at higher densities due to competitive interactions among individuals (Beverton and Holt 1957, Walters and Post 1993). Density-dependent growth has been reported for many temperate fish populations (e.g. Overholtz 1989, Helser and Almeida 1997), and a growing number of studies have also demonstrated this feature in coral reef fish populations (e.g. Doherty 1982, Jones 1987, Booth 1995). Density estimates for *L. miniatus* on the GBR (Mapstone et al. 1998, 2003) are greater for the Mackay and Storm Cay regions, where *L. miniatus* attains a larger asymptotic size, than for the

Townsville region, where a smaller asymptotic size is reached. Therefore, at the current densities in these regions of the GBR, it seems highly unlikely that growth for *L. miniatus* is density dependent, unless the effect of density is contrary to that normally expected.

It is unclear whether the distribution and availability of food or habitat quality are contributing factors to the spatial variation in *L. miniatus* growth. The availability of food is well known to have a direct effect on the growth of fish (Weatherley and Gill 1987). Growth in coral reef fish has been shown to be positively correlated with availability of food (Clifton 1995, Hart and Russ 1996). More convincing evidence that growth in coral reef fish is affected by food availability has arisen from experiments that directly manipulate the availability of food (Jones 1986, Forrester 1990, Kerrigan 1994). Not surprisingly, all of these studies have demonstrated a clear positive relationship between availability of food and growth. Studies of the dietary habits of *L. miniatus* on the GBR indicate the most common prey items are small crabs and sea urchins (Walker 1978). The distributions and abundances of these prey items remain unknown however, precluding any empirical assessment of the effects of food availability on growth of *L. miniatus*. The most likely scenario is that the combined effect of a number of factors, including those discussed above, are responsible for the spatial patterns in *L. miniatus* growth. Exploration of the factors limiting growth in *L. miniatus* remains an important area for further research.

Some generalisations about *L. miniatus* growth can be drawn, despite temporal and spatial variations in growth. There was a high degree of variability in size-at-age, particularly with respect to weight, typical of most coral reef fish and fish populations in general. As a result, a number of age classes accumulate within a narrow size range and the use of length frequency analyses is of little value for estimating growth. The growth pattern for *L. miniatus* was asymptotic for most reefs, with fish approaching their maximum size relatively young at approximately five or six years of age. This pattern of growth is typical of lethrinids (Loubens 1980*b*, Hilomen 1997, Brown and Sumpton 1998, Laursen et al. 1999, Grandcourt 2002) and is similar to other species of reef fish such as some scarids (Choat et al. 1996, Gust et al. 2002), and some large lutjanids (Newman et al. 2000*a*, Newman 2002) and serranids (Ferriera and Russ 1992, 1994) in which asymptotic size is reached at approximately 50% or more of maximum age.

There was a conspicuous absence of fish less than two years old in the samples collected in this study. This is most likely a result of the selectivity of the sampling gear, the existence of a specific juvenile habitat located outside the sampling area, or both. The habitat for juvenile *L. miniatus* has not been identified but is suggested to be located in seagrass beds in deeper water between coral reefs (Williams and Russ 1994). The absence of these younger individuals in this study and others prohibits the estimation and comparison of juvenile growth patterns for the species. The exclusion of juvenile fish from estimates of growth using the VBGF may result in an overestimate of L_∞ and a corresponding underestimate of K (Ferreira and Russ 1994, Craig et al. 1997). It is not clear whether the growth estimates in this study were biased by the absence of juvenile fish. However, the presence in most growth curves of a number of fish larger than the estimates of L_∞ (W_∞), and the propinquity of the estimates of t_0^l (t_0^w) to zero, suggests that any bias, if present, would be small. The only exception was the growth estimate for Bax Reef in the Mackay region, where the estimated L_∞ and W_∞ were considerably larger than the size of any fish sampled in any region. The growth functions for Bax Reef are therefore considered to provide overestimates of L_∞ and W_∞, and consequently underestimates of K^l and K^w due to the strong correlation between these two growth parameters.

The significant regional differences in growth indicate that productivity of *L. miniatus* is likely to vary among regions of the GBR. Fecundity of individuals typically increases with body size, as the available space to store gonads also increases (Roff 1992). Therefore fecundity of *L. miniatus* may be greatest in the Mackay region, where fish reach the largest maximum size, and lowest in the Townsville region where fish grow to a smaller maximum size. Furthermore, densities of *L. miniatus* are higher in the Mackay and Storm Cay regions relative to the Townsville region (Mapstone et al. 1998, 2003). Consequently, the potential may exist for greater overall egg production in the Mackay and Storm Cay regions. However, the relatively low proportion (~25%) of spawning females in the southern area of the GBR (Chapter 4) may counteract this potential for increased reproductive output in these regions. There are, however, no fecundity estimates available for *L. miniatus* in any region of the GBR, precluding further exploration of this hypothesis. Elucidating the regional patterns in fecundity would be a profitable area for future research, particularly for providing quantitative estimates of region-specific egg production.

The temporal and spatial variations in growth revealed in this study also highlight the importance of a multi-scale approach in population studies and assessment of fish stocks. Spatial variation in growth has been demonstrated to be an important factor in maintaining populations of fish above small sizes in the face of cyclical and stochastic patterns of recruitment (Kritzer 2001). Typically, however, fisheries assessment models assume a homogeneous stock, and use only a single estimate of growth to parameterise models for the entire stock. Significant spatial and/or temporal variation in growth among populations within a stock, however, may indicate that different productivity levels exist within the stock. Stock assessments that do not account for such temporal or spatial variation in growth within the stock may overestimate potential yields from less productive populations and/or underestimate potential yields from more productive populations. Consequently, the implementation of management measures based on such biased estimates of yield may result in local or regional depletion and reduction of resilience of the stock as a whole to stochastic or cyclical variations in recruitment. Clearly, variations in growth among populations within a managed stock need to be considered if harvest of stocks is to be managed optimally.

Chapter 6. Spatial patterns in cohort-specific mortality of *Lethrinus miniatus* populations on the Great Barrier Reef.

6.1. Introduction

Mortality is a fundamental parameter for understanding the dynamics of populations. An estimate of the rate of natural mortality (M) is essential for nearly all mathematical models of fish stock dynamics (Hilborn and Walters 1992). M is perhaps the most difficult parameter to estimate directly for exploited species, however, due to the frequent absence of mortality estimates prior to exploitation and the relatively few locations where fish populations remain unexploited (Beverton and Holt 1957, Gulland 1983). Estimates of M may also be confounded by additional processes affecting the observed losses from the population, including catchability, selectivity and availability of fish to the sampling gear (Beverton and Holt 1957, Chapman and Robson 1960, Gulland 1983, Hilborn and Walters 1992, Vetter 1988). Time series methods for estimating M, such as multiple capture-recapture methods and multiple cohort analysis, allow some of these sources of error to be partitioned out (Vetter 1988). The application of such methods is relatively rare, however, due to the time and expense involved in structured sampling over multiple periods. Consequently, reliable estimates of M for fish populations are uncommon. Often the only estimate of mortality that can be estimated empirically for exploited species is total mortality (Z), which includes unknown proportions of M and fishing mortality (F) (Beverton and Holt 1957, Gulland 1983, Hilborn and Walters 1992).

There are few estimates of natural mortality for populations of coral reef fish, particularly for exploited species (Roberts 1996, van Rooig and Videler 1997, Caley

1998, Russ et al. 1998). Reef fish ecology in the last two decades has focussed on determining the relative importance of recruitment and post-settlement processes in shaping population densities (Doherty 1991, Jones 1991). Consequently, estimates of mortality for early post-settlement and juvenile life stages of reef fish, predominantly for small species (<200mm), are beginning to accumulate in the literature (e.g. Doherty and Sale 1986, Jones 1987, Sale and Ferrel 1988, Forrester 1990, Booth and Beretta 1994, Caselle 1999, Schmitt and Holbrook 1999, Forrester and Steele 2000, Holbrook and Schmitt 2003) but estimates of mortality for adult reef fish are still rare, particularly for large species (Russ et al. 1998). Greater emphasis is needed in obtaining estimates of mortality for adult populations of reef fish to gain a full understanding of how mortality rates shape reef fish populations (Davies 1995, Caley 1998).

The most common method of estimating mortality for populations of adult fish is the use of catch curves (Beverton and Holt 1957, Ricker 1975). Vetter (1988) classified catch curves into two types based on when the data were collected and how many age classes were represented. The first type, horizontal (standard) catch curves, include data from several age classes collected at a single point in time or combined from two or more points in time. The use of standard catch curves is subject to a number of assumptions, which include: i) the population is sampled representatively; ii) the regression only includes fish fully recruited to the sampling gear; iii) mortality is constant among age classes and over time; and iv) recruitment is the same each year. The second type, longitudinal catch curves (cohort-specific mortality), use measurements of abundance of a single cohort over successive time periods (e.g. years) and therefore are not subject to the assumptions of constant recruitment or constant mortality among age classes, among cohorts or over time (e.g. Russ et al. 1998).

Estimates of mortality for specific cohorts have been limited predominantly to early post settlement phases (e.g. Rooker et al. 1999, Schmitt and Holbrook 1999) as it is easier to measure abundances of a cohort over shorter time periods. Estimates of cohort-specific mortality for adult fish populations are rare, however, with only a single estimate of cohort-specific mortality available for an adult reef fish population (Russ et al. 1998). This is most likely due to the relatively recent development of age determination techniques for tropical reef fish and the difficulties associated with obtaining adequate samples of single cohorts over a sufficient number of consecutive years to warrant the use of the method. The lack of cohort-specific mortality estimates for adult reef fish populations is unfortunate because recruitment variability is a common feature of reef fish populations (Mapstone and Fowler 1988, Doherty 1991, Doherty and Fowler 1994), suggesting the assumption of constant recruitment associated with the use of standard catch curves is likely to be violated often. Furthermore, the assumption of constant mortality among cohorts (year classes) has not been tested for any adult population of coral reef fish.

The few studies for which estimates of adult mortality of reef fish are available suggest substantial variability in mortality at different spatial scales, including between habitat types within reefs (Aldenhoven 1986, Davies 1995), between reefs (Newman et al. 1996*a*, Kritzer 2002), and among regions (Meekan et al. 2001, Brown and Sumpton 1998, Williams et al. 2003). However, standard catch curves were used to estimate rates of mortality in all of these studies, with the exception of Davies

(1995) who used multiple capture-recapture methods. Thus the observed spatial patterns in mortality may have been confounded at least partly by spatial patterns in recruitment. Knowledge of spatial patterns in mortality is important, particularly for exploited species, as predictions of sustainable yield from most fishery models are highly sensitive to estimates of M (Vetter 1988). For example, Yield per Recruit (YPR) models, which are one of the most widely used stock assessment models, are based on the trade-off between M and growth. Accordingly, reliable estimates of both M and growth are essential in providing accurate estimates of yield from YPR analyses. Ignoring spatial variation in M among populations within a stock may result in biased estimates of yield. The incorporation of a range of mortality estimates from several sub-populations within the stock will provide more realistic outputs from fishery models when spatial variation in M exists among populations within a stock (Vetter 1988).

I took advantage of a large spatial and temporal data set that enabled mortality rates of *L. miniatus* populations to be estimated for individual cohorts from 9 reefs and 3 regions of the Great Barrier Reef (GBR) over a five year period. Furthermore, this data set was collected from reefs that had been closed to fishing for at least eight years prior to sampling. Therefore, assuming few infringements of closure and no age-specific net movement of fish between open and closed reefs (the assumption that *L. miniatus* do not move among reefs is explored further in Chapter 7), estimates of mortality from these reefs should provide reliable approximations of M. The aims of this chapter, therefore, were: 1) to estimate the variation in mortality rates among cohorts of *L. miniatus*; and 2) to determine the spatial patterns in cohort-specific mortality of *L. miniatus* populations on the GBR.

6.2. Methods

6.2.1. Sample collection

Samples of *L. miniatus* were collected yearly from 1995 to 1999 inclusive from six reefs within each of three regions of the GBR using fishery independent catch surveys described in Chapter 2. Only samples collected from reefs closed to fishing were used to estimate natural mortality rates (*M*). Data collected from a total of 9 reefs (three reefs within each of three regions) were used in the analyses (Table 6.1). The fourth reef within each region was not used in any analyses as data were collected from these reefs on only two occasions before they were opened to fishing (see Chapter 2 for details). In addition, one of the reefs in each region was opened to fishing for one year in 1999 (see Chapter 2 for details). Data collected from these three reefs in 1999 were not used in the estimates of mortality, as it was assumed that they would have been subject to significant amounts of fishing mortality since they were opened. As a result, mortality estimates were obtained from data collected from three reefs in each region in 1995-1998, and two reefs per region in 1999 (Table 6.1).

6.2.2. Mortality estimates

An estimate of age is required to estimate mortality because mortality is an estimate of the rate of decrease in abundance with age. Age estimates for *L. miniatus* were obtained from whole otoliths using the procedures outlined in Chapter 2. The frequency of fish sampled in each age class was used as an index of relative abundance of each age class for each reef, given a single day of equal sampling effort for each reef in all years (Chapter 2) and assuming catchability was constant among age classes and years for all age classes fully recruited to the gear. Estimates of mortality were made using age-based cohort-specific catch curves (Beverton and Holt

1957, Ricker 1975) where the natural log-transformed frequency was regressed on age class, and total mortality (*Z*) was estimated as the absolute value of the regression slope. In this case *Z* was taken as an approximation of *M*, because *F* was assumed to be negligible on these reefs because they were closed to fishing.

Table 6.1. Sample sizes of *Lethrinus miniatus* collected from three reefs in each of three regions of the Great Barrier Reef (Townsville, Mackay, and Storm Cay) from 1995 to 1999.

