Stock structure of a coral reef fish, *Plectropomus leopardus*: identification and implications for harvest strategy evaluation

PhD thesis submitted by

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STATEMENT OF CONTRIBUTION OF OTHERS

This thesis includes some collaborative work with my supervisors Dr Gavin Begg, Prof. Bruce Mapstone, Prof. Garry Russ and Dr Rich Little, as well as with Dr Dong C. Lou, Mr Cameron Murchie and Dr André Punt. For all the project components in this thesis I was responsible for the concept and aims, carrying out the laboratory work, the statistical analysis, results interpretation and synthesis, and the writing of all text in the thesis and publications. My supervisors assisted with their advice on these issues, with their contributions reflected by the order of the co-authors for each paper. Rich Little (CSIRO) also assisted with the coding of ELFSim for the purpose of this project. CSIRO Marine and Atmospheric Research assisted with in-kind contribution during a one month stay at the laboratory in Hobart. André Punt assisted with technical and editorial advice for the ELFSim paper. Gavin Begg and Bruce Mapstone also assisted financially towards the Otolith Chemistry paper and with in-kind contributions for the production of this thesis. The samples from which this thesis was derived were provided by Bruce Mapstone and others from the Effects of Line Fishing Experiment done over 11 years on the Great Barrier Reef. Dong C. Lou aged most of the *P. leopardus* samples used in this thesis and assisted with minor editorial advice on the Life History paper. Cameron Murchie assisted with some of the laboratory work for the Otolith Chemistry paper. CRC Reef assisted with financial support towards my stipend, research funds and conference travel support. The School of Marine Biology and Aquaculture assisted with in-kind contribution, research funds and conference travel support. The Great Barrier Reef Marine Park Authority assisted with research funds towards the Otolith Chemistry analysis.

List of papers:

Chapter 2:

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Chapter 3:

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Chapter 4:

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ABSTRACT

The recognition of stocks, or spatially separate groups of individuals with persistent differences in biological characteristics, is important for the sustainable and optimised use of fisheries resources. Stocks with different biological characteristics may respond differently to harvest and therefore have different vulnerabilities to over-exploitation. Recent research suggests that spatial variation in biological characteristics at a range of scales is a feature of many coral reef fishes. An investigation of the temporal stability of spatial differences and the identification of stocks that may require separate management strategies, however, has rarely been undertaken for such fish. Moreover, little is known about the implications of spatial differences in biological characteristics for spatially separate components as well as entire populations of coral reef fishes when subject to various levels of harvest.

This thesis has four primary aims: 1) to investigate the use of otolith chemistry as an indirect indicator of stock structure of three exploited epinepheline serranid coral reef fishes, *Plectropomus leopardus*, *Cephalopholis cyanostigma* and *Epinephelus fasciatus*, on the Great Barrier Reef (GBR), Australia; 2) to investigate the use of otolith morphology as an indirect indicator of stock structure of *P. leopardus*; 3) to investigate the spatial and temporal patterns in life history characteristics of *P. leopardus* as direct manifestations of stock structure; and 4) to examine the implications of spatial variability in life history characteristics of *P. leopardus* for harvest strategy evaluation.

The first two aims were achieved by comparing otolith chemistry (Mn, Sr, Ba) and otolith morphology (otolith length, width, area, perimeter, circularity, rectangularity and Fourier Harmonics) variables among four regions of the GBR,

separated by 100s of kilometres, as well as among three reefs 100s – 1000s of meters apart within each region. The temporal stability in otolith chemistry and morphology signals was also examined by comparing two cohorts of *P. leopardus* and individuals of *C. cyanostigma* and *E. fasciatus* from the same cohorts that were collected two years before and two years after a significant weather disturbance (Tropical Cyclone Justin) in March 1997. Persistent differences in otolith chemistry were found at both broad and fine spatial scales, and differences in otolith morphology were seen at mainly broad spatial scales. Moreover, some aspects of chemical and morphological signals differed between cohorts and individuals collected before and after the Cyclone. The results highlight the need to incorporate data from several years in studies using these techniques to discriminate temporary and possibly misleading signals from those that indicate persistent spatial structure in stocks. These results provide a good starting point for future research on groups of individuals that have lived at least part of their lives in different environments and therefore may have different biological characteristics, although otolith chemistry and morphology should not be used in isolation to determine stock structure.

The third aim was achieved by comparing vital life history characteristics of *P. leopardus* at the same broad regional and finer reef scale as the otolith chemistry and morphology. Temporal stability in stock structure was examined by comparing biological parameters among five consecutive years, from 1995 to 1999. The results matched the patterns indicated by otolith chemistry and morphology and emphasised that the stock structure of *P. leopardus* is far more complex than assumed previously. Mortality, growth, age richness and longevity of *P. leopardus* varied among reefs within regions and some estimates of growth and longevity also varied at the larger regional spatial scale. Several of the spatial patterns in these biological parameters

were complicated by inter-annual variation. Similar to the use of otolith chemistry and morphology, the life history results emphasised the importance of a multi-scaled sampling design, including a temporal component, when using biological characteristics to investigate the stock structure of tropical reef fishes. I proposed a theoretical model for conceptualising the stock identification and management challenge for *P. leopardus* that may be composed of a complex network of reef subpopulations, groups of subpopulations (i.e., regions), and potential stocks with persistent differences in biology.

The fourth aim was achieved using a spatially-structured management strategy evaluation model developed for *P. leopardus* harvested by the GBR line fishery. Relative spawning biomass of the population was estimated from simulations of four hypothetical scenarios of spatial variation in life history characteristics under each of five hypothetical effort scenarios. The life history scenarios involved simulating the *P. leopardus* population with or without differences in a) individual growth and b) mortality rates among four regions of the GBR. The different effort scenarios involved shifting fishing effort among the four regions. The effects of regional closures (no effort) were also examined. Trajectories of mean relative spawning biomass were compared among the different combinations of spatial and effort scenarios. Relative mean spawning biomass trajectories were also compared between two analytical approaches involving aggregating results over regions, as is usually done in fisheries assessments, or treating results separately for each region. The latter comparison directly assessed the impacts of erroneously assuming an homogeneous stock despite regional variation in life history parameters.

Including spatial variation in growth and mortality resulted in greater depletions of relative spawning biomass and longer times to recover relative to pre-

exploitation levels for the population as a whole, as well as for several regions. Aggregating results across regions masked important region-specific patterns in the relative spawning biomass trajectories arising from spatial variation in biology, and so resulted in the wrong conclusions about whether particular management objectives were likely to be realised. These results suggest that spatial variation in growth, in particular, mortality and potentially other life history characteristics should be incorporated in future harvest strategy evaluations for *P. leopardus*. Further, the results suggest that the single management unit currently in place for *P. leopardus* on the GBR may need to be divided into finer spatial units to closer reflect biological stock units to deliver prudent biologically optimal harvests.

The results clearly have some important implications for the management and harvest of *P. leopardus* on the GBR. *P. leopardus,* and probably many other exploited coral reef fishes, should not be viewed or managed as single homogenous populations. Instead these populations should be considered as complex networks of spatially and temporally varying components which although interlinked, may require separate management strategies to assure their long-term sustainability and optimal harvest.

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Chapter 1. General Introduction

There has been increasing attention given to the spatial scale at which marine populations operate (e.g., Stephenson 1999; 2002; Hilborn et al. 2005) following realisation that the spatial and temporal complexity in the population structure of many species has not been considered appropriately in fisheries management (Smedbol and Stephenson 2001; Stephenson et al. 2001; Stephenson 2002). In many situations, species form separate self-sustained populations at finer spatial scales than those typically considered in assessments and management strategies (e.g., Hobday et al. 2001; Stephenson 2002; Andrews et al. 2006). In other situations, only a portion of a single stock is managed and may result in sub-optimal outcomes for the fishery, the stock or both. Moreover, spatial boundaries between separate spawning components of populations may be obscured by migratory behaviours between spawning, nursery or feeding areas, when transient mixing of populations can occur, making stock identification difficult. The importance of spatial structure in populations, however, is not known for many, and indeed perhaps most, harvested species. Some reef associated, demersal fish and shell-fish species for example, form many spatially separate subpopulations of relatively sedentary adults that are closely connected to distinct patches of habitats but interact through unknown levels of larval dispersal. The productivity and harvest of some isolated adult subpopulations can subsequently affect the sustainability of others (Hilborn et al. 2005; Kritzer and Davies 2005). A major challenge facing fisheries scientists and managers is to identify the spatial scale of biologically appropriate management units, or stocks, of species with complex population structures and develop management strategies accordingly. The continuous depletion of fisheries resources around the world,

despite tougher management protocols (FAO 1997; Pauly et al. 2002; Myers and Worm 2003), makes the need for this information an urgent priority.

1.1. Definition of 'stock'

Spatially distinct groups of individuals large enough to be essentially self-reproducing and with different productivities may be referred to as separate stocks (Hilborn and Walters 2001). This is only one of many stock definitions suggested during the several decades-long debate over a universal meaning of the term 'stock' for use across many different disciplines (see reviews by Booke 1981; MacLean and Evans 1981; Begg and Waldman 1999; Waldman 2005). The definition of a stock was traditionally considered comparable to that of separate populations, i.e., reproductively separate units with limited or no exchange of individuals (MacLean and Evans 1981). Recently, there has been a call for a less stringent definition of a stock, however, as the importance of accounting for groups of individuals with persistent phenotypic differences is increasingly emphasised, irrespective of whether those differences are genetically or environmentally caused (Jerry and Cairns 1998; Begg et al. 1999b; Cadrin and Friedland 1999; Swain and Foote 1999). There has also been the development of new techniques to better differentiate between such groups. A stock is now often defined to be of primary relevance to the management objective for a fishery, rather than primarily or exclusively a biological consideration (Begg and Waldman 1999; Waldman 2005). If the management objective is to protect genetic biodiversity, for example, information on the genetic structure of stocks is important. Such information may be less informative, however, if the primary motive is to optimise harvest and prevent over-fishing or localised depletion of less productive components of the population (Thresher 1999). In this case,

spatially separate groups (or subpopulations) of individuals with different life history characteristics should be identified, because such disparate groups may respond differently to fishing mortality and have different vulnerabilities to over-harvest (e.g., Ricker 1958; Adams 1980; Myers et al. 1997; Jennings et al. 1998; Denney et al. 2002). A central aim of this thesis was to identify spatial units relevant to the time-scale of fisheries management of a typically exploited coral reef fish. For this purpose I adopted a broad definition of a stock, as spatially separate groups of individuals with persistent (time-invariant) differences in biological characteristics that are likely to respond relatively uniformly to harvest (sensu Begg and Waldman 1999).

As defined in this thesis, a stock can be equal to a species, population, group or groups of individuals, termed subpopulation(s), which are spatially separate for at least part of their life cycle (Fig. 1.1). A stock in this sense may or may not be genetically distinct, but its life history characteristics are persistently different to those of other stocks. As mentioned above, populations are reproductively isolated, but not genetically distinct to the degree of separate species. In species that have few populations, or have only one population, the term species and population could be used interchangeably. As discussed in Section 1.5, a subpopulation is defined in this thesis as an isolated group of adults that do not mix to reproduce but may exchange larvae. Further, consistent with recent definitions of some marine fishes which are comprised of many spatially separate subpopulations connected by larval dispersal, a population can be termed a metapopulation (Man et al. 1995; Bailey et al. 1999; Young 1999; Smedbol and Wroblewski 2002).

Species
Population
(Metapopulation)

Potential
Stocks
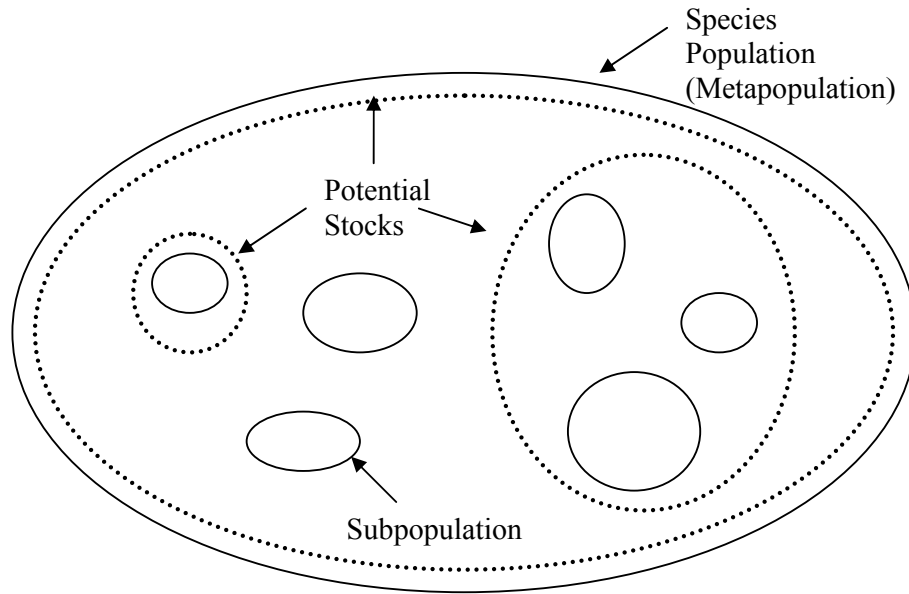
Subpopulation

Figure 1.1 Schematic illustrating the terms used to discuss population structure in this thesis.

1.2. Importance of stock structure

The importance of taking stock structure into account in managing fisheries has been realised for decades, at least for stocks with limited larval exchange. Theoretical work suggests that species that mature later, grow slower and attain larger maximum sizes will decline more rapidly from a constant fishing mortality rate than species that are smaller, grow faster and mature earlier (Adams 1980; Beddington and Cooke 1983; Trippel 1995). The yield per recruit of a late maturing and slow growing species will consequently reach its maximum at lower levels of fishing pressure and at a later age of first capture than a faster growing, early maturing and shorter lived species (Adams 1980). Whilst the effects of fishing mortality on species with different life history strategies have mostly been compared among different taxa (Adams 1980; Brander 1981; Trippel 1995; Jennings and Kaiser 1998; Jennings et al. 1999; Fomentin and Fonteneau 2001), a number of correlative studies between life

history characteristics and declines due to fishing suggest that more subtle variations in biology between intra-specific stocks may have similar effects (Reynolds et al. 2005). Information is needed on the magnitude of differences required between stocks to warrant separate management, in particular for populations with complex spatial structures in which stocks are connected by larval dispersal. Such information, in combination with the identification of life history parameters that may be more sensitive indicators than others of resilience to fishing (e.g., Myers et al. 1997; Jennings et al. 1998; Denney et al. 2002), would considerably aid in the development of appropriate management strategies for exploitation of such species.

Despite the potential implications of stock structure, the common failure to match the spatial scale of management with the spatial scale of biological units is a worldwide problem (Smedbol and Stephenson 2001; Stephenson 2002). Data are frequently aggregated across stocks with different biology in assessments and harvest strategy development, with the potential consequence of losing less productive stocks, or more adversely affecting the sustainability of the entire population (Ricker 1958; Daan 1991; Frank and Brickman 2000; Smedbol and Stephenson 2001). Aggregating data across stocks may also lead to an underestimation of the maximum yield of the population since the yield derived from aggregated data can be less than the sum of yields derived for individual stocks with different harvest potentials (Paulik et al. 1967). Much of the information on implications of aggregating data across stocks assumes the stocks are reproductively isolated. Explicit information is now needed on the implications of aggregating data across biologically different spatial components for species with subpopulations connected by larval dispersal (Fig. 1.1).

1.3. Stock identification techniques

The identification of spatially (and temporally) separate stocks of a population that are homogenous or mixed with respect to some aspects of their life history, and the level of connectivity between them, has been a challenging task for fisheries scientists (Begg et al. 1999b). Differences in life history parameters (i.e., demographic rates and ontogenetic stages), elemental signatures of calcified structures, morphometric and meristic characters, mark-recaptures, parasite composition and genetics have all successfully been used to identify stocks in temperate marine fish (see reviews by Ihssen et al. 1981; Pawson and Jennings 1996; Begg et al. 1999b; Cadrin et al. 2005). Very few have been tested on sub/tropical species (Begg et al. 1998; Patterson et al. 1999; Patterson et al. 2004b). While the choice of stock identification technique may vary depending on the type of data available or due to sampling logistics, it should, in conformity with the definition of a stock, be made with consideration of the management objectives for the species being considered (Begg and Waldman 1999). Different methods will be appropriate if the management goal is to protect genetic diversity than those appropriate if sustainable harvest strategies are sought.

Begg and Waldman (1999) encourage the use of a "holistic approach" to stock identification, in which several techniques are applied to get the best possible picture of the spatial structure of a species. Using a range of techniques simultaneously would not only increase the chance of detecting different stocks, but also increase the confidence in any structure inferred when results match across techniques (Begg and Waldman 1999; Waldman 2005). A holistic approach to stock identification may be especially relevant to species with complex spatial structures since different techniques may be sensitive to different aspects or causes of structure

in populations (Begg and Waldman 1999). Few studies have used multiple techniques to identify stock structures but these emphasise the different resolution (in terms of spatial scale) of patterns gained from genetic versus environmental markers (Casselman et al. 1981; Begg 1998).

1.4. Theory and simulation modelling

Development of theories for conceptualizing stock identification and structure of marine fishes with complex population structures should be encouraged (Stephenson 1999; Smedbol and Wroblewski 2002). The metapopulation concept, in particular, originally developed to study the spatial structure of terrestrial populations (Levins 1969 in Hanski and Gilpin 1997; Pulliam 1988; Hanski and Gilpin 1997) has been very useful in improving our understanding of marine fish population dynamics (e.g., Man et al. 1995; Bailey et al. 1999; Young 1999; Smedbol and Wroblewski 2002). Only recently however, has this theoretical concept been incorporated into simulation models to examine the implications of spatial variability in biology for population dynamics (Crowder et al. 2000; Kritzer and Davies 2005). Crowder et al. (2000) emphasized the importance of identifying source and sink dynamics (sensu Pulliam 1988), with reference to spatial variability in population growth and for the design and placement of marine protected areas (Crowder et al. 2000). Kritzer and Davies (2005) used an age-structured stochastic simulation model to compare the overall dynamics of a reef fish population with no spatial variation in demography to one in which the individuals in one subpopulation attained a larger asymptotic size (L_∞) than others. The incorporation of a subpopulation with larger L_∞ did not create significant differences in the dynamics of population size over time, but some differences appeared among the subpopulations when subjected to large cyclical

changes in recruitment. Simulation studies like these are needed to evaluate the importance of spatial variability in individual life history parameters to the dynamics of populations with complex spatial structures. Moreover, simulation models are being increasingly developed to answer 'what if' questions as part of risk assessments and management strategy evaluations (Haddon 2001). They provide a powerful tool to examine the implications of spatial structure to populations with the added effect of harvest and other potential management regimes. Thus, simulations are used on the one hand, for example in stock assessments, to prescribe specific harvest limits or regulations for a fishery under a limited set of management options, and on the other, to explore general considerations that impact on the interplay between generalised stock dynamics and harvest (as in this thesis).

1.5. Population structure of coral reef fishes

Recent studies suggest that spatial variability in life history characteristics is a common feature of many coral reef fish species (e.g., Aldenhoven 1986; Craig et al. 1997; Adams et al. 2000; Gust et al. 2002; Kritzer 2002; Williams et al. 2003; Mapstone et al. 2004) but there have been few attempts to extend that knowledge to stock identification. Fewer resources have been allocated to research and appropriate management of tropical reef fisheries than to temperate marine resources, probably because of their comparatively low economic value (Russ 1991). Further, tropical reef fisheries are in many developing countries characterised by multi-species and multi-gear artisanal operations, with effort spread unequally across large reef areas, making the collection of even basic catch, effort or biological data difficult (Russ 1991; Sale 2002).

The population structures of many tropical reef fishes are rather different from their temperate counterparts and have the potential to exhibit considerable complexity. Tropical populations often cover large geographical ranges but are associated with archipelagos of reefs representing many distinct patches of habitat. After the pelagic larval stage and settlement on to the reef there is often little movement of adults among patches. Together, these many small, relatively isolated, adult subpopulations may form a meta-population, with interaction among subpopulations primarily by means of larval dispersal (Sale 1998). Archipelagos of coral reefs also often show considerable physical and biological variation among reefs and regions related to latitudinal or other gradients (e.g., across continental shelves) (Wolanski and Pickard 1983; Williams 1991). Subpopulations associated with such reefs have the potential to show corresponding variation in environmentally responsive life history characteristics at a range of spatial scales. Studies so far report variation in life history characteristics over spatial scales from 100s to 1000s of km (Craig et al. 1997; Meekan et al. 2001), to smaller spatial scales among and within reefs (100s m to 10s km, e.g., Aldenhoven 1986; Pitcher 1992; Gust et al. 2002; Kritzer 2002). Few studies, however, have considered commercially harvested species or investigated variation in life history traits at several spatial and temporal scales simultaneously (but see Adams et al. 2000; Meekan et al. 2001; Williams et al. 2003; Mapstone et al. 2004). Recent reports on both fine and broad scale spatial structure, together with the increasing number of coral reef fisheries considered over-exploited (Munro 1996; Sale 2002) demand increased attention to stock identification research and management strategy development for these species.

1.6. Common Coral Trout, *Plectropomus leopardus*

The Great Barrier Reef (GBR) is one of the largest World Heritage Areas spanning 14.8° latitude and incorporating over 3000 coral reefs and shoals. The GBR is subjected to a commercial and recreational Reef Line Fishery (RLF[1]) worth approximately $80 million[2]. Although more than 120 fish species are caught in the RLF, common coral trout, *Plectropomus leopardus*, (subfamily Epinephelinae, family Serranidae; tropical cods and groupers) is the most important species harvested (Mapstone et al. 1996a; Williams 2002). The catch of *P. leopardus* comprises about 30% (1350 t) of the current reef fish Total Allowable Commercial Catch (TACC[3]) and previously accounted for up to 50% of the annual catch (Mapstone et al. 1996).

The multidisciplinary review of previous work of *P. leopardus* that follows here is an essential prerequisite for any stock identification research.The distribution of *P. leopardus* covers the entire GBR and beyond (to southern Japan and Fiji), but individuals are most commonly found on mid- and outer-shelf GBR reefs (Ayling et al. 2000). *P. leopardus* spend their first 25-30 days as pelagic larvae before settlement to benthic reef habitat (Doherty et al. 1994). Tagging studies have shown that there is negligible movement of post-settlement and adult *P. leopardus* among reefs, although post-settlement movements occur within reefs (Davies 1995; Zeller 1998; Zeller and Russ 1998). Unlike many other ephinephelids, which grow slowly and live for a long time (up to 50 years), common coral trout are fast growing and have a relatively short life span (less than 20 years; Ferreira and Russ 1994;

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[1] Information on the Queensland Reef Line Fishery is available at
http://www.reef.crc.org.au/research/fishing_fisheries/statusfisheries/statusline.htm and
http://www.dpi.qld.gov.au
[2] Data extracted from http://chrisweb.dpi.qld.gov.au, January 2006, with permission from Department of Primary Industries and Fisheries.
[3] The Fisheries (Coral Reef Fin Fish) Management Plan 2003 is available at
http://www.legislation.qld.gov.au/LEGISLTN/CURRENT/F/FisherCRFFMP03.pdf

Mapstone et al. 2004). Whilst little is known about its reproductive behaviour, research suggests many, relatively small spawning aggregations form on most individual reefs during late spring to early summer (Samoilys 1997; Zeller 1998) to which individuals show a high degree of fidelity (Zeller 1998).

Although the stock structure of common coral trout on the GBR has not been determined, several studies suggest the potential presence of different stocks. Regional (100s km) or inter-reef (1-10 km) variation has been demonstrated in some life history characteristics of *P. leopardus* on the GBR (Begg et al. 2005), such as abundance (Ayling et al. 2000; Mapstone et al. 2004), reproductive characteristics (Adams 2002), size and age (Russ et al. 1996; Lou et al. 2005) and mortality (Russ et al. 1998; Mapstone et al. 2004). Commercial logbook data on catches of *P. leopardus* have also shown distinct regional variation in catch per unit effort (CPUE) (Mapstone et al. 1996a; Samoilys et al. 2002), further emphasising the possibility of variable productivities between regions and, thus, the presence of several stocks. Current management arrangements, including the TACC, fish size and gear restrictions, recreational bag limits and spatial and temporal closures, however, do not consider localized or regional spatial structure in life history characteristics of *P. leopardus* or any other exploited species on the GBR, with uniform harvest regulations and equal fishery access applying over the entire area.

1.7. Thesis objectives

In light of these issues my thesis has four specific objectives:

1)   To investigate the use of otolith chemistry as an indirect indicator of stock structure of three exploited tropical reef fish, *Plectropomus leopardus*, *Ephinephelus fasciatus, Cephalopholis cyanostigma* (Chapter 2);

2)   To investigate the use of otolith morphology as an indirect indicator of stock

structure of *P. leopardus* (Chapter 3);

3)   To investigate the spatial and temporal patterns in life history parameters of

P. leopardus as direct manifestations of stock structure (Chapter 4);

4)   To investigate the implications of spatial variability in life history parameters

of *P. leopardus* for harvest strategy evaluation (Chapter 5).

The thesis comprises four papers, each addressing one of the above objectives. The papers are conceptually connected however, with the collective aim to improve understanding of the stock structure of an exploited coral reef fish, *P. leopardus*. Otolith chemistry (Chapter 2) and morphology analyses (Chapter 3) were done on otoliths from different *P. leopardus* samples but all specimens used for these techniques were sub-sampled from the same local populations. Whilst *P. leopardus* was the main species under investigation in this thesis, otolith chemistry was also investigated for *E. fasciatus* and *C. cyanostimga* for comparative purposes to explore the general applicability of this technique for serranid coral reef fishes. The *P. leopardus* samples from both chapters were included in the life history analyses (Chapter 4). In Chapter 5 a simulation model was used to investigate quantitatively the potential consequences of interpreting stock information at scales that do not match the underlying structure of a hypothetical harvested population. Although life history information of *P. leopardus* was used from Chapter 4 to parameterise the model, as a real example and for consistency with the rest of the thesis, the intention of the simulations was to answer some general questions rather than to emulate the specific details of *P. leopardus*. In Chapter 6 I bring together the different perspectives of stock structure reported in the preceding chapters and discuss the

main results in the broader context of managing tropical reef fisheries and identify

important areas for future research.

Chapter 2. The use of otolith chemistry to determine stock structure of three epinepheline serranids

2.1. Introduction

The analysis of otolith chemistry is a relatively recently developed technique that has been used successfully to identify stocks in several temperate fishes (e.g., Edmonds et al. 1989; Campana et al. 1995; Proctor et al. 1995; Thorrold et al. 1998) but has been tested on few tropical or sub/tropical marine species (Begg et al. 1998; Patterson et al. 1999; Patterson et al. 2004b). The use of otolith chemistry as a stock identification technique relies on the fact that the otolith, which is mainly composed of calcium carbonate, grows continuously throughout life and is metabolically inert (Campana and Neilson 1985). It also assumes that calcium and other elements in the otolith are derived from the ambient water or due, directly or indirectly, to exogenous physical processes and that these constituents are not susceptible to dissolution or resorption once incorporated into the otolith microstructure. If these facts hold, the aggregate chemical composition of whole otoliths, which integrates the chemical signal over the entire life of the fish, can be a suitable measure for investigating life-time differences between groups of individuals or stocks for management purposes (Campana 1999; Campana et al. 2000). Differences in otolith chemistry between putative stocks may not infer genetic differences, because of links among local populations during spawning or through larval dispersal, but may indicate that different stocks have spent significant periods of their lives in different environments (Campana 1999), and thus give a potential indirect indication of stocks with different life history characteristics.

In this Chapter otolith chemistry was used to investigate the stock structure of three tropical epinephaline serranid species, *Plectropomus leopardus* (common coral trout), *Cephalopholis cyanostigma* (blue-spot rock cod) and *Epinephelus fasciatus* (footballer cod) on the GBR. All three species are commercially and recreationally harvested (Mapstone et al. 1996a; Mapstone et al. 1997; Williams 2002). About 112 t of unspecified cods were landed in 2000 (Williams 2002) and it has been estimated that epinephaline serranids (other than *Plectropomus* spp) comprise around 5% and 10% of the recreational and commercial catches respectively[4]. Whilst *P. leopardus* was the primary species under investigation in this thesis, the otolith chemistry of *E. fasciatus* and *C. cyanostimga* were investigated for comparative purposes to suggest the general applicability of this technique for serranid coral reef fishes. Little is known about the spatial and temporal variation in life history characteristics of *Epinephelus fasciatus* and *Cephalopholis cyanostigma* (but see Moss (2002) for some regional variation of mean size among regions for *C. cyanostigma*). Currently, however, these and all other exploited species on the GBR are managed as single homogenous stocks by spatially uniform regulations applied over the entire GBR (see Chapter 1).

There were two main objectives in this Chapter. First, region-scale structure in stocks of the three species was investigated by comparing aspects of otolith chemistry among four regions of the GBR, broadly separated by 100s km (north to south). Otolith chemical signals of *P. leopardus* were also examined at a finer spatial scale, among neighbouring reefs separated by 100s to 1000s m within each of the four regions. Second, as temporal variation in chemical signals could confound spatially persistent information about stock structure if not accounted for, the

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[4] Green, B.S and Bergenius, M.A.J. 2001. Unpubl. Data, and Mapstone, B.D. 2001. Unpubl. Data. (CRC Reef Research Center, James Cook University, Townsville, Queensland 4811, Australia)

temporal stability in otolith chemistry was examined for all three species. This was achieved by comparing signals from two cohorts of *P. leopardus* with non-overlapping lifetimes either side of a significant weather disturbance (Cyclone Justine in March 1997). Whilst there are on average six tropical cyclones crossing the Australian coast every season[5], Cyclone Justin was an unusually large and persistent cyclone remaining in the Coral Sea adjacent to the GBR for over three weeks in March 1997. Spatially variable effects of the Cyclone, such as an unusually large drop in temperature and salinity across a large area of the GBR, provided a unique opportunity to test the temporal stability of elemental signals in otoliths during a significant environmental perturbation. Temporal stability in the otolith chemistry of *C. cyanostigma* and *E. fasciatus* was examined by comparing samples of each species that were subjected to Cyclone Justin with those that did not experience the event, though for these two species the compared cohorts did have overlapping lifetimes prior to 1997.

2.2. Methods

2.2.1. Background and sample collection

The epinepheline serranids used in this thesis were collected using the same sample design and during the same fieldwork as part of the Cooperative Research Centre for the Great Barrier Reef World Heritage Area Effects of Line Fishing (ELF) Experiment. The ELF Experiment, which started in 1995 and concluded in 2006, included a group of 6 reefs in each of 4 regions extending over 7˚ of latitude along the GBR (Fig. 2.1 Mapstone et al. 1996a; Davies et al. 1998; Mapstone et al. 1998; Mapstone et al. 2004). Of the six reefs in each region, four had been closed to fishing under GBR Marine Park Zoning Plans (zoned Marine National Park B, MNP-B) for

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[5] http://www.bom.gov.au/climate/environ/cyclones.shtml

10 to 12 years at the start of the Experiment and two reefs had been open to fishing (zoned as General Use, GU). Two of the reefs closed to fishing remained closed during the experiment, other than to the annual research line fishing surveys. The other two closed reefs were each subjected to one year of fishing, in 1997 and 1999, after which they were closed again. The two reefs in each region which had historically been open to fishing were subjected to increased fishing pressure for one year similar to the closed reefs. These reefs were then closed for five years before reverting to their original zoning status (GU).

All reefs were sampled each year in the austral spring (October-December) to coincide with the peak spawning period of *P. leopardus*. Each reef was divided into six approximately equal sized, contiguous blocks, and sampled on a single day on each sampling occasion. Standardised commercial reef line fishing effort was distributed uniformly across two depth strata within each block. All fish caught were measured, tagged for later identification, and kept for weighing and extraction of gonads and otoliths. See Davies et al. (1998) and Mapstone et al. (2004) for further sampling details of the ELF Experiment. Samples of *P. leopardus* were aged by CRC Reef staff using standardised methods developed by Ferreria and Russ (1994).
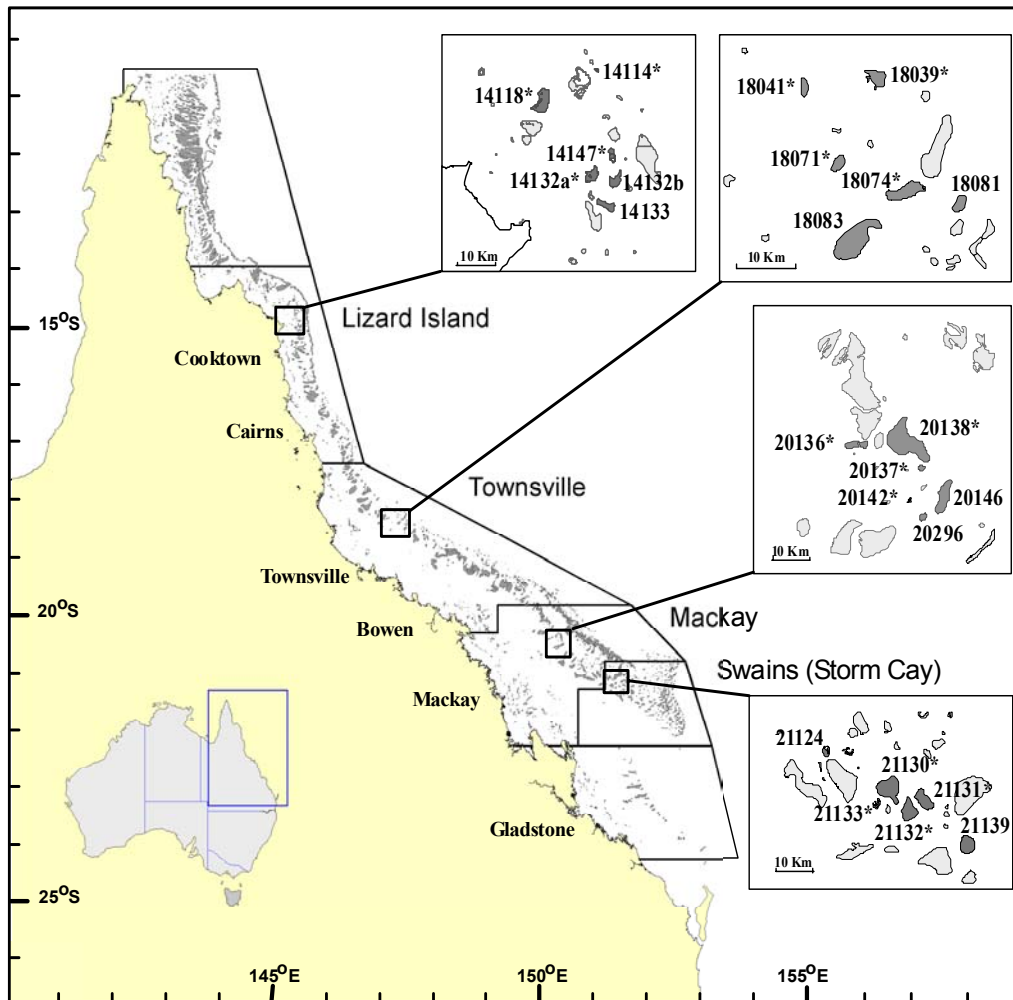
Figure 2.1 Great Barrier Reef (GBR), Australia. Study regions and reefs from which *P. leopardus*, *C. cyanostigma* and *E. fasciatus* were sampled as a part of the ELF experiment. Study regions indicated as Lizard Island, Townsville, Mackay and Swains (Storm Cay is the name of the reef cluster sampled in the Swains Region). * = reefs closed to fishing at the start of the ELF experiment. The lines surrounding the entire reef area represent the borders of the GBR World Heritage Area.

