GEOGRAPHIC VARIATION IN SIZE AT AGE OF THE CORAL REEF FISH, *THALASSOMA LUNARE (*FAMILY: LABRIDAE): A CONTRIBUTION TO LIFE HISTORY THEORY

Thesis submitted by
John ACKERMAN B.Sc. (Hons)
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for the degree of Doctor of Philosophy
in Marine Biology within the
School of Marine Biology and Aquaculture
James Cook University

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ABSTRACT

Key life history traits such as age at maturity, longevity and mortality have all shown correlations with body size. However, the relationship between age and size is particularly important as growth rates (size per time) can have a profound influence on reproductive capabilities and survival. This is especially so in the context of trade-offs between traits, where fast growth may reduce survivability. One way to test trade-offs between life history traits such as growth, reproduction and survival is to examine phenotypic correlations between distinct populations. Life history attributes of populations have been shown to vary over large geographical ranges, in particular those involving a latitudinal or altitudinal gradient. Temperature is likely to be a particularly important factor influencing life histories at these scales, especially for those animals that rely on external sources for body heat. Numerous studies of terrestrial ectotherms have shown that at higher latitudes (or altitudes) body size is often larger than that of lower latitudes. Furthermore, life history theory predicts that at higher latitudes (lower temperatures) individuals should exhibit larger final body sizes but smaller size at age (i.e. slower growth). With slower growth there is likely to be a trend towards later maturation, but greater longevity. With later maturation (at larger sizes) reproductive effort is delayed, however there is the potential for greater fecundity (assuming fecundity increases with body size). However, these theoretical predictions were yet to be tested in coral reef fish. Therefore, the objective of this project was to examine age-based parameters in discrete populations of *Thalassoma lunare*, a widespread and opportunistic wrasse, to evaluate whether reef fish fit predictions of traditional life history theory. Addressing this question is fundamental to our understanding of reef fish populations, the dynamics of interactions and the diversity of coral reef fish. *Thalassoma lunare* is widely distributed, found along much of the East Australian coastline, surrounding Pacific Islands and Indian Ocean. *Thalassoma lunare* is found throughout both inshore, midshelf and outer shelf reefs on the Great Barrier Reef, temperate rocky reef systems and exposed, sheltered and lagoonal sites. Therefore, it was an ideal study organism to look at regional scales for the determination of life history trade-offs in coral reef fishes. The broad aims of this project, therefore, were to 1) describe the age-based biology of *T.*

lunare, and 2) determine whether life history trade-offs exist between growth, reproduction and longevity in this species by comparing populations along a latitudinal gradient within two oceanic basins. Specifically, the variables to be studied were size at age, lifetime growth trajectories, initial growth rates, age and size at maturity, age and size specific sex distributions, mortality and life span.

To describe the age-based biology of *T. lunare*, samples were collected at temporal intervals for a period of two years from the Palm Group of islands, including Pelorus and Orpheus Islands. Age estimates were determined from otolith samples and reproductive parameters were gathered from both macroscopic and histological techniques. To determine whether life history trade-offs exist, geographically separate populations along two latitudinal gradients were examined, one each in the Indian and Pacific Basins, ranging from 4°S to 32°S. Otolith samples for age estimation and gonads for reproductive variables were collected in the East Indian Ocean from Scott Reef (14°S), Tantabiddi, Ningaloo Reef North (22°S), Coral Bay, Ningaloo Reef South (23°S), Beacon Island, the Houtman Abrolhos Islands (29°S) and Rottnest Island (32°S). In the West Pacific Basin samples were collected from Kimbe Bay, Papua New Guinea (PNG; 5°S), Roviana Lagoon, Solomon Islands (8°S), Lizard Island (14°S), the Palm Group of islands (19°S), One tree Island (23°S) and Cabbage Tree Island, Port Stephens (32°S). In addition, two exposed outer shelf reefs were sampled along this latitudinal gradient to account for habitat variation, one at 14°S (approximately 30km east of Lizard Island) and the other at 23°S (exposed outer shelf reef surrounding the One Tree Island Lagoon).