		Year				
Region	**Reef**	**1995**	**1996**	**1997**	**1998**	**1999**
Townsville	Glow	71	34	85	50	54
	Dip	53	20	32	35	23
	Faraday	36	42	40	16	*
	Pooled	**160**	**96**	**157**	**101**	**77**
Mackay	20-142	55	53	41	43	106
	20-137	90	56	36	41	96
	Bax	57	41	51	45	*
	Pooled	**202**	**150**	**128**	**129**	**202**
Storm Cay	21-132	61	41	43	84	124
	21-131	31	31	46	49	69
	21-133	58	32	28	43	*
	Pooled	**150**	**104**	**117**	**176**	**193**

*Reef was opened to fishing in this year. Accordingly, data from this reef in this year were excluded from estimates of *M*.

6.2.3. Cohort-specific mortality

A major assumption in using catch curves to estimate mortality is that all age classes used in the regression are equally selected by the sampling gear used. The selectivity of the gear used in this study to sample *L. miniatus* was estimated for each region (Chapter 7). From these estimates it was assumed that fish six years of age or older were fully selected by the gear. Accordingly, catch curves were used to estimate rates of mortality for cohorts aged six years or older in 1995. Rates of mortality were only estimated for those cohorts with at least one fish captured in each subsequent year. Hereafter, each cohort will be referred to by the age of fish in the cohort in 1995. For example, the cohort aged 6 years in 1995 through 10 years in 1999 will be referred to as the 6yo cohort.

Sample sizes were sufficient to estimate mortality for the 6yo cohort for individual reefs in all three regions. Sample sizes were sufficient to also estimate mortality for the 7yo cohort for the Townsville and Storm Cay regions. Mortality rates were compared among reefs within regions and between cohorts using two nested ANCOVAs (Milliken and Johnson 2001), where reefs were nested within regions. The first ANCOVA compared the regression slopes of the 6yo cohort among reefs in all three regions. The second ANCOVA compared the regression slopes of the 6yo and 7yo cohorts among reefs in the Townsville and Storm Cay regions.

Age frequency data were pooled across reefs within each region to examine regional patterns in cohort-specific mortality over additional cohorts. As three reefs were pooled within each region for the years 1995-1998, and only two reefs pooled in 1999, samples sizes for 1999 were standardised with those from 1995-98 by multiplying the abundances in each age class in 1999 by 3/2. When the data were pooled among reefs within regions, sample sizes were sufficient to estimate cohort-specific mortality for the 6yo-10yo cohorts in the Townsville region, 6yo-9yo cohorts in the Storm Cay region, and 6yo-8yo cohorts in the Mackay region. These data were analysed using three separate ANCOVAs for: a) comparison of the regression slopes of cohorts 6yo-8yo among all three regions; b) comparison of the regression slopes of cohorts 6yo-9yo between the Townsville and Storm Cay regions; and c) comparison of the regression slopes of cohorts 6yo-10yo in the Townsville region only. For all ANCOVAs, Region was a fixed factor, Reef was a random factor nested within Region, Cohort was a fixed factor and Age was the covariate. The interaction between the factors and the covariate provided the tests for significant differences among regression slopes.

Sources of any suggested differences were identified by Least Significant Difference (LSD) adjusted multiple comparisons (Milliken and Johnson 2001). Residual plots and normal probability plots were used to examine the assumptions of homogeneous variances and normality for all data prior to analysis. All data conformed to these assumptions and accordingly no transformations were necessary.

6.3. Results

Mortality rates for the 6yo cohort did not differ significantly among reefs within any of the three regions (Table 6.2). Likewise the mortality rates for the 7yo cohort did not differ among reefs within the Townsville or Storm Cay regions (Table 6.3). Rates of mortality were also similar between the 6yo and 7yo cohorts within the Townsville and Storm Cay regions (Table 6.3). Thus, pooling data across reefs within regions was

Table 6.2. Analysis of Covariance comparing estimates of cohort-specific mortality of *Lethrinus miniatus* for the 6yo cohort among reefs within the Townsville, Mackay, and Storm Cay regions of the Great Barrier Reef.

Test	Source of variation	df	MS	*F*	*p*
Adjusted means:	Region	2	2.567	28.611	**<0.001**
	Reef (Region)	6	0.068	0.247	0.955
Slopes:	Age	1	17.154	62.725	**<0.001**
	Region*Age	2	2.811	10.279	**0.001**
	Reef*Age (Region)	6	0.089	0.325	0.917
	Residual (error)	21	0.273		

Table 6.3. Analysis of Covariance comparing estimates of cohort-specific mortality of *Lethrinus miniatus* between the 6yo and 7yo cohorts and among reefs within the Townsville and Storm Cay regions of the Great Barrier Reef.

Test	Source of variation	df	MS	*F*	*p*
Adjusted means:	Region	1	1.788	10.644	0.021
	Reef (Region)	4	0.158	0.514	0.726
	Cohort	1	0.012	0.40	0.842
Slopes:	Age	1	11.990	39.046	**<0.001**
	Region*Age	1	1.851	6.028	**0.019**
	Reef*Age (Region)	4	0.180	0.587	0.674
	Cohort*Age	1	0.032	0.103	0.751
	Region*Cohort*Age	1	0.007	0.021	0.884
	Reef*Cohort*Age (Region)	4	0.200	0.650	0.631
	Residual (error)	34	0.307		

justified by the similarity in mortality rates among reefs and the 6yo and 7yo cohorts. It was assumed that similar results would hold among reefs within regions for other cohorts.

Cohort-specific mortality varied substantially among regions, but not among cohorts in any region or overall. There was no significant interaction between cohort and region and the ANCOVA indicated mortality rates did not differ significantly among the 6yo-8yo cohorts over all regions (Table 6.4). The average mortality rates of these three cohorts, however, were significantly different among regions (Region*Age interaction, Table 6.4). LSD adjusted multiple comparisons indicated mortality was highest in the Mackay region ($M = 1.12$), followed by the Storm Cay region ($M = 0.78$), and then the Townsville region ($M = 0.39$) (Figure 6.1). Furthermore, mortality rates did not differ significantly among cohorts 6yo-9yo in the Townsville and Storm Cay regions ($F_{3,27} = 1.06$, $p = 0.38$), but when all interaction terms with cohort were removed, the average mortality rates of these four cohorts were significantly higher in the Storm Cay region ($M = 0.71$) than in the Townsville region ($M = 0.31$) (Region*Age interaction, Table 6.5, Figure 6.2). Finally, mortality rates did not differ among cohorts 6yo-10yo in the Townsville region (Table 6.6), and the estimate of M pooled across these cohorts in the Townsville region was 0.29 (Figure 6.3).

Table 6.4. Analysis of Covariance comparing estimates of cohort-specific mortality of *Lethrinus miniatus* among the 6yo-8yo cohorts and among the Townsville, Mackay and Storm Cay regions of the Great Barrier Reef. Estimates of cohort-specific mortality (*M*) for each region, and results of Least Significant Difference (LSD) multiple comparisons among regions are also presented.

Test	Source of variation	df	MS	*F*	*p*
Adjusted means:	Region	2	2.196	9.772	**0.001**
	Cohort	2	0.018	0.81	0.922
Slopes:	Age	1	28.276	125.821	**<0.001**
	Region*Age	2	2.803	12.473	**<0.001**
	Cohort*Age	2	0.013	0.056	0.945
	Region*Cohort*Age	4	0.262	1.165	0.349
	Residual (error)	26	0.225		

LSD test for differences among regions:

Townsville ($M = 0.39$) Mackay ($M = 1.12$) Storm Cay ($M = 0.78$)

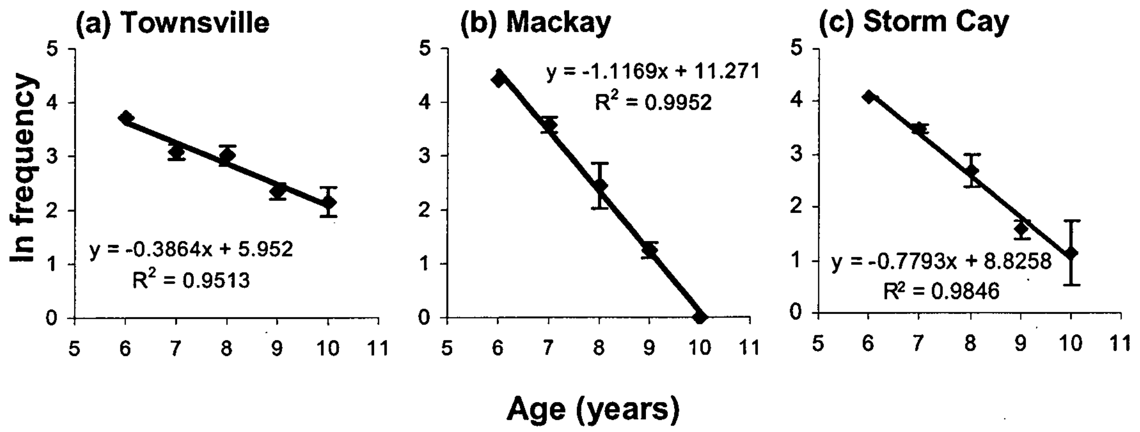

Figure 6.1. Cohort-specific catch curves for *Lethrinus miniatus* from three regions of the Great Barrier Reef, Townsville (a), Mackay (b), and Storm Cay (c). Catch curves were averaged over three cohorts aged 6 years (6yo cohort) to 8 years (8yo cohort) in 1995 (see methods for more details). Error bars are standard errors.

Table 6.5. Analysis of Covariance comparing estimates of cohort-specific mortality of *Lethrinus miniatus* among the 6yo-9yo cohorts in the Townsville and Storm Cay regions of the Great Barrier Reef. (Non-significant higher order interactions were removed from the model in a stepwise reduction process).

Test	Source of variation	df	MS	*F*	*p*
Adjusted means:	Region	1	0.767	3.485	0.071
	Cohort	3	1.208	5.491	**0.004**
Slopes:	Age	1	15.812	71.855	**<0.001**
	Region*Age	1	1.553	7.055	**0.012**
	Residual (error)	33	0.220		

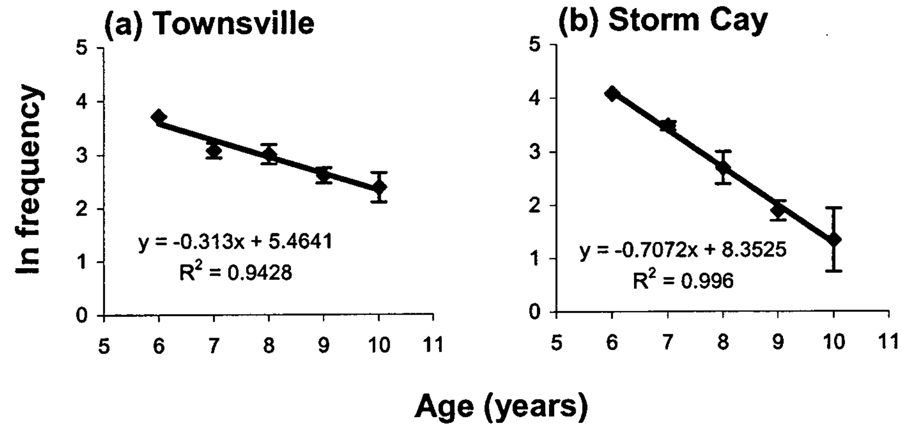

Figure 6.2. Cohort-specific catch curves for *Lethrinus miniatus* from two regions of the Great Barrier Reef, Townsville (a) and Storm Cay (b). Catch curves were averaged over four cohorts aged 6 years (6yo cohort) to 9 years (9yo cohort) in 1995 (see methods for more details). Error bars are standard errors.

Table 6.6. Analysis of Covariance comparing estimates of cohort-specific mortality of *Lethrinus miniatus* among the 6yo-10yo cohorts in the Townsville region of the Great Barrier Reef.

Test	Source of variation	df	MS	*F*	*p*
Adjusted means:	Cohort	4	0.065	9.959	0.725
Slopes:	Age	1	7.977	63.539	**<0.001**
	Cohort*Age	4	0.042	0.338	0.848
	Residual (error)	15	0.126		

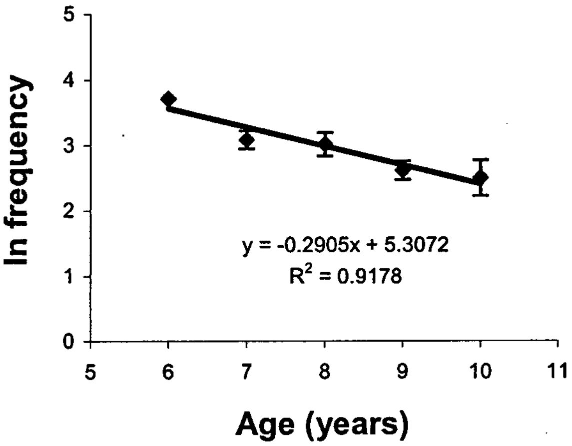

Figure 6.3. Cohort-specific catch curve for *Lethrinus miniatus* from the Townsville region of the Great Barrier Reef. The catch curve was averaged over five cohorts aged 6 years (6yo cohort) to 10 years (10yo cohort) in 1995 (see methods for more details). Error bars are standard errors.