2.2.2. *Plectropomus leopardus*

Otolith chemistry was analysed for samples from 4-year old *P. leopardus* otoliths collected from three reefs within each of the four regions (Fig 2.1; Table 2.1) in each of two sampling years, 1995 and 1999. Four years is the youngest age at which *P. leopardus* in all regions are fully recruited to the fishing gear used in the ELF

Experiment. Although the zoning status of a reef, and the level of fishing pressure on it, were unlikely to have affected otolith chemistry, one reef from each treatment regime in the ELF Experiment was included from each region to avoid such potential biases. Thus, within each region, samples were analysed from one MNP-B reef that was closed to fishing, one MNP-B reef that was open for one year of fishing and then closed, and one GU reef that was subjected to increased fishing for a year prior to closure for five years.

Because otoliths from only 4-year old fish were analysed in 1995 and 1999, the two cohorts included individuals with non-overlapping lifetimes. Consequently, individuals collected in 1995 were not subject to the influence of an unusually large and persistent cyclone (Cyclone Justin) that influenced the southern half of the GBR throughout March in 1997, unlike those 4-year old fish collected in 1999. Standardising sampling by age also minimised the potential for confounding spatial differences in otolith chemistry with ontogenetic effects of element incorporation (e.g., Papadopoulou et al. 1978; Begg et al. 1998; Campana et al. 1999).

Table 2.1. Regions and reefs from which 4-year old *P. leopardus* otoliths were sampled and analysed for otolith elemental signatures. Length range indicates the FL (mm) of *P. leopardus* sampled from each reef.

Region name	Reef name (GBRMPA number)	Length Range (mm)
Lizard Island	Rocky Islet reef A (14032a)	340 - 450
	Rocky Islet reef B (14032b)	340 – 450
	South Direction reef (14147)	351 – 468
Townsville	Knife reef (18081)	345 – 480
	Dip reef (18039)	320 – 462
	Yankee reef (18074)	342 – 450
Mackay	(20142)	346 – 450
	Liff Reef (20296)	341 – 432
	Robertson Reefs (no2) (20136)	341 – 450
Storm Cay	Junk reef (21131)	341 – 442
	Lorries reef (21130)	357 – 450
	Sullivan reef (21124)	340 - 448
	TOTAL	340 - 480

A relationship between elemental incorporation and otolith growth rate (assumed to be correlated to fish length) also can confound spatial or temporal differences in otolith chemistry if there are spatial or temporal patterns in growth (Fowler et al. 1995a; Begg et al. 1998; Campana et al. 2000). The potential for such effects therefore, were minimised by: (1) only including fish with fork length (FL) between 320 and 480 mm (Table 2.1; overall FL for all 4-year olds ranged from 250 to 551 mm); and (2) standardising element concentration by fish FL prior to analyses where a significant relationship existed between element concentration and FL.

A total of 20 *P. leopardus* was sampled from each reef in each year, except from Dip Reef in 1995, when only 14 individuals aged four were collected. This sampling design enabled examination of broad (region) and fine (reef) spatial and temporal (2 cohorts, 1995 and 1999) consistency of otolith elemental signals of *P. leopardus* across much of the GBR, spanning an unusual environmental event

(Cyclone Justin, 1997) that had the potential to significantly influence otolith chemistry.

2.2.3. *Cephalopholis cyanostigma*

A total of 104 *C. cyanostigma* otoliths were analysed from the 1981 year class collected annually from 1995 to 1998 from the three reefs in each region, as described above (Fig. 2.1). There were generally too few otoliths from each reef to allow comparisons among reefs, so *C. cyanostigma* samples were compared across only one broad spatial scale (among regions). Further, because there were too few samples to compare elemental signatures among years, otoliths collected in the years before (1995, 1996) and after (1997, 1998) Cyclone Justin were combined and compared patterns in otolith chemistry over one temporal scale: 'Before' and 'After' the cyclone (Table 2.2). As for *P. leopardus*, if a significant relationship was detected between otolith element concentration and fish fork length (FL), elemental concentration was standardised by this relationship prior to analysis.

Table 2.2. *C. cyanostigma* otoliths analysed for elemental signatures. Numbers indicate individuals included per region and before and after Cyclone Justin in 1997. Length range indicates the FL (mm) of *C. cyanostigma* sampled from each region.

Region	Before Cyclone Justin	After Cyclone Justin	Total	Length Range (mm)
Lizard	13	17	30	210 – 326
Townsville	21	14	35	215 – 271
Mackay	4	14	18	225 – 276
Storm Cay	4	17	21	225 – 288
Total	42	62	104	210 - 288

2.2.4. *Epinephelus fasciatus*

A total of 62 *E. fasciatus* from the 1990 year class collected annually from the four regions over four years (1995 to 1998) was analysed. As with *C. cyanostigma*, there were insufficient samples from each reef to allow comparisons among reefs. Further, limited sample numbers for each year also precluded comparisons among years for this species, meaning that samples were compared only among regions and periods before (1995 + 1996) and after (1997 + 1998) Cyclone Justin (Table 2.3). Again, elemental concentration was standardised by FL where necessary, prior to analysis.

Table 2.3. *E. fasciatus* otoliths analysed for elemental signatures. Numbers indicate individuals included per region before and after Cyclone Justin in 1997. Length range indicates the FL (mm) of *E. fasciatus* sampled from each region.

Region	Before Cyclone Justin	After Cyclone Justin	Total	Length Range (mm)
Lizard	1	10	11	221 – 277
Townsville	6	10	16	236 – 272
Mackay	5	15	20	245 – 311
Storm Cay	7	8	15	221 - 311
TOTAL	19	43	62	221 - 311

2.2.5. Otolith and sample preparation

Sagittal otoliths had been stored in dry paper envelopes from when the fish were captured. Otoliths were carefully cleaned under a dissecting microscope to remove material attached to their surfaces and weighed with an analytical balance (0.0001 g). Otoliths were then prepared for elemental analysis using a modification of the standard procedures explained in Fowler et al. (1995a) and Campana et al. (2000). Firstly, otoliths were placed in acid washed vials and soaked overnight in Milli-Q water, rinsed in Milli-Q water, scrubbed thoroughly (> 2 mins) with an electric toothbrush and rinsed again. Secondly, the otoliths were sonacated for 5 min using an

ultrasonic bath, triple rinsed in Milli-Q water and left in a laminar flow cabinet to dry

for 24 hours. All plastic and glassware were washed in Milli-Q water, soaked in 10%

HNO_3 for over 24 hours and then rinsed again in Milli-Q water prior to use. Thirdly,

otoliths were dissolved in 1 ml ultrapure HNO_3 before dilution with Milli-Q water to

a total of 5 ml. The sample solution was then further diluted with 1% HNO_3 to a ratio

of 1:10 for trace elements and 1:1000 for Sr and Ca (sample: Milli-Q with 1%

HNO_3). Blank samples were prepared similarly, but without the otolith and were

used to correct for background 'noise' in readings and calculate detection limits for

elements.

All samples and blanks contained the internal standards Ga and In at 100

ppb/l. The internal standards were used to correct for the remaining matrix effect not

corrected for by the standard calibration and instrumental drift. All standards, blanks

and samples were prepared in a laminar flow hood to minimise the possibility of

contamination.

2.2.6. ICP-MS analysis

Samples were analysed by solution-based inductively coupled plasma mass

spectrometry (ICP-MS; Ultra Mass700, Varian Instrument Ltd, Melbourne,

Australia) at the Advanced Analytical Centre (AAC), James Cook University. The

ICP-MS was calibrated at the start of each sample processing session or when

showing signs of significant instrumental drift and/or matrix effects (>30%

suppression of the In and Ga signals). Sample blanks were analysed at the beginning

of each ICP-MS processing session, as well as after every 30 otolith samples.

External calibration was used for the quantification of Ca and Sr by using a blank

and two standard solutions with the appropriate known concentrations for Ca and Sr.

The matrix for the blank and standard solution was 1% HNO_3. Standard addition calibration was used for quantification of the other trace elements by analysing a sample followed by two spiked samples (elements of known quantity, here 5 and 50 ppb, spiked into blank samples). After each calibration, spiked samples were also analysed to verify elemental recovery rates.

To avoid confounding spatial or temporal patterns in otolith chemistry with potential instrumental drift, samples of *P. leopardus* were analysed in blocks, with at least one block of samples processed in each session. Each block of random samples contained otoliths from each region and reef. Samples of *C. cyanostigma* and *E. fasciatus* were randomly scattered through these blocks.

An initial scan of four otoliths from each of the three species for 16 elements (Al, As, Ba, Co, Cr, Cu, Fe, Ge, Mg, Mn, NI, Pb, Pd, Sc, V and Zn) indicated that four elements (Ca, Sr, Ba, Mn) were suitable for ICP-MS analysis. The other elements were frequently below detection limits, showed poor reading precision or were likely to be confounded by interferences with other elements. The major isotopes of Strontium (Sr^{88}) and Manganese (Mn^{55}) were analysed, but for Calcium (Ca^{40}) and Barium (Ba^{55}) minor isotopes were examined due to the potential interferences of the major isotope with other elements or due to their instability relative to minor isotopes (Yi Hu pers. comm., AAC).

Detection limits were calculated as three times the standard deviation of the mean blank signal (n=3 readings per blank) averaged over 51 blanks for trace elements and 21 blanks for Ca and Sr. Mean limits of detection were 0.013 µg/g for Ba, 0.064 µg/g for Mn, 17.013 µg/g for Ca and 0.036 µg/g for Sr. Mean estimates of coefficient of variation (percent relative standard deviation, %RSD = SD/mean x 100, n = 3) for otolith samples were 2.800 for Ba, 5.274 for Mn, 51.134 for Ca and

2.476 for Sr. Mean percent recoveries of spiked samples were 106% for Ba (n = 8), 96% for Mn (n = 8) and 94% for Sr (n = 6). Before converting the ICP-MS data to microgram per gram of otolith, readings were corrected for solution concentration and "background noise" (as measured by the blanks). Blank corrections were performed by: (1) fitting a time-dependent function to the blanks analysed during a session and subtracting the blank value predicted from the function for a particular point in time from samples analysed at that time; or (2) when the slope of the function was close to zero, a mean blank value was calculated and subtracted from all the samples of that session. Blank concentrations with extreme values (seven out of 68 blank values with >20 times the expected and other blank values) were excluded from the calculations.

2.2.7. Statistical methods

All element concentration data were inspected for univariate and multivariate outliers. Univariate outliers were determined by the inspection of standardized z scores (values ± 3 sd) and multivariate outliers were defined as cases with an extreme Mahalanobis distance from their groups (i.e., values larger than the critical chi-square at $\alpha = 0.01$ for d.f. = numbers of dependent variables; Tabachnick and Fidell 1983). Extreme values are most likely caused by contamination at the time of sample preparation and were therefore excluded from the analyses. The assumption of homogeneity of variance for each dependent variable was examined using Levene's test and homogeneity of the group covariance matrix by Box's M test (MANOVA, SPSS, 2000). Otolith concentrations of Sr in *P. leopardus* and Mn in *E. fasciatus* were log transformed and concentrations of Ba in *C. cyanostigma* otoliths were ln(x+1) transformed to improve normality and homogeneity of variances. If the

Sr and Mn concentrations were heterogeneous after transformation, the analyses were still performed using the raw data as analysis of covariance (ANCOVA) and multivariate analysis of variance (MANOVA) are relatively robust to departures from this assumption (Underwood 1997) though interpretation of results was more circumspect for such analyses.

Effects of fish FL on elemental concentrations were examined ANCOVA (GLM Procedure, SAS, 2003). Our primary interests in these analyses were: a) to test whether elemental concentration varied with FL for any group of samples; and b) if so, to test whether the slopes of regressions of concentration on FL were homogeneous among groups. If a significant regression was detected and homogeneous among groups, the effect of FL was removed from each elemental concentration using the relationship:

$$C_{ij,adj} = C_{ij} \pm b.(FL_{ij} - MFL._j) \qquad (2.1)$$

where:

C_{ij} = sample concentration for fish i from group j;

$C_{ij, adj}$ = sample concentration of fish i adjusted to mean fork length of group j;

$b.$ = slope of the relationship C_{ij}:FL_{ij} common to all groups;

FL_{ij} = fork length of fish i in group j ;

$MFL._i$ = average fork length within group j.

If significant slopes of the relationship differed among groups, the correction for FL was made separately for each group using the equation above but replacing the common slope ($b.$) with the group-specific slope (b_j). These corrections had the effect of scaling all elemental concentrations from all otoliths to their predicted group mean FL. The procedures were developed by the author of this thesis. It should be mentioned that FL was used for these corrections rather than otolith size,

as some otoliths were slightly broken and otolith size or weight could not be determined. There was a significant relationship between FL and otolith size of otoliths used in Chapter 3 ($r^2 = 0.53$, p < 0.0001, n = 351), however, justifying the use of FL.

The adjusted concentrations for all elements of interest were then analysed by MANOVA to test for spatial and temporal differences in the multi-variate elemental signatures. *A posteriori* univariate ANOVA was used to explore patterns for each of the elements separately when significant effects were indicated in the MANOVA. The univariate linear model for the analysis of each element from otoliths of *P. leopardus* was:

$$x_{ijkl} = \mu_{....} + C_{i...} + R_{.j..} + r(R)_{.k(j).} + CR_{ij..} + Cr(R)_{ik(j).} + e_{l(ikj)} \qquad (2.2)$$

where:

x_{ijkl} = the adjusted concentration for otolith *l* from Cohort *i* Region *j* and reef *k*;

$\mu_{....}$ = the estimate of the population mean concentration over all Cohorts, Regions, reefs and fish;

$C_{i...}$ = the fixed effect of Cohort *i* averaged over Regions and reefs;

$R_{.j..}$ = the fixed effect of Region *j* averaged over Cohorts and reefs;

$r(R)_{.k(j)}$ = the random variation attributable to reef *k* within Region *j* averaged over Cohorts; and

$e_{l(ikj)}$ = unexplained random variation associated with sample *l* within Cohort *i*, Region *j* and reef *k*.

The linear model for univariate analyses of *C. cyanostigma* and *E. fasciatus* otoliths was:

$$x_{ijl} = \mu_{....} + P_{i...} + R_{.j..} + PR_{ij..} + e_{l(ij)} \qquad\qquad (2.3)$$

where:

x_{ij} = the adjusted concentration for otolith *l* from Period *i* and Region *j* ;

$\mu_{....}$ = the estimate of the population mean concentration over all Periods, Regions and fish;

$P_{i...}$ = the fixed effect of Period (before or after cyclone Justin) *i* averaged over Regions;

$R_{.j..}$ = the fixed effect of Region *j* averaged over Periods;

$e_{l(ij)}$ = unexplained random variation associated with sample *l* within Period *i* and Region *j* .

Wilk's Lambda criterion was used to test for group differences in the MANOVAs and Pillai's trace was also inspected as it is more robust to deviation from homogeneity of variances (Tabachnick and Fidell 1983). Pillai's trace will not be referred to further, however, as it did not differ from Wilk's Lambda in any of the analyses. Sums of squares and degrees of freedom of interactions were pooled where the F-ratios of interaction effects were ≤ 1. Pooling increases the degrees of freedom for the denominator and consequently the power of the test of remaining (unpooled) effects. Tukey's honestly significant difference (HSD) test was used to determine which means differed following significant effects in the ANOVAs. Canonical discriminant analysis (CDA) was used to examine the elemental signatures in multivariate space and to investigate whether signatures could be used to classify samples to their Cohort, Period, Region, or reef of origin. Equal prior probabilites and jackknife classification (i.e., "leave-one-out") were used to minimize potential bias in the reclassification of individuals.

2.3. Results

2.3.1. *Plectropomus leopardus*

Concentrations of Mn were below detection limits in 22.2% of the *P. leopardus* samples. These low readings were retained for analysis and were found to be uniformly distributed among groups of samples ($X^2_{0.05,\ 23}$ = 17.71, p > 0.05) indicating that they did not signify spatial or temporal low-points in environmental Mn. The examination of standardised *z* scores and Mahalanobis distances identified a total of 11 outliers (2.4% of total sample number; ranges Ba 12.18 – 0.14 µg/g, log Sr 3.58 – 2.13 µg/g, Mn 2.41 – 0.08 µg/g) which were excluded from the analyses. There was a weak, but significant relationship between FL and Ba concentration ($F_{1.461}$ = 27.37, p < 0.0001, r^2 = 0.0561) and FL and Sr concentration ($F_{1.461}$ = 4.91, p = 0.0271, r^2 = 0.011). Readings of Ba and Sr were therefore standardised for the effect of FL.

MANOVA identified significant differences in elemental signatures in *P. leopardus* otoliths between the two cohorts (1995 and 1999), among regions and reefs nested within regions (Table 2.4). ANOVAs indicated that these differences were due to variation in Ba among reefs within regions (Fig 2.2; Table 2.5), in Mn among regions and between cohorts (Fig 2.3-2.4; Table 2.5) and differences in Sr among regions that were not consistent between cohorts (Fig 2.5). Though Ba concentrations varied widely among reefs in all regions, differences among reefs were statistically significant (HSD, p < 0.05) only in the Townsville Region (between reefs 18039 and 18081; Fig. 2.2) and Mackay Region (between reefs 20136 and 20296; Fig. 2.2). Concentrations of Mn were higher in otoliths from the 1995 cohort than those from the 1999 cohort over all regions (Fig 1.3; Table 1.5) and higher in Lizard and Townsville Regions than in the Mackay and Storm Cay Regions

for both cohorts (Fig 2.4; Table 2.5). Although the ANOVA indicated significant effects for Mn among regions, the HSD test was not sufficiently powerful to discriminate those effects unambiguously and we inferred the most likely differences from the plotted means (Fig. 2.4). Sr concentrations did not differ significantly among regions for the 1999 Cohort, but in the 1995 Cohort were significantly greater in the Lizard and Storm Cay Regions than in the Townsville and Mackay Regions (HSD, $p < 0.05$; Fig. 2.5). Further, Sr concentrations differed significantly between cohorts in the Townsville and Mackay Regions (HSD, $p < 0.05$), but not in the Lizard or Storm Cay Regions (Fig. 2.5).

Table 2.4. Results of MANOVA comparing otolith elemental signatures between two cohorts of 4-year-old *P. leopardus* collected from 3 reefs in each of four regions in 1995 and 1999. P-values in bold indicate significant differences ($p < 0.05$) of the highest-order terms that legitimately could be explored further.

Factor	Wilks' Lambda	F	Num Df	Den Df	p
Cohort	0.2424	6.25	3	6	**0.0282**
Region	0.0251	5.80	9	14.75	**0.0016**
Cohort*Region	0.1769	1.70	9	14.75	0.1759
Reef(Region)	0.9057	1.84	24	1268	**0.0083**
Cohort*Reef(Region)	0.9373	1.19	24	1268	0.2378
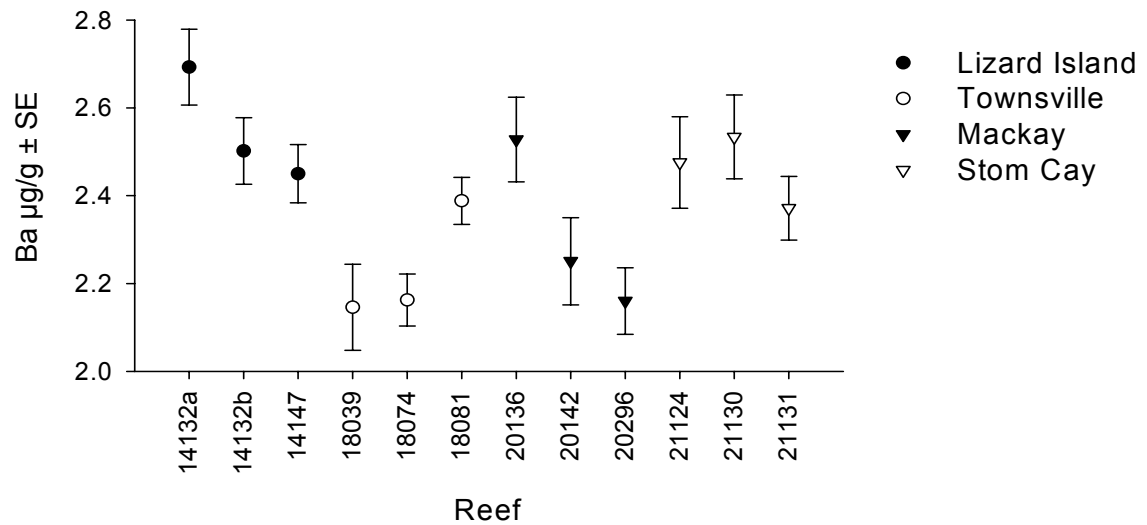
Figure 2.2 Ba µg/g concentrations (mean ± SE) in otoliths of 4-year-old *P. leopardus* collected from 3 reefs in each of four regions on the GBR. Data were pooled across cohorts.

Table 2.5. Results of ANOVAs comparing otolith elemental signatures in two cohorts of 4-year-old *P. leopardus* collected from 3 reefs in each of four regions in 1995 and 1999. Only final analyses resulting from pooling terms with $F \leq 1$ are shown. P-values in bold indicate significant differences ($p < 0.05$) of the highest-order terms that legitimately could be explored further.

Dependent variable	Factor	Df	MS	F	p
Ba	Cohort	1	0.0227	0.06	0.8189
	Region	3	2.4177	3.10	0.0892
	Cohort*Region	3	0.7917	1.95	0.1996
	Reef(Region)	8	0.7801	2.99	**0.0028**
	Cohort*Reef(Region)	8	0.4052	1.55	0.1367
Mn	Cohort	1	0.0690	10.71	**0.0011**
	Region	3	0.0212	3.29	**0.0205**
	Cohort*Region	3	0.0092	1.43	0.2337
	Cohort	1	0.0276	20.02	0.0021
Log Sr	Region	3	0.0094	4.36	0.0425
	Cohort*Region	3	0.0058	4.18	**0.0469**
	Reef(Region)	8	0.0021	1.80	0.0749
	Cohort*Reef(Region)	8	0.0014	1.16	0.3246
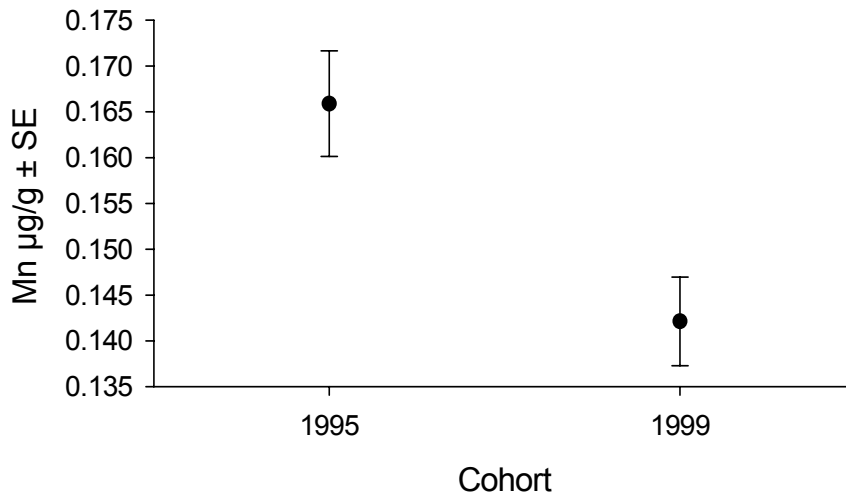
Figure 2.3 Mn µg/g concentrations (mean ± SE) in otoliths from two cohorts of 4-year-old *P. leopardus*, GBR. Data were pooled across reefs and regions.
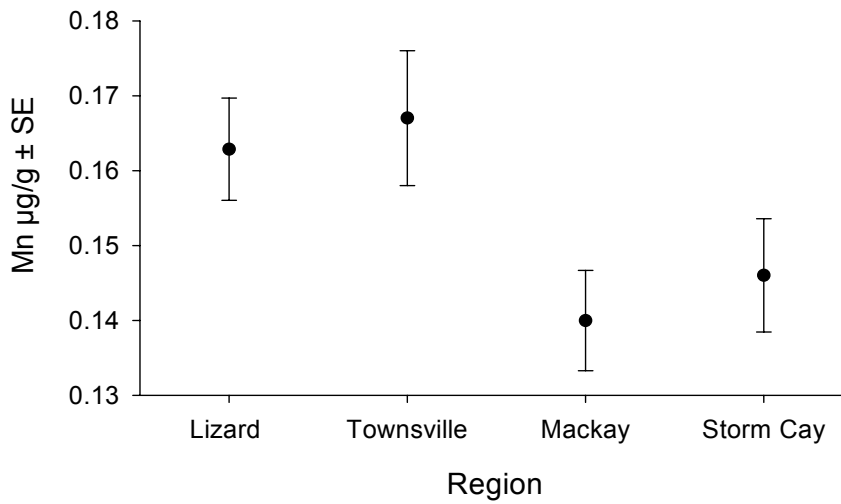
Figure 2.4 Mn µg/g concentrations (mean ± SE) in otoliths of 4-year-old *P. leopardus* collected in four regions on the GBR. Data were pooled across reefs and cohorts.
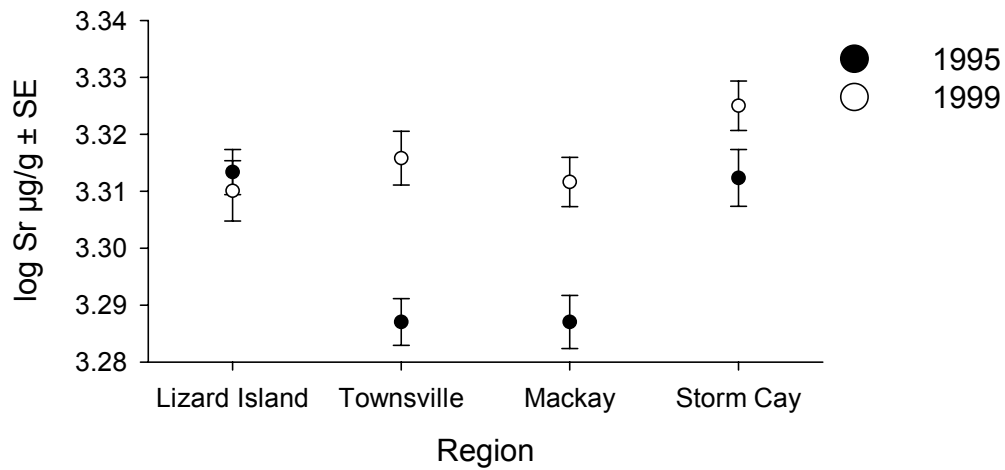
Figure 2.5 Sr µg/g concentrations (mean ± SE) in otoliths from two cohorts of 4-year-old *P. leopardus* collected in each of four regions in 1995 and 1999 on the GBR. Data were pooled across reefs.

Plots of canonical discriminant functions using Cohort, Region or Reef as the separating variable showed no clear separation in multivariate space. In addition, the discriminant analysis showed poor classification results, indicating that individual fish could not be classified with certainty to Cohort (58.3% cross-validated cases), Region (31.3% cross-validated cases) or Reef (11.4% cross-validated cases).

2.3.2. *Cephalopholis cyanostigma*

A total of four extreme sample readings was excluded from further analyses of *C. cyanostigma* data (4.0 % of total sample number; ranges ln (Ba +1) 1.98 – 1.7 µg/g, Sr 1057.93 – 2509.02 µg/g, Mn 0.03 – 0.69 µg/g). A small fraction (3%) of Mn concentrations were recorded below detection limits, but included in the analyses. Ba concentrations were ln(x + 1) transformed to improve normality and variance homogeneity. Slopes of the relationship between Ba concentration and FL differed among regions (homogeneity of slopes test, $F_{3,87} = 4.36$, p = 0.007) hence, the

within-group slope was calculated for each region separately and used to correct for the influence of FL on sample concentration. Sample concentrations of Mn were also corrected for the influence of FL as there was a significant overall relationship between Mn and FL ($F_{1,99} = 23.85$, $p < 0.000$, $r^2 = 0.196$) which was homogeneous among groups (homogeneity of slopes test, $p > 0.05$).

MANOVA detected a significant difference in otolith elemental signatures among regions (Table 2.6). The ANOVAs indicated that these differences were due to regionally variable concentrations of Ba and Mn (Fig. 2.6, 2.7; Table 2.7). HSD tests revealed significantly lower Ba concentrations in the Lizard and Townsville Regions than in the Storm Cay Region and lower concentrations in the Townsville Region than the Mackay Region ($p < 0.05$; Fig. 2.6). A significant difference was also found in Mn concentrations between the Townsville and Mackay Regions ($p < 0.05$; Fig 2.7). The ANOVA also showed a significantly higher concentration of Ba in individuals collected before than after the Cyclone in 1997 (Fig. 2.8; Table 2.7).

Table 2.6. Results of MANOVA comparing otolith elemental signatures in *C. cyanostigma* collected before (1995 – 1996) and after (1997 – 1998) Cyclone Justin (in March 1997) from each of four regions of the GBR. Only final analyses resulting from pooling terms with $F \leq 1$ are shown. P-values in bold indicate significant differences ($p < 0.05$).

Factor	Wilks' Lambda	F	Num Df	Den Df	p
Period	0.9378	2.06	3	93	0.1115
Region	0.7414	3.29	9	226.49	**0.0009**

Table 2.7. Results of ANOVAs of otolith elemental signatures in *C. cyanostigma* collected before (1995 – 1996) and after (1997 – 1998) the Cyclone Justin in 1997 from each of four regions of the GBR. Only final analyses resulting from pooling terms with $F \leq 1$ are shown. P-values in bold indicate significant differences ($p < 0.05$).

Dependent variable	Factor	df	MS	F	p
ln(Ba+1)	Period	1	0.1442	4.86	**0.0298**
	Region	3	0.1081	3.65	**0.0154**
Mn	Period	1	0.00001	0.18	0.6761
	Region	3	0.0187	3.28	**0.0241**
Sr	Period	1	64920.1828	1.86	0.1758
	Region	3	34450.5860	0.99	0.4022
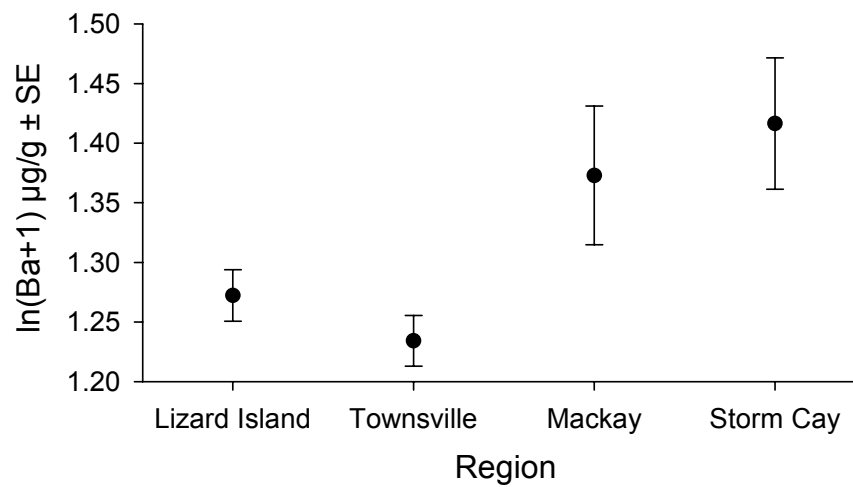
Figure 2.6 Ba µg/g concentrations (mean ± SE) in otoliths of *C. cyanostigma* collected in four regions on the GBR. Data were pooled across the periods before (1995 – 1996) and after (1997 – 1998) the cyclone.
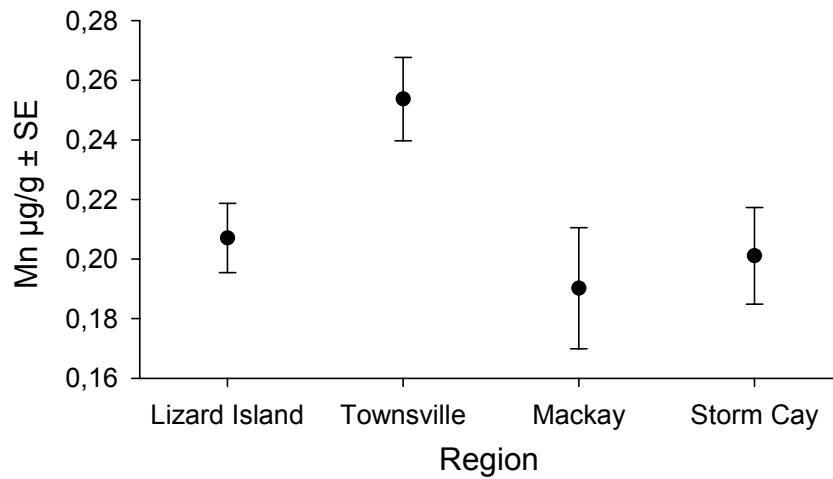
Figure 2.7 Mn µg/g concentrations in otoliths of *C. cyanostigma* collected in four regions on the GBR. Data were pooled across the periods before (1995 – 1996) and after (1997 – 1998) the cyclone.
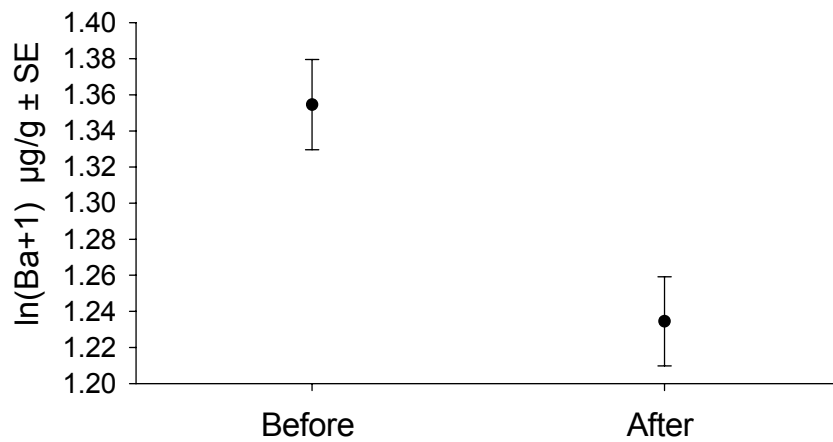
Figure 2.8 Ba µg/g concentrations (mean ± SE) in otoliths of *C. cyanostigma* collected before (1995 – 1996) and after (1997 – 1998) Cyclone Justin. Data were pooled across regions.