Coral reef fish have been shown to exhibit variation in life history traits due to habitat variation. This can be caused by environmental differences in biotic factors such as predation or competition or abiotic factors such as wave action or habitat structure. Therefore, it was imperative that local scale variation (habitat) in life history parameters was examined in conjunction with the large geographic scale study. A gradient of increasing size, survivability and longevity and decreasing mortality was expected from exposed habitats through sheltered to lagoonal habitats. Therefore, three regional sites were chosen along the latitudinal gradients, two located within the Great Barrier Reef (GBR) and one in the Indian Ocean for the examination of local scale life history

differences. These included the Lizard Island Region and the Palm Group of Islands within the GBR and Scott Reef in the Indian Ocean. At Lizard Island, 3 habitat types were identified, exposed reef, sheltered reefs and a lagoon. The Palm Group of islands consisted of 4 sheltered locations and Scott Reef consisted of an outer exposed reef habitat, and two sheltered habitats, an inner reef and the leeward side of a sandy cay.

Otolith increments in *T. lunare* were found to be yearly in formation with no evidence of fish living beyond that of 7 years of age. The plot of size against age showed similar patterns of initial rapid increases followed by a tapering growth trajectory similar to those of other labroid fishes. Whilst mature females were evident in the population at the age and size of 1 year and 70mm Standard Length (SL) respectively, 50% maturity did not occur for females until approximately 2 years of age and 90mm SL. Furthermore, no females were found beyond 5 years of age and 130mm SL, whilst males were only evident in the population after 2 years of age and 90mm SL. This is typical of a protogynous hermaphrodite, where individuals change sex from females to males. Whilst no running ripe gonads were found in the winter months, they were found in April, October and November. In addition, spawning aggregations were observed in July and ripe gonads were found in August. It appears, therefore, that spawning events may occur throughout the year at the Palm Group of islands.

Variations in age-based parameters of *T. lunare* populations across latitudinal gradients throughout the West Pacific Basin and East Indian Ocean were in stark contrast to the predictions. The expected gradient of increasing size and longevity and decreasing mortality was not always observed from lower to higher latitudes. Instead, reef exposure played a significant role in shaping life history parameters of these coral reef fish populations. Gradients from exposed reefs through to sheltered reefs were more likely to cause an increase in size and longevity and a decrease in initial growth rates and mortality.

A general pattern of increasing longevity with increasing latitude was evident in the Indian Ocean but not in the Pacific Basin. Mean 20% longevity estimates from regions in the Indian Ocean were highest at Rottnest Is and the Abrolhos Is, in the south, being significantly greater than those estimates from Ningaloo South and Scott Reef. In

the Pacific Basin, mean 20% longevity estimates followed a habitat cline more so than a latitudinal one. With the exception of One Tree Island Outer Reef, which exhibited large variation due to small sample sizes, the majority of regions with high estimates of longevity were those with relatively sheltered environments, such as the One Tree Island Lagoon and the inshore Palm Group.

Growth at all regions showed similar patterns of initial rapid increases followed by a tapering growth trajectory as those found at the Palm Group of islands. However, both the Indian Ocean and Pacific Basins exhibited little evidence of predicted latitudinal gradients in growth trajectories. There was no evidence of differences in growth parameters between PNG and Port Stephens, two regions separated by the greatest distance. In addition, the Outer Shelf Reef at Lizard Island and the One Tree Island Outer Reef were similar to these two regions, indicative of a habitat difference rather than a large latitudinal gradient. Instantaneous growth rates revealed patterns inconsistent with the theory that higher latitudes (colder waters; 18–25°C) would exhibit slower initial growth rates compared with lower latitudes (warmer waters; 26–31°C). In both oceanic basins the slowest rates were found in the mid-latitudinal regions. Additionally, mortality estimates were also highest at the mid-latitudinal regions.

In general, female fish were mature by 1 year of age, and few mature females remained in the population beyond 4 years of age, with the majority of regions exhibiting substantial numbers of males in the 2-year-old age class. Maturity ogives for the regions in the Indian Ocean show that 50% female maturity was at the lowest ages for the mid-latitudinal regions and highest for the most southern region sampled. One Tree Island Outer Reef and Port Stephens, in the Pacific Basin revealed the lowest age at which 50% female maturity occurred, whilst the highest value occurred at the Palm Group. There was little evidence of a latitudinal pattern regarding sex change in the Indian Ocean; however, a pattern was evident in the Pacific. Populations at the PNG and Solomon Is regions showed the earliest age at sex change, whilst the population at Port Stephens showed a later age of 50% sex change. In general, 50% female maturity occurred at approximately 40% of a population's maximum size and 10 to 20% of a population's maximum age, whilst 50% sex change occurred at approximately 70% of a population's maximum size and 30 to 50% of a population's maximum age. For most populations,

size and age at maturity was generally related to their final body size and size and age at sex change was generally related to size and age at maturity. However, in areas of relatively high densities, e.g. Ningaloo South, OTI lagoon, Solomon Is and PNG, there appeared to be a significantly shorter period between the age at which 50% female maturity occurred and the age at which 50% sex change occurred.