6.4. Discussion

Mortality rates for a number of cohorts of *L. miniatus* examined over a period of five years (1995-1999) were similar among cohorts and among individual reefs within regions but varied substantially among regions of the GBR. Cohort-specific mortality rates were consistently higher in the Mackay region compared with the Townsville and Storm Cay regions, and lower in the Townsville region than the Storm Cay region. Williams et al. (2003) found similar spatial patterns in mortality rates for *L. miniatus* using standard catch curves from a single year of data collected from the same reefs and regions as those sampled in the present study. Although the spatial patterns were similar, the mortality rates were not always comparable between the two studies. Estimates of mortality from the two studies were similar in the Townsville and Storm Cay regions but in the Mackay region, estimates of cohort-specific mortality in the present study ($M = 1.12$) were considerably higher than mortality estimates from standard catch curves ($M = 0.71$) estimated by Williams et al. (2003).

The lower estimate of mortality from the use of standard catch curves by Williams et al. (2003) may be due to strong recruitment pulses having persisted in the age structures in the Mackay region resulting in one or more disproportionately abundant older age classes. Variability in recruitment is a common feature of reef fish populations (Mapstone and Fowler 1988, Doherty 1991, 2002) and the evidence of strong recruitment events has been demonstrated to persist in the age structures for several years (Doherty and Fowler 1994, Russ et al. 1996). Variability in recruitment has been shown to bias estimates of mortality using standard catch curves (Ricker 1975, Allen 1997), whereas estimates of cohort-specific mortality are not affected by variable recruitment as each cohort is analysed independently irrespective of recruitment pulses that might have occurred for the cohort.

Alternatively, the estimates of cohort-specific mortality may have been biased by region-specific annual variations in catchability or availability. Catchability of fish is associated with the probability of capturing a fish when it is accessible to the gear, whereas availability relates to whether fish are locally available to the gear, irrespective of their catchability. Catch rates of *L. miniatus* were variable among years, as evidenced by the variable sample sizes that were collected in each year using the same fishing gear and similar levels of fishing effort. These variable catch rates may be attributable to annual variations in abundance, catchability or availability. Variations in environmental factors such as water temperature and salinity (Quinn 1987, Crecco and Overholtz 1990, Smith and Page 1996, Swain et al. 2000) and behavioural characteristics such as schooling and spawning and feeding migrations (Arreguín-Sánchez 1996, Arreguín-Sánchez and Pitcher 1999) have been shown to affect either catchability or availability of a species. The specific factors affecting catchability of *L. miniatus* are not known but the schooling behaviour (Carpenter and Allen 1989), the potential to move among reefs (Williams et al. 2003, Chapter 7) and occurrence over a large depth range (Newman and Williams 1996) are mechanisms by which the distribution of *L. miniatus* may vary over time, resulting in annual variations in availability. The regression slope for estimates of cohort-specific mortality will be biased by annual variations in catchability or availability as the abundance of cohorts is measured over consecutive years. Conversely, for standard catch curves only the regression intercept will be biased if catchability or availability varies annually and is constant among age classes, as abundance data for all age classes are collected in a single year or pooled over years.

Populations with higher rates of mortality will be characterised by shorter longevities than those with lower rates of mortality. The regional pattern in rates of mortality for *L. miniatus* was, however, not commensurate with regional variation in longevity. For example, the oldest fish was found in the Storm Cay region (20 years), but mortality rates were lowest in the Townsville region, where longevity was shortest (14 years) (See Chapter 7; Figures 7.4 & 7.5). It is possible that the assumption of constant mortality among age classes was violated in one or more regions, suggesting the presence of age- or stage-specific shifts in mortality (Caley 1998). Alternatively, the disparity between estimates of mortality and longevity for each region may have resulted from age-specific movement of fish to and/or from the reefs in these regions, as the estimates of *M* in this chapter explicitly assumed that *L. miniatus* did not move among reefs (this assumption is explored further in Chapter 7). Either mechanism would decouple the expected relationship between mortality estimates from catch curves and longevity. This highlights the dangers associated with extrapolation of the model (catch curves) beyond the data used in the analyses. Thus, it would be inappropriate to extrapolate the estimates of mortality for *L. miniatus* from this study beyond the age classes used in the analyses.

The regional scale of variation in mortality for *L. miniatus* found in the present study is consistent with the findings of Brown and Sumpton (1998) who reported significant differences in *Z* between exploited populations of *L. miniatus* in the Swains and Capricorn Bunker regions of the southern GBR. Brown and Sumpton (1998) estimated Z to be significantly higher in the Capricorn Bunker region ($Z = 0.70$) than in the Swains region ($Z = 0.43$). They attributed the differences in Z to different levels of fishing pressure between the two regions, and assumed similar rates of M between the two populations. Historic levels of commercial catch and effort, however, have been higher in the Swains region than in the Capricorn Bunker region (Mapstone et al. 1996), suggesting fishing mortality may in fact have been higher in the Swains region. Accordingly, variation in M between the Swains and Capricorn Bunker regions can not be discounted.

The spatial patterns in mortality for *L. miniatus* differ from the patterns observed in other reef fish species. Most studies of reef fish mortality have focussed on small site-attached species, such as pomacentrids, and typically variations in mortality are reported among sites within reefs (e.g. Aldenhoven 1986, Davies 1995, Connell 1996) or among neighbouring reefs within a single region (e.g. Newman et al. 1996*a*, Kritzer 2002). Reports of significant regional differences in mortality for reef fish species are rare (but see Meekan et al. 2001), although few studies have examined mortality at this spatial scale. Predation and habitat availability are the two most common processes that have been demonstrated to affect mortality rates in coral reef fish (Jones and McCormick 2002). Both of these processes are likely to operate at relatively small spatial scales. The similarity among neighbouring reefs and significant regional variations in mortality for *L. miniatus* suggest that the processes shaping mortality rates for *L. miniatus* operate at much larger spatial scales than within or between reef habitats.

It is unlikely that that the regional variation in mortality of *L. miniatus* was confounded by the different shelf position of reefs in the Townsville region (more outer-shelf) compared with the Mackay and Storm Cay regions (mid-shelf). As discussed in Chapter 5, several studies have demonstrated significant variation in the assemblages and population parameters of coral reef fish across the continental shelf on the GBR (Williams 1991, Newman and Williams 1996, Newman et al. 1997, Gust et al. 2001, 2002). In particular, Gust et al. (2002) observed significantly higher rates of mortality on outer-shelf reefs than on mid-shelf reefs for three scarid species and one acanthurid species. A positive correlation between densities and mortality rates was considered evidence in support of density-dependent mortality in these species (Gust et al. 2001, 2002). The densities of *L. miniatus* do not vary significantly across the shelf on the GBR (Newman and Williams 1996). Therefore, if cross-shelf variation in mortality of *L. miniatus* does exist, it is unlikely to vary in response to densities. As outlined in Chapter 5, the reefs within the Townsville region are separated across the shelf by at least 15 km. Thus, the similarity in mortality estimates among reefs within the Townsville region is consistent with the hypothesis that cross-shelf variation in mortality is not significant.

Mortality rates were consistent among cohorts of *L. miniatus* at both small (among reefs) and large (among regions) spatial scales, validating the assumption of constant mortality among cohorts at least for the few cohorts analysed. In contrast, significant differences in mortality among cohorts are commonly reported for early post-settlement (Schmitt and Holbrook 1999, Searcy and Sponaugle 2001) and juvenile (Eckert 1987) stages of reef fish. These early life stages of reef fish are common prey species of larger piscivores and predation is considered the dominant mechanism affecting mortality rates of small reef fish (Hixon 1991). Temporal or spatial variations in predation are expected to influence significantly the mortality of some cohorts of newly settled fish more than others (Doherty and Sale 1986, Connell 1996, Hixon and Carr 1997). Conversely, predation on adult reef fish, particularly larger species, is likely to be considerably less as they have fewer predators by virtue of their larger size (Werner and Hall 1974, O'Brien et al. 1976). Thus we might expect rates of mortality to be more similar among cohorts of adults of larger reef fish species such as *L. miniatus*. Russ et al. (1998) provide the only other estimate of cohort-specific mortality for adult reef fish (*Plectropomus leopardus*), but their study was restricted to a single cohort, precluding comparisons of mortality rates among cohorts.

The cohort-specific mortality rates for *L. miniatus* presented here represent some of the only estimates of *M* for an exploited coral reef fish. The accuracy of these estimates, however, remains uncertain, as it was assumed that: 1) there was no movement of *L. miniatus* to or from the reefs in this study; and 2) there were no infringements on the reefs in this study. Movement of *L. miniatus* to or from the reefs in each region may have biased estimates of mortality, particularly if net movement is directional or age-specific resulting in ontogenetic patterns in migration among regions. For example, net movement of fish out of the Mackay region may have resulted in an overestimate of natural mortality in that region because emigrating fish would have been considered to have died. Conversely, net movement of fish into the Townsville region may have resulted in an underestimate of mortality because immigrants would have been assumed to be residents that had survived. Furthermore, if *L. miniatus* do move among reefs on the GBR, populations from reefs open and closed to fishing would be mixed. If such mixing occurs, the estimates of *M* from the reefs closed to fishing in this study would be overestimates, as they would contain an additional component of fishing mortality (*F*) by virtue of exposure of parts of the reef-specific population to harvest when they were outside the reefs closed to fishing. The assumption that *L. miniatus* does not move among reefs is explored further in Chapter 7.

Some level of infringements on reefs closed to fishing on the GBR almost certainly occurs (Russ 2002). Sufficient information on the rates of infringement does not exist for any reefs on the GBR, however, to enable the potential effects of infringements on estimates of *M* to be empirically quantified. It is unlikely that infringement rates vary sufficiently among regions to exclusively account for the substantial (more than three-fold) regional variation in estimates of *M*. The estimates of *M* in this study are likely to be overestimates, however, due to the occurrence of at least some infringements on the reefs sampled.

If the relative magnitude of the mortality estimates are reliable, however, the spatial patterns in mortality have important implications for fisheries management. Populations with lower rates of natural mortality typically exhibit slow population turnover (*K*-selected) and are more vulnerable to over-exploitation than populations with higher rates of natural mortality that typically exhibit fast population turnover (*r*-selected) (Gulland 1988, Hilborn and Walters 1992). Consequently, *L. miniatus* populations in the Townsville region may be more at risk of over-fishing than populations in the Mackay and Storm Cay regions, particularly as fishing effort has been comparable among these regions of the GBR since at least 1988 (Mapstone et al. 1996). Conversely, the high rates of mortality for populations of *L. miniatus* in the

Mackay region indicate a higher rate of population turnover and suggest these populations may be more robust to fishing pressure than those in the Townsville and Storm Cay regions.

The larger size of fish in the Mackay region (Chapter 5), coupled with the higher mortality rates, suggests that productivity is likely to be highest in this region. Productivity is likely to be lowest in the Townsville region due to the smaller size of fish (Chapter 5) and lower rates of mortality. Yield per Recruit (YPR) models, which are one of the most widely used fisheries stock assessment models, estimate the trade-off between mortality and growth rates to predict potential yields under different scenarios of fishing pressure and size at first capture. Such models are likely to predict that potential yields of *L. miniatus* on the GBR are greatest in the Mackay region and lowest in the Townsville region. Recent declines in catches and catch rates of *L. miniatus* in the Townsville region (Williams 2002) provides some circumstantial evidence that populations in this region may be unable to sustain current levels of fishing pressure and could already be suffering from overfishing. Thus, a management strategy that assumes homogeneous production of *L. miniatus* across all regions of the GBR is likely to be inappropriate and may lead to overexploitation of less productive populations, underexploitation of more productive populations, or both. Clearly, the regional differences in structure and dynamics of *L. miniatus* populations needs to be incorporated into fisheries stock assessments for this species if model outputs are to be reliable, and management is to be optimised.

Chapter 7. Exploration of the potential for large-scale movement of *Lethrinus miniatus* to explain regional variation in mortality within the Great Barrier Reef using an age-structured model.

7.1. Introduction

A description of the distribution and abundance of populations in space and time is one of the central goals in ecological studies of populations (Andrew and Mapstone 1987). Movement is one of the most fundamental demographic parameters affecting the distribution and abundance of populations (Quinn and Deriso 1999). Changes in the distribution and abundance of fish populations as a result of movement may occur over a wide range of spatial and temporal scales, including diel feeding migrations (Hobson 1973, Hall et al. 1979, Clark and Levy 1988, Holland et al. 1993, Gibson et al. 1998), ontogenetic shifts in habitat type (Werner and Hall 1988, Frank 1992, Rountree and Able 1992, Eggleston 1995, Light and Jones 1997, Ruzycki and Wurtsbaugh 1999, Dahlgren and Eggleston 2000), spawning migrations (Stabell 1984, Wheeler and Winters 1984, Hampton 1991, Colin 1992, Warner 1995, Bolden 2000, Block et al. 2001) and movements in response to density gradients or in response to exploitation (Robertson 1988, Hilborn and Walters 1992).

The movement patterns of coral reef fish have not been studied as extensively as for many temperate species such as salmonids and anguillids. The only large-scale movement of most coral reef fish is assumed to occur during dispersal of the pelagic larval stages (Sale 1991). Post-settlement reef fish are generally considered to be sedentary, with relatively small home ranges within a reef, and to move between reefs only rarely (Sale 1991, Holland et al. 1993, Davies 1995, 2000, Chapman and Kramer

2000, Marnane 2000, Stewart and Jones 2001). This generalised model for reef fish is most likely biased, however, because most studies of reef fish movement have focussed on small site-attached species that have relatively small home ranges. Movement patterns of larger and potentially more mobile species of reef fish are not well known, but there is increasing evidence indicating that post-settlement individuals of large reef fish are capable of moving significant distances within and between reefs (Moe 1969, Davies 1995, 2000, Holland et al. 1996, Samoilys 1997, Zeller 1997, 1998, Watterson et al. 1998, Bolden 2000, Eristhee and Oxenford 2001, Patterson et al. 2001). A number of studies on smaller reef fish have demonstrated that within-reef movement of post-settlement individuals can be important in determining the local population size and structure of many species (Robertson 1988, Warner 1995, Frederick 1997, Lewis 1997). The extent to which movement is important in structuring populations of larger reef fish species remains unclear.