Similar to *P. leopardus*, plots of the canonical discriminant functions using Period or Region as separating variables revealed no clear separation of the *C.*

cyanostigma otolith elemental data. The discriminant analysis showed poor classification results indicating that individual fish could not be classified with certainty to Period (65.0% cross-validated cases) or Region (33.0% cross-validated cases).

2.3.3. *Epinephelus fasciatus*

Only two extreme data points were identified and excluded from the analyses of *E. fasciatus* data (3.3% of total sample number; Ba 0.88 and 2.36 µg/g, Sr 977.99 and 2719.04 µg/g, log Mn -1.37 and -0.30 µg/g). There was a significant, but weak relationship between FL and Ba µg/g (ANCOVA, $r^2 = 0.094$, p = 0.017), and FL and Mn µg/g (ANCOVA, $r^2 = 0.095$, p = 0.017), but slopes were homogeneous among groups (p > 0.05). The common slopes of each of these relationships were used to correct for the influence of FL on Ba and Mn concentration.

No significant differences in otolith elemental signatures were found among regions or groups of individuals collected before or after the Cyclone in the MANOVA (p > 0.05).

Similar to the other species, plots from canonical discriminant functions for *E. fasciatus* otoliths revealed no separation of the data using either Region or Period as grouping variables. Again, the discriminant analysis showed poor classification results, indicating that individual fish could not be classified with certainty to the Region (26.7% cross-validated cases) or period (60.0% cross-validated cases) from where the samples were collected.

2.4. Discussion

2.4.1. Spatial and temporal variation in chemical signatures

This Chapter revealed significant differences in the otolith chemistry of *P. leopardus* and *C. cyanostigma* at different spatial and temporal scales. These spatial differences indicated that groups of individuals of these two species had spent a significant part of their lives in different environments, providing a basis for potential stock separation. Differences in the otolith chemistry on the east coast of Australia have been reported for temperate reef-estuarine fish (e.g., Dove et al. 1996; Gillanders and Kingsford 2000; Kingsford and Gillanders 2000; Sanchez-Jerez et al. 2002), a coral reef damselfish (Patterson et al. 2004b), and two species of coastal pelagic mackerel (Begg et al. 1998) at spatial scales similar to those identified in this study. With the exception of one other study on the Nassau grouper, *Epinephelus striatus*, in the Caribbean (Patterson et al. 1999), however, this thesis is the only other investigation of the use of otolith chemistry to determine the stock structure of commercially exploited coral reef fish species.

Concentrations of Ba in otoliths of *P. leopardus* indicated potential stock separation at the spatial scale of individual reefs (100s-1000s m), while Sr and Mn signatures suggested stock separation at a regional or greater spatial scale (>100s km); although spatial patterns in Sr concentration depended on the cohort and year of sampling considered. Ignoring such temporal signals could give misleading information about stock structure. A single homogenous stock of *P. leopardus* may have been suggested if only Sr signatures from the cohort collected in 1999 had been considered, while the possibility of three potential stocks was apparent from the otolith elemental signatures in the 1995 collection (Fig. 2.5). Potential stock separation at the larger (regional) spatial scale was also suggested for *C. cyanostigma*

based on otolith concentrations of Mn and Ba. It could not be determined, however, whether stock structure at the finer spatial scale (among reefs) also would have been detected for this species because sample numbers were insufficient to investigate variation in otolith elemental concentrations among reefs.

These spatial patterns in otolith chemistry are consistent with what might be expected from the presumed sedentary (reef-specific) habit of most serranids post settlement (e.g., Chapman and Kramer 2000; Stewart and Jones 2001). Davies (1995) showed that *P. leopardus* individuals are extremely unlikely to move among reefs after settlement and Mosse (2002) found that *C. cyanostigma* were also faithful to particular sites over long periods (at least 5 years). Such sedentary behaviour would increase the likelihood of detecting local and regional variations in environmental conditions, even among individual reefs, manifest as spatial patterns in otolith chemistry.

Although different mean elemental signatures in otoliths of *P. leopardus* and *C. cyanostigma* suggested the separation of stocks, elemental signatures of individuals could not be used to classify individual fish to their region, reef or time of capture. These results contrast with a recent survey of a newly settled damselfish *Pomacentrus coelestis*, collected from reefs in the Lizard Island Region and in the southern GBR by Patterson et al. (2004), who reported spatial differences in Ba/Ca ratios (among regions), Mn/Ca ratios (reef within regions) and Sr/Ca ratios (sites within reefs) for the post-settlement part of the otolith and could successfully classify individuals to region and year. It is likely that the within-stock variation of chemical signatures among individual fish that are several years old and of different ages, is much greater than in newly settled fish and that this would result in greater overlap of individual chemical signatures from different potential stocks. Such overlap may

explain the limited use of otolith chemistry in the species examined here to classify individual fish to a particular place or time of capture.

Similar to this study, other investigations of the inter-annual stability in otolith chemical signatures of marine fishes have found differences between years in at least one, and often several, of the elements examined (e.g., Campana et al. 1995; Patterson et al. 1999; Gillanders and Kingsford 2000; Rooker et al. 2001; Gillanders 2002; Patterson et al. 2004a). Temporal variation in Mn concentrations was detected for *P. leopardus* (between cohorts) and in Ba for *C. cyanostigma* (between groups of individuals collected before and after Cyclone Justin). Although Mn and Ba chemical signatures were not persistent from year to year, they varied consistently over time across all the regions for both species. In contrast, Sr concentrations in *P. leopardus* varied between cohorts (or among years of capture) differently in different regions. Consequently, when using otolith chemistry to investigate stock structure it is preferable to compare signatures among individuals from the same age, but collected over several years, to minimise confounding spatial variation in otolith chemistry with particular times of sampling and to derive a generalisable, time-averaged assessment of the spatial structure of a stock. Limited sample sizes for *C. cyanostigma* and *E. fasciatus* precluded assessment of whether the spatial patterns in otolith microchemistry would also be temporally variable for those species.

The lack of significant variation in otolith chemistry among regions for *E. fasciatus* might indicate that *E. fasciatus* stocks are homogeneous over much of the GBR, though the evidence is certainly not conclusive. It also might be that the sample sizes provided insufficient statistical power or that the analytical technique combined with the range of elements used were not sufficiently sensitive to delineate

stock structure of this species at the spatial and temporal scales examined, if indeed such structure exists in those stock(s).

2.4.2. Reasons for temporal and spatial variation in otolith chemistry

Several possible reasons could explain the spatial and temporal differences in otolith elemental compositions detected from fish collected across the GBR. The reasons include variations in the physical (e.g., water hydrodynamics and temperature) and biological (e.g., diet) environment, and differences in the ontogenetic or physiological regulation of elemental incorporation.

Experiments have found that concentrations of Sr and Ba in otoliths can be directly correlated with concentrations in the water (Gallahar and Kingsford 1996; Bath et al. 2000). Spatial and temporal variability in otolith chemistry would be expected on the GBR given the natural variability in biological and hydrodynamic factors among reefs and regions in the GBR (Wolanski 1994). Although only a small cluster of reefs was sampled in each region, some broad spatial scale features with regards to continental shelf depth and width and potential influence of oceanic water from the Coral Sea will be reflected in these regions. The Lizard Island Region is situated on a relatively shallow (~30 m) and narrow part of the continental shelf where the reef matrix is dense and any substantial water movement is restricted to the narrow inter-reef passages. Several elongated reefs on the shelf break limit oceanic inflow from the Coral Sea. The shelf widens with increasing latitude (Fig. 2.1) and slopes in the Townsville Region to a depth of about 100 m. The reef matrix in this region is the least dense in the GBR and waters are influenced by the bifurcation of the westerly flowing South Equatorial Current, which splits between 15°S and 22°S into the south flowing East Australian Current and north flowing

Coral Sea Coastal Current (Tangdong and Lindstrom 2002). Over 50% of the inflow from the Coral Sea across the shelf occurs over a 150 km wide area in the Townsville Region (Brinkman et al. 2002). The continental shelf widens even further in the Mackay and Storm Cay Regions where the reef matrix is again dense, restricting the inflow of oceanic water (Wolanski 1994).

Upwelling of deep nutrient rich oceanic water can occur by several oceanographic mechanisms and has been reported to various degrees in all regions of the GBR (e.g., Andrews and Gentien 1982; Andrews 1983a; Wolanski 1994; Middleton et al. 1995). Ba has a nutrient type distribution in seawater, i.e., the element is depleted in surface water and enriched at depth (Millero and Sohn 1992) and Ba/Ca ratios in corals have been shown to reflect nutrient upwelling (Lea et al. 1989; Fallon et al. 1999). Upwelling events, therefore, could influence the variation in Ba concentration in otoliths of *P. leopardus* and *C. cyanostigma* at different spatial and temporal scales. Similarly, the variability in Mn detected among regions for both *P. leopardus* and *C. cyanostigma* could be due to different terrestrial influences. Mn enters surface waters via the atmosphere, but mainly via rivers and land (Millero and Sohn 1992). The reefs in the Lizard Island Region are located much closer to the coast compared to the other regions, and are potentially more prone to terrestrial influences. Although none of the reefs included in this study is close enough to the coast to be directly affected by river plumes other than on very rare occasions (Devlin et al. 2001), and no obvious cross shelf patterns in elemental concentrations were apparent, the possibility exists that some of the regional patterns in otolith chemistry are complicated by cross-shelf influences. Without the sampling of water masses and otoliths concurrently, however, the potential reasons for differences in otolith chemistry remain speculative.

There is ambiguous evidence that otolith elemental incorporation, in particular Sr, is influenced by temperature and salinity (Campana 1999; Thresher 1999). The maximum difference in monthly average sea surface temperature between the latitudes examined in this study is less than 2 °C (Lough 1994). There was no apparent consistent spatial trend in any of the elemental concentrations in otoliths with respect to latitude that would suggest temperature gradients as a potential explanation for the spatial differences in otolith chemistry among regions. There is a possibility, however, that the temporally variable concentrations of Mn and Sr for *P. leopardus* and Ba for *C. cyanostigma* collected before and after the Cyclone Justin event in 1997 were related to cyclone-associated changes in temperature or salinity, or both. Cyclone Justin caused a relatively large and rapid drop in water temperature over the southern half of the GBR (south of ~17-18°S) during this time, with bottom temperatures dropping in just one month (March) to below the average winter minimum not usually reached until July[6]. This study revealed a significant increase in Sr otolith concentrations in at least two regions in *P. leopardus* collected after the Cyclone. It also discovered decreased concentrations of Mn in *P. leopardus* otoliths and elevated otolith concentrations of Ba in *C. cyanostigma* that had experienced the cyclone. This inference, however, does not agree with any of those studies that have investigated the effect of temperature on elemental concentrations in otoliths within, or close to, the temperature range occurring in the regions examined. Several studies have reported a positive correlation between temperature and Sr incorporation in otoliths (Kalish 1989; Lough 1994; Hoff and Fuiman 1995; Bath et al. 2000), while others found no effect of ambient temperature on Sr:Ca ratios (Tzeng 1996; Kawakami et al. 1998). No temperature related effects on Ba incorporation in

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[6] Australian Institute of Marine Science. 2005. Unpubl. Data. (Available from http://www.aims.gov.au/pages/facilities/weather-stations/aws-ytd.html) [Accessed on: 1 February 2005.]

otoliths were detected by Fowler et al. (1995a; 1995b), Bath et al. (2000) or Elsdon and Gillanders (2002). A reduction in Mn concentrations in otoliths at higher temperatures was found by Fowler et al. (1995a), while Elsdon and Gillanders (2002) found no temperature effects on Mn:Ca ratios.

Other factors related to the Cyclone, such as potential changes in salinity due to associated heavy precipitation might also be implicated in the elevated levels of Sr (*P. leopardus*) and Ba (*C. cyanostigma*) and decreased levels of Mn (*P. leopardus*) in otoliths collected after the event. As for temperature, similarly ambiguous are the results from investigations of the relationship between salinity and Sr in the marine environment (Thresher 1999). Fluctuations in salinity among and within years will rarely be more that 1.5 ppt (34 to 35.5 ppt) (Andrews 1983a) on the outer shelf of the GBR. In contrast to our results, Fowler et al. (1995a, b) found a positive relationship between Sr otolith concentrations and salinity (at 26 to 36 ppt), while Chesney et al. (1998), Hoff and Fuiman (1995) and Proctor et al (1995) found no effects on Sr in the range of 9.5 to 40 ppt. Similarly, Fowler (1995b) reported no effects of salinity on concentrations of Mn and Ba.

Differences in other factors such as ontogeny (e.g., Thresher et al. 1994; Proctor et al. 1995), physiology (e.g., Kalish 1989), growth rates (e.g., Thresher et al. 1994) and diet (e.g., Sanchez-Jerez et al. 2002) also cannot be ruled out as potential factors influencing differences in otolith elemental composition in *P. leopardus* and *C. cyanostigma*. Effects of physiology and ontogeny should have been substantially minimised in *P. leopardus* by examining fish of the same age and similar sizes. As mentioned previously, however, there is a possibility that the comparison of fish of different sizes and ages might have confounded potential temporal and spatial differences in the otolith chemistry of *E. fasciatus* and to some degree of *C.*

cyanostigma. It is clear that laboratory experiments investigating the influence of the physiological regulation on otolith elemental incorporation are needed if we are to understand the reasons for spatial and temporal differences in otolith chemistry. It should be emphasised however, that independent of the reasons for the variation in otolith elemental concentrations, studies of patterns in otolith chemistry can still be used to investigate stock structure of a species so long as several years are covered in the sampling program and sampling is carefully stratified to account for variations among fish of different ages or year classes.

Patterns of variation in otolith chemistry were not consistent among species, with the different species showing different patterns in Ba, Mn and Sr concentrations at different spatial and temporal scales. Similar elemental concentrations in different species should be expected if the incorporation of trace elements in otoliths was directly related to the concentration of the elements in the water and the species incorporated elements into their otoliths with the same mechanisms. This was suggested for two species of damselfish on the GBR in which the elemental signatures of one species could even be used to successfully classify another to the region and year of capture (Patterson et al. 2004). In the first field comparison of otolith elemental fingerprints among five estuarine species Swearer et al. (2003) concluded that species that were closely related showed more similar chemical compositions in their otoliths than more distantly related species, and that differences were most likely due to diet or physiology or both. Potential differences in the physiology, diet, growth rate, ontogeny and age of the three species examined in this thesis could all be possible reasons for the different patterns in otolith chemistry, however, and would obviate statistical comparisons among species.

2.4.3. Conclusion and future directions.

Patterns in otolith chemistry of *P. leopardus* and *C. cyanostigma* provide a good starting point to direct further research on groups of individuals that have lived at least part of their lives in different environments, and therefore may have different life history characteristics. Otolith chemistry results should not be used in isolation to determine the stock structure of these species and the *E. fasciatus* population, however, as supplementary information is needed to aid the identification of structures in the stocks considered here that are relevant to sustainable fisheries management. Information on the spatial and temporal structure of other phenotypic characteristics (e.g., otolith morphology and meristics), including specific information on patterns in life history characteristics (e.g., growth, mortality rates and maturity), should be collected to confirm, refute or suggest additional levels of structure, with the overall aim of achieving a 'holistic' picture of the stock structures of these species (sensu Begg and Waldman 1999; Chapter 1). In the following Chapters of this thesis, the stock structure of *P. leopardus,* therefore, was investigated further by examining patterns in otolith morphology (Chapter 3) and vital life history characteristics (Chapter 4) across the same spatial and temporal scales examined for otolith chemistry.

Chapter 3. The use of otolith morphology to determine stock structure of *Plectropomus leopardus*.

3.1. Introduction

Variations in morphological characteristics of otoliths have proved useful for identifying fish stocks for a range of temperate marine species (e.g., Bird et al. 1986; Castonguay et al. 1991; Smith 1992; Campana and Casselman 1993; Friedland and Reddin 1994; Begg et al. 2001; Smith et al. 2002), but have not been examined for species on tropical reefs. Similar to otolith chemistry (Chapter 2), differences in morphological characteristics between putative stocks indicate that stocks either differ genetically or have at least spent some periods of their lives in different environments (Begg et al. 1999b; Cadrin 2000) and therefore have the potential to develop different population characteristics that may be manifest as different productive capacities. Otolith morphological features used as indicators of stock separation generally fall within one of three categories. The first category includes the traditional one-dimensional linear measurements of size-related attributes such as otolith length and width (e.g., Begg and Brown 2000; Bolles and Begg 2000) and distances between specific features on the otolith (e.g., Turan 2000). Internal otolith measurements, such as nucleus length (e.g., Messeih 1972; Neilson et al. 1985) and width of hyaline bands or increments (e.g., Hopkins 1986; Begg et al. 2001) also fall within this category. The second category comprises two-dimensional size measurements, such as area, perimeter (e.g., Campana et al. 1994; Begg and Brown 2000; Bolles and Begg 2000) and different shape indices, including circularity and rectangularity (e.g., Friedland and Reddin 1994; Begg and Brown 2000; Bolles and Begg 2000; Tuset et al.

2003). A third, more recent morphological technique examines the two-dimensional outline of otolith shape using Fourier analysis (e.g., Bird et al. 1986; Smith 1992; Campana et al. 1994; Begg and Brown 2000; Smith et al. 2002). Fourier analysis produces a series of cosine and sine curves from the coordinates of a traced outline which, when added together, describe the outline of the traced form. The cosine and sine curves can be defined mathematically in a series of Fourier descriptors and used as variables to compare otolith shapes among individuals or potential stocks (Christopher and Waters 1974; Younker and Ehrlich 1977.).

The aim in this Chapter was to examine the use of otolith morphology for determining the stock structure of *P. leopardus* on the GBR. As for otolith chemistry (Chapter 2), both the broad and fine scale spatial patterns of *P. leopardus* were investigated by comparing aspects of otolith morphology among fish collected from four regions of the GBR, separated by 100s km (north to south), and from neighbouring reefs separated by 100s to 1000s m within each of the four regions. In addition, I consider the potential for temporal variation in otolith morphology, possibly related to particular time-dependent events or reflecting variation among different cohorts of fish. If present, temporal variation could confound the spatial information if samples were taken from only one time and so otolith morphological characteristics were compared from two cohorts of *P. leopardus* with non-overlapping life histories either side of a significant environmental disturbance (Cyclone Justin; Chapter 2). As for the investigation of otolith chemistry, spatially variable effects of Cyclone Justin provided an opportunity to test for potential interaction between the temporal variation and spatial patterns in otolith morphology.

3.2. Methods and data analysis

3.2.1. Sample collection

Otolith morphological variables were analysed from 4-year old *P. leopardus* collected in 1995 and 1999 from three reefs within each of the four regions (Fig. 2.1 in Chapter 2; Table 3.1). Although the zoning status of a reef and the level of fishing pressure on it were unlikely to have affected otolith morphology, one reef from each treatment regime in the ELF Experiment was included from each region (See Chapter 2) to avoid potential biases in spatial variation related to particular fishing histories. Thus, within each region, samples were analysed from one MNP-B reef that was closed to fishing, one MNP-B reef that was open for one year of fishing and then closed, and one GU reef that was subjected to increased fishing for a year prior to closure for five years.

Table 3.1. Study years, regions and reefs from which *P. leopardus*, were sampled and analysed for otolith morphology.

Region name	Reef name (GBRMPA number)	1995, 1999 replicates	Length range (mm)
Lizard Island	Rocky Islet Reef A (14132a)	20, 6	304-495
	Rocky Islet Reef B (14132b)	20, 6	306-481
	South Direction Reef (14147)	20,12	350-468
Townsville	Knife Reef (18081)	8, 4	370-451
	Dip Reef (18039)	7,12	318-462
	Yankee Reef (18074)	20, 8	322-464
Mackay	Unnamed Reef (20142)	20, 18	322-456
	Liff Reef (20296)	20, 16	303-427
	Robertson Reefs (no2) (20136)	20, 11	342-514
Storm Cay	Junk reef (21131)	20, 15	345-422
	Lorries reef (21130)	20, 11	328-475
	Sullivan reef (21124)	18, 19	280-424
TOTAL		213, 138	303-514

Sagittal otoliths from up to 20 4-year old *P. leopardus* were sampled from each reef in each year (Table 3.1). Otoliths from fewer than 20 fish were analysed only if less than this number were collected from a reef. This sampling design enabled the examination of broad (region) and fine (reef within region) spatial and temporal (1995 and 1999 cohorts) patterns in otolith morphology of *P. leopardus* across much of the GBR, spanning an unusual environmental event (Cyclone Justin, 1997) that had the potential to significantly influence the results.

3.2.2. Morphological analysis

A microscope image (10x magnification) was projected onto a computer screen using a video camera (Panasonic GP-KR222E). Whole otolith area, length, perimeter and width (Fig. 3.1) and two shape indices, circularity and rectangularity, were collected from each otolith using the OPTIMAS image analysis system (OPTIMAS 1999). Rectangularity was calculated as the area of the otolith divided by the area of its minimum enclosing rectangle, and circularity as the perimeter of the otolith squared divided by its area (OPTIMAS, Silver Spring, MD, 1999). The perimeter of the otolith was traced in a counter clockwise direction and digitized into 128 x-y equidistant coordinates using the distal edge of the otolith rostrum as a common starting point for the coordinates. A Fast Fourier Transform (FFT) was calculated as a Cartesian FFT (OPTIMAS, Silver Spring, MD, 1999). The Cartesian FFT used the 128 x-y coordinates as complex numbers (a + *i*b), where a was the real component and *i*b the imaginary component, representing the amplitudes of the cosine and sine waves, respectively. The resultant 128 set of complex

numbers or descriptors were subsequently normalized for differences in otolith position by setting the 0th descriptor to 0, and in size and rotation of the otolith by dividing all the descriptors with the 1st descriptor. The normalized descriptors (a' + *i*b') were used to calculate the absolute value (Harmonic) of each descriptor according to the following (Christopher and Waters, 1974):

$$Harmonic = \sqrt{a'^{2}_{n} + (ib')^{2}_{n}} \tag{3.1}$$

The Harmonics were then used in combination with the other morphological variables and shape indices to compare otoliths between cohorts and among regions and reefs within regions.

The higher the number of equi-distant points and subsequent complex numbers included in the model, the closer the fit to the original shape. The main features of the otolith shape, however, are generally captured by the first 10-20 Harmonics (e.g., Campana and Casselman 1993; Friedland and Reddin 1994). The minimum number of Fourier descriptors required to explain at least 90% of the recorded shape of the otoliths was calculated following the range finding procedure of Smith et al. (2002). A total of 128 descriptors were collected from two randomly selected otoliths from each reef and cohort (24 in total) and normalized for position, size and rotation as described above. The shape of each otolith was reconstructed (by computing the inverse FFT) using all the descriptors and then reconstructed using only the first and last descriptors. The Euclidian distance between the inverse FFT using all the descriptors and the inverse FFT using only the first and last descriptors was defined as the maximum percent error of reconstruction, i.e. 100% reconstruction error (Smith et al. 2002). Because the Cartesian descriptors are asymmetrical around the middle frequency, both ends of the array are required in the

reconstruction. Otolith shape was reconstructed, therefore, using the first two and last two descriptors, the first three and last three descriptors, and so on until the first and last 22 descriptors were used. This range finding test allowed us to estimate the decrease in mean percent reconstruction error by using more and more descriptors and it was estimated that 14 of the first and last descriptors were required for the reconstruction error to be less than 10%. See Figure 3.1 for a comparison of the otolith shape reconstructed from the first and last 14 descriptors and all 128 descriptors. These descriptors, therefore, were used in the statistical analyses to compare the spatial and temporal patterns in otolith shape of *P. leopardus.*
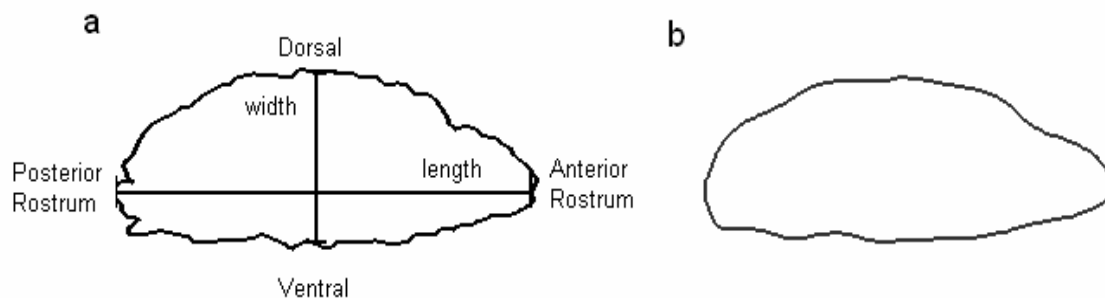
Figure 3.1 Example of a *P. leopardus* otolith reconstructed by using a) all of the 128 Fourier descriptors that were collected, and b) the first and last 14 descriptors. Otolith orientation and measures of length and width are indicated.

3.2.3. Statistical methods

The assumptions of normality and homogeneity of variance for each morphological variable were examined using Shapiro-Wilk's and Levene's tests respectively, and homogeneity of the group covariance matrix tested by Box's M test. Variables of circularity, breadth and area were log transformed and Fourier harmonics 2, 4, 9, 11 – 14,

120 – 121, 114 – 118 and 123 – 127 square root transformed to conform to the assumption of normality and homogeneity of variances.

A relationship between otolith morphology and otolith growth rate (assumed to be correlated to fish length) may confound spatial or temporal differences in otolith morphology (Campana and Casselman 1993). The potential for such effects were minimised by: (1) including fish with as narrow FL range (between 280 and 514 mm) as possible but still achieve sufficient sample numbers (overall FL for 4-year olds sampled during the ELF Experiment in 1995 and 1999 ranged from 250 to 551 mm); and (2) standardising morphological variables by FL prior to further analyses where a significant relationship existed. The effect of FL on each morphological variable was examined by ANCOVA (Winer et al. 1992). My primary interests in these analyses were: a) to test whether morphological variables differed with FL for any group of samples; and b) if so, to test whether the slopes of regressions of morphological variable on FL were homogeneous among groups. If a significant regression was detected and homogeneous among groups, the effect of FL was removed from each measurement using the relationship:

$$O_{ij,adj} = O_{ij} + b.(FL_{ij} - MFL_{.j}) \tag{3.2}$$

where

$O_{ij, adj}$ = otolith morphological measurement of fish i adjusted to mean fork length of group j;

O_{ij} = original otolith morphological measurement for fish i from group j;

$b.$ = slope of the relationship $O_{ij}:FL_{ij}$ common to all group;

FL_{ij} = fork length of fish i in group j; and

MFL.$_j$ = average fork length within group *j*.

If significant slopes of the relationship differed among groups, the correction for FL was made separately for each group using the equation above, but replacing the common slope (*b.*) with the group-specific slope (*b$_j$*). These corrections had the effect of scaling all morphological variables from all otoliths to their predicted group mean FL.

MANOVA (Tabachnick and Fidell, 1983) was used to investigate the effects of sex (females, males and individuals in the process of changing sex; i.e., transitionals) on otolith morphology. Separate MANOVAs were computed for the one- and two-dimensional shape variables and the Fourier Harmonics using a three-way crossed model (outlined below) with fixed factors: Cohort, Region and Sex. Data were pooled across reefs within regions due to insufficient sample numbers to test for reef-specific effects (Table 3.2). Due to the low numbers of transitionals, the MANOVA was computed both with and without this variable of sex to investigate the robustness of the results.

Table 3.2. Cohort and regions from which samples of *P. leopardus* were used to investigate the effects of sex on otolith morphology. Numbers are sample sizes.

Region name	Cohort	Sex female	male	Transitionals
Lizard	1995	30	12	4
Island	1999	16	4	1
	1995	25	6	2
Towsnville	1999	16	6	1
	1995	28	24	2
Mackay	1999	15	24	
	1995	26	19	1
Storm Cay	1999	10	28	2
TOTAL		166	123	13

A MANOVA was also used to test for spatial and temporal differences in otolith morphology using a three-way crossed model with fixed factors: Cohort and Regions, and a random factor: reef (nested within region). A Principal Component (PC; Tabachnick and Fidell, 1983) Analysis was done first on the combined data set of both the shape variables and Fourier Harmonics to reduce the number of variables to be incorporated in the MANOVA. The number of PCs to extract and subsequently include in the MANOVA was determined by examining the size of the eigenvalues (representing the variance explained by each PC), as well as their relative contribution to the percent variance explained compared to the other eigenvalues (i.e., scree test; Tabachnick and Fidell 1983). The latter determines the number of PCs beyond which the addition of more PCs would contribute little to the variance explained by the solution (Tabachnick and Fidell 1983). Wilk's Lambda criterion was used to test for group differences in the MANOVAs. Sums of squares and degrees of freedom of interactions were pooled when the F-ratios of interaction effects were ≤ 1.

A posteriori ANOVA was used to explore patterns for each of the PCs separately when significant effects were indicated in the MANOVA. The univariate linear model for the analysis of each PC was:

$$x_{ijkl} = \mu_{....} + C_{i...} + R_{.j..} + r(R)_{.k(j).} + CR_{ij..} + Cr(R)_{ik(j).} + e_{l(ikj)} \qquad (3.3)$$

where

x_{ijkl} = the PC score for otolith l from Cohort i, Region j and reef k;

$\mu_{....}$ = the estimate of the population mean PC score over all Cohorts, Regions, reefs and otoliths;

$C_{i...}$ = the fixed effect of Cohort i averaged over Regions and reefs;

R$_{.j..}$ = the fixed effect of Region j averaged over Cohorts and reefs;

r(R)$_{.k(j)}$ = the random variation attributable to reef k within Region j averaged over

Cohorts; and

$e_{l(ikj)}$ = unexplained random variation associated with otolith l within Cohort i,

Region j and reef k.

HSD tests were used to determine which means differed following significant effects detected in the ANOVAs. The communalities (representing the proportion of the total variance of a variable accounted for by the PC) and variable loadings of the PCs that were significant in the ANOVAs were subsequently examined. A loading below 0.45 indicated that the variable explained less than 20% of the PC and therefore, was not interpreted further.

Finally, two forward stepwise canonical discriminant analyses (CDAs; Tabachnick and Fidell, 1983) were computed using the shape variables and Fourier harmonics to examine the otolith morphology of *P. leopardus* in multivariate space and investigate whether otolith morphology could be used to classify samples to spatial scale and cohort of origin. The factor used as a separating variable in the CDA depended on the significant effects determined in the MANOVA (i.e., Cohort, Region or Reef(Region) or any interactions between these factors). The CDA was used in this way as a confirmatory technique. Wilk's Lambda criterion was used to test for significant differences between the discriminant functions. Equal prior probabilites and jackknife classification (i.e., "leave-one-out") were used to minimize potential bias in the reclassification of individuals.

3.3. Results

Slopes of the relationship between FL and several otolith morphological variables for *P. leopardus* differed among a range of spatial scales and between cohorts (Table 3.2). The within-group slope, therefore, was calculated for each group according to the level at which the slopes of the relationship differed and used to correct for the influence of FL (Table 3.2). The common between-group slope was used to correct for the influence of FL on some variables as there was a significant overall relationship between the variable and FL which was homogeneous among groups (ANCOVA homogeneity of slopes test, p > 0.05; Table 3.2). No morphological variable was significantly correlated with FL after standardisation. Furthermore, shape variables and Fourier harmonics were not significantly different between otoliths of females, males or transitionals (MANOVA, p > 0.05). The same results were achieved when the MANOVA was computed without the transitionals. The morphological data, therefore, were pooled across sex for the remainder of the analyses.

3.3.1. Principal Component Analysis

Four PCs were extracted from the analysis of the combined data set of shape variables and Fourier Harmonics and included in the MANOVA (Table 3.3). The communalities ranged between 0.11 and 0.88, with some morphological variables better defined by the PC solution than others (Table 3.3). About 44% of the total variance in the morphological data was explained by the four extracted PCs (17.9%, 10.2%, 9.9% and 5.9% by PC I, II, III, IV, respectively). A combination of higher order Harmonics describing the finer details of the otolith outline, and lower order Harmonics, perimeter, length, and

circularity representing the broad shape of otoliths, explained most of the variation in PC I and III (Table 3.3). Variation in the broader details of otolith shape also accounted for most of the variation in PC II and IV with otolith area, breadth, perimeter, length and Harmonic 8 explaining most of the variation in PC II and breadth and Harmonic 127, explaining most of the variation in PC IV (Table 3.3).

Table 3.3. Results of homogeneity of slopes test for the influence of fish fork length (FL) on otolith morphological variables of 4-year old *P. leopardus*. The level of correction represents the level at which the slopes were heterogeneous. For example, the level of correction "reef(Region)" means that the slopes of the relationship between FL and a morphological variable differed among reefs nested within regions and that the slope for each reef was used to correct for the influence of FL. Level of correction "FL" means that there was a significant overall relationship between FL and a morphological variable, but that the slopes of this relationship were homogenous among reefs(Region), Regions and Cohorts. Only variables with a statistically significant relationship with FL are shown.