There was significant variation in age-based demographic parameters between habitats, within regions. However, this variation was often not consistent with the predictions that a gradient would exist from the exposed through sheltered to lagoonal habitats of increasing size and age and reduced estimates of mortality, as observed habitat parameters differed between regions. Longevity estimates between habitats, within regions, were only evident at the Palm Group and Scott Reef regions. This is surprising, as these two regions were less heterogeneous in exposure compared with the surrounding habitats of Lizard Island. However, growth trajectories exhibited differences between sheltered and exposed locations of Lizard Island with little difference found between habitats within the other two regions. Mortality, whilst fitting predictions at one region, was generally not consistent between regions. Differences in mortality estimates were only evident between the exposed and sheltered reefs of Lizard Island.

Whilst a gradient of slower growth, later maturation, larger final body sizes and increasing longevities have been shown to exist in terrestrial ectotherms, for coral reef fish this may not always be the case. Age-based parameters of *T. lunare* appear to be more susceptible to habitat variation than large regional scales and/or large temperature differences. Therefore, exposed outer reef habitats are more likely to impose smaller final body sizes, potentially reduced longevities and increased mortality in contrast to the more sheltered inshore environments. Further work is now necessary to determine the biotic and abiotic factors that affect populations of coral reef fish across these habitat scales, especially traits such as age at maturity, longevity and mortality. Additionally, research is needed to link these life history attributes with phylogenetic information. Finally, modelling the extent to which phenotypic flexibility exists amongst traits between genetically similar populations will increase our understanding of evolved strategies to account for habitat heterogeneity.

One aspect is evident however, for *T. lunare* to attain a large size, regardless of habitat, it needs to grow old. In habitats where survivability is low, and consequently size is comparatively small, reproductive output maybe reduced. If this is the case, then these populations may be contributing little to the overall gene pool. In contrast, those populations attaining larger sizes (and ages) may be contributing substantially and therefore these populations need to be maintained to sustain the resilience of the species as a whole.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1. GENERAL INTRODUCTION

1.1. Body size and relationship with other life history traits

One of the most obvious and important characteristics of any organism is its body size (Peters 1983; LaBarbera 1989; Hanken & Wake 1993). However, body size has often been overlooked (Schmidt-Nielsen 1984) even though differences can exist across orders of magnitude, even between species that are closely related (Munday & Jones 1998; Ackerman et al. 2004). Yet it plays a fundamental role in physiological (Roff 1981; Platt & Silvert 1981), behavioural (Schlesinger & Shine 1994), evolutionary (LaBarbera 1989; Hanken & Wake 1993) and ecological (Calder 1983; Ackerman & Bellwood 2003) processes. The influence of body size on the ecology of animals may be sub-divided into community (Hutchinson & MacArthur 1959; Damuth 1981; Griffiths 1986; May 1986; Blackburn & Gaston, 1996) and individual levels (Avery 1996; Churchfield 1996). On a community level, species numbers and densities are often correlated with body size (Damuth 1981; Peters 1983; May 1988). On an individual level, size may influence such aspects as energetics, habitat utilisation, food acquisition, food handling capabilities, and predation (Churchfield 1996; Miller 1996). Therefore, body size can be an important determinant of life history variation with profound consequences on the ecology and evolution of life history traits (Calder 1983; Schmidt-Neilsen 1984; LaBarbera 1989).

Key life history traits such as longevity, age at maturity, fecundity, generation time and offspring size have all been shown to have positive relationships with body size (Calder 1984; Begon & Mortimer 1986). Furthermore, life history traits such as mortality (Blueweiss et al. 1978, Sogard 1997) and specific metabolic rate (metabolic rate relative to mass; Schmidt-Nielsen 1984) have been shown to have strong negative relationships. Therefore, much of the demographic variation between species can be accounted for simply by variation in body size. However, many life history variables have units of time (Charnov 1993), such as age at maturity, growth rates or maximum life span. Age, therefore, becomes an important tool in understanding population demographics and life history attributes. Introducing age structure is the basis of the 'life

table' leading to classical demography and life history theory (Stearns 1992). Furthermore, size and age and the relationship between them are specifically important demographic tools necessary to our understanding of population turnover rates (Choat et al. 2003) and therefore to our understanding the evolution of life history theory (Stearns 1992).