Reef fish species belonging to the Lethrinidae family do not appear to be territorial (Carpenter and Allen 1989) and are thought to be more mobile than reef fish in many other families (Jones 1991). Unlike most smaller reef fish, the relatively deep open sand/rubble areas between reefs, which often extend for several kilometres, do not appear to create a boundary for the movement of *L. miniatus* adults, as they are commonly caught in areas of sand and shoal between reefs to depths of at least 128m (Williams and Russ 1994, Newman and Williams 1996). Tagging studies generally have been unsuccessful at tracing movements of *L. miniatus* (Brown et al. 1994) because of remarkably low recapture rates but three individuals were tagged and recaptured by a Queensland amateur fishing organisation (SUNTAG, Australian National Sportfishing Association unpublished data). One of these fish was recaptured six months after release on the same reef it was tagged but the other two fish had moved at least 20 km across several reefs in periods of six months and two years. Furthermore, both fish were less than 320 mm FL and so most likely to be three years old or younger (Chapter 5), suggesting that *L. miniatus* is at least capable of moving relatively large distances at a young age. Similar movements have been observed for *L. nebulosus* in Japan where in the first 18 months of life fish moved up to 7 km from their release site (Kaneshiro 1998). In this chapter, the degree of large-scale movement of *L. miniatus* that would be required to explain the significant regional variations in mortality demonstrated in Chapter 6 was explored.

Movement, like mortality, is perhaps one of the most challenging demographic parameter to quantify, particularly for fish, as it can only be measured directly by observing the relocation of known individuals and then calculating the net effect on the population. Consequently, determining the movement patterns of more mobile fish using conventional tagging techniques becomes expensive, as the probability of recapturing or resighting individuals decreases with increasing area and size of the population relative to the number of tagged individuals. It is possible to explore the extent of potential movement by examining changes in age frequency distributions. The disappearance of fish from a population can only result from mortality, net emigration or both. Given an estimate of mortality, net immigration or emigration can be estimated from variations between observed and predicted age frequency distributions, where net movement is defined as the difference between immigration and emigration. Naturally, net movement will inevitably be an underestimate of absolute movement as it is extremely unlikely that all movement will be exclusively immigration or emigration. An estimate of zero net movement, therefore, does not necessarily indicate that there is no movement but may also result if immigration is equal to emigration.

The aim of this chapter was to explore the magnitude and direction of potential movement of *L. miniatus* that would be required to explain the significant regional variation in mortality shown in Chapter 6. While there are a range of other hypotheses that also might explain the observed regional variation in mortality, it was more feasible to explore movement given the available data. In this chapter, I developed an age-structured model to compare the fit of a model age structure to observed age frequency distributions when no movement is assumed in the model with the fit to age frequency distributions explicitly incorporating movement. This provided a simple estimate of the net movement required in each of three regions of the GBR to explain the observed regional variation in age structures.

7.2. Methods

7.2.1. Model structure

The following age-structured model was developed to explore the extent of movement of *L. miniatus* that would be required to reproduce observed age structures from reefs closed to fishing within the Townsville, Mackay and Storm Cay regions of the GBR if natural mortality was uniform over regions. The number of fish in region r, was determined by survivorship from the previous year and the age-specific net movement using the equation:

$$N^r_{a,y} = \begin{cases} R^r_y & \text{if } a = 2 \\ (N^r_{a-1,y-1} + d^r_{a,y}).e^{-M} & \text{if } 2 < a \leq 20 \end{cases} \qquad (7.1)$$

where:

$N^r_{a,y}$ is the number of fish in region r at age a in year y;

R^r_y is the relative recruitment of fish aged two years in region r in year y;

M is the instantaneous rate of natural mortality across all regions, ages and years for fish aged two years and older; and

$d^r_{a,y}$ is the age-specific net movement of fish in region r at age a in year y.

Each region was considered to constitute a single homogeneous population as the structure of *L. miniatus* populations from reefs within each region were generally similar while population structures differed significantly among regions (see Chapters 5 and 6). Movement of post-recruits (>2 years of age) was modelled in the form of emigration or immigration to or from each region. No attempt was made to explicitly model connectivity of post-recruits among regions. This would have required explicitly modelling the fishing and population dynamics of *L. miniatus* in areas open to fishing and the movement of *L. miniatus* over specific distances. There is limited demographic information available for populations of *L. miniatus* from fished areas of the GBR or for the rate at which *L. miniatus* might traverse known distances, so such a model was beyond the scope of this chapter.

Recruitment was defined as the number of two year old fish entering the population, as age frequency data for fish younger than two years of age was not available. No assumption was made about the origin of recruits or larval dispersal among regions. The number of recruits in each region was expressed as a proportion of the total number of fish in all age classes in each region. Estimates of recruitment to each region in each year, $R_{r,y}$, were estimated as the number of two-year-old fish necessary to maximise the fit to observed age frequency distributions in each region and year with the prescribed rates of natural mortality. Consequently, estimates of recruitment varied among regions and years.

Fishing mortality was assumed to be zero as the reefs within each region from which I had data were nominally closed to fishing (Chapter 2). Thus, the only source of mortality experienced by the populations in each region was assumed to be natural mortality, *M*. It was necessary to assume a common rate of *M* across all regions since movement is confounded with mortality and it is not possible to separate the effects of mortality and movement on increases or decreases in the size of populations in each region. Based on the assumption that net immigration or emigration of *L. miniatus* occurred in each region and the net effect of this movement within the area of the GBR bounded by the three regions was zero, a common estimate of *M* pooled across all regions would be less confounded with movement than separate estimates of *M* from each region, which would be biased by either net immigration or emigration. Three levels of this common natural mortality were used to test the sensitivity of the model to variations in natural mortality. These natural mortality estimates were obtained by pooling age frequency data across all regions and using the methods adopted in Chapter 6 to estimate cohort-specific rates of natural mortality for as many cohorts as possible that were six years or older in 1995. Six years of age was considered to be a conservative estimate of the age at which *L. miniatus* became fully selected by the sampling gear (see results from this chapter, Williams et al. 2003). The minimum, maximum and mean estimates of mortality from these cohort-specific catch curves were then used as input values of *M* for the model. *M* was also assumed to be constant across all age classes and years.

Movement was only modelled for fish three years of age or older, as fish were considered to be recruiting to the population at age two. Net movement of fish in each age class (>2 years) in all regions was assumed to increase after recruitment. Assuming a constant rate of movement, the proportion of fish moving will decrease with age because most, if not all, old fish would have already moved. Accordingly, a logistic curve was used to model age-specific net movement in each region. The cumulative proportion of fish immigrating or emigrating in each region, age class and year was estimated using:

$$C^{r}_{a,y} = \frac{d^{r}_{y}}{1+e^{-\ln 19(a-a^{r}_{50,y}/a^{r}_{95,y}-a^{r}_{50,y})}} \tag{7.2}$$

where:

$C^{r}_{a,y}$ is the cumulative proportion of fish immigrating or emigrating in region *r* at age *a* in year *y*;

d^{r}_{y} is the asymptote of the logistic curve and represents the total frequency of fish immigrating (positive value) or emigrating (negative value) in each region *r* and in each year *y* relative to the total population in each region;

$a^{r}_{50,y}$ is the age at which 50% of 'moving' fish have moved in each region *r* and in each year *y*; and

$a^{r}_{95,y}$ is the age at which 95% of 'moving' fish have moved in each region *r* in each year *y*.

The age-specific net movement of fish in region *r* at age *a* in year *y*, $d^r_{a,y}$, was estimated from the cumulative proportion of fish moving in each region and year using:

$$d^r_{a,y} = C^r_{a,y} - C^r_{a-1,y-1} \tag{7.3}$$

7.2.2. Model implementation

Observed age frequency data were pooled across reefs closed to fishing within each region. The age-structured model (equation 7.1) was run to generate age frequencies which were fitted to the observed age frequencies of *L. miniatus* for each region by maximising the negative log-likelihood of the model parameters, and then adjusted to improve the fit by adding or removing fish from each age class. Age frequencies were expressed as relative frequencies because a different number of reefs were sampled within each region in some years (see Chapter 2) and estimates of absolute abundance for each region were not available. The model was fitted separately to each of five years of age frequency data (1995-1999) to provide some indication of the temporal variability in recruitment and movement patterns and to three levels of natural mortality to determine the sensitivity of the model to variations in mortality.

To examine the effects of movement of fish, it was necessary to account for the effect of selectivity and reconstruct the 'natural' age frequency distributions for each region. Selectivity of the gear from which samples came was assumed to be constant among all regions with respect to length as the same gear was used to sample the populations in all regions (Chapter 2) and selectivity is assumed to be size selective rather than age selective. However, regional differences in the size at age (Chapter 5) suggest that the ages selected by the gear may have varied among regions. To obtain age-specific selectivity curves for each region, length frequency data were first pooled across all regions and years to obtain a length frequency distribution for the whole population. A logistic function was fitted to all length classes smaller than the mode of the length frequency distribution under the assumption that the mode represented the length at which *L. miniatus* first became fully selected by the gear and that selectivity of *L. miniatus* followed a logistic curve. The proportion of each length class selected by the gear was estimated using the logistic function:

$$Q_l = (1+e^{-\ln 19(l-l_{50})/(l_{95}-l_{50})})^{-1} \tag{7.4}$$

where:

Q_l	is the proportion of each length class, l, selected by the gear;
l_{50}	is the length at 50% selectivity; and
l_{50}	is the length at 95% selectivity.

Age-specific selectivity curves for each region were derived from the parameters of the length-specific selectivity curve (equation 7.4) and the predicted size at age for fish in each region estimated by the von Bertalanffy growth function (VBGF) (Chapter 5) using:

$$Q_a^r = (1+e^{-\ln 19(l_a^r-l_{50})/(l_{95}-l_{50})})^{-1} \tag{7.5}$$

where:

Q_a^r is the proportion of each age class, a, in region r selected by the gear; and

l_a^r is the length at age a in region r predicted by the VBGF (Chapter 5).

The effect of selectivity on the age frequency distributions for each region was 'removed' and the 'natural' age frequency distributions were reconstructed for each region by dividing the frequency of fish in each region and age class by its age-specific probability of capture using:

$$f_a'^r = \frac{f_a^r}{Q_a^r} \tag{7.6}$$

where:

$f_a'^r$ is the observed frequency of fish in region r at age a adjusted for gear selectivity; and

f_a^r is the observed frequency of fish in region r at age a; and

Q_a^r is the proportion of each age class, a, in region r selected by the gear.

7.2.3. Initial model fit without movement

The model was initially fitted to the reconstructed observed age frequency distributions in each region without immigration or emigration ($d_{a,y}^r = 0$) in all regions. Consequently, the initial fit of the model provided predicted age frequency distributions that were identical for each region as there was no movement in any region and mortality was constant among regions. The initial fit was only used to provide a baseline fit with which to compare the effects of movement in subsequent runs of the model.

7.2.4. Final model fit with movement

The model was then fitted to the reconstructed observed age frequency distributions explicitly incorporating immigration and emigration in each region to determine whether movement of post-recruits could explain differences between the observed and predicted age frequency distributions from the baseline fit of the model. The model was fitted to the reconstructed observed age frequency distributions by solving equation 7.1 and maximising the negative log-likelihood of the model parameters R_y^r and $d_{a,y}^r$ using the SOLVER routine in MS EXCEL (Haddon 2001). Outputs from the model included estimates of relative recruitment to each region and the relative magnitude, direction and age specificity of movement of post-recruits in each region.

7.3. Results

7.3.1. Estimates of cohort-specific mortality

Rates of cohort-specific mortality were estimated for six different cohorts aged six to 11 years in 1995 from age frequency data pooled across all three regions (Figure 7.1). From these six estimates of cohort-specific mortality, the minimum (M = 0.35), maximum (M = 0.50) and mean (M = 0.425) estimates were used to provide a range of natural mortality values with which to explore model sensitivity to uncertainty in M.