Variable	df	F	p	Level of correction
Log Breadth	8, 306	1.99	0.0467	reef(Region)
Log Circularity	8, 306	1.99	0.0479	reef(Region)
Length	3, 315	4.05	0.0075	Region
Log Area	8, 306	2.01	0.0452	reef(Region)
Perimeter	8, 306	2.34	0.0187	reef(Region)
Rectangularity	1, 341	14.43	0.0002	FL
Sqrt Harmonic 2	1, 349	11.15	0.0009	FL
Harmonic 3	1, 349	10.32	0.0014	FL
Sqrt Harmonic 4	1, 349	6.90	0.0090	FL
Harmonic 5	3, 314	3.44	0.0171	Cohort*Region
Harmonic 6	7, 314	2.12	0.0410	reef(Region)
Harmonic 7	1, 349	13.56	0.0003	FL
Sqrt Harmonic 9	7, 307	2.30	0.0270	Cohort*reef(Region)
Sqrt Harmonic 13	1, 349	8.05	0.0048	FL
Sqrt Harmonic 14	7, 317	3.31	0.0021	reef(Region)
Sqrt Harmonic 114	1, 327	8.69	0.0034	Cohort
Sqrt Harmonic 115	7, 307	2.48	0.0170	Cohort*reef(Region)
Sqrt Harmonic 116	7, 317	3.95	0.0004	reef(Region)
Sqrt Harmonic 117	7, 317	2.89	0.0061	reef(region)
Sqrt Harmonic 118	3, 314	2.90	0.0354	Cohort*Region
Harmonic 119	1, 349	6.79	0.0096	FL
Sqrt Harmonic 120	3, 325	2.91	0.0346	Region
Sqrt Harmonic 121	7, 307	2.10	0.0435	Cohort*reef(Region)
Harmonic 124	3, 314	4.01	0.0080	Cohort*Region
Harmonic 125	1, 349	10.79	0.0011	FL
Harmonic 126	1, 349	31.76	<0,0001	FL
Harmonic 127	1, 327	4.37	0.0373	Cohort

Table 3.4. Variable communalities and loadings on the four significant PCs explaining 44% of the total variance in the otolith morphological data of 4-year old *P. leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the GBR.

Variable	Communalities	PC I	PC II	PC III	PC IV
		Loadings			
Perimeter	0.88	0.39	0.69	0.51	0.01
Length	0.85	0.07	0.57	0.71	0.14
Log Area	0.81	-0.05	0.80	0.32	-0.27
Log Breadth	0.80	-0.03	0.70	-0.10	-0.55
Harmonic 127	0.78	0.18	-0.16	0.65	0.55
Log Circularity	0.76	0.67	0.13	0.42	0.33
Sqrt Harmonic 4	0.70	0.80	0.04	-0.21	-0.09
Harmonic 6	0.64	0.72	0.18	-0.27	-0.11
Harmonic 5	0.58	0.63	-0.29	0.27	-0.15
Harmonic 8	0.51	0.17	0.57	-0.38	0.09
Harmonic 10	0.49	-0.32	0.44	-0.29	0.34
Sqrt Harmonic 2	0.49	0.70	0.00	-0.04	0.03
Harmonic 3	0.49	-0.40	-0.05	0.57	0.01
Harmonic 122	0.45	0.43	0.40	-0.25	0.21
Sqrt Harmonic 13	0.44	0.58	-0.08	-0.07	-0.30
Sqrt Harmonic 117	0.41	0.42	-0.21	0.11	-0.42
Harmonic 7	0.41	0.54	-0.23	0.06	0.25
Sqrt Harmonic 120	0.40	0.37	0.26	-0.32	0.30
Sqrt Harmonic 11	0.37	0.54	-0.12	0.03	-0.25
Harmonic 119	0.37	0.45	-0.30	0.22	-0.14
Harmonic 125	0.35	-0.22	0.02	0.55	0.03
Sqrt Harmonic 115	0.35	0.33	-0.12	0.22	-0.42
Sqrt Harmonic 121	0.31	0.39	-0.37	0.16	-0.01
Harmonic 124	0.30	0.48	0.11	0.03	0.24
Sqrt Harmonic 116	0.26	0.30	0.14	-0.35	0.18
Sqrt Harmonic 118	0.26	0.49	0.02	-0.11	0.06
Sqrt Harmonic 114	0.18	0.19	0.00	-0.37	0.10
Sqrt Harmonic 12	0.18	0.22	-0.11	0.33	-0.05
Harmonic 126	0.16	0.32	0.18	0.04	0.13
Sqrt Harmonic 9	0.14	0.09	-0.20	-0.05	0.30
Sqrt Harmonic 123	0.14	0.27	-0.03	-0.17	0.18
Rectangularity	0.13	-0.25	-0.17	-0.18	0.08
Sqrt Harmonic 14	0.11	0.30	-0.09	-0.02	0.10

The MANOVA of the four PCs identified significant effects on the PC scores of otolith morphology of the interaction between regions and cohorts (1995 and 1999;

Cohort*Region interaction, Table 3.4). ANOVAs indicated that these differences were due to variation in PC II among regions and PC IV among reefs within regions, with both spatial patterns varying depending on the cohort in consideration (Table 3.5). Differences in PC II were due to differences between the Lizard Island and Mackay Regions in 1995 and between cohorts in Mackay (Fig. 3.2a; HSD, $p < 0.05$). The apparent inconsistency between the significant reef within region effect in the ANOVA (PC IV) and no such reef effect detected in the MANOVA is most likely explained by the difference between only two reefs in the Lizard Island Region, with a significantly lower mean PC IV score on Reef 14132a than on Reef 14147 in 1995, while the reverse was observed in 1999 (Fig. 3.2b; HSD, $p < 0.05$). There was also a significant difference between cohorts on Reef 14132a (Lizard Island) and Reef 20296 (Mackay Region; Fig. 3.2b; HSD, $p < 0.05$).

Although only explaining 18% (PC II and IV combined) of the variation in the morphological data, the PC analysis suggested the presence of at least two stocks of *P. leopardus* on the GBR in 1995, one in the northern part of the GBR (Lizard Island) and one in the southern part (Mackay), whereas one homogeneous stock was suggested in 1999.

Table 3.5. Results of MANOVA comparing PC I - IV scores of otolith morphology from two cohorts of 4-year old *P. leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the GBR. p-values in bold indicate significant differences ($p < 0.05$).

Factor	Wilks' Lambda	F	Df	p
Cohort	0.3800	2.04	4, 5	0.2269
Region	0.0513	2.34	12, 14	0.0687
Cohort*Region	0.0315	3.04	12, 14	**0.0269**
Reef(Region)	0.8880	1.19	32, 1167	0.2126
Cohort*Reef(Region)	0.8900	1.18	32, 1167	0.2318

Table 3.6. Results of ANOVAs comparing otolith PC scores of otolith morphology from two cohorts of 4-year old *P. leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the GBR. Only final analyses resulting from pooled terms with $F \leq 1$ are shown. p-values in bold indicate significant differences ($p < 0.05$). Only PCs with significant differences are shown.

Variable	Factor	df	MS	F	P
PC II	Cohort	1	1.5165	1.60	0.2067
	Region	3	0.8057	0.47	0.7126
	Reef(Region)	8	1.7209	1.82	0.0732
	Cohort*Region	3	3.0900	3.26	**0.0217**
PC IV	Cohort	1	0.3246	0.11	0.7473
	Region	3	3.2901	8.11	**0.0083**
	Cohort*Region	3	3.5574	1.21	0.3675
	Reef(Region)	8	0.4059	0.43	0.9011
	Cohort*Reef(Region)	8	2.9452	3.14	**0.0020**
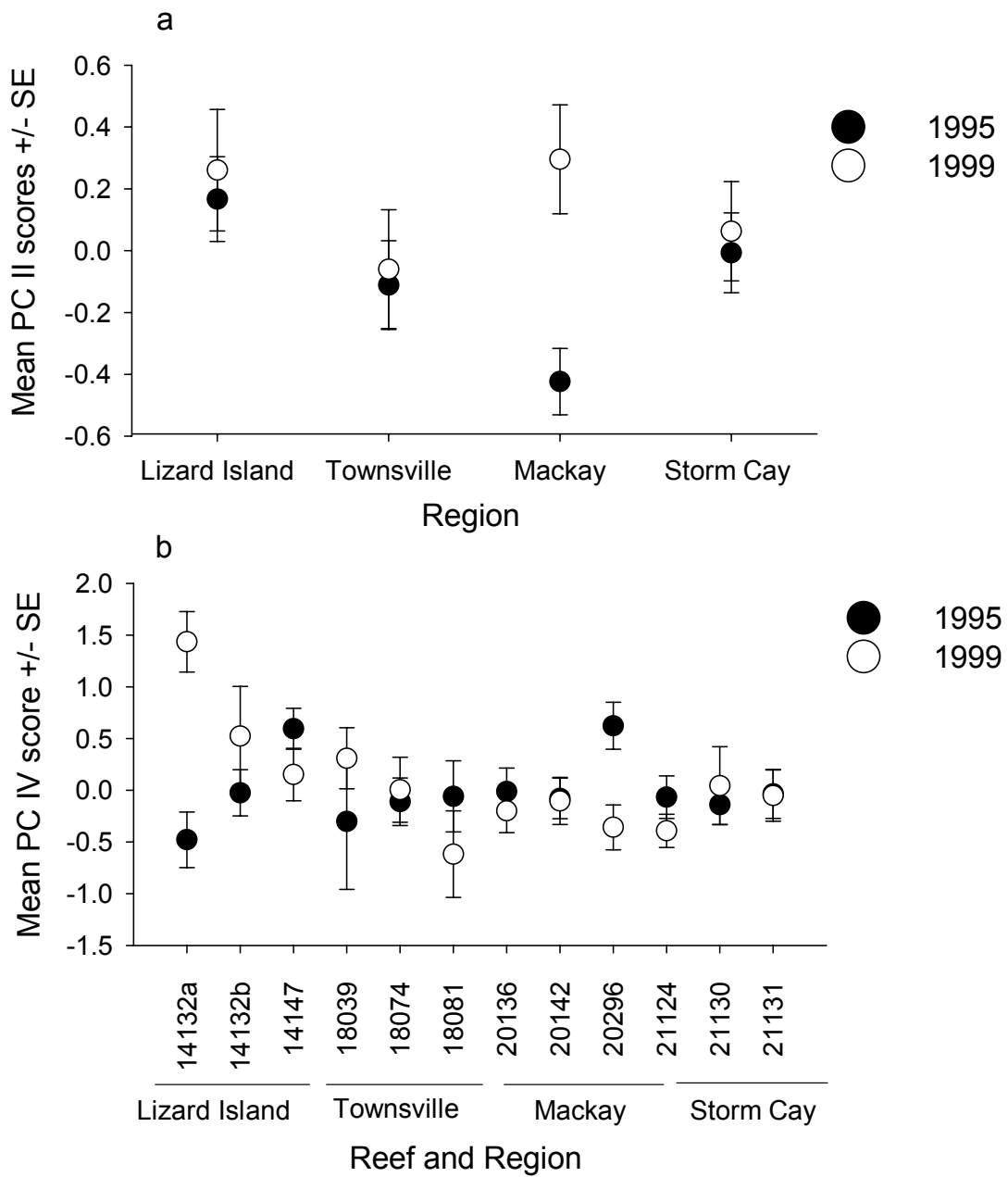
Figure 3.2   Mean scores of a) PC II per region and cohort, and b) PC IV per reef within region and cohort of 4-year old *P. leopardus* collected from three reefs in each of four regions in 1995 and 1999 on the GBR.

3.3.2. Discriminant analyses

Two stepwise canonical discriminant analyses (CDA) were computed for the morphological variables (Fourier harmonics and shape variables combined) in response to the significant Cohort*Region effect in the MANOVA of the PC scores. First, separate CDAs were done for each region using Cohort as the separating variable and second, separate CDAs were done for each cohort using Region as the separating variable. The region specific CDA using Cohort as a separating variable showed a significant first discriminant function (DF) for all four regions, accounting for 100% of the variance in the data (Table 3.6a). Some separation was observed in the distribution of the DF I scores between the two cohorts within each region, although the temporal pattern was not consistent across regions (Fig. 3.3). Likewise, the cohort specific CDA using Region as a separating variable showed some separation among the four regions in the first two significant DFs of Cohort 1995 (explaining 59.9% and 30.7% of the variance, respectively) and one significant function of Cohort 1999 (explaining 100% of the variance, Table 3.6b). The means of the DF I scores in the Lizard Island and Townsville Regions were distinctly greater than those of the Mackay and Storm Cay Regions in 1995 (HSD, $p < 0.05$; Fig. 3.4a) and in 1999 Townsville DF scores were greater than those from the Mackay and Storm Cay Regions (HSD, $p < 0.05$; Fig. 3.4b).

Different combinations of Harmonics 9, 114, 118 describing the finer details of the otolith shape, and Harmonic 124 and shape variables area and circularity representing the broad details of otolith shape, were selected into the DFs to maximize the separation of cohorts within regions (Table 3.7). The primary variables selected for separating regions in each of the cohorts were similar to those selected in the region specific CDA,

although the variables were not the same in each cohort (Table 3.7). Between 66.7% and 76.3% of *P. leopardus* within a region could be correctly classified to their cohort of origin (Table 3.8). Fewer cohort specific individuals could be classified to a Region however, with 34.3% and 39.7% correctly classified for cohorts sampled in 1995 and 1999, respectively (Table 3.9).

Table 3.7. Significance test of a) region specific and b) cohort specific CDA of shape variables and Fourier harmonics combined from otoliths of 4-year old *P. leopardus* collected from three reefs in each of four regions in two cohorts, 1995 and 1999 on the GBR. Only significant discriminant functions (DF) are shown.

a)

Spatial scale	Factor	DF	Wilks' Lambda	X^2	df	P
Lizard Island	Cohort	I	0.7818	19.21	2	<0.0001
Townsville	Cohort	I	0.6863	20.89	3	0.0001
Mackay	Cohort	I	0.7685	26.34	4	<0.0001
Storm Cay	Cohort	I	0.7683	25.43	3	<0.0001

b)

Cohort	Factor	DF	Wilks' Lambda	X^2	df	P
1995	Region	I to III	0.7573	56.72	12	<0.0001
1995	Region	II to III	0.8918	23.36	6	0.0006
1999	Region	I	0.91	11.95	3	0.0075
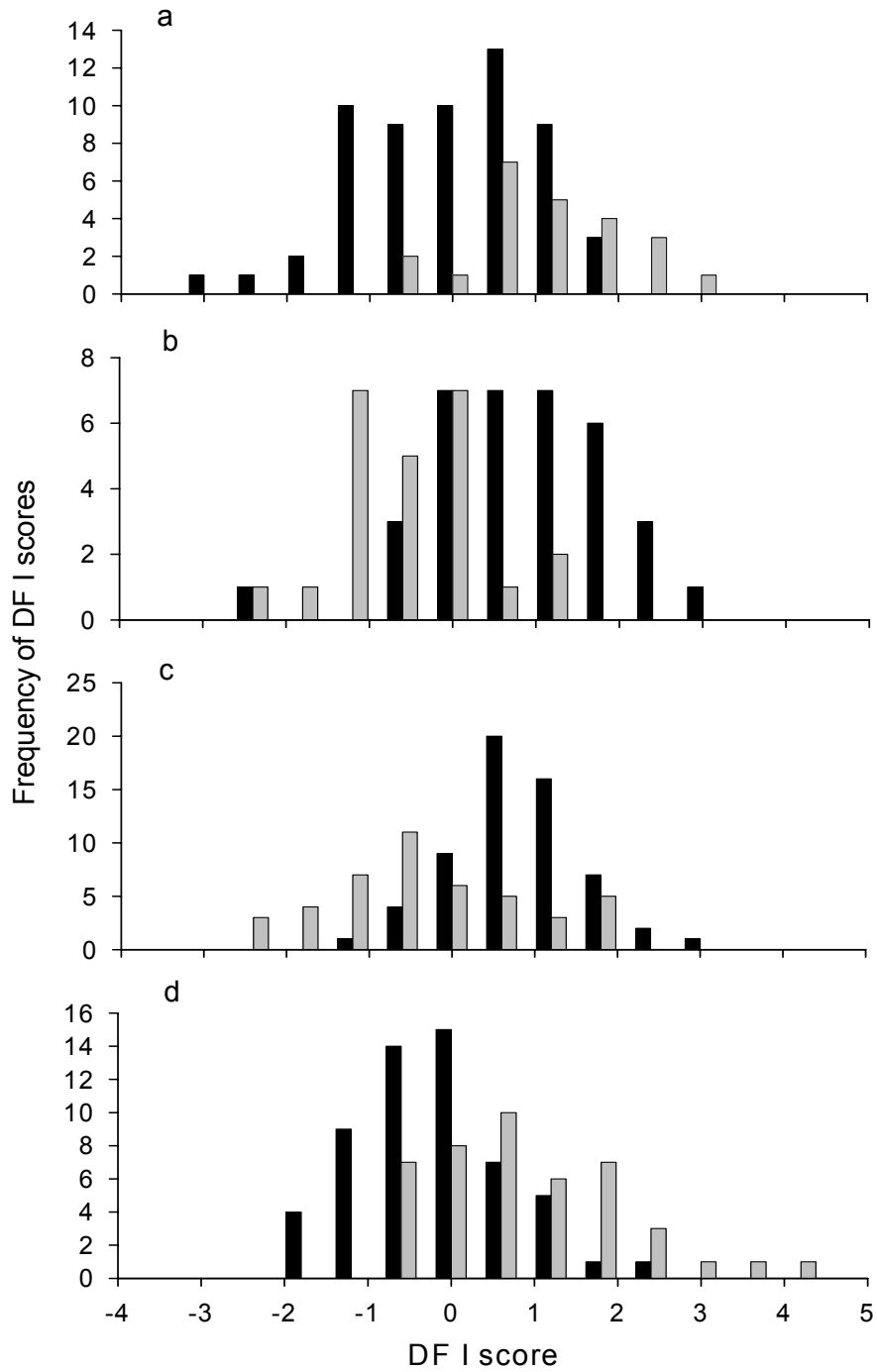
Figure 3.3 Frequencies of DF I scores from otolith morphological variables (Fourier Harmonics and shape variables combined) per cohort (sampled in 1995 and 1999) for regions a) Lizard Island, b) Townsville, c) Mackay, and d) Storm Cay of 4-year old *P. leopardus* from the GBR. (The data were pooled across reefs within regions).
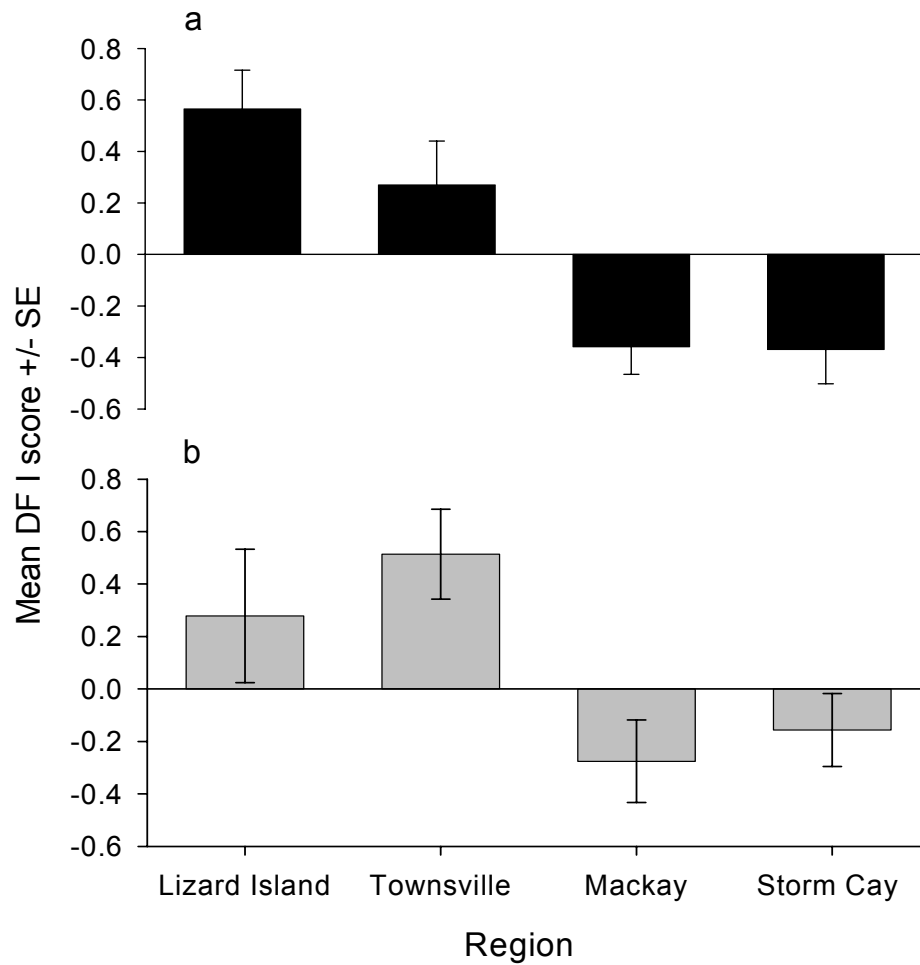
Figure 3.4 Mean ± SE of DF I scores from otolith morphological variables (Fourier Harmonics and shape variables combined) per region for a) Cohort 1995, and b) Cohort 1999 in 4-year old *P. leopardus* from the GBR. (The data were pooled across reefs within regions).

Table 3.8. Canonical coefficient function representing correlation between the morphological variables (Fourier Harmonics and shape variables combined) and significant DFs, separating two Cohorts (1995 and 1999) of 4-year old *P. leopardus* within each of four regions, GBR. All variables selected in the models are shown, but variables with loadings < 0.45 are not interpreted further.

Variable	Lizard Island DF I	Townsville DF I	Mackay DF I	Storm Cay DF I	1995 DF I	1995 DF II	1999 DF I
Log Area			-0.62		0.59	-0.37	
Rectang.				0.38			
Log Circ.		-0.58					1
Sqrt Harm. 9		0.49	0.57				
Sqrt Harm. 114				0.62			
Sqrt Harm. 115	-0.24						
Sqrt Harm. 118	0.84				-0.46	0.23	
Sqrt Harm. 123			0.35				
Sqrt Harm.124		0.22		0.49	0.45	0.52	
Sqrt Harm.125			0.41		-0.12	0.69	

Table 3.9. Correctly classified individuals of 4-year old *P. leopardus* per cohort (1995 and 1999) in each of four regions of the GBR.

Cohort	Lizard Island	Townsville	Mackay	Storm Cay
1995	63.79	71.43	78.33	76.79
1999	73.91	83.33	70.45	63.64
Total	66.70	76.30	75.00	71.00

Table 3.10. Correctly classified individuals of 4-year old *P. leopardus* per region on the GBR in each of two cohorts (1995 and 1999).

Region	1995	1999
Lizard Island	39.66	17.39
Townsville	28.57	58.33
Mackay	45.00	53.49
Storm Cay	41.07	11.36
Total	39.70	34.30

3.4. Discussion

3.4.1. Spatial and temporal variation in otolith morphology

Differences in the otolith morphology of *P. leopardus* were detected at different spatial and temporal scales across the GBR. Although the patterns in otolith morphology of *P. leopardus* were not always consistent between different types of shape variables, two main inferences can be made from these results. Firstly, similar to otolith chemistry, the results indicate that this technique can be useful for identifying groups of individuals of this species that are likely to have spent a significant part of their lives in different environments and therefore suggest potential stock separation. Overall otolith morphology suggested the presence of at least one southern and one northern stock along the GBR, although stock boundaries were temporally variable for some aspects of morphology. It is possible that the main morphological characteristics of otoliths are established in the larval stage and that large amounts of larval dispersal and mixing among areas result in overlap of signatures among stocks. Finer details of otolith shape, however, are most likely influenced by environmental processes during the post-larval phase and may therefore provide insights to the separation of stocks during post-larval life.

Although otolith morphology also suggested variation at a finer, among reef, spatial scale (1-10s km) the significant difference in the multivariate morphological measurement (PC IV) were only between two reefs in the Lizard Island Region. Based on otolith morphology therefore, it seems unlikely that such fine-scale separation is a common phenomenon of *P. leopardus* on the GBR (but see Chapter 2 and 4 for persistent differences among reefs in otolith chemistry and life history characteristics, respectively).

Nevertheless, the presence of some difference among reefs emphasizes the importance of careful and sufficient sampling to capture the range of values manifest in fine-scale, presumably random, variation within regions and so avoid erroneously ascribing to regional structure features that are really a reflection of local-scale variation.

The second inference from the results is that regional patterns in otolith morphology are not always consistent among cohorts and may be subject to temporally dynamic events such as large-scale environmental perturbations or the origin of recruitment of a cohort (if otolith morphology is in part genetically determined). Ignoring such temporal signals could give misleading information about stock structure. A single homogenous stock of *P. leopardus* may have been suggested if otolith morphology based on the 1999 PCA results alone were considered, while at least two potential stocks would be inferred from both the PCA of the 1995 data and CDA analyses of the 1995 and 1999 data (Fig. 3.2a; 3.4a). In addition, cohorts were distinguishable within all regions based on the frequency distributions of DF scores. Other investigations of the inter-annual stability in otolith morphology of marine fishes have found differences between years, as well as age groups (Castonguay et al. 1991; Campana and Casselman 1993; Begg and Brown 2000; Begg et al. 2001). Consequently, similar to otolith chemistry, when using otolith morphology to investigate stock structure, it is preferable to compare multiple cohorts with individuals of the same age, collected over several years.

The spatial and temporal patterns in otolith morphology are in part consistent with the assessment of stock structure of *P. leopardus* on the GBR based on otolith chemistry (Chapter 2). Differences in otolith chemistry of *P. leopardus* collected from the same spatial and temporal scales as considered here for otolith morphology suggested the

presence of two or three regional stocks. Similar to patterns in otolith morphology, spatial variation in otolith chemistry among regions varied dependent on the cohort being considered. In contrast to the spatial patterns in otolith morphology, however, otolith chemistry also indicated the potential presence of persistent spatial differences at the finer reef scale. Thus, although the number and potential boundaries of phenotypic stocks based on otolith chemistry and morphology remained uncertain, the combined results of these studies emphasized the potential presence of several stocks of *P. leopardus* on the GBR and suggest some regional north-south demarcation among stocks. Differences in both otolith morphology and chemistry indicated that the movements of adults of *P. leopardus* may be limited and are consistent with the presumed sedentary (reef-specific) habit of most serranids post-settlement (e.g., Chapman and Kramer 2000; Stewart and Jones 2001). These results confirm those of several tagging studies of *P. leopardus* on the GBR which found that individuals are unlikely to move among reefs post-settlement (Davies 1995; Zeller 1998; Zeller and Russ 1998). Such limited inter-stock movement of adults means that the recovery rate of stocks after significant harvest is largely (if not solely) dependent on some unknown level of larval dispersal. Further investigations, therefore, are required to clarify the implications of this potential stock structure of *P. leopardus* to ensure sustainable harvests at scales appropriate to both management and the stock structure of the fish.

3.4.2. Reasons for temporal and spatial variation in otolith morphology

Little is known about what processes influence the expression of traits responsible for otolith shape (Ihssen et al. 1981). Differences in growth rate has been the main reason

given for differences in linear morphological variables of otoliths (e.g., Reznick et al. 1989; Secor and Dean 1989; Begg et al. 2001), as well as outline shape variables (e.g., Castonguay et al. 1991; Campana and Casselman 1993; Begg and Brown 2000; Smith et al. 2002). In this study, *P. leopardus* samples were restricted to a certain size range to minimize the potential of a growth rate effect that could confound spatial or cohort related differences in otolith morphology. Significant differences in growth rates (indicated by mean FL of 4-year olds), however, were apparent among reefs within regions (see Chapter 4), while there was no consistency in the patterns of variation in FL and any of the otolith morphological variables. It is possible that the large variation in FL among reefs would have masked potential differences in broad-scale regional differences in growth rates or that some other developmental rate, such as maturation or reproductive output, were more important in influencing otolith morphology of *P. leopardus*.

Spatial and temporal variation in otolith morphology might be expected in *P. leopardus* populations along the GBR given the natural variability in biological and hydrodynamic features across reefs and regions (Wolanski 1994), which in turn could affect fish developmental rates. There was no monotonic latitudinal trend apparent in any of the otolith morphological variables, such as would be expected if morphological features were related to a temperature gradient. The maximum difference in monthly average sea surface temperature among the latitudes examined in this thesis is typically less than 2 °C (Lough 1994). In contrast, there is regional (broad spatial scale) variability in the upwelling and inflow of cool nutrient rich oceanic water across the continental shelf of the GBR (e.g., Andrews and Gentien 1982; Andrews 1983b; Wolanski 1994;

Middleton et al. 1995) which could potentially influence fish developmental rates through changes in food availability or 'step-wise' patterns in water temperature.

There is also a possibility that the temporal variability in otolith morphology of *P. leopardus* collected before and after Cyclone Justin in 1997 was related to changes in temperature or other environmental variables caused by the cyclone (see Chapter 2). This study revealed a significant difference in otolith morphology between non-overlapping cohorts sampled in 1995 and 1999 in the Mackay Region, which is one of the regions where the changes in temperature would have been greatest.

3.4.3. Conclusion and future directions

Differences in otolith morphology proposed the potential presence of at least two regional stocks of *P. leopardus* on the GBR, although some aspects of the spatial patterns varied with the cohort considered. As for differences in otolith chemistry, an examination of the relevance of these temporal and spatial patterns for fisheries management should be the next step. If the proposed stocks have persistently different life history characteristics and, potentially, different fishery productivities, less productive stocks may be subjected to greater harvest and increased risk of local depletion if the GBR population continues to be subject to uniform harvest strategies. Information on vital life history characteristics (e.g., growth, mortality, maturity), therefore, is needed to examine the potential impacts of fishing and related harvest strategies for the postulated stocks.

Otoliths are often collected during routine sampling undertaken as part of the monitoring and assessments of exploited fish stocks. As a result there may be large archives of otoliths potentially available for morphology and chemistry analyses in most

fisheries laboratories. Patterns in otolith morphology, therefore, may provide a cost and time effective starting point for further research on groups of harvested coral reef fishes that have lived at least parts of their lives in different environments.

Chapter 4. The use of vital life history characteristics for the identification of appropriate management units of *Plectropomus leopardus*.

4.1. Introduction

It is important to ensure a match between the spatial scale of management units and the spatial scale of biological processes in the development of management strategies for harvested fish populations (Smedbol and Stephenson 2001; Stephenson 2002). Biological units, or stocks, with different life history characteristics may respond differently to fishing pressure and therefore require different harvest strategies for optimal and sustainable exploitation (Ricker 1954; Adams 1980). The identification of all stocks in species that are 'population rich' (Iles and Sinclair 1982), such as many demersal shell and reef fish species, Atlantic salmon, cod and herring, however, can be very difficult in practice. Consequently, the failure to appropriately consider biological units in management strategy development is a global problem (Stephenson 2002).

Stock identification by means of life history characteristics has been used extensively for temperate fish species (e.g., Casselman et al. 1981; Fairbairn 1981; Horn et al. 1998; Begg et al. 1999a; Hanchet 1999; Begg et al. 2005), but equivalent studies on tropical reef fish were until recently lacking. Recent findings demonstrating spatial variability at a range of scales in life history characteristics of some reef associated fishes (e.g. Gust et al. 2002; Kritzer 2002; Williams et al. 2003), however, emphasise (but rarely discusses) the potential existence of stocks with different productivities within reef fish populations or metapopulations. The population structure of many demersal coral reef fishes is quite different from temperate demersal species. Coral reef fish populations are often comprised of many spatially separate sedentary adult subpopulations, each

associated with distinct patches of reef in a highly variable environment (Wolanski 1994) and connected only by unknown levels of larval dispersal. These species, therefore have the potential to show variation in life history characteristics at a range of spatial scales.

Whether a subpopulation or groups of subpopulations of coral reef fishes can be termed stocks in the traditional sense, i.e. reproductively separate units with limited exchange of individuals (MacLean and Evans 1981) is uncertain because of the inadequate knowledge of the degree of larval dispersal among reefs. The focus of this Chapter however, is to identify biological units that might behave differently at time scale(s) important for fisheries management of a typically exploited coral reef fish, *Plectropomus leopardus,* for which spatial variation in life history characteristics have been reported (e.g., Russ et al. 1998; Adams et al. 2000; Mapstone et al. 2004).

The specific aims of this Chapter were to investigate both broad scale (100s km) and fine scale (100s - 1000s m) spatial patterns in a suite of life history parameters as biological indicators of stock structure of *P. leopardus,* to test for consistency with patterns indicated from otolith chemistry and morphology. Because temporal variation in life history characteristics could confound the spatial patterns (Begg et al. 1999a; Begg 2005), these parameters were also compared from 1995 to 1999.

4.2. Methods

4.2.1. Sample collection

Only *P. leopardus* collected between 1995 and 1999 from the closed reefs in each of the four regions as part of the ELF Experiment were used in this study (Fig. 2.1; Table 4.1). Estimates of growth and mortality from individuals on these reefs were considered the

closest approximation to those of natural populations not modified significantly by fishing (Mapstone et al. 2004). As some levels of illegal fishing on these reefs cannot be ruled out, however, estimates of mortality were referred to as total mortality, Z (Beverton and Holt 1957), comprising both natural mortality and unknown fishing mortality from potential infringements of closed areas, rather than strictly natural mortality (M).

Table 4.1. Study years, regions and reefs within regions from which *P. leopardus* were sampled and analysed for growth and mortality estimates. All reefs had been closed to fishing for seven to 12 years at the start of the Experiment. Reef ID = GBR Marine Park Authority reef number, Age = number of samples aged, Wt = number of samples weighed, FL = number of samples measured for fork length, OPEN = years open to fishing; Excluded = years following fishing for which data were excluded from analyses.