1.2. Size at age and trade-offs between life history traits

The relationship between body size and age is of particular importance to the life historian, as growth rates are a key element in life history evolution (Roff 1992). Growth rate can have a profound influence on the survivability and reproductive capabilities of an organism. Whether this be growing faster or growing for a longer period. For example, larger individual size at age has been related to decreased mortality in a range of organisms (Avery 1996; Sogard 1997, Rilling & Houde 1998). Furthermore, larger size at age can advance maturation times and increase fecundity (Forsythe & Hanlon, 1988; Roff 1992). However, in contrast, faster growth has also been found to reduce longevity (Metcalfe & Monaghan 2003). Hence, a trade-off may exist between these traits, in which the unit of resource allocated to growth cannot be allocated to survival (Grubb 1989, Stearns 1992, Roff 2002). There are several reasons why faster growth may be linked to a reduction in longevity. Firstly, increased growth rates can be an effect of increased resource acquisition, which may increase the susceptibility of the organism to predation (Gotthard 2000). Secondly, faster growing individuals may be more susceptible to starvation during periods of limiting resources (Blanckenhorn 2000). However, in addition to extrinsic causes, there have been links with intrinsic factors (Monaghan & Metcalfe 2000; but see Morand & Ricklefs 2001). Different genetic strains of mice and rats exhibiting different growth rates have revealed variable longevities, regardless of diet (Rollo 2002).

Trade-offs between traits, especially between reproduction and survival and reproduction and growth, are an essential part of life history theory. There are four ways in which trade-offs of life history variables can be examined (Reznick, 1985 and highlighted in Roff 2002). These are

1)   Phenotypic (or environmental) correlations, which measure the association between two life history traits between individuals, populations or species.

2)   Experimental (or environmental) manipulations, which manipulate a trait of interest whilst attempting to keep all other factors constant (or at the very least random)

3)   Genetic analysis (correlations), either through co-variation between individuals within and among families (sib-analysis) or

4)   Genetic analysis (correlations) through selection experiments.

To gain a full understanding of the nature of trade-offs between traits and the causal mechanisms behind them it is necessary to include both phenotypic and genetic analysis (Roff 2002). However, if the limitations are recognised (i.e. there may be additional variables associated with the correlation) and causal mechanisms are suggested rather than attributed, then they are particularly important in recording life history variation in nature. Furthermore, studies examining phenotypic correlations are imperative to generating testable hypothesis regarding life history traits and trade-offs (Bronikowski & Arnold 1999).

Why do high rates of reproduction or high growth rates lead to high rates of mortality? Understanding the patterns or processes that limit longevity, growth or reproduction is of fundamental importance to explaining the diversity of life (Partridge 1989; Stearns 1992). As mentioned, one way to test these patterns and the processes governing them is to perform manipulative experiments or common-garden laboratory experiments. However, in some animal groups this is difficult due to logistic difficulties associated with keeping the animals in enclosures for their reproductive life span. Therefore, one way to avoid these problems is to examine trade-offs amongst demographic traits between species or populations. However, interspecific comparisons are heavily reliant upon a complete and reliable phylogeny. In contrast however, an examination between geographically distinct populations (either latitude or altitude) of conspecifics (Charlesworth, 1980) does not have the same constraint.

1.3. Latitudinal and altitudinal variation in life history characteristics

Size at age has often been shown to vary over large geographic ranges involving a latitudinal or altitudinal gradient (Atkinson, 1994). Temperature is likely to be a particularly important factor influencing life histories at these scales, especially for those animals that rely on external sources for body heat (Sebens, 1987, Atkinson 1996). Temperature is known to have a significant effect on metabolic rate, growth and overall size of ectotherms (Brett, 1979; Rilling & Houde, 1998; Wood & O'Dor, 1999; but see Sinclair et al. 2002). Over 40 years ago, it was realised that with an increased rearing temperature, the resultant body size of a poikilotherm decreased (Ray, 1960; Nunney & Cheung 1997). This proposal followed that of Bergmann's rule where the mean body sizes of endotherms increased with decreased temperature and therefore, at higher latitudes (or altitudes) body size is often larger than that of lower latitudes (but see Mousseau, 1997). However, whilst this is usually examined between species using mean estimates of species size and latitude (see Manly 1998), it has also received attention within species, at the population level (Mayr 1956; Ashton et al. 2000; Freckleton et al. 2003). Much of the variation in life history traits at this level has focused upon butterflies (Gotthard et al. 1994), squid (Forsythe, 1993), frogs (Berven & Gill, 1983) and reptiles (Gregory & Larsen, 1996). Much less has been done on the life histories of coral reef fish (Caley, 1998; but see Schultz & Warner, 1991) and very few studies have examined variation of life histories of reef fishes over large spatial scales (but see Meekan et al. 2001 and Choat et al. 2003).