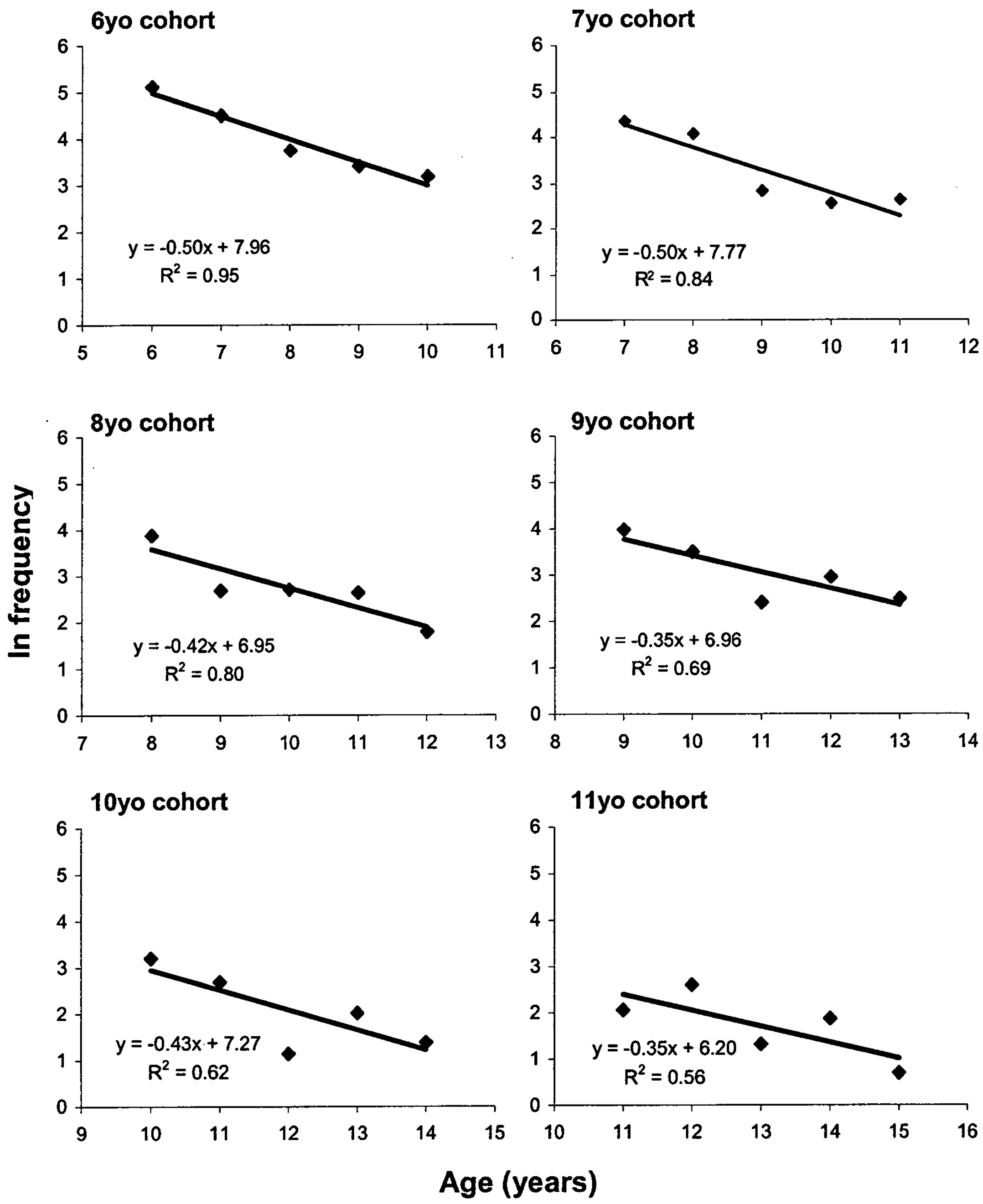

Figure 7.1. Cohort-specific catch curves for *Lethrinus miniatus* based on age frequency data pooled across three regions of the Great Barrier Reef (Townsville, Mackay and Storm Cay). The cohorts were aged from 6 years (6yo cohort) to 11 years (11yo cohort) in 1995.

7.3.2. Regional gear selectivity

Samples of *L. miniatus* pooled across all three regions were 50% selected by the sampling gear at approximately 360 mm FL and 95% selected by approximately 430 mm FL (Figure 7.2). The age-specific selectivity for each region calculated from the region-specific von Bertalanffy growth parameters varied slightly among regions but *L. miniatus* was close to full selection by the gear at six years of age in all regions (Figure 7.3).

7.3.3. Initial model fit without movement

The model provided a better fit to the observed age structures for the Storm Cay region than for either the Townsville or Mackay regions when the model was initially fitted without allowing for movement of fish in any region (Figure 7.4). In the Townsville region, the model considerably overestimated recruitment (abundance of two year old fish) and the abundance of three and four year olds but underestimated the abundance of fish aged six years and older in all years. In three of the five years (1996, 1997 and 1999) the model underestimated recruitment in the Mackay region and overestimated the abundance of three and four year old fish. In the Storm Cay region the model showed no bias to either under or overestimate recruitment among the five years, although the abundance of some of the younger age classes between three and five years were overestimated in some years. Variations in natural mortality over the range used as inputs (M = 0.35 – 0.50) did not have a large effect on the predicted age frequency distributions (Figure 7.4). The only effect variation in natural mortality had was to increase the estimates of recruitment with increased mortality rates.

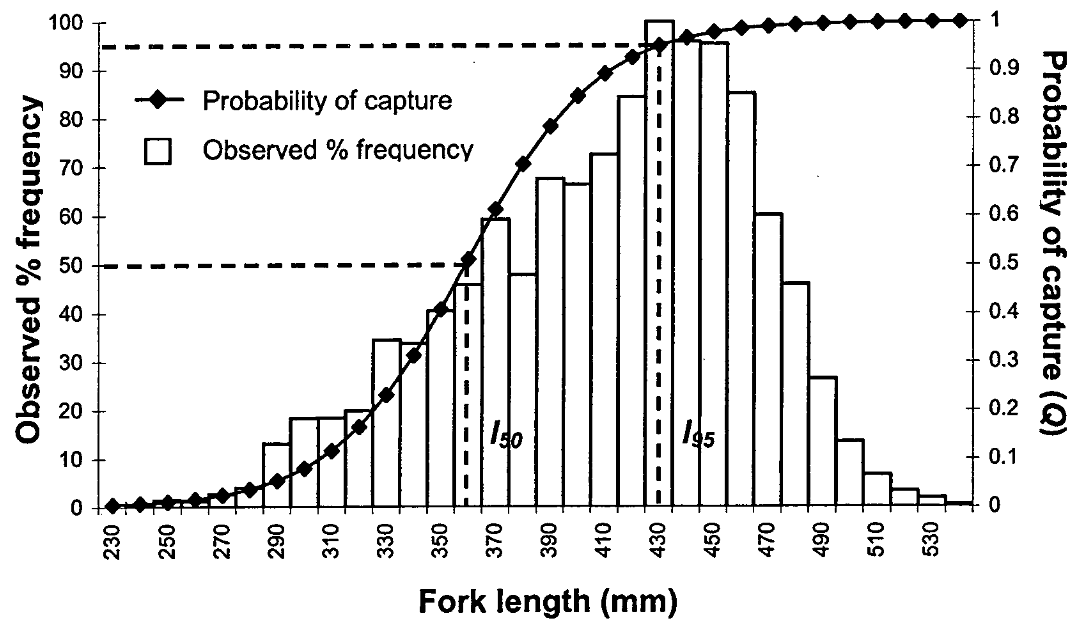

Figure 7.2. Length-specific selectivity of *Lethrinus miniatus* (curve) estimated from length frequency data (open bars) pooled across three regions of the Great Barrier Reef (Townsville, Mackay and Storm Cay). Dotted lines indicate the estimated l_{50} and l_{95} which represent the length at which *L. miniatus* was 50% and 95% selected by the sampling gear respectively.

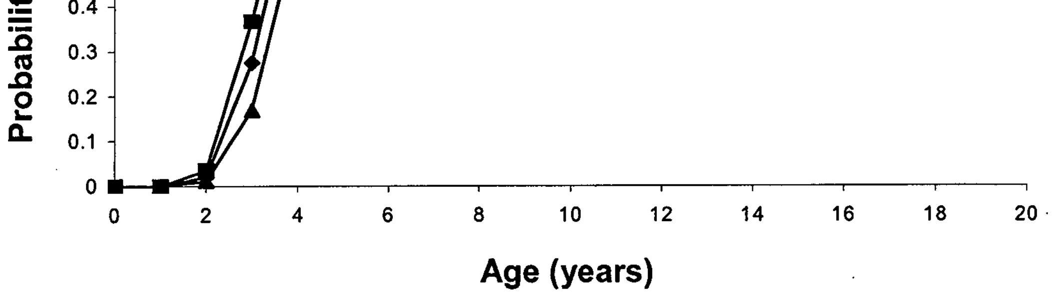

Figure 7.3. Age-specific selectivity of *Lethrinus miniatus* from three regions of the Great Barrier Reef (Townsville, Mackay and Storm Cay) estimated from the length-specific selectivity (Figure 7.2) and region-specific size-at-age estimated by the von Bertalanffy growth function.

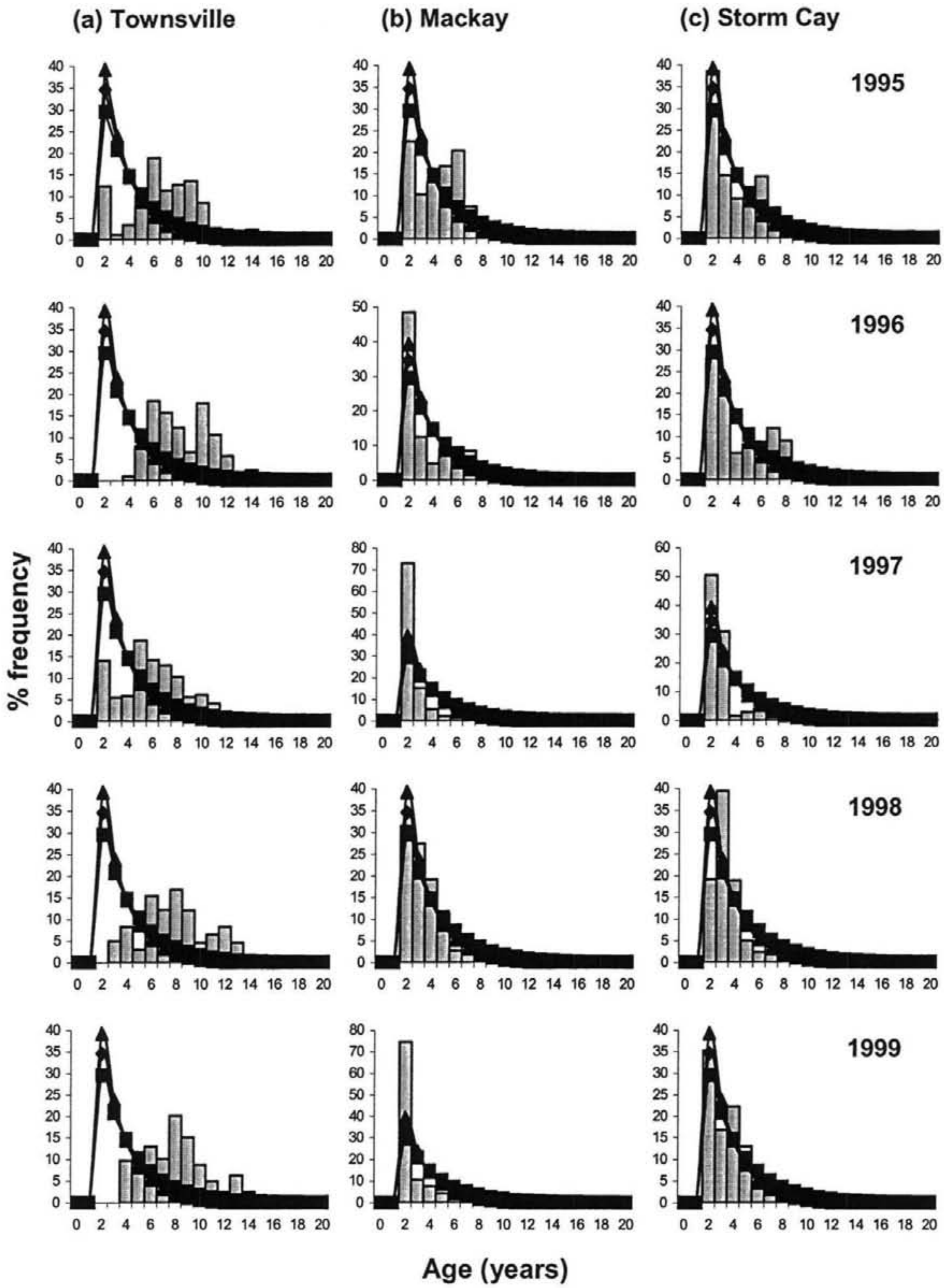

Figure 7.4. Initial fit of the model assuming no movement of *Lethrinus miniatus* post-recruits in three regions of the Great Barrier Reef, Townsville (a), Mackay (b) and Storm Cay (c) in five consecutive years from 1995 to 1999. Solid bars represent observed age frequency distributions and lines represent predicted age frequency distributions from the model for three input values of natural mortality, $M = 0.35$ (■), $M = 0.425$ (◆) and $M = 0.5$ (▲).

7.3.4. Final model fit with movement

Incorporating immigration and emigration of post-recruits into the model provided a good fit to the observed age frequency distributions in all three regions and in all years (Figure 7.5). Similar to the initial fit, the effect of the different input values of natural mortality was small for all regions and years when immigration and emigration were included in the model (Figure 7.5). The predicted age-specific net movement of fish averaged over five years was substantially different for each region (Figure 7.6).

The model predicted significant net immigration of fish into the Townsville region for all input values of natural mortality. A large proportion of age classes three to six years were predicted to be immigrants, although significant net immigration continued until at least 10 years of age (Figure 7.6).

In the Mackay region, the model predicted net emigration of some age classes for all input values of natural mortality. Emigrants were predicted to be three and four year old fish when natural mortality was 0.35 or 0.425, while only three year old fish were predicted to be emigrating when natural mortality was 0.50 (Figure 7.6).

The model predicted immigration of some age classes in the Storm Cay region for all input values of natural mortality. Six year old fish were predicted to be immigrants when natural mortality was 0.35 or 0.425, while seven year old fish were predicted to be immigrants when natural mortality was 0.425 or 0.5 (Figure 7.6).