Region	Reef ID	1995 Age	1995 Wt	1995 FL	1996 Age	1996 Wt	1996 FL	1997 Age	1997 Wt	1997 FL	1998 Age	1998 Wt	1998 FL	1999 Age	1999 Wt	1999 FL	Total Age	Total Wt	Total FL
Lizard Island	14114	66	1	65				72	79	79	70	66	72	51	51	53	259	197	269
	14118	219	91	227	145	76	155	123	130	132	142	156	161	OPEN --Excluded------			629	453	675
	14132a	303		318	67	81	82	OPEN -----------------------Excluded-------------------------------------									370	81	400
	14147	237	8	251	46	48	49	56	63	63	116	125	126	131	138	138	586	382	627
Townsv.	18039	176	179	180	42	46	47	119	133	135	160	146	161	105	111	111	602	615	634
	18041	106	112	114	32	32	33	120	120	121	110	124	131	OPEN ---Excluded-----			368	388	399
	18071	314	319	322	144	145	146	154	161	168	169	169	180	222	221	225	1003	1015	1041
	18074	297	277	308	106	115	117	OPEN ----------------------Excluded---									403	392	425
Mackay	20136	310	333	740	258	261	247	OPEN---- --------------------Excluded----------------------------------									568	594	987
	20137	299	315	640	161	170	174	71	80	83	151	151	152	134	138	141	816	854	1190
	20138	265	286	534	217	222	229	104	107	107	238	253	256	OPEN---Excluded------			824	868	1126
	20142	260	274	509	242	252	254	128	134	138	193	202	202	215	224	226	1038	1086	1329
Storm Cay	21130	300	269	500	265	276	287	OPEN ----------------------- Excluded-------------------------------------									565	545	787
	21131	278	277	423	228	206	240	202	220	224	270	220	280	279	291	295	1257	1214	1462
	21132	297	309	487	262	282	288	134	144	146	134	140	146	266	297	299	1093	1172	1366
	21133	255	260	264	142	147	151	89	72	93	107	109	109	OPEN------Excluded---			593	588	617
	Total	3982	3310	5882	2357	2359	2499	1372	1443	1489	1860	1861	1976	1403	1471	1488	10974	10444	13334

4.2.2. Spatial and temporal patterns of life history characteristics

4.2.2.1. Growth

The regression relationships between ln transformed fish weight (dependent variable) and ln transformed FL were as a measure of relative growth compared among years, regions (with the data pooled across reefs within regions) and reefs (nested within regions) by ANCOVA (GLM Procedure; SAS, 2003). Transformation of both weight and length was necessary to conform to the assumption of linearity. Year and Region were considered fixed effects and reef a random variable. Significant effects including the covariate (ln(FL)) were the primary interest in the analysis, since those terms would indicate variation in the slope of the weight-length relationship over spatial or temporal scales. Data from the Lizard Island Region in 1997 were excluded from the analysis because of low sample numbers for individual reefs in that year.

Mean length and weight of *P. leopardus* at age four were compared among Years, Regions (both fixed effects) and reefs (random and nested within regions) using ANOVA. Only reefs from which at least five fish were caught were included in the analyses.

The von Bertalanffy growth function (VBGF) was fitted to length and age data from *P. leopardus* samples collected from each reef and region in each year by non linear least-squares estimation. A common t_0 was estimated and used when estimating L_∞ for all spatial and temporal comparisons to correct for potential gear-selective biases towards the larger individuals in the population (Ferreira and Russ 1994). The most reliable estimate of a common t_0 was gained by adding to the length-at-age data, supplementary length data from individuals aged one to three years collected by spear-fishing in 1995 from two of the green reefs in each region (see Welch 1999). The spear-fishing survey had the same basic design as the ELF line

fishing surveys to ensure data from both sampling methods were compatible (Welch 2001). The following VBGF was used:

$$L_{t,r} = L_{\infty,r} (1 - e^{-K_r(t-t_0)})$$

where:

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

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

K_r is the rate at which L_∞ is approached in region or reef r; and

t_0 is the common age at a theoretical length of zero.

The spatial and temporal consistency of the growth parameter L_∞ was then assessed using ANOVA. Three factors were included in this analysis: Year, Region (fixed effects) and reef (nested within region) (random effect). The highest order interaction (Year*reef(Region)) could not be included in the ANOVA as reef averages were compared and there was no replication of estimates within reefs.

4.2.2.2. Longevity and age distribution

The 90th percentiles of age (A_{90}) were used as an estimate of longevity of *P. leopardus* and age richness (A_R) was used as a proxy for age frequency distributions (Begg et al. 2005). A_R was calculated as the number of age classes above three years present in the population on each reef in each year. A_{90} and A_R values were compared using ANOVA with the same design as for the comparison of K and L_∞.

4.2.2.3. Mortality

Mortality rates of *P. leopardus* were estimated from age-based cohort-specific catch curves (Beverton and Holt 1957; Ricker 1975) using log-linear regressions of

frequency of individuals of each cohort caught in successive years, where the slope of the relationship between log-frequencies and ages provides an estimate of instantaneous total mortality (Z; Beverton and Holt 1957) for a cohort. Mortality rates were only estimated for individuals that were four years or older (Mapstone et al. 2004). Only cohorts with at least one individual per age class sampled in a minimum of three consecutive years were included in the analysis.

Sample numbers were sufficient to compare mortality rates of the cohorts that were 5 and 6 years old (yo) in 1995 among two reefs within the Lizard Island and Townsville Regions and three reefs within the Mackay and Storm Cay Regions. Mortality rates of the 4, 6 and 7 yo (in 1995) cohorts could be compared among two reefs from the Townsville Region and three reefs within the Mackay and Storm Cay Regions. ANCOVA was used to compare among regions and reefs within regions the slopes of the regression relationship between ln transformed frequency (dependent variable) and year, meaning that each regression represented a single cohort. Year was included as the covariate to conform to the assumption that each group in the ANCOVA was based on the same range of values for the independent variable (Winer et al. 1992). Sums of squares and degrees of freedom of interactions were pooled in a step-down fashion where the F-ratios of higher order interactions were ≤1. Pooling increases the degrees of freedom for the denominator and consequently the power of the test of remaining (unpooled) effects in the analyses.

The Student-Newman-Keuls (SNK) test for multiple comparisons of slopes and means (Zar 1996) was used to determine which slopes and means differed following significant effects in the ANCOVAs and ANOVAs, respectively.

4.3. Results

4.3.1. Spatial and temporal patterns of growth

4.3.1.1. Weight-length relationships

The ANCOVA showed significant variation among reefs within regions in the weight - length relationship of *P. leopardus* that also interacted with years (Table 4.2a). This interaction was explored further by separate ANCOVAs for each region with the factors reef (random) and year (fixed). In all regions there was a significant FL*Year*reef interaction (Table 4.2b), indicating that there were no persistent spatial differences in the weight – length relationship of *P. leopardus*. SNK comparisons of slopes revealed that there was a significant variation in the reef-specific weight - length relationship among years for most reefs in all regions (p < 0.05; Table 4.3), with the only exceptions being one reef in each of the Lizard Island (Reef 14114) and Townsville (Reef 18041) Regions. Most reefs showed a small but overall increase in the slope (*b*) of the reef-specific weight – length relationship with time, indicating that small *P. leopardus* were generally lighter and large fish generally heavier at a given FL in later years than in earlier years (p < 0.05; Fig. 4.1a-d). The patterns in each region were generally similar among most reefs. There was also small but significant variation among reefs within regions in most years in the Lizard Island and Townsville Regions, but less so in the Mackay and Storm Cay Regions (SNK, p < 0.05). The overall increase in the reef-specific slopes of the weight – length relationship with time was also evident in the significant main effect of year in the overall analysis (the slope in 1995 was significantly smaller than for all other years and 1996, 1997 were significantly smaller than 1998, 1999; p < 0.05; Table 4.3a). The consistency in this inter-annual pattern among almost all reefs may suggest that the overall Year effect (Table 4.2a) was indeed general and spatially

robust, although an unequivocal conclusion cannot be made without investigating this further.
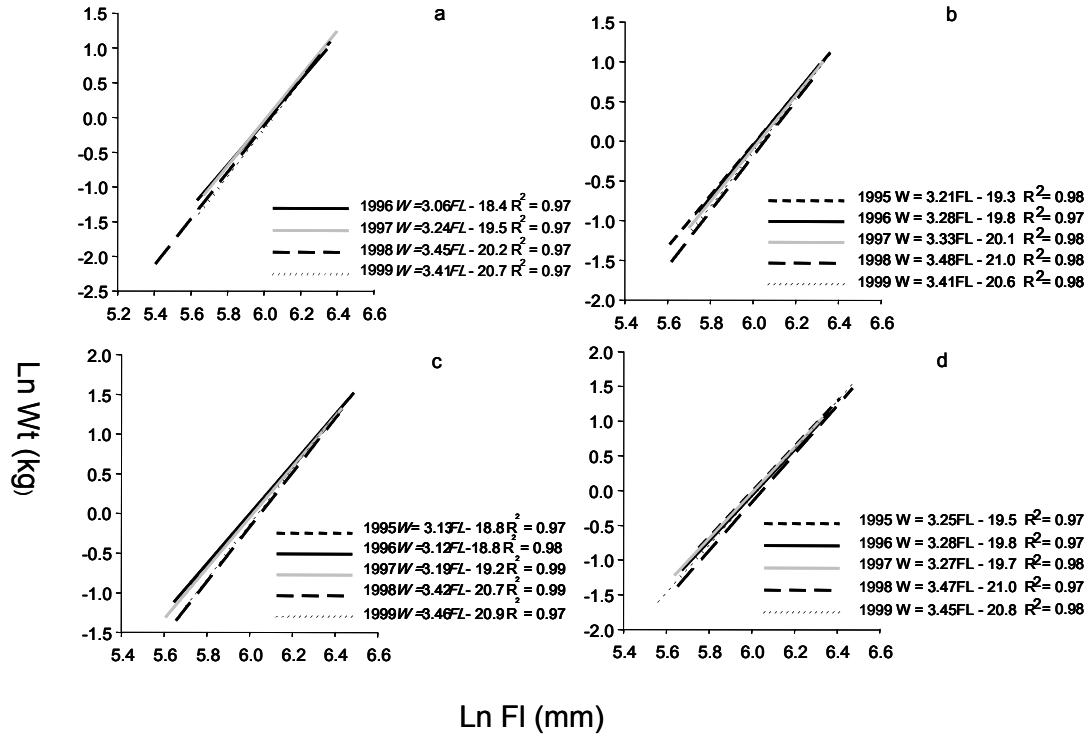
Figure 4.1 Regression relationships between ln weight (W; kg) and ln FL (mm) of *P. leopardus* collected between 1995 and 1999 from a reef in the a) Lizard Island (reef 14147) b) Townsville (reef 18071) c) Mackay (reef 20137) and d) Storm Cay (reef 21132) Regions on the GBR. The linear equation and correlation coefficient (R^2) of each regression relationship are also shown.

Table 4.2. Results of a) overall and b) region-specific ANCOVA homogeneity of slopes test comparing the slope of the relationship between body weight and the covariate FL of *P. leopardus* collected from four reefs in each of four regions in each of five years (1995 – 1999) on the GBR. Only interaction effects including the covariate are shown. p-values in bold indicate significant differences (p < 0.05) of the highest-order terms that legitimately could be explored further.

a)

Source of variation	$df_{1,2}$	Mean Square	F	p
FL * Year	4, 28	0.315	14.61	<0.0001
FL * Region	3, 11	0.100	3.56	0.0509
FL * Reef(Region)	11, 9968	0.028	4.42	<0.0001
FL * Year * Region	11, 28	0.028	1.29	0.2813
FL * Year * Reef(Region)	28, 9968	0.022	3.38	**<0.0001**

b)

Region	Source of variation	df	Mean Square	F	p
Lizard Island	FL * Year	3	0.027	3.78	0.0010
	FL * Reef	2	0.018	2.51	0.0816
	FL * Year * Reef	4	0.047	6.49	**<0.0001**
	Error	870	0.007		
Townsville	FL * Year	4	0.038	6.21	<0.0001
	FL * Reef	3	0.064	10.42	<0.0001
	FL * Year * Reef	8	0.024	3.96	**0.0001**
	Error	2353			
Mackay	FL * Year	4	0.260	45.60	<0.0001
	FL * Reef	3	0.012	2.21	0.0846
	FL * Year * Reef	8	0.011	1.96	**0.0479**
	Error	3300			
Storm Cay	FL * Year	4	0.190	26.98	<0.0001
	FL * Reef	3	0.015	2.13	0.0945
	FL * Year * Reef	8	0.017	2.35	**0.0163**
	Error	3445			

Table 4.3. Results of the SNK tests for comparisons of slopes of the relationship between body weight and the covariate FL of *P. leopardus* among years 1995 to 1999 for each reef within regions. Reefs and years with different letters indicate significant differences ($p < 0.05$). When no letter is assigned to a reef it means that that reef was not included in the analyses.

Region	Reef	1995	1996	1997	1998	1999
Lizard Island	14114			A	A	A
	14118		A	B	C	
	14147		A	AB	B	B
Townsville	18039	A	AB	AB	AB	B
	18041	A	A	A	A	
	18071	A	AB	B	C	BC
	18074	A	B			
Mackay	20136	A	B			
	20137	A	A	A	B	B
	20138	A	A	A	B	
	20142	A	AB	A	C	B
Storm Cay	21130	A	B			
	21131	A	A	A	B	A
	21132	A	A	A	B	B
	21133	AB	C	C	B	

4.3.1.2. Length of 4-year old fish

There were also significant differences in average FL of 4-year old *P. leopardus* among reefs within regions that interacted with years (Table 4.4a). Further, there was a significant overall main effect of region (Table 4.4a). Average FL of four-year-old *P. leopardus* was similar in the Lizard Island and Storm Cay Regions, but differed from those in Townsville and Mackay ($p < 0.05$; Fig. 4.2). To explore further the significant Year*reef(Region) interaction effect, ANOVAs were computed for each region separately (Table 4.4b). These results revealed that the interaction effect was due to a significant reef*Year effect only in the Storm Cay Region (Table 4.4b). Average FL of 4-year olds increased over the five year period on three of the four reefs in this region, although the relative change in FL from year

to year differed among reefs (SNK, p < 0.05; Fig. 4.4). In contrast, there was no significant variation in FL of 4-year olds in the Townsville Region and a significant main effect of reef only in the Lizard Island and Mackay Regions (Table 4.4b; Fig. 4.3a and b). There was also a significant overall increase in FL with time in both the Lizard Island and Mackay Regions (Table 4.4b; SNK, p < 0.05).

Table 4.4. Results of a) overall and b) region-specific ANOVAs comparing average FL (mm) of 4-year old *P. leopardus* collected from four reefs in four regions in each year between 1995 and 1999 of the GBR. p-values in bold indicate significant differences (p < 0.05) of the highest-order terms that legitimately could be explored further.

a)

Source of variation	$df_{1,2}$	Mean Square	F	p
Year	4, 28	24929.490	9.94	<0.0001
Region	3, 12	75186.616	3.54	**0.0483**
Reef(Region)	12, 2707	21252.190	2.82	0.0008
Year * Region	12, 28	4428.961	1.77	0.1049
Year * Reef(Region)	28, 2707	2507.023	1.60	**0.0246**

b)

Region	Source of variation	df	Mean Square	F	p
Lizard Island	Year	4	15540.749	10.63	**<0.0001**
	Reef	3	53481.406	36.59	**<0.0001**
	Year *Reef	6	1480.457	1.01	0.4164
	Error	382			
Townsville	Year	4	3085.948	1.72	0.1447
	Reef	3	3926.198	2.18	0.0889
	Year * Reef	7	2101.624	1.17	0.3185
	Error	536			
Mackay	Year	4	12880.505	8.46	**<0.0001**
	Reef	3	17350.870	11.40	**<0.0001**
	Year * Reef	7	1470.208	0.97	0.4550
	Error	967			
Storm Cay	Year	4	11859.616	7.74	<0.0001
	Reef	3	10250.285	6.69	0.0002
	Year * Reef	8	4538.875	2.96	**0.0028**
	Error	822			
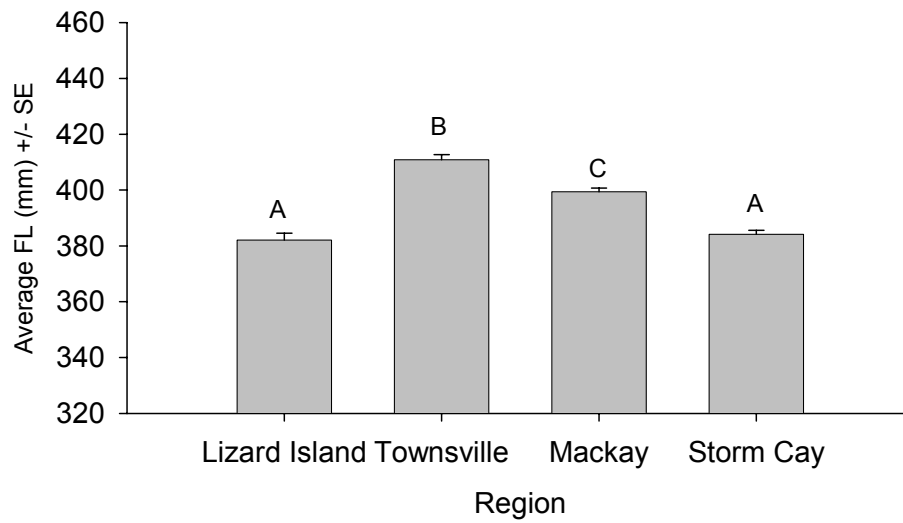
Figure 4.2 Average FL (mm) of 4-year old *P. leopardus* from four regions (data pooled across reefs and years) on the GBR. The letters above the bars represent the results of SNK multiple comparison tests. Similar letters indicate no significant differences among means and different letters indicate a significant difference (p < 0.05).
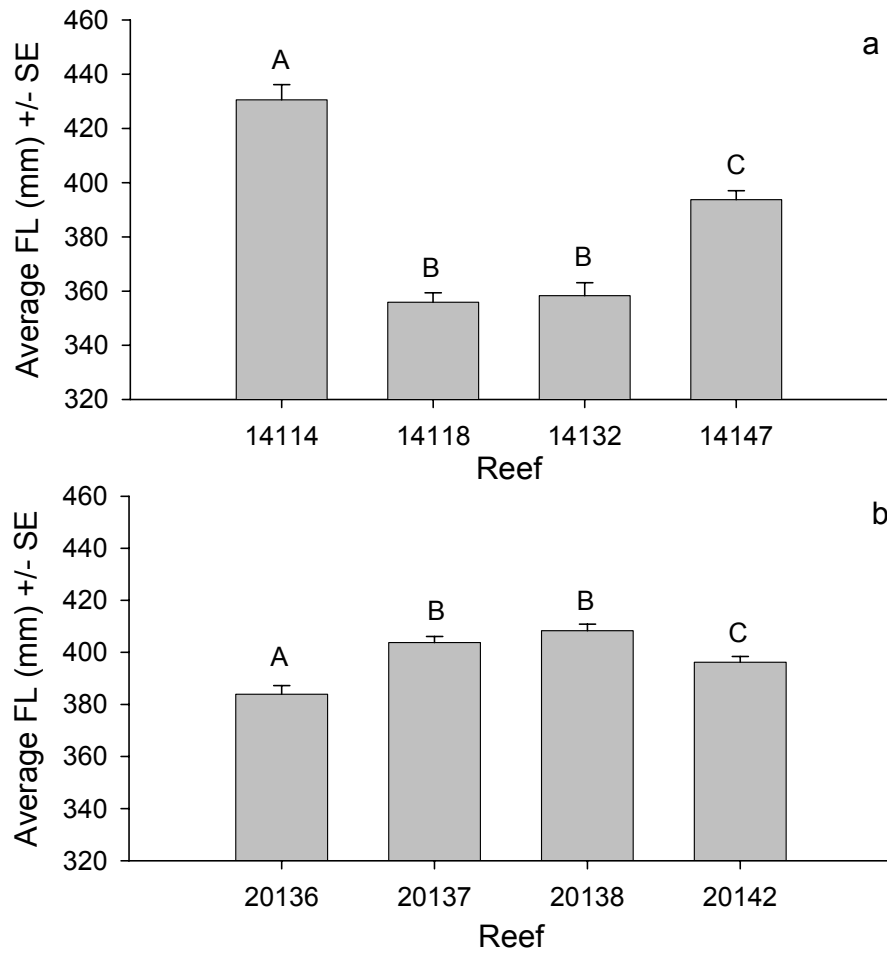
Figure 4.3 Average FL (mm) of 4-year old *P. leopardus* collected from four reefs in the a) Lizard Island and b) Mackay Regions on the GBR. The letters above the bars represent the results of SNK multiple comparison tests. Similar letters indicate no significant differences among means and different letters indicate a significant difference ($p < 0.05$).
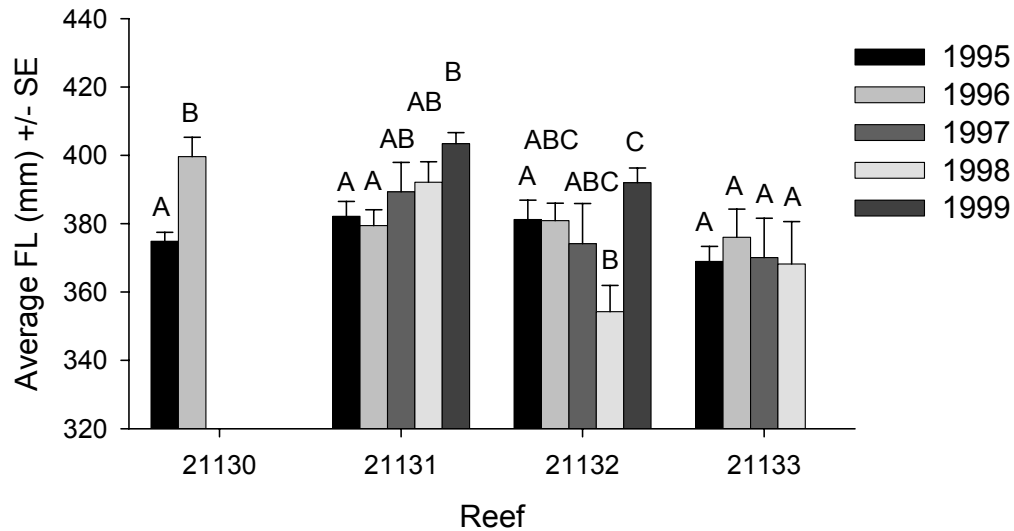
Figure 4.4 Average FL (mm) of 4-year old *P. leopardus* from four reefs collected yearly between 1995 and 1999 in the Storm Cay Region on the GBR. The letters above the bars represent the results of SNK multiple comparison tests. Similar letters indicate no significant differences among means and different letters indicate a significant difference ($p < 0.05$). (There are no bars for 1997-1999 for 21130 and 1999 for 21133 as these reefs were open to fishing during these years, and the data were not included in the analyses.)

There was a strong correlation between weight and length of four year old *P. leopardus*. Thus, similar patterns appeared in comparisons of fish weight among reefs and regions as in comparisons of FL and so the results of the weight analyses are not included here.

4.3.1.3. Von Bertalanffy growth parameters

Von Bertalanffy growth curves for *P. leopardus* differed considerably among regions and over years (Fig. 4.5). Estimates of the VBGF parameter L_∞ varied significantly only among years averaged over all reefs and regions (Table 4.5a). Estimated L_∞ was

greater in the first year of sampling (1995) than in later years (1997 to 1999; SNK, p

< 0.05; Fig. 4.6).
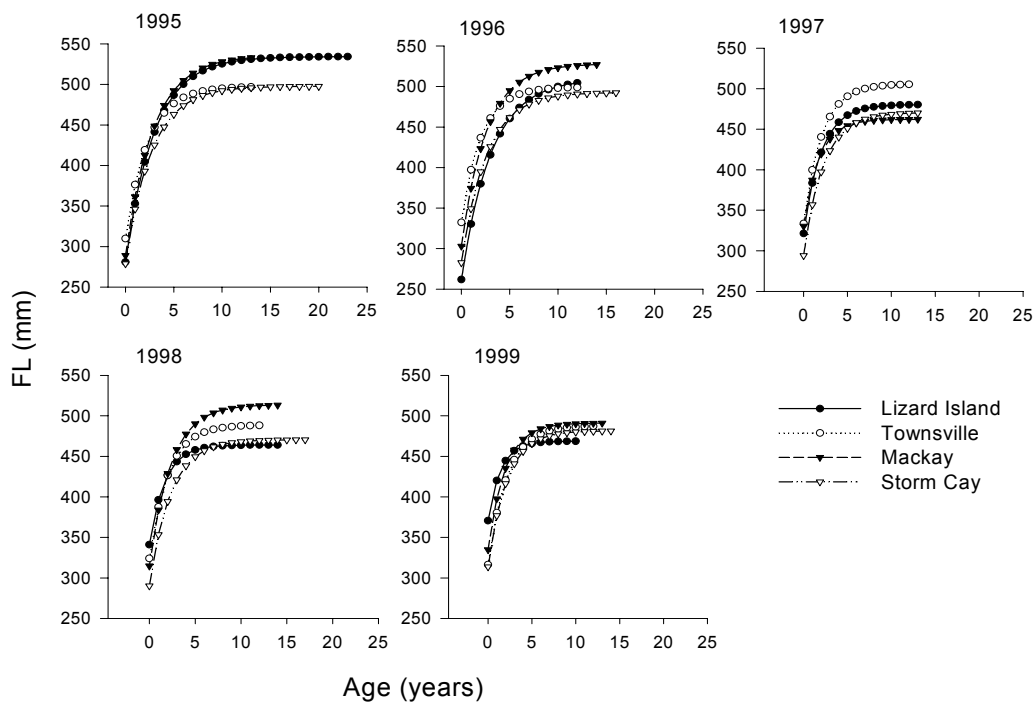
Figure 4.5 VBGF fitted to *P. leopardus* length-at-age data collected from four regions over five years (1995 to 1999) on the GBR.

Table 4.5. Results of the ANOVA comparing average VBGF parameter L_∞ estimated from *P. leopardus* collected from four reefs in four regions in each year between 1995 and 1999 of the GBR. p-values in bold indicate significant differences (p < 0.05).

Source of variation	df	Mean Square	F	P
Year	4	3770.570	6.37	**0.0007**
Region	3	2391.440	1.96	0.1747
Year * Region	12	935.946	1.58	0.1487
Reef(Region)	12	1223.443	2.07	0.0514
Error	31	591.627		
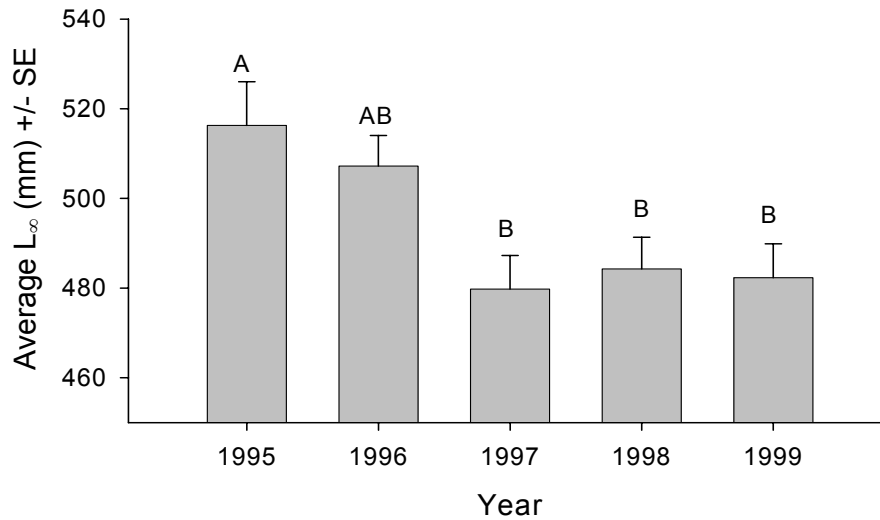
Figure 4.6 Average L_∞ (mm) of *P. leopardus* collected between 1995 and 1999 on the GBR. The letters above the bars represent the results of the SNK test. Similar letters indicate no significant differences among means and different letters indicate a significant difference (p < 0.05). (Data are pooled across four reefs in each of four regions.)

4.3.2. Longevity and age richness

The average 90th percentiles of age (A_{90}) showed a significant Year*Region interaction and both A_{90} and average age richness (A_R) showed significant Reef(Region) effects (Table 4.6a and b). The Year*Region interaction for A_{90} was due to lower values of A_{90} in Lizard Island and Townsville Regions than in the two southern regions in 1999 (SNK, p< 0.05; Fig. 4.8a) and significantly different values between 1996 and 1999 in the Lizard Island Region (SNK, p < 0.05; Fig. 4.8a). The variation in A_{90} and A_R among reefs was generally low, with significant differences among reefs in A_{90} found only in the Lizard Island Region and differences among reefs in A_R in the Lizard Island and Townsville Regions (SNK, p < 0.05; Fig. 4.8b and 4.9).

Table 4.6. Results of the ANOVA comparing average (a) 90th percentiles of age (A_{90}) and (b) age richness (A_R) of *P. leopardus* from four reefs in four regions in each year between 1995 and 1999 on the GBR. p-values in bold indicate significant differences ($p < 0.05$) of the highest-order terms that legitimately could be explored further.

a) A_{90}

Source of variation	df	Mean Square	F	p
Year	4	2.989	5.50	0.0018
Region	3	4.172	1.80	0.2007
Year * Region	12	1.733	3.19	**0.0046**
Reef(Region)	12	2.318	4.26	**0.0006**
Error	31			

b) A_R

Source of variation	df	Mean Square	F	p
Year	4	2.401	1.97	0.1230
Region	3	12.300	2.02	0.1646
Year * Region	12	1.088	0.89	0.5646
Reef(Region)	12	6.083	4.98	**0.0002**
Error	31			
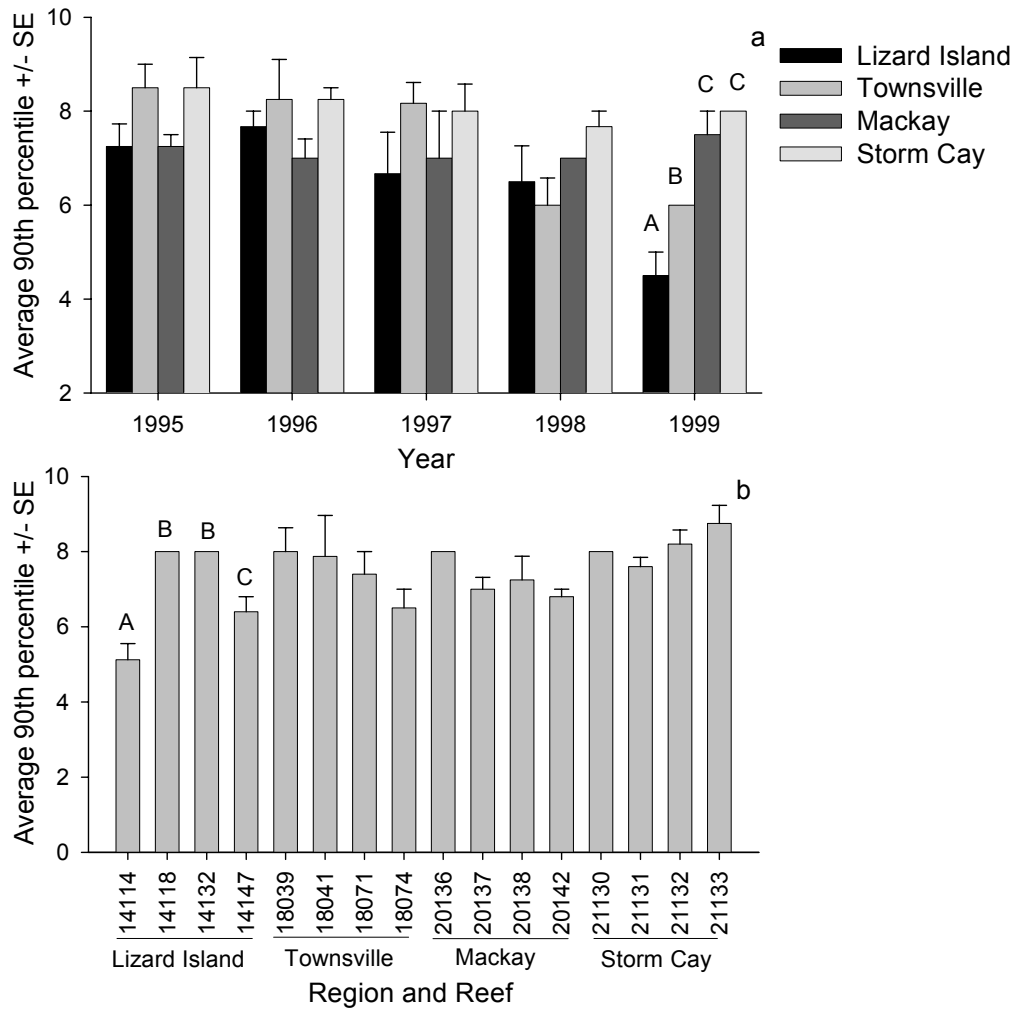
Figure 4.7 Average 90th percentiles of age of *P. leopardus* from a) four regions within each of five years between 1995 and 1999 and b) four reefs within four regions (data pooled across years) on the GBR. The letters above the bars represent the results of SNK tests. No letters or similar letters indicate no significant differences among means and different letters indicate a significant difference ($p < 0.05$).
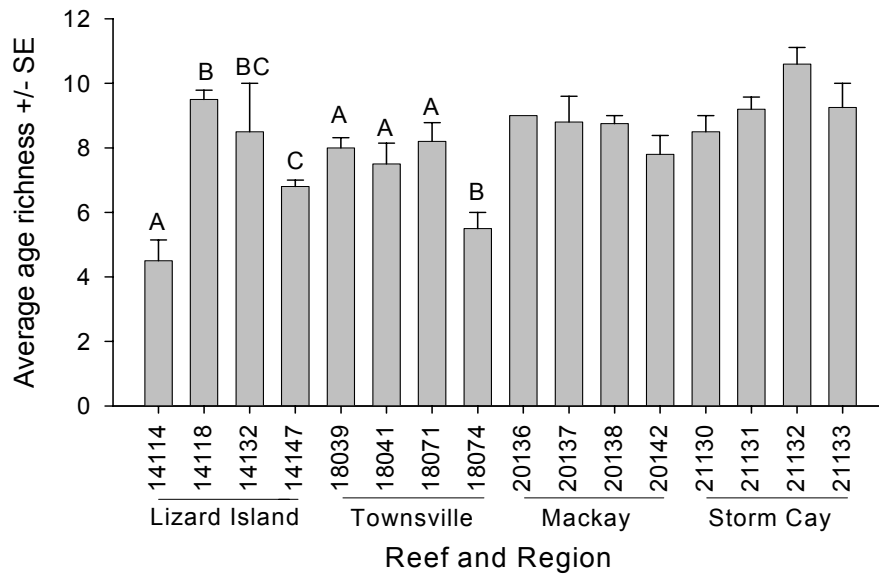
Figure 4.8 Average age richness of *P. leopardus* from four reefs within four regions on the GBR (data pooled across years). The letters above the bars represent the results of SNK tests. No letters or similar letters indicate no significant differences among means and different letters indicate a significant difference (p > 0.05).