1.4. Contribution of reef fish to life history theory

Much is known about terrestrial organisms, especially *Drosophila* spp., due to fast generation times and ease at which they can be experimentally manipulated. However, a comprehensive understanding of fish life histories is generally limited to that of guppies (*Poecilia reticulata*; Reznick and co-workers) and Atlantic silversides (*Menidia menidia*; Conover and co-workers). Both Reznick and Conover and their associated co-workers have done much over the last 15-20 years with regards to understanding fish life histories, trade-offs and causal mechanisms. However, our understanding of reef fish life histories is limited (but see Warner 1984a, 1984b, 1995 for reproductive strategies). This is especially so regarding age-based demography. Historically, difficulties associated

with identifying and counting incremental marks in calcareous structures from tropical fish have impeded age-based studies on coral reefs (Choat et al. 2003). However, thinly sectioned otoliths have greatly reduced the difficulties encountered when attempting to estimate the age of tropical fish. Furthermore, the increased occurrence of studies validating the periodicity of increment formation within sagittal otoliths has enabled age-based studies in tropical regions to develop (Cappo et al. 2000, Kalish 2002).

Examination of reef fishes could make a substantial contribution to understanding life history theories. They are widely distributed, inhabiting a variety of environmental gradients, which is likely to cause significant variability amongst life history traits (Gust et al. 2002). Furthermore, recent evidence suggests that they may offer additional insights into life history variation, as they do not necessarily fit general predictions. For example, a negative relationship has been demonstrated between longevity and body size within the Family Serranidae (Mosse 2001). Smaller cods live in excess of 40 years, whilst the larger trout rarely live beyond 15 years. This is contrary to the positive relationship predicted by traditional life history theory. However, we have little understanding of how these demographics vary over large spatial scales (i.e. latitude), or to what extent they can vary. Life history theory predicts that at higher latitudes (lower temperatures) coral reef fish would exhibit larger final body sizes but smaller size at age (i.e. slower growth). With slower growth there is likely to be a trend towards later maturation, but greater longevity (Stearns & Koella, 1986). With later maturation (at larger sizes) reproductive effort is obviously delayed and therefore potentially decreased, however there is the potential for greater fecundity (assuming fecundity increases with body size). Yet, these fundamental theories remain to be tested in coral reef fishes. In addition, some reef fish undergo adult sex change, a taxonomically widespread strategy but generally uncommon (Warner 1984b, Rogers & Sargent 2001). This introduces an additional and complex variable to be considered when examining life history models (Charnov, 1993).

Labrids (Wrasse) are both abundant and speciose components of reef fish assemblages. Worldwide there are estimated to be approximately 450 species of labrids (Parrenti & Randall 2000), with a large proportion of those found in tropical regions. What we know to date suggests they are mostly protogynous hermaphrodites (i.e. sex

change from female to male), which has been one of the major reasons for their representation in the scientific literature. Much of our understanding of the ecology and evolution of sex changing species has come from the ability to collect these abundant and conspicuous fish. Yet, excluding a few species, including the Caribbean bluehead wrasse (*Thalassoma bifasciatum*), there has been little information on age-based life history aspects of tropical labrids. Notwithstanding, the recent developments of age and growth studies in the tropics (Meekan et al. 2001, Choat & Robertson 2002).

The labrid family is an ideal group to identify some of the patterns involved with latitudinal variation due to their abundance and distribution. They are known to occur throughout the tropical, subtropical and temperate regions and they are one of the most abundant and speciose family. Large variations in body size (50mm to 2300 mm) within the family provide a good opportunity to investigate the correlations between body size and other life history traits. In addition, labrids are mostly protogynous hermaphrodites, enabling a relatively unique trait (to life history theory) to be examined. The moon wrasse (*Thalassoma lunare*; Labridae), a tropical reef species found in large abundances along both the west and east coasts of Australia to as far south as Rottnest (32°S) and Montague Islands (36°S) respectively is ideal for the examination of these large scale patterns. It is an abundant, opportunistic reef fish (Connell 2000), with adult fish generally larger than the majority of fish found on a reef (Ackerman & Bellwood 2000). It ranges from the Red Sea to the West Pacific, through tropical, subtropical to temperate regions. It is one of the most widespread reef fish in the southern hemisphere, found at equatorial regions ranging to 36° S. Found locally to be one of the top 5 most abundant labrids (Fulton et al. 2001), yet surprisingly, there is little information on its life history characteristics. However, the extensive distribution of this reef fish allows for the examination of age-based demographic parameters across large regional scales. In addition, the potential for widespread dispersal of pelagic larvae avoids the need to separate ancestral effects from genetic responses. This reduces the opportunity of local genetic differentiation (Schultz & Warner, 1991; Warner 1997, Shulman, 1998), therefore variation in life history parameters between populations are likely to be a response to environmental conditions.