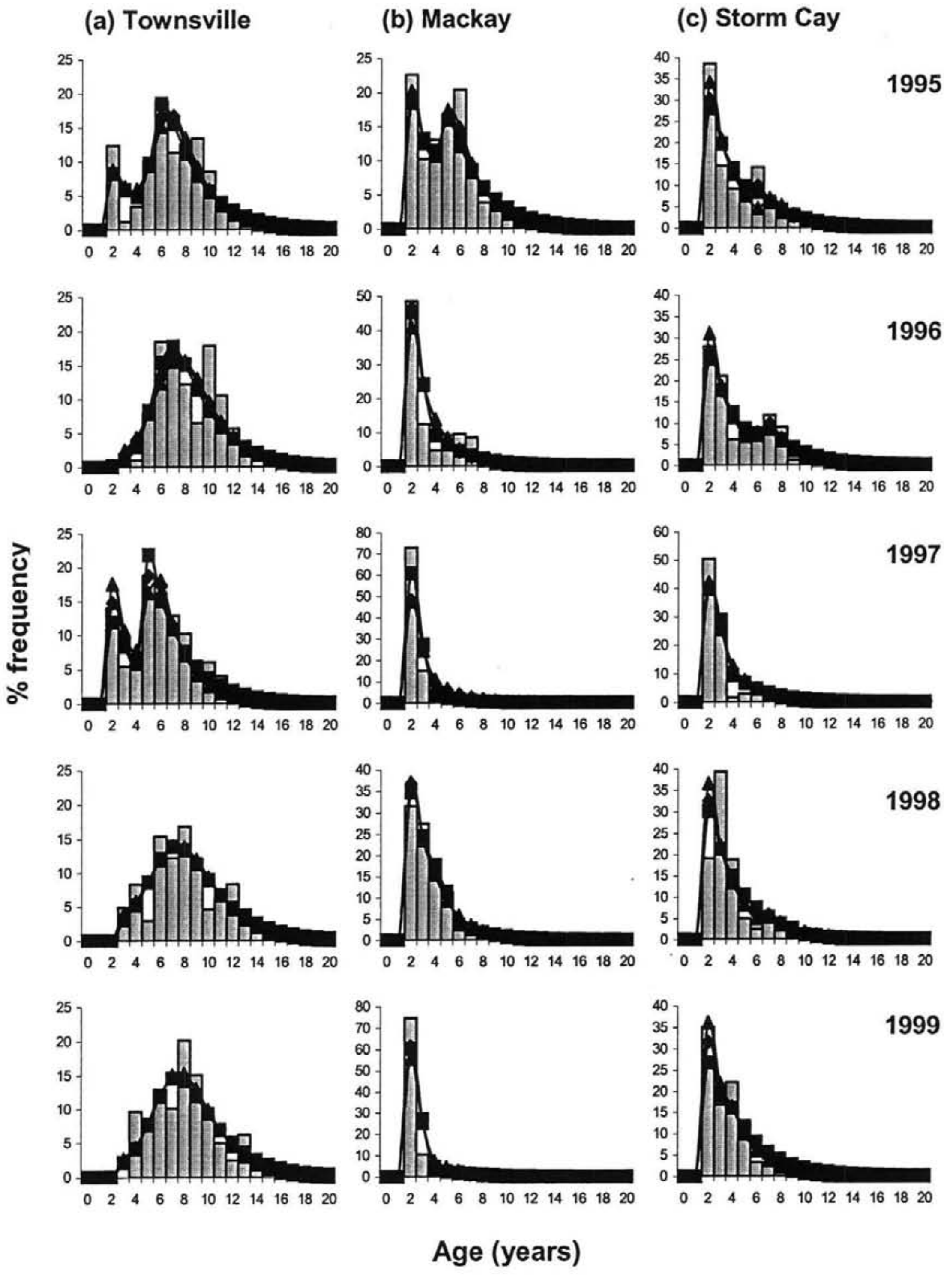

Figure 7.5. Final fit of the model incorporating immigration and emigration of *Lethrinus miniatus* post-recruits in three regions of the Great Barrier Reef, Townsville (a), Mackay (b) and Storm Cay (c) in five consecutive years from 1995 to 1999. Solid bars represent observed age frequency distributions and lines represent predicted age frequency distributions from the model for three input values of natural mortality, $M = 0.35$ (■), $M = 0.425$ (♦) and $M = 0.5$ (▲).

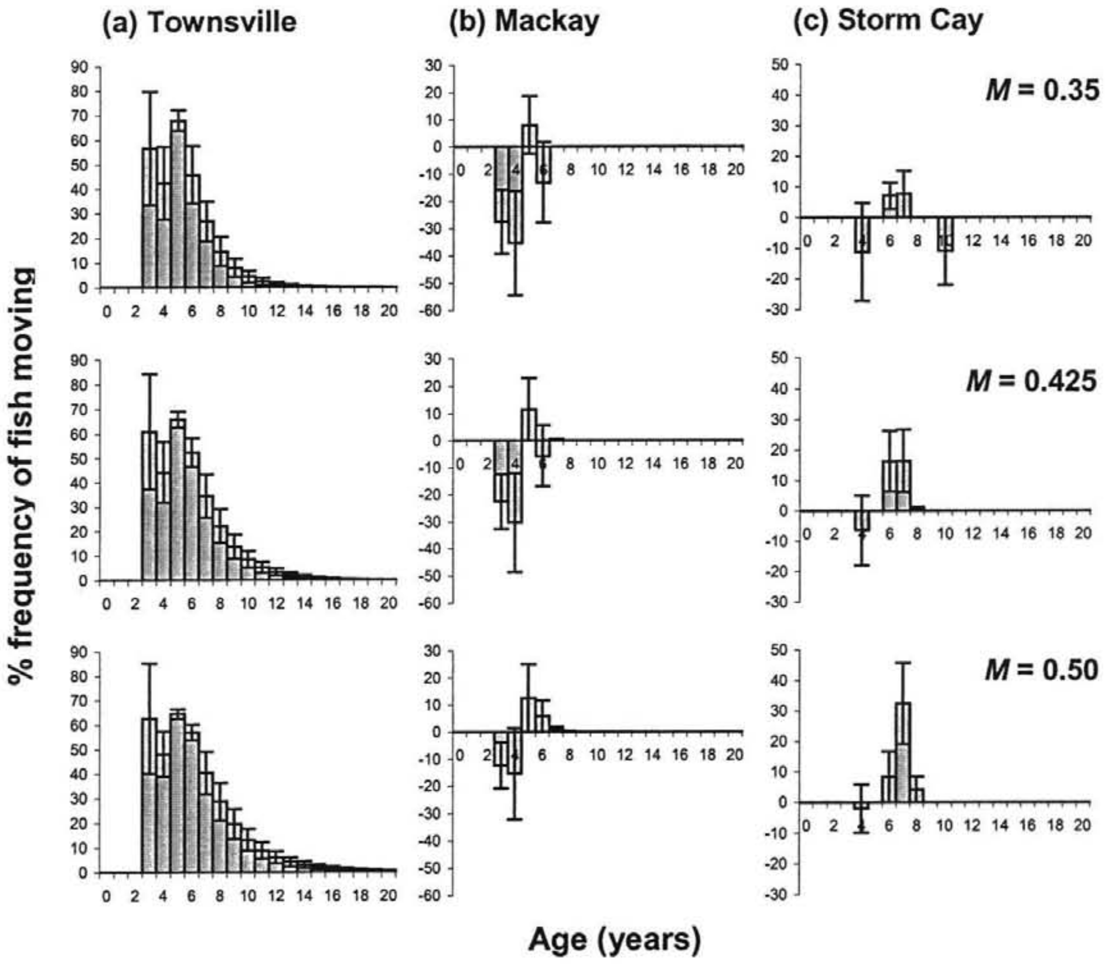

Figure 7.6. Predicted age-specific net immigration (positive values) and emigration (negative values) of *Lethrinus miniatus* averaged across five years from 1995 to 1999 for three levels of natural mortality in three regions of the Great Barrier Reef, Townsville (a), Mackay (b), and Storm Cay (c). Each bar represents the relative frequency of fish in an age class that have immigrated or emigrated expressed as a percentage of the number of fish remaining in the age class. Error bars are standard error.

Estimates of relative recruitment (number of two year old fish relative to the total number of fish in each region) varied significantly among regions (Figure 7.7). Rates of relative recruitment were very low in the Townsville region (~5%) compared with the Mackay and Storm Cay regions, while relative recruitment rates did not differ significantly between the Mackay (~40-44%) and Storm Cay (~30-36%) regions.

Estimates of relative recruitment did not vary significantly within regions with changing values of natural mortality (Figure 7.7).

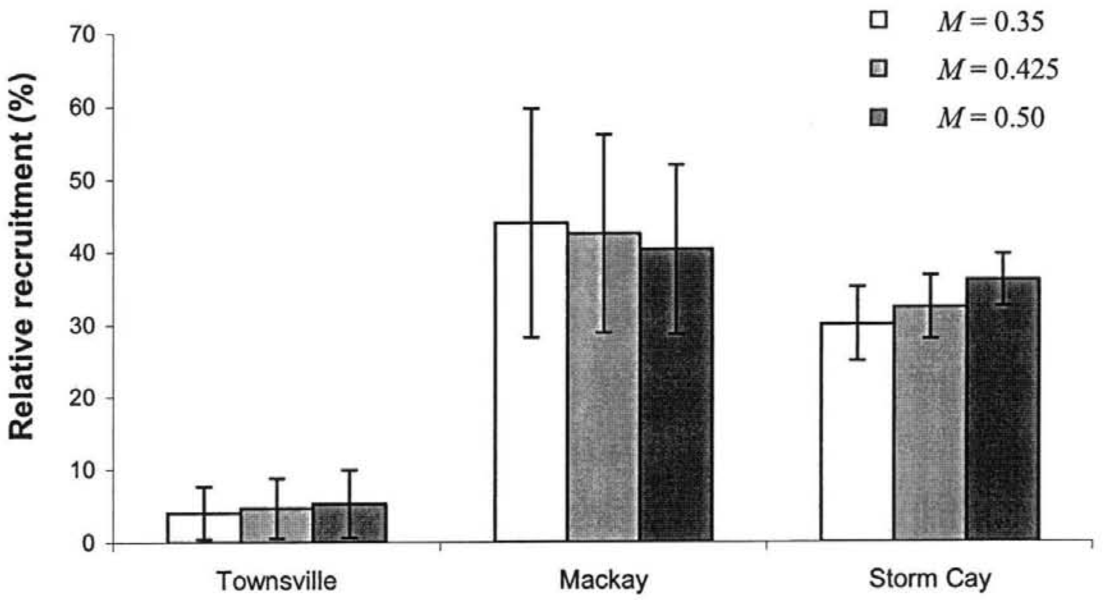

Figure 7.7. Predicted relative recruitment of *Lethrinus miniatus* to three regions of the Great Barrier Reef (Townsville, Mackay and Storm Cay) for three levels of natural mortality (M) averaged across five years from 1995 to 1999. Relative recruitment is defined as the number of two year old fish in a region expressed as a percentage of the total number of fish in the region. Error bars are 95% confidence intervals.

7.4. Discussion

The results from this chapter suggest that movement of *L. miniatus* to or from regions of the GBR would be required to account for the observed regional variation in age structures if natural mortality rates do not vary among regions. In particular, the model predicted substantial net immigration to the Townsville region and, to a lesser extent, the Storm Cay region and net emigration of fish from the Mackay region.

Immigration to the Townsville region was predicted over a wide range of age classes, whereas immigration to the Storm Cay region and emigration from the Mackay region were predicted to be limited to only a few age classes. These predictions of age-specific net movement were not significantly affected by a range of natural mortality rates between 0.35 – 0.50 y^{-1} that were used as inputs in the model.

7.4.1. Potential hypotheses for movement of L. miniatus

One hypothesis that might explain the model results is that regional differences in recruitment and subsequent densities result in the dispersal of *L. miniatus* post-recruits away from the centre and towards the extremes of their distribution on the GBR. The distribution of the regions is such that the Mackay region is located approximately at the centre of the distribution of *L. miniatus* on the GBR, the Townsville region is located at the northern extreme of the species distribution (approximately 300 kilometres north of the Mackay region) and the Storm Cay region is located approximately half way between Mackay and the southern extreme of the species distribution on the GBR (Figure 7.8). Catch rates of *L. miniatus* are generally greater from reefs within the Mackay region than reefs within the Storm Cay region, which in turn are greater than catch rates from reefs within the Townsville region (Mapstone et al. 2003). This suggests that relative densities of *L. miniatus* are likely to be highest in the Mackay region, lowest in the Townsville region and intermediate in the Storm Cay region. This regional pattern of densities of *L. miniatus* is also reflected in the relative recruitment to each region predicted by the model. Assuming movement rates of *L. miniatus* are similar among regions, higher densities in the Mackay region would result in net movement of fish away from the Mackay region towards the extremes of their range (Figure 7.8).