### 4.3.3. Patterns of mortality

No significant differences were detected in mortality rates between the 5 and 6 yo cohorts or among regions or reefs within regions for these cohorts. Mortality rates differed significantly among the 4, 6 and 7 yo cohorts, however, as well as among reefs within regions (Table 4.7). Although the ANCOVA indicated significant reefs within regions and cohort effects, the SNK tests were not sufficiently powerful to discriminate those effects unambiguously. The regression plots of frequencies versus year and the estimated mortality rates (i.e., slope values) indicated that over all regions the 4 yo cohort showed a lower rate of mortality than the 7 yo cohort (Fig. 4.10) and more variable mortality rates among reefs in the Townsville and Mackay Regions than in the Storm Cay Region (Fig. 4.11).

Table 4.7. Results of the ANCOVA comparing mortality rates among reefs and Regions for the 4, 6 and 7 yo cohorts of *P. leopardus* sampled between 1995 and 1999 on the GBR. Only final analyses resulting from pooling terms with $F \leq 1$ and interaction effects including the covariate are shown. p-values in bold indicate significant differences ($p < 0.05$).

Source	df	Mean Square	F	p
Year * Region	2	0.0380	0.07	0.9340
Year * Reef(Region)	5	0.5489	2.49	**0.0392**
Year * Cohort	2	1.6885	7.66	**0.0010**
Year * Region * Cohort	4	0.2198	1.00	0.4154
Error	70	0.2206		
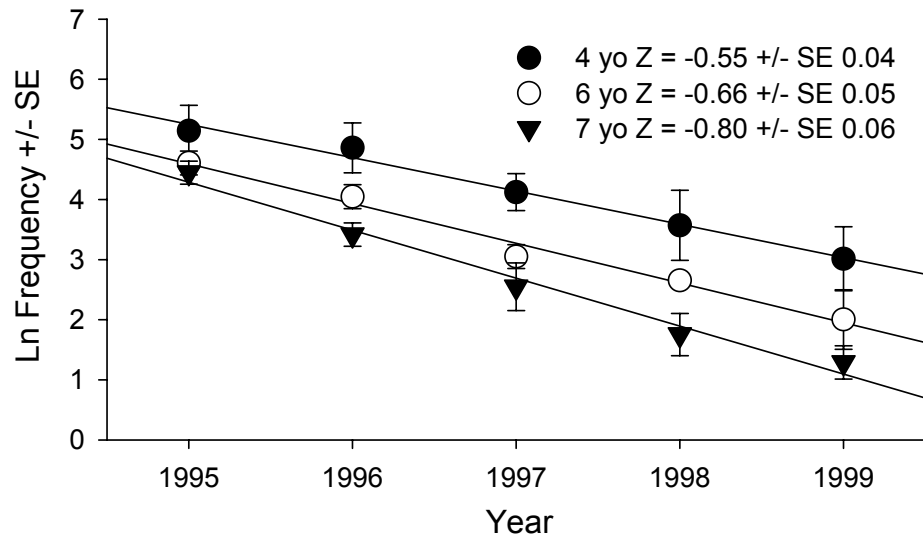
Figure 4.9 Cohort-specific mortality rates (±SE) for three cohorts (4, 6 and 7 yo) of *P. leopardus* from four regions on the GBR. The slope values (Z±SE) are presented for each cohort, with the slope values representing the estimated mortality rates.
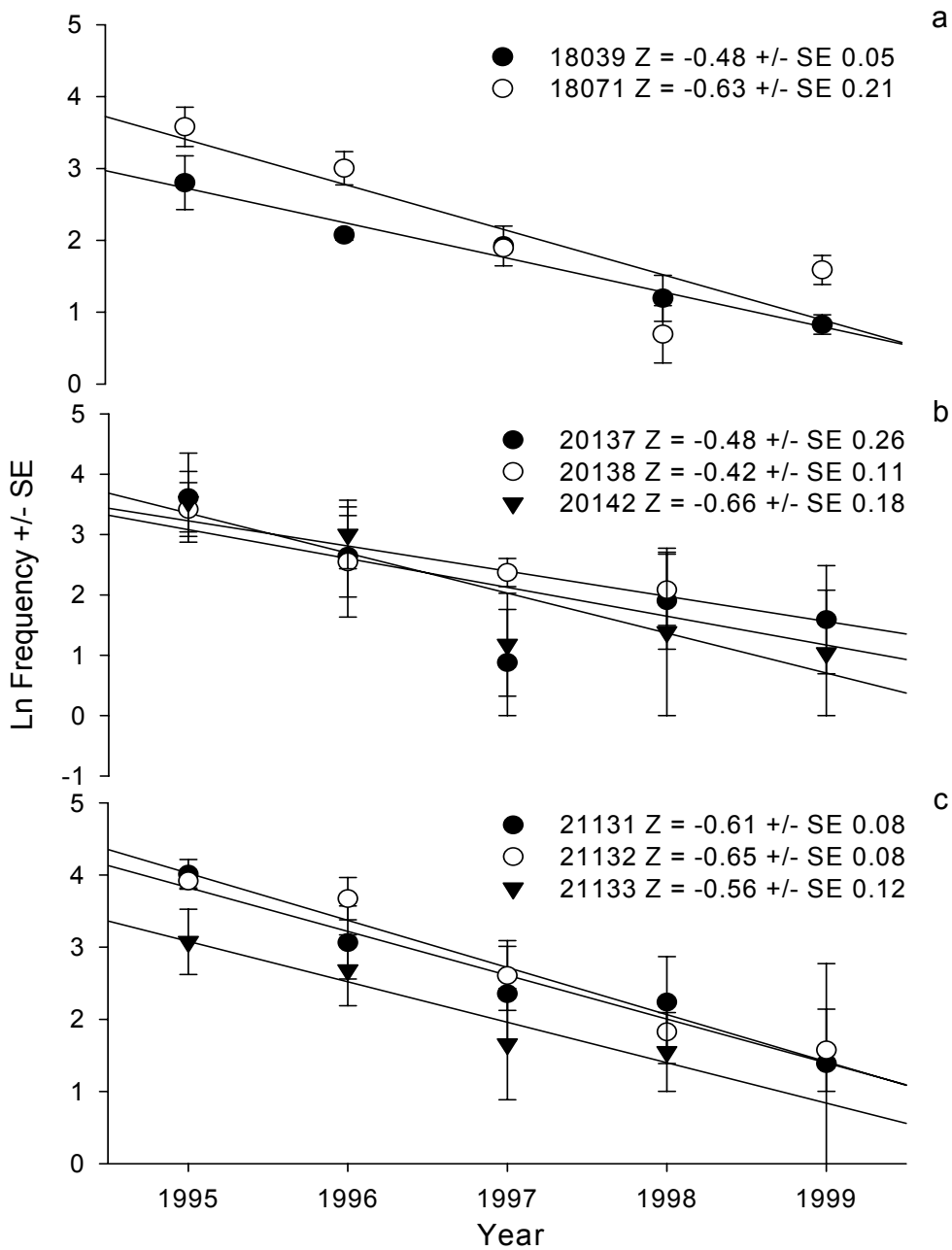
Figure 4.10 Mortality rates (±SE) of *P. leopardus* estimated by cohort-specific catch curves from (a) two reefs in the Townsville Region, and three reefs within the (b) Mackay and (c) Storm Cay Regions on the GBR. Data were averaged over the 4, 6 and 7 yo cohorts. The reef name and slope values (Z±SE) are presented, with the slope values representing the estimated mortality rates for each reef.

4.4. Discussion

4.4.1. Patterns in life history characteristics as an indication of stock structure

The results from this study indicate that the GBR population of *P. leopardus* consists of a complex network of subpopulations, groups of subpopulations (i.e., regions) and potential stocks with persistent differences in life history parameters; supporting results from analyses of otolith chemistry (Chapter 2) and morphology (Chapter 3). Mortality rates and most growth parameters of *P. leopardus* varied among neighbouring reef subpopulations separated by only hundreds to thousands of metres within regions, while some aspects of growth also varied among larger regional scales (Table 4.8). Whilst several growth patterns also varied across years, some persisted through time, indicating potential stock structure that was temporally stable at both fine and broad spatial scales. Mortality rates also varied among specific cohorts, with overall mortality rates fluctuating as much as 68%. There were differences in longevity among regions that also varied across years, and some persistent differences in age richness and longevity among reefs within regions (Table 4.8).

Table 4.8. Summary of statistically significant results (X) of spatial and temporal patterns in life history characteristics of *P. leopardus* on the GBR. Wt = weight, FL = fork length, L_∞= asymptotic length (VBFG parameter), A_{90} = 90th percentile of age, A_R = age richness.

Variable	Reef(R)*Year	Region*Year	Reef(R)	Region	Year	Cohort
Wt-FL	X				X	
FL4yo	X		X	X		
Z			X			X
L_∞					X	
A_{90}		X	X			
A_R			X			

These results are consistent with other studies of *P. leopardus* that show regional differences in reproductive strategies (Adams et al. 2000; Adams 2002), population densities (Ayling et al. 2000; Mapstone et al. 2004), mean size and age (Mapstone et al. 2004) and reef to reef variability in mortality (Russ et al. 1998). Combined also with other multi-scale studies of tropical reef fishes (e.g., Adams et al. 2000; Gust et al. 2002; Kritzer 2002; Kingsford and Hughes 2005; Robertson et al. 2005b), these results suggest that complex population structures are a feature of many tropical reef fishes. Moreover, it is evident from these results that a hierarchical sampling design is essential to enable separation of the range of values of life history characteristics at different spatial scales. Such separation is particularly important to avoid erroneously ascribing characteristics to broad-scale stocks that are in reality features of variation among local scale sub-populations.

These results also emphasized the importance of a temporal component when investigating the population structure of coral reef fishes. The existence of temporal variability in life history characteristics has been reported frequently for temperate stocks (e.g. Begg et al. 1999a; Marteinsdottir and Begg 2002; Overholtz 2002), while my research and that of others suggest that such variability is also likely in tropical reef fishes (Russ et al. 1996; Williams et al. 2003; Begg et al. 2005). Life history characteristics are susceptible to changes in local environmental conditions (Yamahira and Conover 2002) and archipelagos of reefs show considerable physical and biological variation at a range of spatial and temporal scales (Wolanski 1994). It is therefore not surprising that *P. leopardus,* which rarely move among reefs post-settlement (Davies 1995; Zeller 1998; Zeller and Russ 1998), show corresponding variation in life history characteristics across a range of spatial and temporal scales. Repeated and simultaneous sampling of population components at appropriate scales

is important to minimize the risk of confounding spatial variation in life history characteristics with circumstances that appear only at particular times of sampling.

4.4.2. Potential processes causing spatial and temporal patterns in life history characteristics

Differences in biological parameters or other phenotypic expressions across spatial scales do not indicate whether the underlying causes are genetic, environmental or both (Ihssen et al. 1981). Van Herwerden et al. (2006) showed that there was very little genetic variation across the GBR in either mitochondrial or nuclear markers of *P. leopardus*, with the exception of some genetic differentiation in the Townsville Region, suggesting larval dispersal across most regions. Such genetic markers are neutral to selection, however, and do not provide information about possible differences in genes that influence fitness (Conover 1998). Adaptive traits are faster evolving and may exhibit structure at much finer spatial scales than neutral markers, even in marine populations with the potential for great levels of gene flow (Conover 2000). Thus, spatial variation in life history characteristics of *P. leopardus* could be the result of local adaptation or reflect the naturally occurring environmental variability among reefs and regions (Wolanski 1994).

Environmental processes that could affect life history characteristics on a regional scale might be related to continental shelf depth and width (i.e., the shelf on the east coast of Queensland gets deeper and wider with increasing latitude), terrestrial influences and upwelling, or features varying with latitude, such as, temperature. Spatial differences in life history characteristics have commonly been related to temperature gradients associated with latitude (e.g., Choat et al. 2003).

Although there were no persistence latitudinal trends in life history characteristics, relatively small temperature variations regionally might interact with other biological processes to contribute to regional differences in the biology of *P. leopardus*.

Temperature may also explain some temporal differences in life history characteristics. For example, longevity decreased from 1995 to 1999 in the Lizard Island Region over the sampling period (Fig. 4.8a). This could be due to an increasing trend in mean water temperature between 1996 and 1999 (26 to 29.5° C) that was not recorded on reefs at the southern distribution of the GBR (AIMS[7]). This observation is consistent with other studies showing that individuals live longer in colder temperatures than their conspecifics in warmer temperatures (Meekan et al. 2001; Choat et al. 2003; Ruttenberg et al. 2005).

A combination of density-dependent processes has been suggested as a likely explanation for finer among-reef scale variations in mortality rates (Gust et al. 2002; Williams et al. 2003), growth rates (Gust et al. 2002, Kritzer 2002) and average ages (Gust et al. 2002). Differences in density of *P. leopardus* among reefs within regions have been reported (Ayling et al. 2000) indicating at least the existence of a prerequisite for density-dependent processes that could be explaining small-scale spatial patterns in biology.

Fishing could also have affected some of the life history characteristics of *P. leopardus*. Although the sampled reefs were closed to fishing during the study period, potential illegal fishing and legal historic fishing on these reefs prior to closure in 1987 may have altered some of the life history characteristics of cohorts that were still alive during the time of this study. For example, Williams et al. (2003) proposed that historic fishing (1960s – 1980s) influenced the differences among

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[7] Australian Institute of Marine Science. 2005. Unpubl. Data. (Available from http://www.reeffutures.org/topics/bleach/loggers_advance.cfm) [Accessed on: 16 March 2006.]

regions in demography of *Lethrinus miniatus* on the GBR. Although there are no records of historic and or illegal fishing pressure on individual reefs, the possibility exists that historic fishing had some effect on growth and cohort strength (and so estimates of A_{90}) of *P. leopardus* cohorts over 8 years old in 1995 to 12 years old in 1999. Furthermore, illegal fishing could have affected age structures (and so estimates of A_R) by selectively removing the older age classes. Historic fishing is not likely to have influenced the variation in mortality rates however, as *Z* was only estimated for individuals (4 to 7 yo) that were either not alive before the study period or too young to be caught by the fishing gear.

4.4.3. Conclusion and future directions

Management and assessment of exploited stocks, including stock identification should be an evolving process (Kutkuhn 1981; Begg 2005), where key life history characteristics of targeted species are continuously monitored. The results of this Chapter showed that temporal variation in life history characteristics of *P. leopardus* is as significant as the spatial variation present. Potential stocks with persistent differences in biology, therefore, can only be revealed conclusively from a comparison of parameters through time such that temporal variation in stock structure can be either ruled out or accounted for when interpreting spatial patterns. Spatial and temporal variation in the biology of *P. leopardus* should be incorporated into future simulation studies to evaluate consequences to individual stocks, as well as to the entire population (Chapter 5). Further research is also required to determine the number of stocks present on the GBR, stock boundaries and the degree of larval connectivity among them.

Spatial differences in some features of the biology of *P. leopardus* suggest the potential for significant variability in productivity among reef-associated and regional subpopulations or stocks. In combination with unevenly distributed fishing effort on the GBR, these results imply that the single management unit currently considered for *P. leopardus* may need to be divided into smaller units to closer reflect those of the biological units or stocks with different productivities and, ultimately, capacities to support optimised sustainable harvest strategies.

Chapter 5. Implications of spatial variability in life history characteristics for harvest strategy evaluations.

5.1. Introduction

The importance of stock structure and spatial variation of life history characteristics in stock assessment and harvest strategy development has been realised for decades, but the failure to ensure a match between the spatial scale of biological and management units is a common and unresolved problem (Smedbol and Stephenson 2001; Stephenson 2002). Data are frequently aggregated across stocks despite the risk of losing less productive stocks and threatening the sustainability of the entire population (Ricker 1958; Daan 1991; Frank and Brickman 2000; Smedbol and Stephenson 2001). Aggregating data across stocks for the purpose of assessment and management may also lead to underestimation of the maximum sustainable yield of the population, which may be less than the combined yields of individual stocks (Paulik et al. 1967). Further, the most appropriate management strategy for one stock may not necessarily be the most appropriate for another (Crozier et al. 2004; Rahikainen and Stephenson 2004). A major challenge facing fisheries scientists and managers, therefore, is not only to identify individual stocks, but also to determine the magnitude of differences required in life history characteristics among stocks to warrant separate management arrangements, particularly of species that are population rich (Iles and Sinclair 1982) and connected by larval dispersal.

Spatial variability in life history characteristics has recently been recorded for several coral reef fishes at a range of scales (e.g., Russ et al. 1996; Russ et al. 1998; Gust et al. 2001; Adams 2002; Kritzer 2002; Williams et al. 2003; and see Chapter 4), but the stock structures of these species are uncertain. However, results from this

thesis indicated potential stocks of *P. leopardus* with persistent differences in life history characteristics at both regional (100s km) and inter-reef (100s -1000s m) spatial scales (Chapter 4). These results question whether most of the current (2002–2004) harvest regulations, which are applied uniformly across the entire GBR World Heritage Area, are appropriate for this species or optimal for the fishery. This issue will remain unresolved until the implications of the observed spatial variability have been investigated and the sustainability of *P. leopardus* determined.

The main aim of this chapter was to address the first part of this question related to the uniform harvest strategy for the fish. General scenarios were simulated of what might happen if the stock structure was incorrectly interpreted when considering management of a harvested coral reef fish population. Although *P. leopardus* displayed stock structure (i.e., persistent differences in life history characteristics) at both the finer reef and larger region spatial scales (Chapter 4), this research took the initial first step to examine consequences of stock structure at the larger scale. The larger spatial scale was considered primarily because that is more likely to be a scale at which managment strategies could be tailored to account for specific variation in biological features of a stock. Information from *P. leopardus* was used in the simulations to resemble realistic differences that may occur among regional stocks and in the context of a real fishery. The simulations were not, at this stage, however, intended to investigate the consequences of all the nuances of spatial and temporal variation in life history characteristics found for the *P. leopardus* population on the GBR (including those found Chapter 4) or to represent a formal stock assessment procedure.

The aim of this research was achived using the Effects of Line Fishery Simulator, ELFSim, designed for management strategy evaluation (MSE) and the *P.*

leopardus population on the GBR (Mapstone et al. 2004). An MSE generally involves evaluating the consequences of various management strategies on a population through a set of resource or fishery performance indicators, so that fishery and biological responses to different strategies can be compared in relation to various management objectives identified by stakeholders (Smith 1993). Whilst the main purpose of ELFSim is to evaluate potential management strategies for the *P. leopardus* fishery in the context of multiple stakeholder objectives (Mapstone et al. 2004), it provided a tool to examine the consequences of spatial variation in life history characteristics observed for a harvested population with a complex spatial structure, composed of over 3000 reef based subpopulations and potential stocks connected by larval dispersal (Chapter 4).

The specific objectives of this Chapter were therefore:

1. to compare the implications on assessments of the relative spawning biomass (RSB; biomass of mature females) of

    i. accounting for regional (100's km) variation in growth and mortality observed for *P. leopardus*;

    ii. ignoring such regional variation and aggregating data across regions with assumed homogeneity of life history characteristics; and

2. to compare the impacts on RSB of alternative strategies for regulating fishing effort with or without reference to regional variation in the life history characteristics of harvested *P. leopardus*.

5.2. Materials and methods

5.2.1. ELFSim overview

There are three model components to ELFSim: (i) biological operating model; (ii) fishery model; and (iii) management model. The biological model simulates the 3822 reef-associated adult subpopulations of *P. leopardus* and larval dispersal amongst them on the GBR (Fig. 2.1 in Chapter 2). Successful dispersal of larvae among reefs varies stochastically and decreases with increasing distance between reef pairs, and some self-recruitment to natal reefs is allowed. There is no movement of post-settlement *P. leopardus* among reefs (Davies 1995; Zeller 1997). The biological model is age-, sex- and size-structured and is parameterised from empirical data collected as a part of the Effects of Line Fishing (ELF) Experiment (see Chapter 2; Campbell et al. 2001; Mapstone et al. 2004), and other published studies (see Mapstone et al. 2004). Individuals aged 0 and 1 years are subject to density-dependent mortality and the model allows for temporal variation in age-specific natural mortality.

The fishery model features fishing by the commercial, charter and recreational sectors of the GBR Reef Line Fishery. The biological model is initialised from an assumed unexploited status in 1965 to 1998 and tuned to reproduce the reported historical fishing catch from 1989-1998 given the known amount of fishing effort during the same years. The biological model is then run forwards in time (projections) and interacts dynamically with various effort scenarios prescribed under static management strategies that can also include other management instruments (e.g., seasonal or spatial closures, alternate minimum legal sizes). During the projection period (in this case from 1999-2025), the fishery model allocates fishing effort to reefs under the constraints imposed by the management strategy

implemented by the management model. The annual amount of effort for each sector in the projection period is specified and distributed among months according to the historic empirical monthly distribution of effort. The effort is then distributed spatially to 6 x 6 nautical mile grid cells according to a ranking process based on prior (up to the immediately preceding time step) cell-specific catch and effort levels, and whether the cell is open or closed to fishing. The effort allocated to a cell is subsequently distributed to the reefs within each cell in proportion to reef perimeter. The amount (kg) of *P. leopardus* caught per month from each reef depends on reef specific effort, fishable biomass, the specified gear selectivity, minimum legal size (MLS) limits and catchability coefficients (which are sector-specific).

In the management model, a range of harvest strategies can be specified such as effort level, area closures and MLS. The different management strategies can then be compared by examining the values of a range of performance indicators such as relative spawning biomass (RSB), relative available biomass (biomass selected by the gear and above the MLS), catches, catch rates and size and age metrics, among others. In this Chapter, I investigated the patterns of RSB of mature females resulting when different effort-regulated harvest strategies were applied to the *P. leopardus* subpopulations under alternative scenarios of spatial variation in life-history characteristics. For further details of ELFSim see Mapstone et al. (2004).

5.2.2. Model specifications

Although ELFSim is developed to include the entire GBR World Heritage Area (GBRWHA), only four regions were included in this study in line with the stock identification studies (Chapter 2-4): Lizard Island, Townsville, Mackay and Swains Regions (Fig. 2.1), encompassing 1800 reef subpopulations of *P. leopardus*. These

four regions have been sampled over several years as part of the ELF Experiment to collect biological information for *P. leopardus* and other species caught in the GBR line fishery (see Chapters 2-4). Empirical estimates of region-specific growth and mortality could thus be used in ELFSim to explore consequences of spatial variation in vital life history rates that influence relative spawning biomass (RSB). A combination of four spatial life history and five effort scenarios were modelled (Table 5.1). The suite of simulations allowed analysis of the effects of general and region-specific growth crossed with effects of general and region-specific mortality under the five effort scenarios imposed on each of the life history scenarios.

Table 5.1. a) Life history and b) effort scenarios simulated to examine their implications for the relative spawning biomass of *P. leopardus*.

a)

Life history scenario	Details
No Spatial Structure (NoSS)	Individuals in all regions had the same (or overall) mortality (M) and growth (G) measured empirically as the average across regions.
Spatial Structure Growth & Mortality (SSGM)	Individuals in each region had region-specific growth (G_r) and mortality (M_r) rates measured empirically.
Spatial Structure Growth only (SSG)	Individuals in all regions had the same overall M but region-specific G_r.
Spatial Structure Mortality only (SSM)	Individuals in all regions shared the same overall G but had region-specific M_r.

b)

Effort scenario	Details
Expected Fishery Productivity Effort (EPE)	Effort was distributed among regions in proportion to the expected fishery productivity of *P. leopardus* subpopulations in the regions. Productivity was considered proportional to the average catch per unit effort (CPUE; fish/line hour) of legal sized coral trout estimated from structured line-fishing surveys over the years 1995-2000 on reefs in each region closed to fishing for 10+ years, (Mapstone et al., 2004).
Inverse of Expected Fishery Productivity Effort (InEPE)	Effort was distributed among regions in inverse proportion to the expected fishery productivity of the regions.
Status Quo Effort (SQE)	Effort was distributed among regions according to the regional distribution of effort recorded by the fishery in 1996[8].
Uniform Effort (UE)	Effort was distributed uniformly among regions.
No Effort (NoE)	No effort was applied to any region.

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[8] The 1996 catch level was used as a target in setting the current total allowable commercial catch (TACC). The effort level in this year is therefore assumed to approximate the effort level subjected to the population to catch the TACC, and thus used as the status quo level of effort in these simulations.

Catch per unit effort (CPUE) from ELF catch surveys on unfished reefs was taken as an indicator of underlying (unexploited) fishery productivity on reefs in each region. CPUE increased from north to south, with Lizard Island being the least productive region and Swains the most productive region (Lizard Island = 4.0, Townsville = 6.3, Mackay = 9.0 and Swains = 12.0 number of fish/line hour). The effort distributed among regions in each non-zero effort scenario (Table 5.1) was set to the total effort (in line-days) for the four regions in 1996 recorded in the fishery logbook and survey data collected by the Queensland Department of Primary Industries and Fisheries (Mapstone et al. 1996a; 2004; Williams 2002). Effort was calculated for the three different sectors of the fishery in 1996 and comprised 65165 line-days of commercial effort, 22821 line-days of charter-based recreational effort and 125491 line-days of private (individual) recreational effort.

The 'no effort' (UE, Table 5.1b) scenario was used to investigate the recovery rates of RSB in the hypothetical situation of closure of the fishery (Table 5.1b). The other four scenarios were used to investigate the consequences of potential shifts in effort among regions, either because of regulation or intrinsic fleet adjustments (Table 5.1b). For the 'status quo effort' (SQE) scenario, effort was distributed among regions and sectors according to distributions of effort reported for each sector in 1996, whilst for all other effort scenarios the same proportional distribution was used for all sectors (see Fig. 5.1a for proportions of the 1996 effort distributed among regions and sectors). Sector specific differences were not addressed in the results, however, since the performance indicator of interest (RSB) is independent of any sector specific activity.

My allocation of effort to regions under the different effort scenarios was distributed without explicit reference to the different amounts of available fishing

habitat in the regions. ELFSim allocates effort to reefs in proportion to their reef perimeter, however, and so the amount of effort per unit of reef perimeter (i.e., days of effort/km of reef perimeter) or effort density was computed for all regions under each effort scenario and the proportional distribution of effort density compared with the distribution of effort I imposed for each effort scenario (Fig. 5.1b). The results clearly indicated that differences in the regional distribution of absolute effort closely corresponded with regional patterns in effort density, indicating a relatively uniform amount of habitat (reef perimeter) among regions (Fig. 5.1b).
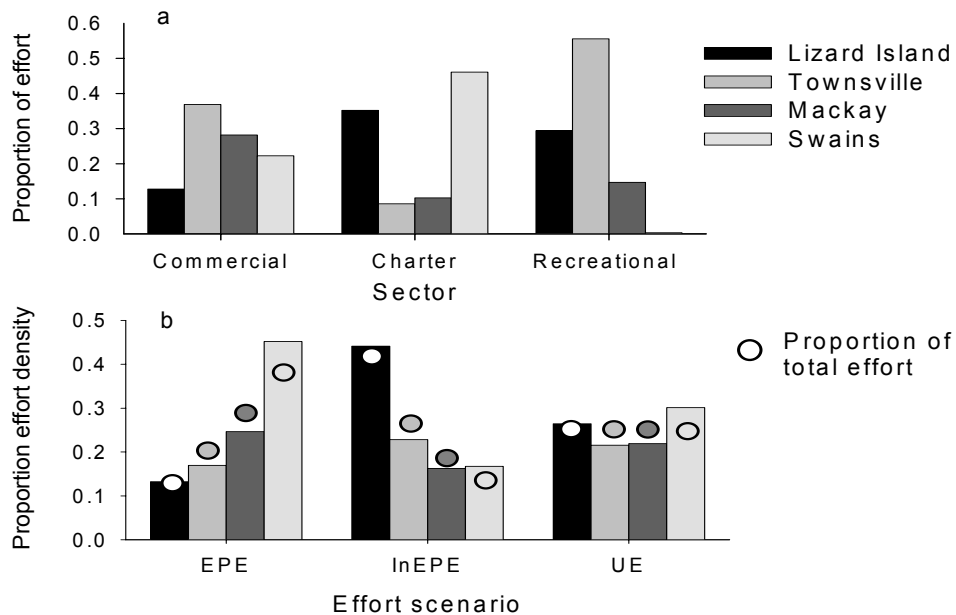
Figure 5.1 a) Proportion of total effort (line-days) under the status quo (SQE; 1996) effort scenario distributed for the commercial, charter and recreational sector in each of four regions; b) Proportion of effort density (regional effort per unit of reef perimeter) under the EPE, InEPE and UE scenarios compared to proportions of total effort distributed in each of four regions. These proportions were the same for all three sectors.

Approximately 33% of the GBRWHA was closed to fishing for all simulations reflecting the current (post-2004) regulations of the GBRMPA Zoning Plan 2003[9]. Ten replicate initialisations of the historical period (1965-1998) were run for each life history scenario, each based on the same empirically observed fishery data. Each of these initialisations was then followed by two replicate projections to 2025 under each effort scenario, resulting in a total of 20 replicate simulations for each combination of four life history and five effort scenarios (a total of 400 simulation projections).

5.2.2.2. Biological parameters

Estimates of growth and mortality rates were calculated for *P. leopardus* collected through structured line-fishing surveys as part of the ELF Experiment (Mapstone et al. 1996b; 2004; Campbell et al. 2001; Chapter 4). Whilst previous research of *P. leopardus* show variation in life history characteristics at several spatial and temporal scales (Chapter 4), this Chapter investigated the consequences of structure at the larger regional spatial scale. Life history information obtained in Chapter 4 was used to estimate regional parameters, without the intention of depicting the exact spatial structure of the population, but to resemble realistic difference in growth and mortality among hypothetical stocks. Although the ELF Experiment sampled reefs both open and closed to fishing in each region, only samples from the four reefs that had been closed to fishing were used here to parameterise the biological operating model of ELFSim. Whilst some levels of illegal fishing cannot be excluded (Mapstone et al. 2004; Chapter 4), estimates of growth and mortality from *P.*

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[9] See 'http://www.reefed.edu.au/rap/sitemap.html' for the current zoning plan

leopardus on these reefs were assumed to be our best available estimates of natural rates (Mapstone et al. 2004) for the purposes of these simulations.

The von Bertalanffy growth function (VBGF) is used in ELFSim to describe the relationships between FL and age (see Chapter 4). Region-specific (G_r) and overall (G) average estimates of the VBGF parameters L_∞ (the mean asymptotic FL) and K (the rate at which L_∞ is approached) were used to examine consequences of spatial variation in growth. Estimates of L_∞ were statistically different among years (Chapter 4) and so region-specific estimates of K and L_∞ were computed for each year separately and then averaged across years. The parameters for the overall growth were calculated for each year separately with the data pooled across reefs and regions, and then averaged across years.

A power function is used in ELFSim to convert FL to total fish weight (see Chapter 4). Previous research suggested no large scale spatial variation among regions in this relationship (Chapter 4), and so an overall estimate (with the data pooled across regions) of the coefficient *a* and exponent *b* were computed and the single power function $W_{FL} = 2.57 \ X \ 10^{-09} \ FL^{3.28}$ used to convert FL (mm) output by ELFSim to total fish weight for all regions (kg).

ELFSim allows for three types of natural variation in mortality. First mortality may vary ontogentically through age-specific mortality rates. Second, mortality on each spatial stratum (e.g., reef) may vary stochastically among months around its mean value. Finally, mortality may vary non-randomly (i.e., planned) among strata. All three types of natural variation were included in simulations presented. Rather than vary mortality non-randomly among reefs, however, ELFSim was modified to vary mortality among regions, with each reef within a region having the same mean mortality but still varying stochastically through time around that

mean independently of other reefs. Mortality rates (M) of *P. leopardus* were estimated from age-based cohort-specific catch curves using log-linear regressions (see Chapter 4). Region-specific mortality rates (M_r) were determined from the average regression slope across region- and cohort-specific catch curves derived in Chapter 4. The overall estimate of mortality (M) was computed from the average regression slope of cohort specific catch curves estimated from the data pooled across regions. Age-specific estimates of M were incorporated by assuming that natural mortality was greater for younger (ages 0 and 1) than older animals, with fish aged 2 and older having the same constant rate (Mapstone et al. 1996b; Campbell et al. 2001; Mapstone et al. 2004). M_r was used for individuals of 2 years and older. The natural mortality of 1 and 0 year olds were then adjusted proportionally based on the ratio of the M_r (ages 2+) to the mean M for ages 2+ over all regions.

The results are presented in the following format. First, average RSB trajectories under no effort (NoE) and different life history scenarios are shown for each region to illustrate depletions and recoveries of mean spawning biomass relative to the pre-exploitation level (1965 in ELFSim). As I was interested in comparing mean spawning biomass trajectories from different life history and effort scenarios in relative terms, and no stock assessment of *P. leopardus* has been undertaken, values of spawning biomass are presented relative to their pre-exploitation (virgin 1965) or status quo (1996) level[8], rather than in absolute values. Second, trends in the average RSB trajectories are compared for all life history scenarios and all other effort scenarios for each region. To investigate the implications of shifting effort among regions compared to the status quo effort (SQE) distribution, average RSB over the last five years of the projection period under each life history and non-SQE effort scenario are compared after indexing them to the average RSB over the last five

years for the SQE scenario for the corresponding life history scenario. Thus, the comparisons are for RSB at the end of projections under a given life history scenario as a proportion of that which would have been observed for the same life history scenario under the SQE effort distribution. RSB levels are also reported in relation to a management objective identified at a MSE stakeholder workshop organised by the CRC Reef Research Centre, 2004[10]. This objective is to maintain average RSB equal to or greater than the 1996 level 50% of the time. Finally, assessments of average RSB from all the different life history and effort scenarios are compared after being either aggregated across regions or calculated on a region-specific basis. All results were evaluated by a graphical comparison of the different trajectories and their standard errors (calculated from the replicate, independent runs of the model for each scenario). Thus, no statistical probability evaluations were performed on the model outputs.

5.3. Results

5.3.1. Growth and mortality input parameters

P. leopardus in the Lizard Island Region reached the largest asymptotic sizes (L_∞), but at a slower rate (K) compared both to the other regions and to the overall estimate aggregated across regions (Table 5.2). *P. leopardus* in the Mackay Region showed the highest age-specific mortality rates and individuals in the Townsville Region the slowest mortality rates. The largest differences between region-specific and overall parameter estimates were found in the Lizard Island Region for growth and in the Townsville Region for mortality (Table 5.2).