However, one problem associated with population studies over large spatial scales are variables that cannot be controlled for. Variables, such as habitat structure, food availability, predation, wave energy or abundance, amongst others, may alter over these spatial scales (Williams 1982, Sale 1991, Caley 1995 Crossman et al. 2001) in conjunction with temperature. All of which have long been known to have consequences on life history characteristics (Brett 1979, Reznick & Endler 1982, Jones 1991). Especially age and size at maturity and age and size specific mortality (Stearns 1992). Whilst it is not possible to measure all habitat associated differences, the examination of demographic differences in populations separated by large spatial scales need to account for potential habitat variation before observations concerning geographic variation can be related to predictions.

The examination of age-based demographic variation across variable spatial scales is an important aspect of understanding coral reef fish dynamics, as it has significant implications for a range of conservation and management based practices. Demographic variation has direct implications for a population's ability to maintain or increase its abundance, as reproductive output is often positively correlated with the size and/or length of the reproductive lifespan of the individual (Roff 1992). Therefore, significant variation in reef fish demography across regional (or local) scales may translate into some populations being more important to the reproductive output of the species than others (Kritzer 2002). This potential demographic variation has strict consequences for decision making in spatially based management/conservation practices for Marine Protected Areas (MPA's) or Representative Area Programs (RAP's), such as those currently in place within the Great Barrier Reef, Australia.

1.5. Variables to be examined

Whilst all life history traits figure undoubtedly towards a species reproductive capability and ultimately its survival, principle life history traits have been defined as; size at birth; growth pattern; age at maturity; size at maturity; number, size and sex ratio of offspring; age- and size-specific reproductive investments; age- and size-specific mortality schedules and length of life (Stearns 1992). Tropical reef fish are invariably pelagic spawners, either in groups or as spawning pairs, where eggs and sperm are

ejaculated into the water column where fertilisation occurs (Domeier & Colin 1997).
They are washed off the reef, usually as the spawning occurs on an outgoing tide, where
the larvae spend days to months in blue water before returning to a reef. This mode of
reproduction makes it extremely difficult, if not impossible, for tropical marine
ichthyologists to determine demographic variables such as size at birth and number, size
and sex ratio of offspring. However, through the use of sectioned otoliths, age and size
based demography can be investigated with a high level of certainty. Therefore, in this
study the variables to be focused upon will be age, size, lifetime growth trajectories,
initial growth rates, age and size at maturity, age and size specific sex distributions,
mortality and life span. Additionally density dependent processes have been implicated
numerous times in the variation of life history attributes (Warner & Hoffman, 1980;
Jones, 1991; Warner, 1991). Therefore, density estimates will be incorporated into the
analyses to determine whether high or low abundances can explain any of the variation.

1.6. Objectives

The main objective of this study is to test predictions of life history theory by
examining age-based demographic traits within one species of the labrid family. This
project will provide a unique contribution to general life history theory by focusing on a
large geographic scale extending over 24° of latitude in two oceanic basins. Through the
examination of these populations over this large regional scale it will provide the basis
for understanding important trade-offs between age- and size-based demographic traits in
reef fish. Furthermore, it will provide us with baseline information with which to further
evaluate the causes of demographic differences within species groups. More specifically,
Chapter 2 will examine the basic biology of *T. lunare*, in particular, the temporal nature
of incremental marks in the otoliths, the maximum age, the sexual size and age structure,
and maturity and sex change schedules. These data will establish the fundamental
demography of this species to allow for a more in depth examination of age- and size-
based traits across variable spatial scales. Chapter 3 will describe a technique for
assessing growth rates amongst populations, as current methods are inadequate, even
though growth rates are an important component of understanding life history variation.
Chapter 4 will examine maximum life span, size at age, growth rates, age and size at
initial sexual maturity, age and size at sexual transition and natural mortality rates