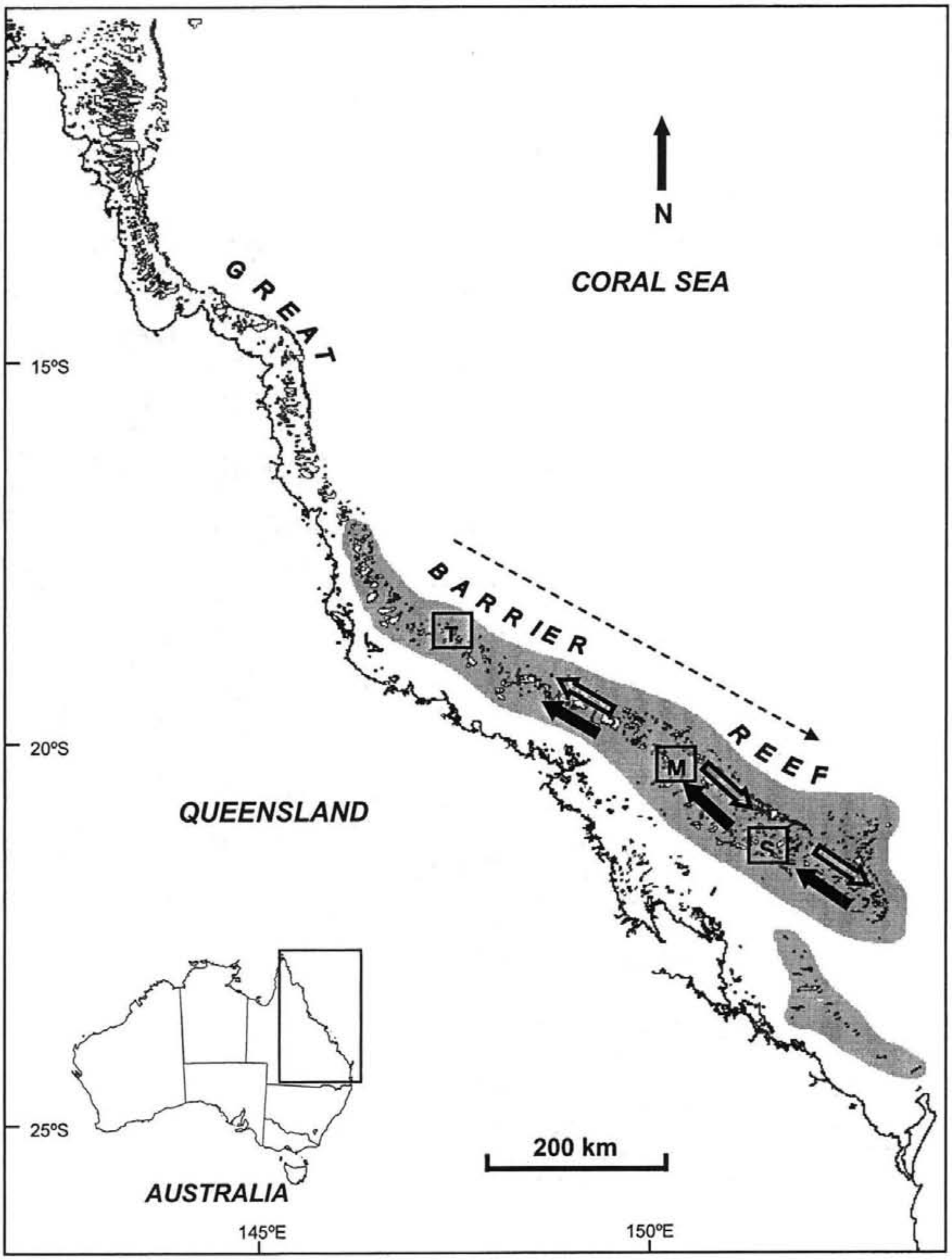

Figure 7.8. Hypothesised movement of *Lethrinus miniatus* post-recruits among the Townsville (T), Mackay (M), and Storm Cay (S) regions of the Great Barrier Reef (GBR). Transparent arrows indicate net movement for hypothesis 1) dispersive net movement away from distribution centre. Solid arrows indicate net movement for hypothesis 2) general northward net movement (See text for details of hypotheses). Dashed arrow indicates possible net direction of larval dispersal. Shaded area indicates distribution of *L. miniatus* on the GBR.

The predicted net emigration of fish from the Mackay region and net immigration into the Townsville region is consistent with this dispersion hypothesis. Furthermore, the predicted net immigration of six and seven year olds in the Storm Cay region is also consistent with this hypothesis. Under the dispersion hypothesis, a net immigration of fish into the Storm Cay region would be expected, as the number of immigrants arriving from the Mackay region should be higher than the number of emigrants leaving the Storm Cay region and moving towards the southern extreme of the species distribution. It would be interesting to sample populations of *L. miniatus* from reefs near the southern extreme of their distribution on the GBR to determine whether the age frequency distributions provide evidence of immigration in older age classes, similar to that in the Townsville region. While large-scale dispersal is a well documented feature for stocks of Icelandic cod (*Gadus morhua*) (Hovgård and Christensen 1990) and haddock (*Melanogrammus aeglefinus*) (Frank 1992), such large-scale dispersal has not been documented for any species of reef fish.

An alternative hypothesis is that net movement of *L. miniatus* occurs in a general northerly direction on the GBR, towards the Townsville region (Figure 7.8). The influence of the East Australian Current on the GBR results in a general southerly flow of water over the regions in this study (Wolanski 2001). Consequently, net transport of *L. miniatus* larvae on the GBR may occur in a southerly direction (Figure 7.8). The prediction of high relative recruitment in the Mackay and Storm Cay regions compared with the Townsville region is consistent with a net southerly dispersal of larvae. Furthermore, the proportion of spawning female *L. miniatus* was significantly greater in the northern area of the GBR compared with the southern area of the GBR (Chapter 4), suggesting that a large proportion of *L. miniatus* larvae on the GBR may originate from the northern area. Net movement of post-recruit *L. miniatus* towards the northern extreme of their distribution may represent an evolutionary advantage for the species to maintain its current distribution on the GBR. The major assumption of this hypothesis is that the northern area of the GBR provides a more suitable habitat for reproduction and spawning of *L. miniatus* than the southern regions. Significant migrations to spawning sites have been documented for a number of other large reef fish, particularly the large serranids. Some of the reported distances moved to reach a spawning site include up to 10 km for *Epinephelus polyphekadion* in Palau (Johannes et al. 1995), 17 km for *Plectropomus leopardus* on the GBR (Zeller 1998), 72 km for *E. morio* in the Gulf of Mexico (Moe 1969), and from 110 km (Colin 1992) to 220 km (Bolden 2000) for *E. striatus* in the central Bahamas. The strong evidence of immigration in the Townsville region and somewhat weaker evidence of emigration in the Mackay region is consistent with this hypothesis. The evidence of immigration in the Storm Cay region is not consistent with this hypothesis, although the evidence of immigration was weak.

A further hypothesis is that net movement of *L. miniatus* occurs across the shelf of the GBR, rather than latitudinally, parallel to the coastline. As mentioned in previous chapters, the shelf position of the reefs within the Townsville, Mackay and Storm Cay regions is not consistent among regions. Prediction of net immigration in the Townsville region and net emigration in the Mackay region would be consistent with an hypothesis of net movement of *L. miniatus* from the inner and mid-shelf reefs towards the outer-shelf reefs. The limited evidence of net immigration to the Storm Cay region, however, is not consistent with this hypothesis. Significant cross-shelf movements from inshore and estuarine habitats to mid and outer-shelf reef habitats on the GBR have been documented for *Lutjanus argentimaculatus* (Russel et al. 2003) and suggested for other large lutjanids including *L. sebae*, *L. malabaricus* and *L. erythropterus* on the GBR (Williams 1991, Williams and Russ 1994). The collection of demographic data across the continental shelf for *L. miniatus* in all three regions may provide an indirect test of this hypothesis for this species.

It will be necessary to obtain direct estimates of movement from tagged or known individuals to rigorously test these hypotheses. Recapturing sufficient numbers of individuals of a species capable of moving large distances, however, will be problematic. Brown et al. (1994) tagged and released 667 *L. miniatus* in a single region of the GBR and only received a single return in a five-year period. The lack of recaptures was attributed to the dispersal of *L. miniatus* into deeper water away from the reefs on which they were released. Recent advances in satellite archival tags may provide an alternative tool for tracking large-scale movements in fish, but the size of these tags currently limits their use to larger fish such as sharks, tuna and billfish.

7.4.2. Implications of model assumptions

The model predictions of large-scale net movement of *L. miniatus* are based on a number of major assumptions, which have important implications for the model predictions. It was necessary to assume a constant rate of natural mortality across regions, as movement and mortality are confounded, making it impossible to determine the relative contribution of each to the loss of individuals from populations in each region. The effect of different natural mortality rates on the predictions of age-specific net movement in each region was to increase the predicted immigration to each region, but this increase was slight, at least for the range of mortality rates used in the model. The assumption of a constant rate of natural mortality across regions conflicts with the results presented in Chapter 6 that demonstrated significant regional variation in natural mortality when net movement of fish among reefs was assumed to be zero.

Regional variation in natural mortality, however, may still have direct effects on the model predictions. For example, the predicted emigration from the Mackay region may include an unknown quantity of increased natural mortality, such that the rate of natural mortality is higher in this region than the mortality rates used in the model. Similarly, if the rate of natural mortality in the Townsville region was in fact lower than the mortality rates used in the model, increased survival of residents may account for some of the predicted immigration to this region.

If *L. miniatus* move among reefs on the GBR, the estimates of *M* used in the model are likely to be overestimates. The reefs used in the model were closed to fishing and it was assumed that there were no infringements on these reefs. Movement of *L. miniatus* among reefs, however, would result in the mixing of fish from reefs both open and closed to fishing. Consequently, estimates of *M* from populations sampled from reefs closed to fishing would also contain an unknown component of fishing mortality (*F*) arising from the movement of fish to reefs closed to fishing following exposure to harvest.

Frederick (1997) demonstrated convincingly that post-settlement movement of a number of reef fish species significantly biased estimates of mortality when movement was ignored. Natural mortality rates of *L. miniatus* estimated in Chapter 6 assumed no net movement among regions and consequently may be biased due to either immigration or emigration. In particular, the estimate of natural mortality for the Mackay region was 1.12 y^{-1} (Chapter 6), which corresponds to a loss of nearly 70% of a cohort each year. It seems likely that this estimate is an overestimate, given *L. miniatus* on the GBR has a potential longevity of 20 years (Brown and Sumpton 1998, Williams et al. 2003). Estimates of natural mortality for other relatively large reef fish with similar longevities typically range between 0.1 – 0.5 y^{-1} (Munro and Williams 1985, Russ et al. 1998, Newman et al. 2000*a*,*b*, Kritzer 2002). The more likely scenario for *L. miniatus* is that regional variation in natural mortality and large-scale net movement both contribute to the observed differences in age frequency distributions and subsequent estimates of mortality among regions.

Net age-specific movement of *L. miniatus* in the model was assumed to follow a logistic function. However, if net age-specific movement of *L. miniatus* follows a different pattern, the net direction of movement across all age classes in each region predicted by the model would remain the same, as the deviations between the observed and predicted age frequency distributions from the initial model fit without movement, under the same model assumptions, would be unchanged.

L. miniatus also were assumed to remain stationary on a reef until they reached three years of age, after which they were considered capable of moving in or out of a region. This assumption was necessary as recruitment was assumed to occur at two years of age and so movement of two year old fish would have confounded estimates of recruitment. SUNTAG (unpublished data) provide the only evidence of movement of young *L. miniatus* among reefs on the GBR, while (Kaneshiro 1998) provide evidence for movements up to 7 km off Okinawa Island, Japan for early juvenile *L. nebulosus*, a closely related species (Lo Galbo et al. 2002).

The model also assumed that the number of two year old fish in each region represented an estimate of relative recruitment to each region. If early post-settlement and juvenile mortalities of *L. miniatus* vary substantially among regions, then the estimates of relative recruitment to each region may be biased, as recruitment was estimated in the model by fitting to the observed frequency of two year old fish. Unfortunately nothing is known about the early post-settlement or juvenile stages of *L. miniatus*, precluding further examination of this idea. Other authors have demonstrated significant spatial variation in post-settlement and juvenile mortality of reef fish among sites within individual reefs (e.g. Jones 1997, Beukers and Jones 1998, Stewart and Jones 2001, Holbrook and Schmitt 2003), but variation at larger spatial scales has not been documented.

7.4.3. Implications of large-scale movement

Movement of *L. miniatus* among reefs on the GBR almost certainly occurs, although the exact magnitude and spatial scale over which it occurs is unknown. Such relatively large-scale movement has important implications for the spatial scales over which demographic processes operate. Lewis (1997) demonstrated that post-settlement movement of numerous reef fish species among patch reefs within an individual reef significantly affected the size of populations on isolated patch reefs, thus masking variability in recruitment. On a similar spatial scale, Frederick (1997) found that post-settlement movement of several reef fish species among patch reefs significantly biased estimates of mortality when movement was ignored. For *L.*

miniatus, movement among reefs may have the consequence of decoupling demographic processes such as recruitment and mortality from the size of populations at the scale of individual reefs. Therefore, for more mobile species such as *L. miniatus* it will be important to obtain quantitative estimates of recruitment, mortality and movement rates over larger spatial scales (Jones 1991), such as clusters of reefs or regions, to obtain reliable estimates of population structure.

The prediction of large-scale movement of *L. miniatus* in this study has important implications for the design of Marine Protected Areas (MPA). Recently, MPAs have gained considerable popularity as fisheries management tools for coral reef fisheries (Roberts and Polunin 1991, Dugan and Davis 1993, Russ 2002). The effectiveness of MPAs, however, will depend on numerous factors, including transfer rates of larvae and adults between MPAs and fished areas, size of the MPA, and rates of growth, mortality and exploitation of the species (Polacheck 1990, DeMartini 1993, Bohnsack 1998, Murray et al. 1999, Russ 2002). Net movement of fish from within MPAs to fished areas can provide harvestable biomass for the fishery (Alcala and Russ 1990, DeMartini 1993, Russ and Alcala 1996, Roberts et al. 2001, Russ 2002). However, excessive net movement from a MPA may reduce the biomass and spawning stock within the MPA, thus reducing potential export of larvae from the MPA into fished areas (Rakitin and Kramer 1996, Crowder et al. 2000, Russ 2002, Zeller et al. 2003). Direct evidence of adult reef fish movement across the boundaries of MPAs has been documented on only a few occasions (Holland et al. 1993, 1996, Davies 1995, 2000, Zeller et al. 2003). The potential for large-scale movement of *L. miniatus*, at least among reefs on the GBR, suggests that MPAs may need to be larger than individual reefs if they are to protect potentially more mobile species, such as *L. miniatus*, for significant parts of their lives. For example, if MPAs were implemented at the scale of individual reefs, then movement of fish among reefs both open and closed to fishing may dilute the effects of closure. Mapstone et al. (2003) demonstrated that the mean age and relative abundance of *L. miniatus* differed significantly between reefs open to fishing and the reefs used in this study, which were closed to fishing. This suggests that net movement of *L. miniatus* in the three regions is not large enough to completely eliminate the effects of protection on reefs closed to fishing, even where only single reefs were closed.