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[10] Little LR, Begg GA, Goldman B, Ellis N, Mapstone BD, Punt AE, Jones A, Sutton S, Williams A. 200X. Modelling multi-species targeting of fishing effort in the Queensland Coral Reef Fin Fish Fishery. Report to the Fisheries Research and Development Corporation

Table 5.2. Region-specific and overall estimates of the VBGF parameters and age-specific mortality rates. L_∞ = mean asymptotic FL (mm), K = the rate at which L_∞ is approached, t_0 = the age at theoretical length zero, and M_x = mortality rate at age x. Overall = estimate from the data aggregated across all regions. ( ) = percent change of the region-specific parameter relative to the overall estimate.

Management unit	L_∞		K		T_0	M_0 yr		M_1 yr		M_{2+} yrs	
Overall	521.6		0.3		-0.9	0.85		0.75		0.64	
Lizard Island	616.2	(+18.1)	0.26	(-13.3)	-1.75	0.79	(-7.1)	0.69	(-8.0)	0.59	(-7.8)
Townsville	537.7	(+3.1)	0.27	(-10.0)	-1.52	0.56	(-34.1)	0.49	(-34.7)	0.42	(-34.4)
Mackay	549.7	(+5.4)	0.28	(-6.7)	-0.95	0.99	(+16.5)	0.86	(+14.7)	0.74	(+15.6)
Swains	512.0	(-1.8)	0.3	(-0.0)	-0.67	0.69	(-18.8)	0.61	(-18.7)	0.52	(-18.8)

5.3.2. Depletions and recoveries

There was considerable variation (i.e., standard errors presented in the figures) around the mean RSB trajectories of *P. leopardus* when data were aggregated across regions, as well as when regions were treated separately. The variation was the result of stochastic treatment of natural mortality and recruitment in the model. Despite the variability within an effort scenario, however, some general patterns emerged, as well as some differences. In all scenarios, mean RSB decreased approximately linearly during the historic period (as the population was subject to an assumed linearly increasing fishing effort from zero in 1965 to the observed values in 1989-1998) to between 50 - 80 % of pre-exploitation levels in 1999, depending on the region or life history scenario considered (Fig. 5.2). When the results were aggregated spatially with no fishing effort applied in the projections, recovery of mean RSB was slightly faster under NoSS than under SSGM with recovery rates under the SSG and SSM intermediate (Fig. 5.2a). Mean RSB under all life history scenarios had fully recovered at the end of the projection period (Fig. 5.2a).

When analysed by region, however, simulations showed variable levels of depletion and recovery patterns of mean RSB (Fig. 5.2b-e) and for some regions the mean RSB trajectories were quite different to those of the aggregate results. The Lizard Island Region showed the greatest differences from both the aggregated results as well as among life history scenarios (Fig. 5.2a, b). Mean RSB decreased to 55 - 60% of pre-exploitation levels in 1998 under the SSGM and SSG scenarios respectively, and recovered substantially slower than under the NoSS and SSM scenarios (Fig. 5.2b) or under the SSGM and SSG scenarios of the aggregated results (Fig. 5.2a). The SSGM and SSG scenarios had not fully recovered by the end of the projection period in this region. The mean RSB trajectories of the Townsville Region were quite similar to those of the aggregate results (q.v. Fig. 5.2a and c). Whilst RSB trajectories differed among life history scenarios in the aggregated results (Fig. 5.2a), there were no apparent differences among RSB trajectories for the different life history scenarios in the Mackay Region (Fig. 5.2d). RSB had recovered and stabilized at pre-exploitation levels by 2007 under all scenarios (Fig. 5.2d). The aggregated RSB trajectories were lower for some life history scenarios than they were for the Mackay Region, which means that aggregate results would have overestimated depletion and under-estimated recovery rate for those life history scenarios (q.v. Fig. 5.2a and d). Similarly, only relatively slight differences were found between mean RSB trajectories for the different life history scenarios in the Swains Region (Fig. 5.2e). Moreover, RSB depletion was slightly less under the SSGM scenario (80%) and the recovery faster under SSG than assessed by the aggregate results (q.v. Fig. 5.2a and e). With the exception of the SSGM and SSG scenarios in the Lizard Island Region, the recovery of RSB was relatively fast in all regions, reaching approximately pre-exploitation levels in 15 years.

Figure 5.2 Time trajectories of mean spawning biomass relative to pre-exploitation levels (RSB) for the *P. leopardus* population estimated for the a) results aggregated across four regions, b) Lizard Island, c) Townsville, d) Mackay and e) Swains Regions for different life history scenarios with no fishing effort in the projection period (1999 – 2025).

5.3.3. Effort scenarios

5.3.3.1. Patterns in RSB trajectories

The effects of different effort scenarios on mean RSB trajectories were only slight when considered by the results aggregated across regions (Fig. 5.3). Mean RSB during the projection period remained stable at about 65% of pre-exploitation levels under the SSGM scenario and between 75-80% under the other spatial scenarios (Fig. 5.3a-d). The variability around each mean RSB trajectory (error bars) also was small.
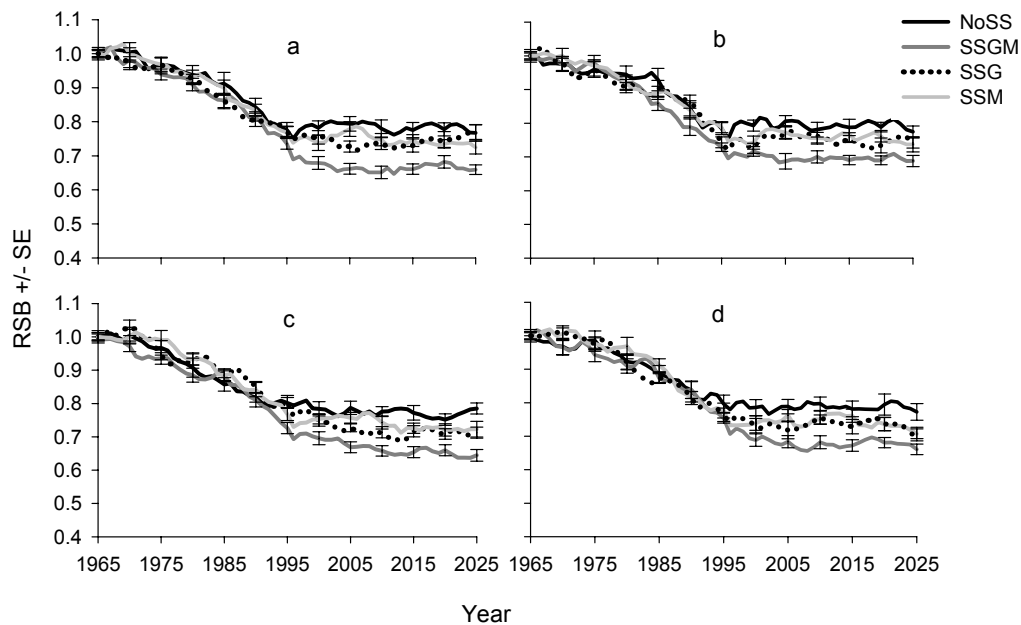
Figure 5.3 Trajectories of mean spawning biomass relative to pre-exploitation levels (RSB) for the overall *P. leopardus* population (results aggregated across four regions) under different life history scenarios (NoSS, SSGM, SSG and SSM) and effort scenarios: a) EPE, b) InEPE, c) SQE and d) UE levels.

The effects of different effort scenarios on mean RSB trajectories in the Lizard Island Region (Fig. 5.4A) were very different to those suggested by the aggregate results (Fig. 5.3) for some life history scenarios. Under the SSGM and SSG scenarios and EPE or SQE levels of effort, mean RSB stabilised at pre-exploitation levels that were 10% lower than for the same scenarios of the aggregated data (q.v. Fig. 5.3 and Fig. 5.4A a, c). The effects of EPE and SQE levels on mean RSB under NoSS and SSM, however, were very similar to that of the aggregated results. When the Lizard Island Region were subjected to UE and InEPE scenarios, mean relative RSB at the end of the projection period was considerably lower than the equivalent RSB of the aggregated results for all life history scenarios (q.v. Fig. 5.3 and Fig. 5.4A b, d). Particularly noticeable were the low mean SB levels under the SSGM scenario which, when subjected to InEPE and UE were reduced to 17% and 30% of pre-exploitation levels, respectively, and were still declining in 2025 (Fig. 5.4A b, d). In contrast, mean SB in all other regions stabilized relatively quickly and remained stable throughout the projection period for all life history and effort scenarios (Fig. 5.4B, 5.5A, B). There were small differences in mean RSB among life history scenarios under all effort scenarios for the Townsville Region (Fig. 5.4B) and under EPE, SQE and UE for the Swains Region (Fig. 5.5B a, c, d). Under the InEPE scenario in the Swains Region (Fig. 5.5B b) and all effort scenarios in the Mackay Region (Fig. 5.5A a-d) there were no differences in mean RSB among life history scenarios. Mean RSB in the Townsville and Mackay regions (Fig. 5.4B a-d, 5.5A a-d), and of the Swains Region under the InEPE scenario (Fig. 5.5B b), stabilised at somewhat greater levels than for the aggregate results (Fig. 5.3). In contrast, under the EPE scenario mean RSB of the Swains Region stabilised at about 10% lower than for the aggregate results.
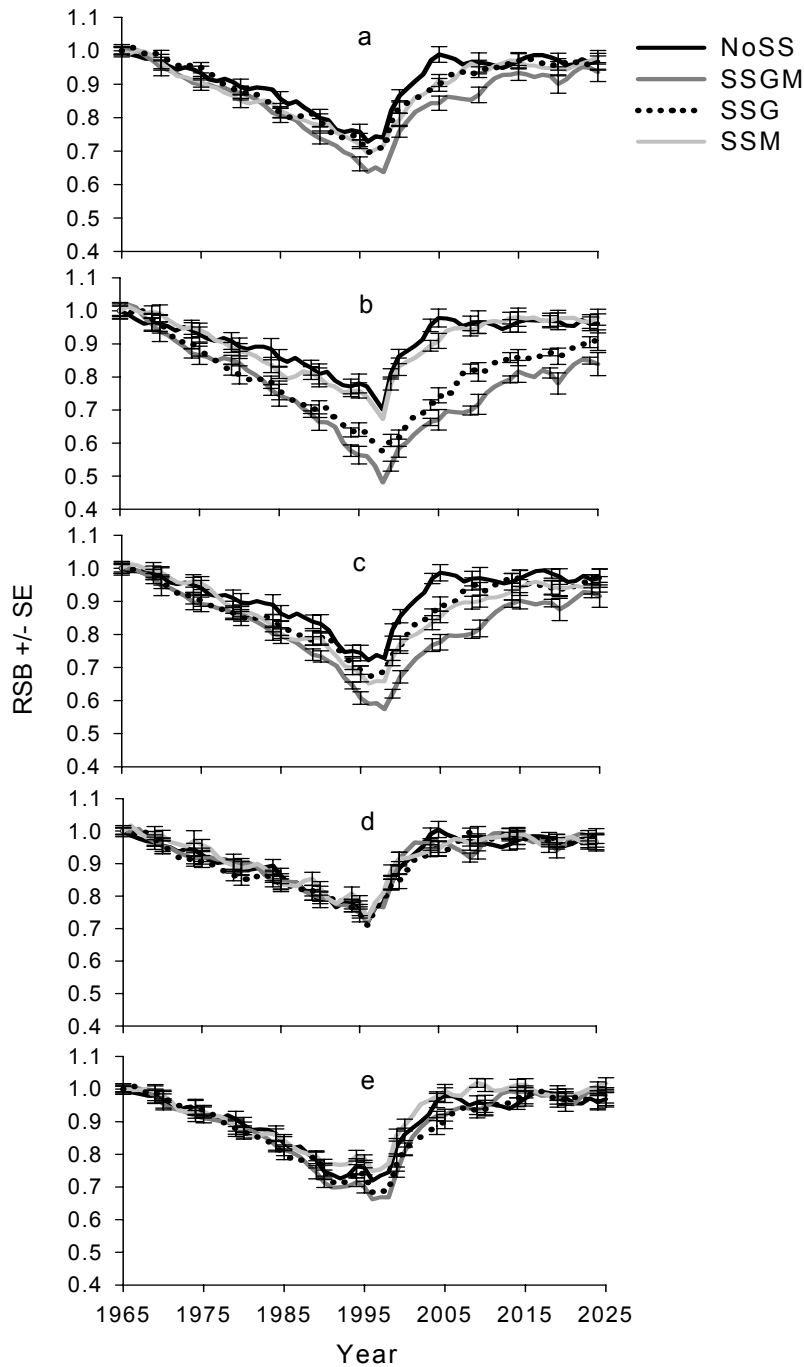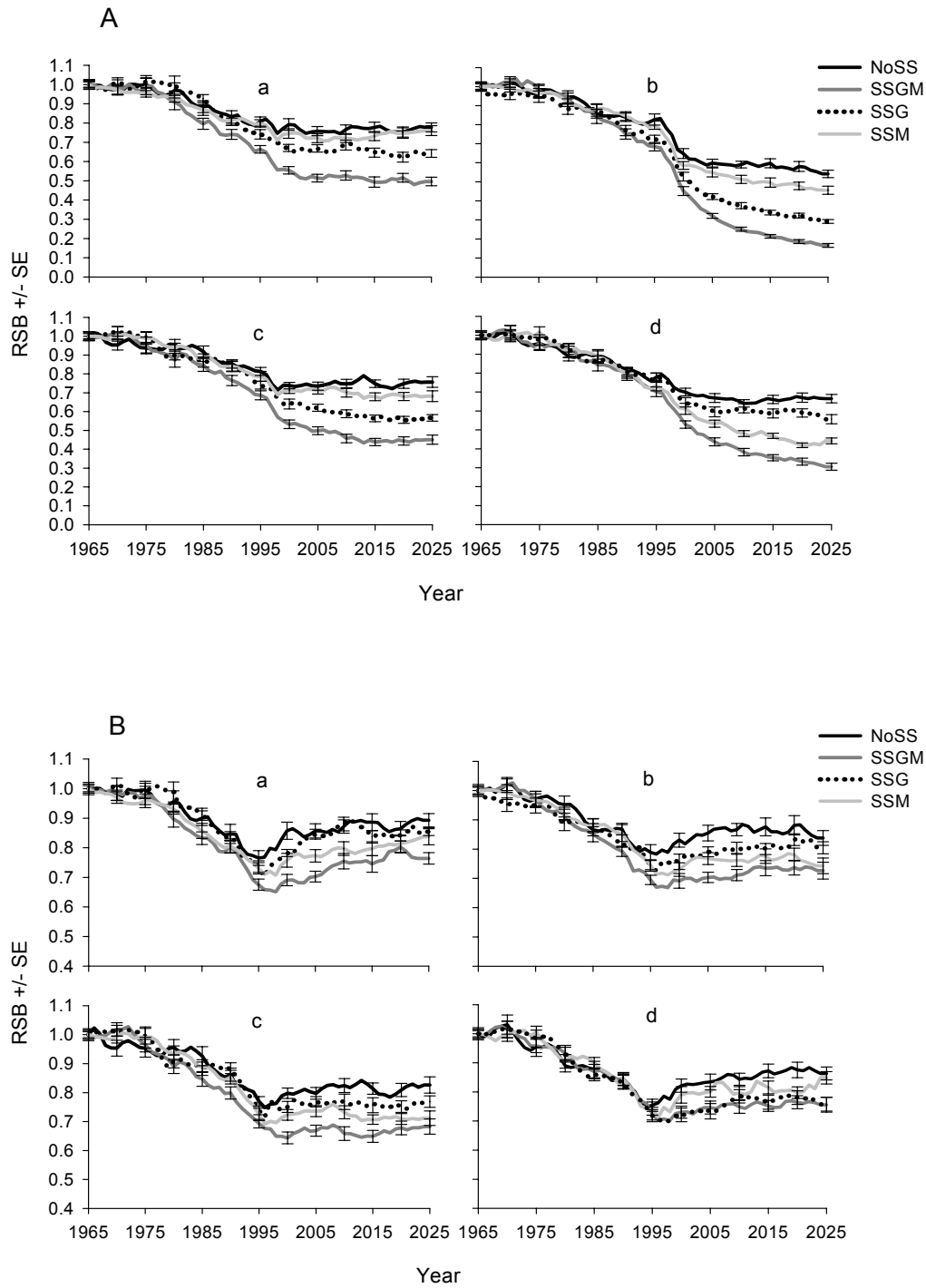
Figure 5.4 Time trajectories of mean spawning biomass relative to pre-exploitation levels (RSB) for *P. leopardus* in the Lizard (A) and Townsville (B) Regions under different life history scenarios (NoSS, SSGM, SSG and SSM) and effort scenarios: a) EPE, b) InEPE, c) SQE and d) UE levels.
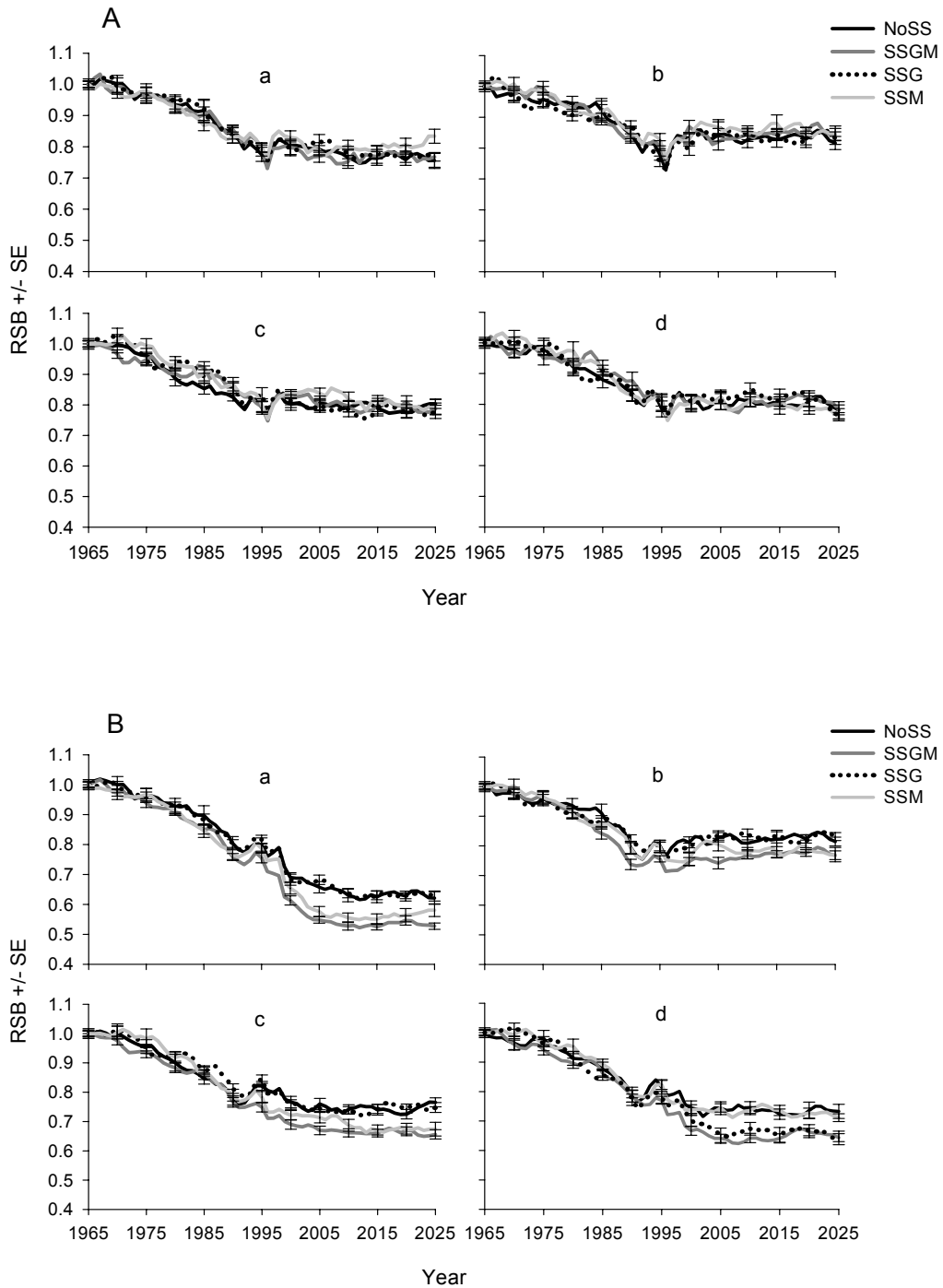
Figure 5.5 Time trajectories of mean spawning biomass relative to pre-exploitation levels (RSB) for *P. leopardus* in the Mackay (A) and Swains (B) Region under different life history scenarios (NoSS, SSGM, SSG and SSM) and effort scenarios: a) EPE, b) InEPE, c) SQE and d) UE levels.

When differences occurred in mean RSB among life history scenarios (irrespective of effort scenario), trajectories generally decreased to lower relative levels under SSGM and SSG than the NoSS and SSM scenarios (Fig. 5.3–5.5). In the Lizard Island Region, where the differences among life history scenarios were particularly large, mean RSB decreased less under the SSG scenario than under SSGM, but more than under SSM and NoSS (Fig. 5.4). Further, a 34% and 16% decrease in mortality in the Townsville and Mackay Region, respectively, and only small differences in growth for both regions (Fig. 5.4, 5.5), resulted in comparatively small differences between the region-specific RSB trajectories and the overall trajectories. These results suggest that spatial variation in growth may have substantially greater effect on relative levels of RSB than the equivalent or greater spatial variation in mortality.

5.3.3.2. Patterns in mean RSB over the last five years of the projection period relative to mean RSB at status quo effort levels

Mean RSB over the last five years of the projection period for the EPE, InEPE and UE scenarios relative to those under the SQE scenario were similar across life history and effort scenarios when considered as aggregated results (Fig. 5.6a). These results suggest that the population as a whole may be robust to potential shifts in effort across the regions in the future.

Mean RSB at the end of the projection period relative to mean RSB at status quo levels were also similar across life history scenarios in the Townsville, Mackay and Swains regions (Fig. 5.6c, d and e). One exception was the somewhat greater depletions of mean RSB relative to SQE levels for the Swains Region when effort was shifted to EPE levels (~80%; Fig. 5.6e). In contrast, mean RSB at the end of the

projection period for the Lizard Island Region under the UE and InEPE scenarios was lower than in the aggregate data and the Lizard Island specific mean RSB at SQE (q.v. Fig. 5.6a and b). The effects of different effort levels on RSB also varied for different life history scenarios in the Lizard Island Region. The effects of fishing were greatest under SSGM and lowest under NoSS. For example, for the InEPE scenario RSB at the end of the projection period was close to 70% under NoSS but only 40% under the SSGM scenario (Fig. 5.6b) compared to the SQE results.
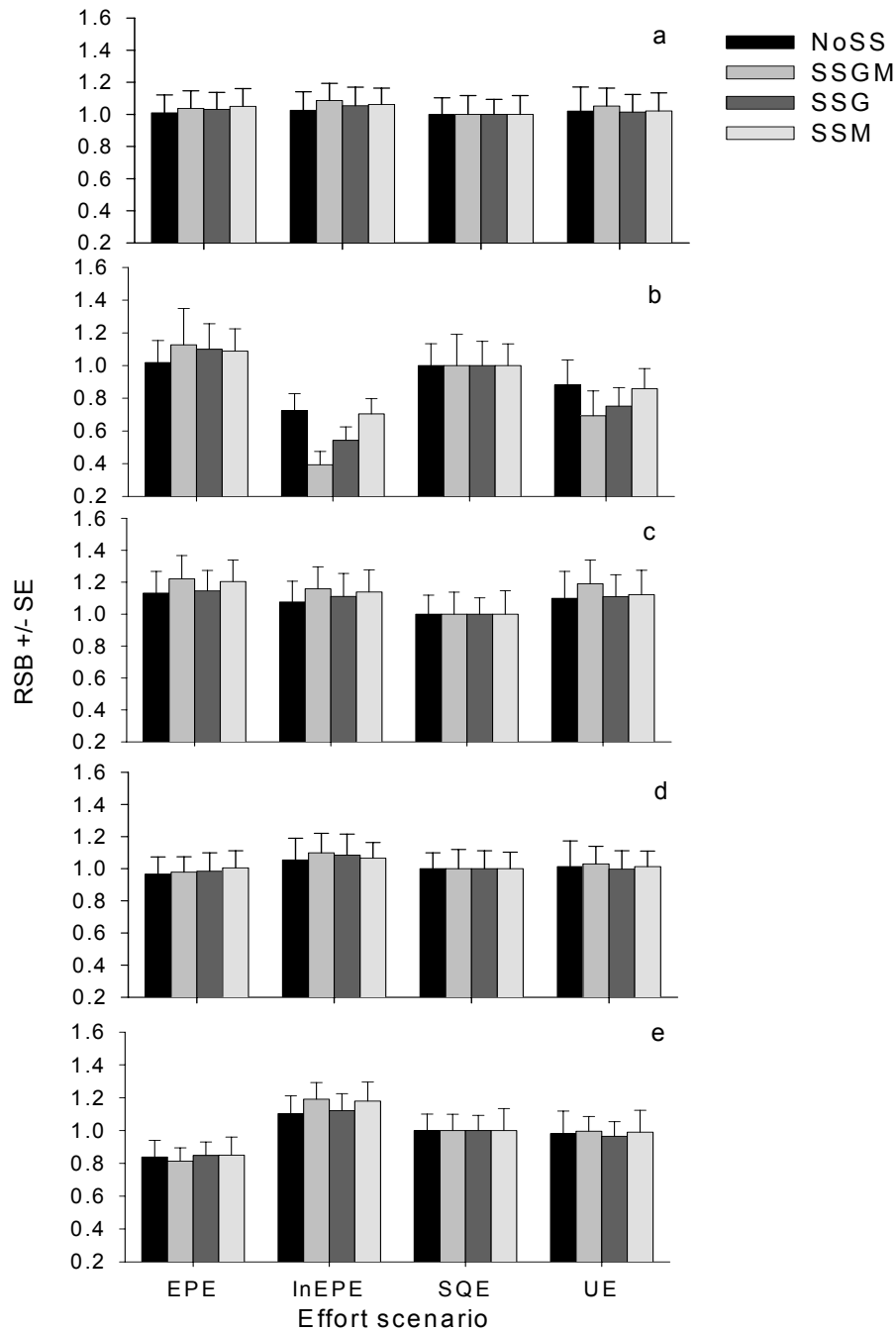
Figure 5.6 Mean RSB from the last five years of the projection period relative to mean RSB from the last five years of the projection period under the status quo (1996) effort scenario for a) results aggregated across regions, b) Lizard Island, c) Townsville, d) Mackay, e) Swains regions under different life history scenarios (NoSS, SSGM, SSG and SSM) and effort scenarios: a) EPE, b) InEPE, c) SQE and d) UE levels.

5.3.3.3. RSB status relative to management objectives

Mean RSB of the aggregate results was greater than status quo levels more than 50% of the time (in years) under NoSS and SSM for all effort scenarios, but SQE and thus met the management objective for these life history and all effort scenarios (Fig. 5.7a). For SSGM and SSG, however, levels of mean RSB did not meet the management objective under any effort scenario except for SSG under InEPE (Fig. 5.7a).

Region-specific analyses, however, showed that mean RSB levels were greater than status quo levels more than 50% of the time in the Mackay Region for all life history and most effort scenarios, under all life history scenarios under EPE, InEPE and UE in the Townsville Region, only under InEPE in the Swains Region, and only under NoSS for the EPE scenario in the Lizard Island Region (Fig. 5.7b-e). Particularly striking was the large difference between the NoSS and SSGM scenarios under EPE in the Lizard Island Region and the overall low percentage of time that RSB was equal to or above status quo levels for all other effort scenarios (Fig. 5.7b).
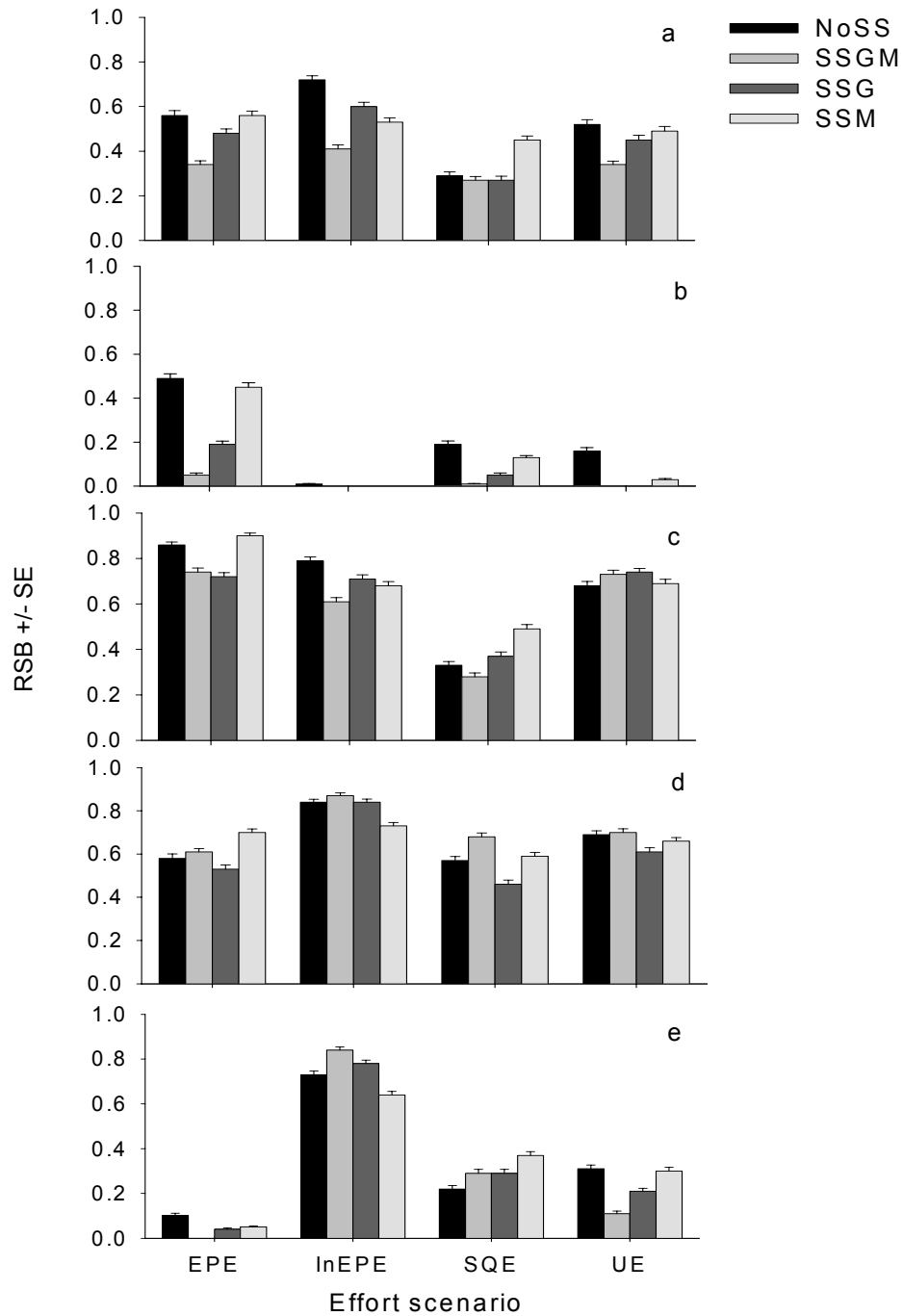
Figure 5.7 Proportion of time (in years) that mean RSB was greater than status quo levels of RSB for the a) results aggregate across regions, b) Lizard Island, c) Townsville, d) Mackay, e) Swains regions under different life history scenarios (NoSS, SSGM, SSG and SSM), and under four different effort scenarios: a) EPE, b) InEPE, c) SQE and d) UE levels.

5.4. Discussion

5.4.1. Consequences of ignoring spatial variability in biology

The simulation results presented above illustrate the potential importance of accounting for spatial variation in vital life history characteristics when evaluating the sustainability of coral reef fish populations subject to different harvest strategies. First, including spatial variation in growth and mortality of *P. leopardus* in the harvest strategy evaluation resulted in greater depletion levels in 1998 and longer periods of recovery to pre-exploitation levels of RSB than when there was no spatial variation in life history characteristics for the population as a whole, as well as for the northern regions (Lizard Island and Townsville). Second, the presence of spatial variation in vital life history rates resulted in greater effects of various harvest strategies on RSB for the population as a whole, as well as for the Lizard Island and Townsville regions. Third, not accounting for spatial variation in biology increased the probability of making the wrong conclusion about whether a management objective was realised.

It is probable that the implications of spatial variation in biology of *P. leopardus* on the GBR would be the similar for other coral reef fishes with comparable life histories. Recent research has revealed that variability in biology of coral reef fishes among both large and small spatial scales is the norm rather than the exception (e.g., Robertson et al. 2005a), with spatial variation of other exploited species being of similar magnitude to that of *P. leopardus* (e.g., *Lethrinus miniatus*; Williams et al. 2003).

5.4.2. Consequences of aggregating data across biological units

Aggregating RSB outputs across regions rather than analysing outputs by region had important implications for the harvest strategy evaluation, especially when *P. leopardus* had different region-specific life history rates. The aggregated results masked important region-specific patterns in the *P. leopardus* RSB trajectories under different effort scenarios, irrespective of whether spatial variation in biology was present. The results of this Chapter suggest that aggregating results across several spatial components with different biological characteristics when evaluating and subsequently setting harvest strategies, increases the probability of depleting some spatial components more than expected or intended. In addition, there is an increased probability in under-utilising the resource in other spatial components, where the relative spawning potential is greater than what appears in the aggregated results. Moreover, ignoring spatial variation in life history characteristics among regions and aggregating results across regions increased the potential for making the wrong conclusion about the performance of alternative harvest strategies against specified management objectives.

As the regions, or stocks (Chapter 2-4), in our simulations are of different geographical sizes and therefore contain different absolute numbers of reef subpopulations, some regions had a disproportionate effect on the aggregated patterns simply through contributing a greater amount of absolute spawning biomass. Townsville was the largest region in the simulations and mean patterns of RSB from this region were only slightly different to those of the aggregated results. Conversely, Lizard Island was the smallest region and RSB patterns from this region showed the greatest contrast to the aggregated results.

Despite the knowledge of spatial variation in biology among stocks with little or no larval exchange and associated consequences (Ricker 1958; Paulik et al. 1967; Frank and Brickman 2000), the pooling of data across stocks in assessment and management strategy evaluations is a worldwide and common practice (Stephenson 2002). The simulations presented in this Chapter quantify the consequences of such simplifications for stocks connected by larval dispersal and provide an important basis for considering how to address those consequences. In addition, there are often great difficulties associated with the identification of all stock components in species that are population rich, such as coral reef fishes, Atlantic salmon, cod and herring (sensu Iles and Sinclair 1982). Simulation models are enormously useful for exploring potential consequences of aggregating results in such populations with many spatial components.