between geographically distinct populations of *Thalassoma lunare* in both the East Indian Ocean and West Pacific Basin. Furthermore, in Chapter 5, local scale variation will be examined at several geographically separate regions, as latitudinal studies need to control for local scale variation in environmental conditions due to environmental differences obscuring any large-scale demographic patterns (Roni & Quinn, 1995). Local scale variation will be assessed at the habitat level, with differences based upon exposure, i.e. exposed reef fronts, sheltered reefs and lagoonal habitats. Moreover, a cross-shelf comparison (along $14^{o}S$) will be examined as large demographic differences have been reported for reef fish across this environmental gradient (Gust et al. 2002). Variation of the above demographic variables will therefore be at three scales; local (habitat), cross-shelf and regional (latitude and oceanic basins). Furthermore, density estimates will be obtained in conjunction with the above demographic traits and interactions between these will provide us with insights into potential trade-offs within the life history of a protogynous coral reef fish.

CHAPTER 2. PERIODIC OTOLITH INCREMENT FORMATION AND TEMPORAL SPAWNING IN THE MOON WRASSE, *THALASSOMA LUNARE* (FAMILY LABRIDAE), AT THE PALM GROUP OF ISLANDS, GREAT BARRIER REEF (GBR).

2.1. Introduction:

Information such as growth, size and age at maturity, reproductive output, mortality rates and longevity estimates are all key demographic parameters necessary for the development of fundamental life history theory and consequently understanding the mechanisms of evolution (Stearns 1992). Age is a fundamental component of these demographic parameters and can be obtained for teleosts through the examination and analysis of growth zones in bodily structures such as scales (Robillard & Marsden 1996), bones (Cass & Beamish 1983, Brennan & Cailliet 1989) and otoliths (Meekan et al. 2001, Gust et al. 2002, Choat et al. 2003). Otoliths are the most commonly used structure for fish as it has shown to be the most reliable in age determination (Jones 1992). In fact, in 1999 alone over 800,000 otoliths were examined worldwide, purely for the purpose of age estimation in the use of fisheries stock assessments (Campana & Thorrold 2001).

Otoliths are crystalline concretions comprised mainly of calcium carbonate, precipitated from the surrounding endolymph fluid onto a matrix of proteins (the most common of which is otolin). Rings can be observed, and counted, in the otoliths due to an optical contrast between the protein rich and protein poor zones, most commonly due to an increase in growth over the warmer summer months, in comparison to the cooler winter months. Each alternate opaque and translucent band may therefore represent one year (i.e. a period of fast and slow growth). However, much has been written about the need for confirming whether these bands are in fact annual (Beamish & McFarlane 1983; Francis 1995; Campana 2001). Several different validation techniques are possible, with some ranked higher than others, according to a proposed index of scientific merit (Campana 2001). However, much of the validation argument has revolved around definitions.

Apart from the difference between precision and accuracy, the argument can be divided into two broad categories. Firstly, the periodicity of the incremental marks (i.e.

whether they are in fact formed annually) and secondly, whether the number of bands is estimated accurately (i.e. how close an estimated age is likely to be the true age (Francis (1995)). As it is difficult for most studies regarding fish ages to directly estimate whether an age is accurate, as true ages are unknown, the periodicity of the incremental mark is commonly what most authors allude to regarding validation. However, regardless of the inconsistencies with validation terminology, there is little evidence to suggest that these incremental marks are formed with a periodicity other than once a year (Fowler & Doherty 1992, Cappo et al. 2000, Kalish 2002, Caldow & Wellington 2003). Much of the need for validation has arisen due to the difficulties associated with the estimation of age from the otoliths of deep-water species, where growth-zones are often narrow and difficult to read and longevities can be in excess of 100 years (Cailliet et al. 2001). However, sectioned otoliths for tropical reef fish allow for discernable recognition of incremental marks (Fowler 1990). Furthermore, longevities have rarely been found beyond the age of 50 years. Therefore, validating otoliths for tropical reef fishes at every geographic location within its range, as suggested by Geffen (1992), is likely to be unnecessary (Choat et al. in prep).