7.4.4. Summary and conclusions

In summary, this chapter demonstrated, through the use of an age-structured model, that significant movement of *L. miniatus* to or from regions, particularly immigration to the Townsville region, would be required to explain the significant regional variation in age structures and estimates of *M*. A number of major assumptions were made in the development of the model, however, the most tenuous being the assumption of a common *M* among regions of the GBR. At this stage it is not possible to separate the confounding effects of mortality and movement on the population structure of *L. miniatus* without independent estimates of movement. The most likely scenario appears to be that both movement and regional variation in mortality account for the observed regional differences in age structures.

Assuming the assumptions of the model are valid, there are at least three hypotheses that may explain the results from the model, including: 1) a dispersive net movement away from the distribution centre; 2) a general northward net movement to take advantage of prevailing currents for larval dispersal; and 3) a cross-shelf net movement from inner and mid-shelf reefs towards outer-shelf reefs. Comprehensive tagging studies will be necessary to test these alternate hypotheses, but tagging studies on this large spatial scale are likely to be logistically difficult for a reef fish of such potentially high mobility.

Finally, this chapter highlights the importance of determining the scales at which movement in larger coral reef fish occurs. Movement of adult fish can decouple the relationship between demographic processes such as recruitment and mortality from the size of the population. Therefore, to obtain reliable estimates of population structure it will be essential to determine the spatial scales at which all demographic processes, including movement, operate.

Chapter 8. General Discussion

8.1. Spatial patterns in population biology

Recently there has been a call for the compilation of more spatially explicit data sets of population parameters for a range of species to clarify generally the spatial scales that are most important in shaping coral reef fish populations (Choat 1998, Sale 1998, Choat and Robertson 2002). Several recent studies have started to build our knowledge of spatial pattern and the importance of spatial scale for coral reef fish populations (e.g. Hart and Russ 1996, Newman et al. 1996*a*, Adams et al. 2000, Meekan et al. 2001, Gust et al. 2002, Kritzer 2002, Williams et al. 2003). The results from this thesis have contributed further to this knowledge of spatial pattern for coral reef fish. Some generalisations can be made from this thesis with respect to spatial patterns in population parameters of *L. miniatus*. Generally, the spatial scales at which variation was observed varied among population parameters. Significant large-scale differences were observed in some parameters (size at sex change, proportion of spawning females, growth, and mortality), small-scale differences were only observed for one parameter (growth) and no spatial differences were observed in some parameters (spawning season, sex ratios, and age at sex change). A comparison of these results with other studies of spatial patterns in population parameters (e.g. Aldenhoven 1986, Pitcher 1992, Connell 1996, Hart and Russ 1996, Newman et al. 1996*a*, Adams 2000, 2002, Gust et al. 2002, Kritzer 2002, Platten et al. 2002) revealed substantial differences among species. That is, the spatial scale at which a particular population parameter varies appears to differ among species. This point was also highlighted by Choat and Robertson (2002) who demonstrated a significantly different spatial pattern in age and growth between an acanthurid and a scarid species.

This thesis also highlights the importance of obtaining estimates for as many population parameters as possible simultaneously. The interaction among population parameters suggests that measuring only one parameter, or a small subset of parameters, may result in a misleading interpretation of the overall dynamics of the population. A good example of this is the estimates of natural mortality from Chapter 6 and the modelling of post-recruitment movement in Chapter 7. Taken in isolation, the estimates of natural mortality would suggest that *L. miniatus* in the Mackay region were dying at an extraordinarily high rate of nearly 70% of a cohort each year. However, it is possible that emigration of post-recruits from the Mackay region may contribute to the apparent high rate of natural mortality in this region. Such insights could not have been obtained by examining only a single population parameter (*M*).

Historically, there has been significantly more research effort devoted to studying populations of small, rather than large bodied, reef fish. This is due, in part, to the greater ease with which smaller, more sedentary reef fish can be studied but also to their apparent numerical dominance on the reef. Larger species of reef fish are typically targets for coral reef fisheries and, therefore, knowledge of their population biology has significance for fisheries management. Roberts (1996) noted this imbalance and called for more studies on larger, commercially important reef fish species. The results from this thesis, and from other recent studies (e.g. Adams et al. 2000, Williams et al. 2003), have contributed towards correcting the imbalance by providing estimates of a range of population parameters for large, commercially important reef fish.

8.2. Future directions

This thesis has highlighted a number of areas that require further research. These areas relate specifically to *L. miniatus*, as well as to coral reef fish, and in some cases to fish in general.

8.2.1. Spawning omission and protogyny in coral reef fish

Sadovy (1996) emphasised that better estimates of the reproductive output of coral reef fish populations were urgently needed. An obvious but important component necessary to estimate reproductive output is a measure of the size of the spawning population, usually expressed as the number of mature females. It is often assumed when estimating reproductive output that all mature females in a population participate in spawning each year. The results from Chapter 4, and from other recent studies (Chauvet 1991, Fennessy and Sadovy 2002) have demonstrated that, at least in some species, a significant proportion of mature females do not spawn each year. For these species, reproductive output would be overestimated if all females were assumed to be spawning each year. From a management perspective it will be necessary to regard the non-spawning mature females as effectively 'immature' as they do not contribute to egg production in a given spawning event. Clearly better predictions of reproductive output can be gained by determining the frequency and causal factors of spawning omission.

8.2.2. Protogyny in coral reef fish

Almost 50% of coral reef fish families contain species that are thought to be protogynous hermaphrodites (changing sex from female to male) (Warner 1984, Sadovy 1996). The controlling mechanism for sex change, however, remains unclear for the majority of protogynous fish, including *L. miniatus*. The traditional view was that sex change occurred at a genetically predetermined size or age (Ghiselin 1969). More recently, there is increasing evidence that sex change in coral reef fish is under social control (Sadovy 1996). It will be important to determine which mechanism controls sex change, particularly for exploited species, as the response of the population to fishing will vary between these two mechanisms. More information on sex ratios and detailed behavioural studies and/or manipulative experiments are necessary to test the different hypotheses of sex change in coral reef fish populations. Only from this information can we predict with more certainty the potential effects that fishing may have on reproductive output of populations. Ultimately this will lead to a better understanding of the reproductive biology of coral reef fish populations and consequently better informed management of harvested stocks.

8.3.3. Movement studies of large coral reef fish

Net movement of fish in or out of a population can significantly modify the population structure and bias estimates of density, mortality and recruitment history (Robertson 1988, Warner 1995, Frederick 1997, Lewis 1997). However, movement is a population parameter that is too often ignored in studies of coral reef fish populations. Net movement of adult coral reef fish is usually assumed to be negligible, but rarely has it been quantitatively measured. Most studies that have directly measured movement rates of adult coral reef fish have been limited to smaller species (e.g. Lewis 1997, Frederick 1997). However it is the larger species that are likely to be more mobile and move over greater distances (DeMartini 1998). There is an urgent need to quantify the movement patterns of larger reef fish species and to measure the effects of movement on the population structure and estimates of other population parameters. Information on movement patterns is also important for the design of marine protected areas (MPAs), as the effectiveness of MPAs will be governed by the net movement (spillover) of fish into adjacent fished areas (Russ 2002).

The use of conventional tagging techniques for tracking the movement patterns of more mobile fish is likely to be more difficult than for small sedentary species, as the probability of recapturing or resighting individuals decreases with increasing area and size of the population, relative to the number of tagged individuals. The indirect technique used in Chapter 7 to predict potential movement of *L. miniatus* is one alternative method for estimating net movement rates. However, this technique requires accurate estimates of the population age structure and a reliable independent estimate of mortality. Recent advances in satellite archival tags may provide an alternative tool for tracking large-scale movements in fish, but the size of these tags currently limits their use to larger fish such as sharks, tuna and billfish.

8.3. Implications for fisheries management

The results from thesis have a number of important implications for the management of *L. miniatus* populations on the GBR and the management of coral reef fish in general.

8.3.1. Harvest controls for L. miniatus

Specific restrictions for *L. miniatus* on the GBR include a minimum size limit of 350 mm TL (approximately 320 mm FL) for all fishers, which is intended to allow 50% or more of fish to reach maturity and spawn before becoming vulnerable to the fishery.

Based on the maturity estimate from Chapter 4, the current minimum size limit appears to be meeting its objective as 100% of females were mature at 320 mm FL. However, this estimate of maturity was obtained from a single region of the GBR. It will be important to determine whether maturity varies among regions of the GBR to establish whether the current minimum size limit is appropriate for all regions of the GBR.

Chapter 4 also established that 50% of females in the southern area of the GBR do not spawn in all seasons until they reach 450 mm FL. From a management perspective the females that do not spawn in a given season are effectively 'immature' for the years they do not contribute to egg production. Therefore, although the current minimum size limit may be allowing 100% of females to reach maturity before becoming vulnerable to the fishery, it is likely that many of these females, at least in the southern area of the GBR, do not spawn before being caught. The use of a minimum size limit for *L. miniatus* is further complicated by the protogynous sexual strategy of *L. miniatus* (changing sex from female to male). Chapter 4 revealed that the entire male population of *L. miniatus* are vulnerable to capture, and therefore *L. miniatus* may be particularly vulnerable to sperm limitation arising from overfishing of males. An increase in the current minimum size limit, or the introduction of a maximum size limit, are two mechanisms that may offer some protection from harvest to a proportion of the male population.

A spawning closure for the GBR Line Fishery is proposed for three nine-day periods around the new moons in October, November and December (QFMA 1999). The proposed closures are intended to protect the spawning activity of reef fish, particularly spawning aggregations of the main target species *Plectropomus leopardus* (QFMA 1999). The information presented in Chapter 4 indicates that the proposed closures do not coincide with the peak spawning period for *L. miniatus* and so the spawning stock of *L. miniatus* will gain little, if any, protection of spawning activity from the proposed spawning closures. Furthermore, the efficacy of spawning closures depends on more than just aligning the closure with peak spawning periods. For a spawning closure to be most effective (i.e. more effective than closures at other times), there must be evidence supporting the intentional targeting of spawning aggregations or an increase in catchability of a species during the spawning season. There is little evidence consistent with either of these scenarios for any species in the GBR Line Fishery (Mapstone et al. 2001).

8.3.2. Spatially explicit management

Traditional fisheries management defines a fish stock as a homogeneous population of fish with uniform population parameters (Ihssen et al. 1981, Smith and Jamieson 1986, Gauldie 1991). Indeed, current management of *L. miniatus* implicitly assumes a single homogenous 'stock' with no spatial structure throughout the entire species range on the GBR. Clearly, the results from this thesis have revealed that significant spatial variation exists within the 'stock' of *L. miniatus* on the GBR, particularly at the regional spatial scale.

Populations of *L. miniatus* on the GBR are likely to comprise a single genetic stock, however, as van Herwerden et al. (2003) were unable to detect significant genetic variability among populations of *L. miniatus* from six reefs within three regions spread throughout the distribution of *L. miniatus* on the GBR, including four reefs sampled for this thesis (Dip, Glow, Bax, 20-137). The existence of genetically homogenous populations of *L. miniatus* on the GBR, but significant spatial variation in population biology, suggests that the presence of genetic differences among populations are not always necessary for populations to be considered as separate stocks or management units.

The significant variation in population parameters among regions may reflect regional variation in productivity of *L. miniatus*. For example, productivity of *L. miniatus* is likely to be higher in the Mackay region, where recruitment is greater, fish reach a larger maximum size and have higher rates of natural mortality than in the Townsville region, where recruitment is lower, the maximum size of fish is smaller and rates of natural mortality are lower. Under the current management arrangements for *L. miniatus*, where spatial variation in productivity is not accounted for, it is possible that less productive components of the stock (e.g. Townsville) are being overfished while potential yields are not being realised from more productive components of the stock (e.g. Mackay).

At face value, such spatial structure provides strong evidence in support of spatially explicit management strategies that accommodate the observed spatial patterns in population biology. However, spatially explicit management strategies will be difficult to implement, particularly for coral reef fisheries, due to the high costs involved with the need for continued spatial assessments of the stock and the difficulties associated with enforcing the boundaries for spatially explicit management controls. An alternative, perhaps more conservative, approach would be to adopt a management strategy that explicitly incorporates the spatial structure into the stock assessment but applies a single management strategy across the stock as a whole that is least likely to result in the collapse of any component of the stock.

8.4. Summary and conclusions

This thesis demonstrated significant spatial and temporal variation in population biology of *L. miniatus* on the GBR. The largest differences in population parameters were observed at the spatial scale of regions, suggesting that productivity of *L. miniatus* may vary among regions of the GBR. This thesis highlighted the importance of incorporating such variation into stock assessment models and ultimately into management measures to avoid over-exploitation of less productive components of the stock. This thesis also highlighted the importance of including a range of population parameters in studies of fish population dynamics. Ultimately, more multi-scale studies are needed that incorporate both spatial and temporal scales, and a range of population parameters. The importance of spatial variation in population parameters, and the scales at which they vary, can only be determined through such multi-scale approaches.

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