5.4.3. Consequences of different effort levels

Whilst the effects of changing effort distributions on RSB were small in most regions, increasing effort levels had a relatively large effect in the Lizard Island Region where the shift in effort was the greatest. Less expected, was the comparatively low levels of RSB at the end of the projection period in the Lizard Island Region under the status quo levels of effort. Moreover, when spatial structure was accounted for, the management objective RSB = RSB_{1996} 50% of the time was only realised in the Mackay Region with status quo levels of effort. The results in this Chapter suggest that to increase the probability of achieving this management objective, effort would have to be reduced in the Townsville Region from status quo levels to EP, IEP or U levels, in the Swains Region to IEP levels and in the Lizard Island Region to levels beyond those explored here. These results suggest that

region-specific management may be warranted for *P. leopardus* and potentially other coral reef species caught in the GBR line fishery with similarly variable biological characteristics. It is important to note, however, that RSB did not crash under any of the effort scenarios investigated, and remained above most biological reference points specified under the precautionary approach to fisheries management (Mace and Gabriel 1999), suggesting that the *P. leopardus* population is likely to be relatively robust to contemporary harvest strategies.

An overall increase in total effort in the GBR line fishery is unlikely as there is a cap on commercial licences, a total allowable commercial catch of 1350 t for *P. leopardus*, regulation of charter fishing permits and declining participation in the recreational sector (Coral Reef Fin Fish Management Plan 2003[11]). Some degree of redistribution of effort could occur among regions, however, as fishers are not restricted by their licenses to fish a particular area within the GBR, and therefore have the option to seek alternative fishing grounds as a consequence of regulatory, social, economic or environmental factors. Begg et al.[10] estimated that a small number of commercial reef line fishers fished new areas in a year of operation and used other ports than their original home port for a variety of social, economic or environmental reasons affecting them on an individual basis. Although the percentage was small, it emphasises the possibility of a greater effort shift among regions in response to changes affecting many fishers simultaneously. For example, a recent increase in no-take areas (i.e., areas closed to fishing and other extractive activities) from 4 - 33.4% of the GBRWHA (Day et al. 2002) may have resulted in commercial fishers moving into new areas, although the extent and persistence of such changes are not yet clear.

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[11] Fisheries (Coral Reef Fin Fish) Management Plan 2003
http://www.legislation.qld.gov.au/LEGISLTN/CURRENT/F/FisherCRFFMP03.pdf

5.4.4. The importance of growth versus mortality

Growth and mortality are key population parameters determining the biomass production of fish populations (Hilborn and Walters 2001). Individual growth rate and asymptotic body size are important determinants of maturation, which is often dependent on size rather than age in fishes, and weight-at-length, which is highly correlated to fecundity (Roff 1992). Rates of M are often indicative of a population's rate of turn-over of individuals, with persistent high mortality rates indicative of a population with a rapid turn-over rate and high harvest potential compared to a population with lower mortality rates (Gulland 1988; Hilborn and Walters 2001). As expected by theory, my results of different RSB trajectories among life history scenarios and regions for a particular scenario were the consequence of a trade-off between growth and mortality. Less expected, however, were the disproportionately larger effects on RSB of changing growth than effects of changing mortality.

P. leopardus is protogynous and changes sex from female to male. Sex change and maturity are most likely size-dependent processes (Adams et al. 2000; Adams 2002). A greater asymptotic size in the Lizard Island Region under the SSGM scenario (region-specific growth and mortality) resulted in individuals reaching maturity and changing sex at a relatively younger age compared to under the NoSS scenario (no spatial variability in growth and mortality). Consequently, there were fewer older (and larger) females in the Lizard Island Region under SSGM and fish had less time to reproduce as females before reaching a size at which they changed sex. Moreover, as selectivity by the fishing gear is also size dependent (Fulton et al. 1999), individuals under SSGM were selected by the fishing gear at a younger age in the Lizard Island Region than elsewhere and more of the mature biomass would be vulnerable to harvest earlier than under NoSS or in other regions.

Thus, whereas in other regions, the MSL protected females from harvest until age 3 or 4, in the Lizard Island Region mature females were being harvested from around age 2. All of these processes would have contributed to the greater depletions and effects of fishing on RSB in the Lizard Island Region under SSGM than NoSS, or than in other regions with smaller asymptotic sizes.

The 18% increase in the asymptotic size under SSG in the Lizard Island Region caused a disproportionately greater depression of the RSB depletions and recoveries than an 8% decrease in mortality under SSM. Similar effects were noted in the Townsville Region. Therefore, it can be concluded that processes associated with growth had a greater effect on the sustainability of the stock in a region than equivalent, or even larger, proportional changes in mortality. The greatest effect of increased mortality is likely to be at the extreme of the size and age distribution, when most individuals would have already changed sex into males and therefore disappeared from the mature female biomass (and so assessments of RSB).

The results of variable RSB trajectories with changing growth and mortality parameters were expected and consistent with the different postulated effects of fishing on species with different life history characteristics (Jennings and Kaiser 1998; Jennings et al. 1999; Hilborn and Walters 2001). Results from this Chapter show that mean RSB at the end of the projection period was less for regions (and scenarios) with larger asymptotic size, which agrees with the general theory and empirical evidence that a species or stock that contains individuals that can attain a larger maximum body size cannot sustain the same amount of fishing as one that generally contains smaller fish (e.g., Adams 1980; Trippel 1995; Jennings et al. 1998; Russ and Alcala 1998; Jennings et al. 1999; Fomentin and Fonteneau 2001). In addition, regions with relatively high rates of mortality, and therefore potentially a

rapid population turn-over rate, were relatively less affected by fishing compared to regions with lower mortality rates (Gulland 1988; Hilborn and Walters 2001). Whilst in this study growth and mortality were varied in isolation of other life history characteristics, it is most likely that spatial variation among regions would result in, or be the result of, variation in other characteristics to which growth and mortality are correlated. For example, a positive correlation between body size- and age-at-maturity observed among stocks within species (Trippel 1995), and the increase in fecundity per unit of biomass with increased body size (Roff 1992), are all likely characteristics to further influence the vulnerability of a stock to fishing under variable growth scenarios.

5.4.5. Other model considerations

As with all simulation models, ELFSim is subject to some assumptions (e.g., the stock-recruitment relationship and larval dispersal matrix) which could affect the results of this study. A new assumption, added as a result of the inclusion of spatial variation in biology in ELFSim, concerned whether the spatial scale and boundaries specified for the management units or regions matched those of true biological units or stocks. Distinct regional difference in CPUE (Mapstone et al. 1996a; Samoilys et al. 2002), densities (Ayling et al. 2000), reproductive characteristics (Adams 2002), and growth (Mapstone et al. 2004; Chapter 4) of *P. leopardus* emphasise the possibility of variable productivities among regions, and therefore agree with the use of regions as the appropriate management units, but there is insufficient data available to date to reliably characterise the nature and locations of transitions or boundaries among regions. Further, a comparison of life history characteristics at several spatial and temporal scales in Chapter 4 also found differences in life history characteristics among reefs within regions. These results emphasise the importance

of incorporating finer scale spatial variation in biology into future simulation studies to evaluate consequences to individual stocks, as well as to the entire *P. leopardus* population, and to resolve the spatial characteristics of transitions among the regions I have examined.

Whilst this study accounted for regional differences in growth and mortality, there is a possibility of spatial variation in other important life history characteristics. Regional variation in size- and age-at-maturity and sex change (Davies et al. 2006), and regional variation in recruitment could have large influences on patterns in RSB through time. In addition, the potential occurrence of maternal effects, e.g., that older larger females produce larvae with a greater chance of survival (e.g., Marteinsdottir and Steinarsson 1998; Berkeley et al. 2004; Wright and Gibb 2005) could further exacerbate the consequences of ignoring spatial variability in biology in harvest strategy evaluations.

Finally, in ELFSim it is assumed that only a relatively small proportion of larvae recruit back to the reef where they were spawned. Although high levels of larval exchange among local reef subpopulations have been predicted, recent population modelling also indicates that a few subpopulations with some levels of self-recruitment are likely and probably essential for the long-term sustainability of the entire population (James et al. 2002). Partial self-recruitment of a coral reef fish on the GBR has also been directly shown by the recapture of larval fish with marked otoliths (Jones et al. 1999). Even moderate levels of self-recruitment to reefs or groups of reef subpopulations could potentially increase the consequences of spatial variation in biology, especially if the RSB of such subpopulations is reduced by fishing. Bode et al. (2006) predicted the occurrence of source-sink dynamics between two subregions in the northern part of the GBR (Crowder et al. 2000). As with high

levels of self recruitment, uni-directional larval flow could clearly greatly increase the effects of differences in biology across various spatial scales, especially if the majority of fishing effort was concentrated, even temporarily, in a 'source' area. The effects of high levels of self-recruitment and source-sink dynamics are other phenomena that clearly need to be investigated in future simulation studies

5.4.6. Conclusion and future directions

Not accounting for spatial variation in growth and mortality when undertaking harvest strategy evaluations can lead to the wrong conclusion about the effects of different harvest strategies on the population RSB as a whole, as well as the individual spatial components of the population. If predictions about the relative levels of performance indicators are unreliable, so are the predictions about whether management objectives are realised.

The spatial patterns in biology of *P. leopardus* simulated in this study were clearly simplified compared to the complex spatial (and temporal) structures in life history characteristics revealed in Chapter 4 (and other work referenced therein). The results of this study provide some important future research recommendations, however, and have potential management implications that require consideration. The results suggest that the single management unit currently considered for *P. leopardus* may need to be divided into finer spatial units to more closely reflect the scale of the biological units or stocks (Stephenson et al. 2001; Rahikainen and Stephenson 2004). This may also be the case for other coral reef fish populations, for which variation in life history characteristics has been reported at similar spatial scales and of the same magnitude as *P. leopardus*. The results in this study (and Chapter 4) also suggest that temporal and finer scale spatial variation in the biology of *P. leopardus*, as well as variation in other vital life history characteristics now

need to be investigated in simulation studies to evaluate consequences of harvest strategies for individual stocks, as well as the entire population. As for other fish species with complex spatial population structures, future simulation modelling is also necessary to investigate implications of varying levels of larval connectivity among spatially variable population components.

Chapter 6. General Discussion

My thesis is one of the first to demonstrate the use of a range of techniques to identify stocks of a coral reef fish with persistent differences in biological characteristics. The results suggest that the stock structure of *Plectropomus leopardus,* a typically exploited coral reef fish, and therefore potentially other coral reef fishes, is far more complex than assumed in current coral reef fisheries management schemes. Whilst it is not new that spatial variability in biology is a feature of coral reef fishes, studies reporting such variability have only recently investigated multiple spatial and temporal scales simultaneously (see recent studies by Adams et al. 2000; Gust et al. 2001; Kritzer 2002; Williams et al. 2003; Mapstone et al. 2004; Davies et al. 2006; Williams et al. 2006). The results of this study show that both of these aspects are necessary in stock identification studies (Chapters 2 – 4). Some characteristics used to identify stocks varied not only at several different spatial scales, but patterns also changed with the time of sampling. More importantly, previous studies on spatial variation in life history characteristics of coral reef fishes have rarely discussed their results in the context of potential stock structures or the implications of such structures for sustainable fisheries management (but see Williams et al. 2003; Mapstone et al. 2004; Williams and Shertzer 2005; Davies et al. 2006 for some brief discussions). This thesis is one of the first to illustrate the likely implications of spatial variability in biology for individual population components, as well as the entire reef fish population when subject to different levels of fishing. That stocks with different life history characteristics may respond differently to fishing is also not new (e.g., Ricker 1958; Adams 1980), but what has been less appreciated are the ramifications of spatial variability in biology among harvested stocks, connected

by larval dispersal. Overall, this thesis, which also proposes a theoretical model to conceptualise the stock structure of *P. leopardus*, adds significantly to the embryonic, but urgently needed theory on stock structure of coral reef fishes.

6.1. The utility of phenotypic stock identification techniques for coral reef fishes.

Otolith chemistry and otolith morphology are two techniques frequently used to identify phenotypic stocks in temperate regions because they are cost-effective environmental and/or genetic markers. This thesis is one of the first to test the use of these techniques on coral reef fishes (see also Patterson et al. 1999 for use of otolith chemistry). The value of these techniques is that they may identify retrospectively groups of individuals that have lived for significant periods of their lives in different environments (Campana 1999), and therefore indirectly indicate groups that may have different life history characteristics. The results of this thesis suggested that spatial patterns in otolith chemistry and morphology (Chapters 2 and 3) did indeed reflect the spatial variability in biology of *P. leopardus* (Chapter 4), albeit at somewhat different spatial sensitivities. The results also revealed that whilst spatial patterns of some apsects of otolith morphology, chemistry and life history characteristics were persistent through time, others were not. Consistent with temperate stock identification studies using these techniques, I therefore suggest that these techniques should not be used in isolation to identify stocks of other coral reef species until their ability to reflect spatial patterns in biology has been repeatedly verified, i.e., at multiple times of sampling. For example, there is no obvious reason why *E. fasciatus,* for which no differences in otolith chemistry were detected, would not show differences in life history characteristics at similar spatial and temporal scales as *P. leopardus,* considering their relatively similar life histories and

taxonomic proximity. In situations where collections of otoliths are already available and differences are detected, these techniques do provide means to direct future research on groups of individuals that have been spatially separated for extended periods of their lives.

Whilst otolith chemistry and life history characteristics of *P. leopardus* varied among both finer reef and larger region spatial scales, otolith morphology varied predominantly among regions. The two former techniques thus seem to be sensitive to variations at different spatial scales. Waldman (2005) proposed that one aspect to variable spatial sensitivities of different stock identification techniques is related to the depth of the stock separation, which is a result of the spatial extent of the separation and length in time that putative stocks have been isolated. The most obvious (and also the greatest) difference in depth of separation would be between genetically different stocks and phenotypically different stocks that are purely environmental in origin. Genetic differentiation is notably a slower process than environmentally driven phenotypic differentiation in marine fishes, and often results in separation at relatively larger spatial scales due to large population sizes and high rates of larval exchange. Understanding the spatial sensitivities of the stock identification techniques used in this thesis, and therefore the depth of the separation, is complicated as these phenotypic characteristics can be environmentally or genetically determined, or both.

A study by van Herwerden et al. (2006) showed little genetic differentiation in the *P. leopardus* population on the GBR, suggesting extensive larval dispersal across most regions. This study used markers that are neutral to local genetic adaptation, however, which is driven by natural selection to maximise fitness (Conover 1998). Adaptive traits evolve faster and may result in spatial structures at

finer spatial scales than neutral markers (Conover 2000). Moreover, increased evidence of significant self-recruitment of fishes to some coral reefs (Jones et al. 1999; Swearer et al. 1999; Jones et al. 2005), genetic structuring of natural markers in other coral reef fishes over small spatial distances (e.g., McMillan and Palumbi 1995; Shulman and Bermingham 1995; Rocha et al. 2005), and recent empirical evidence for adaptive genetic differentiation in growth rate of a juvenile coral reef fish (Buechler 2005) emphasise the possibility of spatial variability in phenotypic stocks being the result of genetic adaptation for at least some variables. It could be possible that the phenotypic variables that showed persistent spatial differences (at either the reef or regional spatial scale) are genetically determined, whilst the variables with changing spatial patterns through time are reflecting a variable environment. Distinguishing between the underlying causes of the spatial variability in phenotypic characteristics is particularly difficult but not essential for fisheries management. For most fisheries management objectives it is important to establish whether differences in life history characteristics exist and whether these are persistent through time, but less important to establish the origins of such differences. Determining the causes of spatial phenotypic variability is an important process, however, if the management objective is to protect genetic biodiversity of fished stocks (Swain and Foote 1999). Further information on these issues and different spatial and temporal sensitivities of different stock identification techniques is needed to increase our understanding of spatial structuring, as well as to increase our capacity to explain the origins of observed patterns in stock structures.

6.2. Stock structure of *P. leopardus*

Otolith chemistry, otolith morphology and life history characteristics revealed a great complexity in the population structure of *P. leopardus* on the GBR. The results suggest that the population is composed of a complex network of reef subpopulations with spatially and temporally variable life history characteristics and groups of subpopulations (i.e., regions), that might represent stocks with persistent differences in biology. Whilst the results in my thesis provide some spatially structured information of *P. leopardus*, and may be used to guide stock identification research for other commercially exploited coral reef fish, the complexity of the results recommends future consideration of the following issues. First, in the present study only a single cluster of neighbouring reefs in each of the four regions was investigated. Some phenotypic characteristics showed persistent differences among reefs within a region, suggestive of stocks at the spatial scales of reefs. Other characteristics suggested stocks at the spatial scale of regions. There is a clear possibility that if a range of biological characteristics of *P. leopardus* were examined between and outside the areas investigated, preferably on a continuum between neighbouring clusters considered here, increased number of stocks might be suggested. Although it is unlikely that the exact number of stocks present, in the 3000+ reef archipelago of the GBR will be resolved, their potential presence should be investigated as far as possible, together with their most likely stock boundaries and temporal persistence, and spatial variation in biology among them considered in future monitoring programs and management strategy development.

Second, it is known that less productive stocks will not be able to sustain the same amount of fishing as a stock that is more productive. Little has been known, however, of the magnitude of difference required in the biological characteristics

among stocks to warrant separate management strategies and whether some biological characteristics are more sensitive than others in maintaining fished populations. This thesis provides some significant information with regards to these issues (Chapter 5) that will be discussed below.

Third, very little is known about the connectivity of different stocks through the exchange of larvae among sedentary spawning subpopulations. Such information is fundamental to the understanding of the replenishment of different stocks and consequently how much fishing the collection of stocks can sustain, and where across the range of a population fishing impacts are likely to be most important. It is likely that the stock-recruitment relationship may be operating on a larger spatial scale than that of the processes determining other life history characteristics in coral reef fishes. The production of larvae in one area, influenced by area-specific environmental processes and potential management strategies, may therefore affect the productivity in another area (Hilborn et al. 2005). Information on the exchange of larvae among areas is notoriously difficult to collect, however, and estimates of larval recruitment have until recently been only estimated from indirect methods such as catch trends reported in commercial logbooks and population information from structured research surveys. High levels of larval exchange among local subpopulations in the northern region of the GBR have been predicted, but recent population modelling indicated that a few subpopulations with high levels of self-recruitment were essential for the long term sustainability of the entire metapopulation (James et al. 2002). Partial self-recruitment of a coral reef fish on the GBR has also been directly shown by the recapture of larval fish with marked otoliths (Jones et al. 1999). Further, Bode et al. (2006) predicted the occurrence of source-sink dynamics between two groups of reefs using the simulated larval

dispersal dataset of James et al. (2002). If spatial variability in life history characteristics of *P. leopardus* were at least partially genetically driven, it is possible that the reefs (or regions) with persistent differences in biology represent spatial population components with high levels of self-recruitment. These reefs may also function as sources to sink reefs, which in turn receive larvae from several different reefs and therefore show comparatively variable life history characteristics across time.

Finally, the current estimates of life history characteristics in this thesis are derived from areas that were closed to fishing, and as such gives an approximation of natural vital rates. It is likely however, that fishing itself has had an effect on the life history characteristics of *P. leopardus* in areas open to fishing on the GBR (e.g., Adams et al. 2000; Mapstone et al. 2004), and which could complicate further detailed studies to identify stocks and management strategy development of this species. Information on the approximate 'natural state' of subpopulations or stocks is important, however, and can be used to estimate their productive potential. In developing management strategies these estimates can then be taken as a point of reference against which to measure impacts of fishing and the status of harvested components of the populations.

6.2.1. A theoretical model of stock structure of *P. leopardus*

I propose a theoretical model of the *P. leopardus* population on the GBR to conceptualise the stock structure challenge facing fisheries scientists and managers working on coral reefs (Fig. 6.1), as an extension of the simple schematic in Chapter 1 (Fig.1.1). This model is an adaptation of the model of Stephenson et al. (2001b), which was devoid of the specific criteria of a metapopulation, supplemented with the

terminology of an extended nested version proposed for species with different levels of stock complexity (Smedbol and Stephenson 2001). In particular, theoretical models such as this can provide a useful guide for scientists and managers to 1) appreciate the importance of larval connectivity among subpopulations, 2) understand the spatial scale of importance in maintaining individual subpopulations as well as the overall population, and 3) plan for management units that are appropriate to the spatial scale of biological units but also are logistically appropriate (Smedbol and Wroblewski 2002).

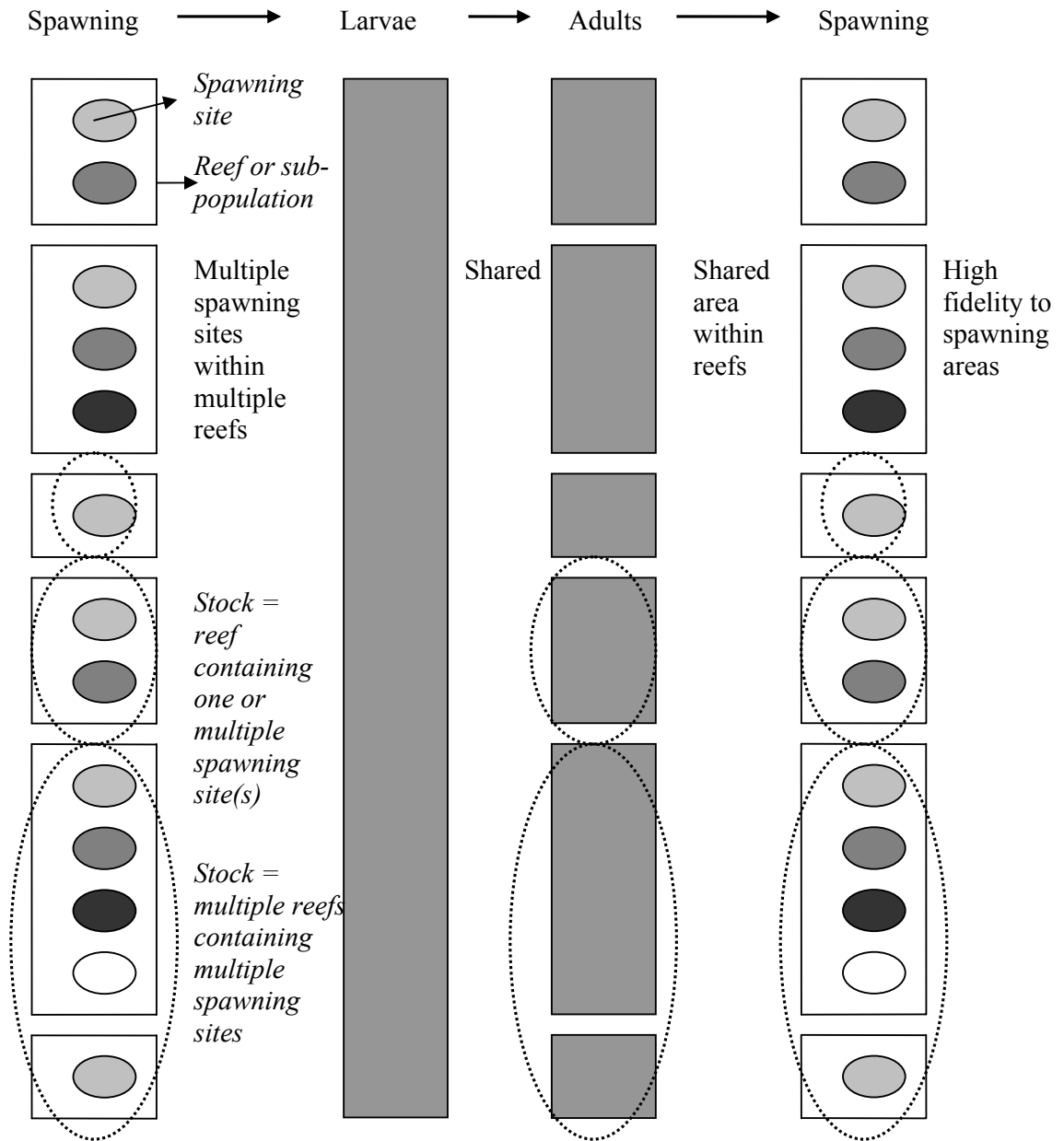**Figure 6.1** Conceptual model of *P. leopardus* stock structure, adapted from Stephenson et al. (2001) and Smedbol and Stephenson (2001). The smallest spatial unit is the area occupied by the spawning component, the second smallest component is the reef and the largest spatial component is the area covered by the larval dispersal stage. Dotted ovals indicate potential spatial components of unit stocks.

The finest spatial unit of the model is the spawning component or aggregation site. There is likely to be several spawning aggregation sites of *P. leopardus* on each reef (Samoilys 1997; Zeller 1998) to which individuals show a high degree of fidelity (Zeller 1998). The second smallest component is the reef. Tagging studies have shown that there is negligible movement of adult *P. leopardus* among reefs of the GBR, but that post settlement movements occur within reefs (Davies 1995; Zeller 1997, 1998; Zeller and Russ 1998). The larvae of *P. leopardus* are pelagic and spend about 25-30 days in the plankton prior to settlement to demersal habitats (Doherty et al. 1994), making it likely that at least some proportion of larvae are widely dispersed. Thus, the pelagic stage makes up the largest spatial component of the model and is the one about which we know least. As mentioned above, however, recent advances in hydrodynamic computer modelling and the recapture of larval fish with marked otoliths emphasise the potential existence of reefs with high self-recruitment on the GBR (Jones et al. 1999; James et al. 2002; Bode et al. 2006).

My definition of a stock is a group of spatially separate groups of individuals with persistent differences in biological characteristics that will respond uniformly to particular harvest strategies (sensu Begg and Waldman 1999), even if there is some degree of larval dispersal among stocks. Accordingly, the results from my thesis suggested potential structuring of stocks of *P. leopardus* at the fine reef scale and also at the larger regional scale incorporating multiple reefs (Fig. 6.1) for a range of phenotypic variables. The results from this thesis also revealed temporal variability and complex time – space interactions of other variables. The conceptual model presented therefore not only lay bare any persistent spatial structuring of the biological processes of *P. leopardus*, but also provides a point of reference for overlaying appropriate biological as well as logistically feasible management units.

Considering the over 3000 reef subpopulations on the GBR, each with one or several spawning components, and the fact that a management strategy of any one spatial component may affect the individuals of another through larval dispersal, makes the need for understanding what may be an appropriate management unit to regulate harvest an urgent priority.

6.3. Implications of spatial structure in life history characteristics.

Whilst the fisheries literature on temperate species has numerous studies of spatial variability in biology, the implications of such variability for the long term persistence of harvested populations are rarely discussed. Consequently, stock assessments and management strategies rarely consider such variability, and if they do, results are often based on data aggregated spatially (Stephenson 2002). My thesis took the essential next step and simulated a range of hypothetical scenarios to examine the consequences of spatial variability in life history characteristics of *P. leopardus* among regions on the GBR. Three main messages can be taken from the results and these messages can most likely be generalised to other coral reef fishes. First, there is a potential for losing information on individual spatial components in the population by reporting results aggregated spatially. Second, including spatial variability in growth and mortality is important when predicting the relative effects of fishing on individual spatial components as well as the population as a whole. Third, the results emphasise the importance of considering some life history characteristics more than others when forecasting the sustainability of harvested coral reef fishes. For *P. leopardus,* spatial variability in individual growth characteristics was more important to consider than equivalent proportional differences in natural mortality rates. The increased vulnerability of regions with

larger maximum individual sizes is predicted by the general theory of the effects of fishing on species (Adams 1980; Trippel 1995), and supported by correlations between various different life history characteristics of inter-specific stocks and declines due to fishing (reviewed by Reynolds et al. 2005). Although the von Bertalanffy growth parameters and mortality estimates were in reality not significantly different at the spatial scale of regions (relative to the variability among other factors in the analyses; Chapter 4), the simulation results emphasise the importance of accounting for even subtle differences in life history characteristics of *P. leopardus*. A similar message is likely to apply to other commercially important coral reef fishes for which similar magnitudes of variability have been reported (Williams et al. 2003; Mapstone et al. 2004; Williams et al. 2006).

Considering that significant, and sometimes temporally stable, variations in some life history characteristics of *P. leopardus* were seen also at the finer spatial scale of reefs (Chapter 4), the next necessary step should be to extend ELFSim to investigate the implications of such finer spatial scale variation in life history characteristics. ELFSim should also be extended to examine the consequences of the temporal variation present in several characteristics of this species (Chapter 4). Further, the importance of other life history characteristics should be investigated, such as age-at-maturity which is commonly correlated to stock vulnerability (Myers et al. 1997; Jennings et al. 1998) and size-at-maturity, both of which display regional differences in *P. leopardus* (Davies et al. 2006). Finally, the current results need to be viewed in the light of the assumption that larvae are distributed among reefs based on the exponential decline in dispersal with the distance between them. A hydrodynamically mediated spatially structured larval dispersal model (an extension of the model in James et al. 2002) is currently being incorporated in ELFSim. This

will allow for the investigation of the implications of spatial variation in biology of various species under potentially more realistic larval dispersal regimes. The results of this thesis provide some central pointers of the possible implications of spatial variability in coral reef fish populations with large dispersal potentials and emphasise the need for such further work.

6.4. Management implications:

As for many marine fishes, coral reef fish are typically managed uniformly across their spatial ranges, despite potential disparities in the productivity among spatially separate components. The results of spatial variability in biology among putative stocks (Chapters 2-4) and potential implications of such variability (Chapters 5), suggests that the current spatially uniform management strategies may not be optimal for *P. leopardus* or for the fishery dependent on their harvest. For example, the current management arrangements of *P. leopardus* permit a total allowable commercial catch (TACC) on the GBR, with no restrictions of where this catch can be harvested (except for the closures of some reefs within the GBR National Park). The simulation results in Chapter 5 suggest that a potential shift in effort from more to less productive population components could have potentially detrimental consequences for the latter. In addition, if structured source-sink stock-recruitment dynamics are a feature of the *P. leopardus* larval connectivity matrix on the GBR (as per Bode et al. 2006)*,* severe depletion of multiple spatial components could occur if fishing depleted key sources of larvae with disproportionately high likelihoods of recruitment success.

A possible solution would be to divide the current single management unit in place for *P. leopardus* into finer spatial units, to closer reflect stocks with different

biology. Although it seems unlikely that harvest management strategies, such as catch and effort controls stratified according to spatial structures in stocks, will be feasible at the reef scale (hundreds of meters to tens of kilometres), they could potentially be implemented at regional scales (hundreds of kilometres). For example, the TACC could be divided among regions according to their expected productivities. In one of the first examples of spatially explicit fine scale management to protect individual spawning components of herring in Nova Scotia, the TAC is distributed after annual surveys in proportion to the size of the spawning component (Stephenson et al. 2001). Although such an undertaking would clearly be impractical on the GBR, with thousands of reefs, each with potentially several spawning aggregations (Samoilys 1997; Zeller 1998), this example is an important first step towards finer scale spatial management to safeguard all spatial components in populations with complex spatial structures.

Marine protected area (MPA) strategies on the other hand, certainly could take advantage of the knowledge of persistent variation at reef spatial scales, as well as independently temporally variable reefs or groups of reefs, at least for some reefs in highly fished areas. No-take areas currently close 33.4% of the GBR World Heritage Area to fishing, and in many cases the spatial scale of a closed area is as small as an individual reef. No-take areas in their present form are not used as a fisheries management tool on the GBR. They were established to protect coral reef biodiversity, bioregions and major habitats. Marine reserves are being advocated as the primary alternative to traditional fisheries management strategies (such as catch and effort quotas) for multi-species, multi-gear, artisanal coral reef fisheries in developing nations, where policy tools such as catch and effort quotas are difficult to implement (e.g., Alcala and Russ 1990; Roberts and Polunin 1991; Russ 1991;

Munro 1996; Bohnsack 1998). The coral reef fishery on the GBR is notably different from operations in developing countries by its large spatial scale, offshore operations, commercial importance, and the targeting of few species such as coral trout[12]. No-take areas, located to include persistently high-production reefs wherever possible, in combination with traditional fisheries management policies (Russ 2002), however, should certainly be considered as potential future viable fisheries management options within the GBRWHA.

Until we know more about the ecological significance of the stock structure (Smedbol and Stephenson 2001) of *P. leopardus* and other coral reef fishes, however, defining appropriate units for *P. leopardus* to use for spatially explicit management of fishing on the GBR will be difficult. In the meantime, we should opt for a precautionary approach to management (Mace and Gabriel 1999), in which the knowledge of spatial variation in biology that we do have, and the uncertainty associated with spatial structure (i.e., variation in life history parameters with time) at both the reef and region spatial scales is taken into account and a conservative TACC, for example, is applied for the whole area. It should be noted that some current management strategies, such as minimum legal sizes and region-specifically timed fishing closures during spawning times appear to be in line with the precautionary principle, and have been important to maintaining the *P. leopardus* population at a seemingly sustainable level (Mapstone et al. 2004)

6.5. Conclusion

This multi-scale investigation of a typically exploited reef fish suggested that the *P. leopardus* population in the GBRWHA is composed of a complex network of subpopulations with spatially and temporally variable life history characteristics,

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[12] For more information on the GBR RLF see http://www2.dpi.qld.gov.au/fishweb/15895.html#12.

groups of subpopulations and potential stocks with persistent differences in life history parameters. Patterns in otolith chemistry and morphology proved useful techniques for suggesting patterns in life history characteristics and can be used to direct future research to determine the phenotypic stock structure of harvested populations. Simulation modelling suggested the importance of accounting for spatial variability in life history characteristics on a broad regional spatial scale in management strategy development, or the effects of harvest can be substantially underestimated for individual regions as well as for the entire population. Simulation results also emphasise the implications of aggregating results spatially, under which information on the different productivities of individual regions may be lost.

The results of this thesis emphasise that stock identification should be an evolving process, where key life history characteristics of targeted species are continuously monitored. Until more is known about larval connectivity, the long-term changes in life history characteristics and the consequences of finer among reef spatial differences in life history characteristics, the precise implementation of spatially explicit management may be difficult to resolve. In the meantime, the results from this thesis can be used for the development of a precautionary management strategy to account for groups of fish that function as individual units or stocks in response to harvest and management. *P. leopardus,* and probably many other coral reef fishes, therefore, should not be managed as single homogenous populations, but instead be viewed as complex networks of spatially and temporally varying components that, although interlinked, may require separate consideration for sustainable management and optimal harvest.

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