Age-based data are fundamental to understanding life history aspects of tropical reef fish. Growth rate, age at maturity, mortality and longevity (Campana 2001) are crucial to understanding population dynamics, rates of population growth and survivability. Whilst otolith examination for age estimation is widespread, age-based parameters have been estimated using other techniques, such as length-based measures (Eckert 1987, van Rooij et al. 1995). However, estimates of age-based parameters following length-based analysis of cohorts have often led to erroneous estimates of longevity (see van Rooij & Videler 1997 in contrast with Choat et al. 2003). This is because asymptotic growth trajectories, a common growth pattern in reef fish (Choat et al. 1996, Meekan et al. 2001, Choat & Robertson 2002), make it difficult to distinguish one cohort from another when length is the focal variable. Furthermore, some reef fish are long lived (estimated through the examination of otoliths) which make it difficult to follow young individuals into the oldest age categories. This is especially so for fish living beyond a few years. In reef fish, this appears to be the rule rather than the exception with many species living beyond 5 years of age and with some living beyond 30 years of age (Mosse 2001, Choat & Robertson 2002, Choat et al. 2003). However, reef fishes of the labroid clade, including wrasses and parrotfishes, often exhibit

relatively rapid indeterminate growth, high mortality rates and reduced life spans (Hostetter & Munroe 1993, Choat et al. 1996, Choat et al. 2003, Choat et al. in prep). In contrast, Eckert (1987), through the use of length-based visual techniques, estimated the life span of the relatively small labroid, *Thalassoma lunare*, and the subject of this study, to be on average 12 years old with a 10% probability of attaining ages of 19 years. Examination of incremental marks in otoliths has yet to confirm this relatively old age for a labroid of this size.

The study of labroids has contributed significantly to our limited understanding of tropical reef fish life histories (see Warner 1984a and Schultz & Warner 1989, 1991). The majority of work in this group however, has largely been focused upon reproductive strategies (Robertson 1972, Choat & Robertson 1975, Robertson & Warner 1978, Warner 1984b, Jones 1980b). Labroids are generally sequential protogynous hermaphrodites, often with two male strategies (diandry; Warner 1988). The first with a colour pattern indistinguishable from the female (initial colour phase pattern), that either spawns with females in groups, or sneaks into pair spawning individuals (Henson & Warner 1997). The second, with a terminal phase (TP) colour pattern, which in all species (except one) is brighter than the female or Initial Phase (IP), maintains spawning territories, with larger individuals holding prime position on the reef. These individuals may pair spawn with individual females up to 60 times in any one day (Warner & Schultz 1992, Warner et al. 1995). Sex change has been demonstrated to be socially induced, either based on the removal of the largest (presumably male) individual (Munoz & Warner 2003a) and/or the sex ratio becoming overly female biased (Shapiro & Lubbock 1980).

Recent work however, has shown that the largest females may not change sex under altered social conditions (Munoz & Warner 2003b). Rather the second or third largest female will do so. Munoz & Warner (2003b) hypothesise that once a certain size threshold has been reached the advantage of changing sex to male is outweighed by the size of the female ovaries and therefore fecundity and their overall reproductive output will in fact be compromised. Additionally, Choat et al. (in prep) have shown that all females of the large labrid, *Cheilinus undulatus*, may not change sex, as the oldest individuals in their sample were female.

Despite the large body of literature on sex change in wrasses, very few have examined age-based demography, or its relationship with sex specific stages (but see

Jones 1980a). Whilst age-based data has been gathered for those species used to examine various aspects of life history theory, such as sex change (Cowen 1990) and ontogenetic migration (Gillanders 1997), there is still the need for additional baseline biological data to link the role of size, age and growth to that of maturity, mortality and longevity. These data on the basic biology of the species are essential to evaluate the types of variation we may expect in *T. lunare* life history parameters. This was achieved by addressing the following objectives at the Palm Group of islands:

1)   What is the temporal nature of the incremental bands in the sagittal otoliths?

2)   What is the maximum age?

3)   What is the sexual size and age structure?

4)   When did individuals mature?

5)   If protogynous, when did sex change occur? and;

6)   At what time of the year did they reproduce?

2.2. Methods:

2.2.1 Sampling locations:

Sampling of *Thalassoma lunare* begun in December 1999 through to the end of 2001 with collections occurring approximately eight times throughout each year. Sites were located in the Palm Group of islands (18° 40'S 146° 30'E) along the Great Barrier Reef (GBR). These included the western (leeward) sides of both Pelorus Island and Orpheus Island (Figure 2.1).

2.2.2 Sampling procedures:

Collections of individual fish were through the use of hand-spears. Fish were weighed and measured for fork and standard length (FL and SL respectively) to the nearest mm. Sagittae were removed, cleaned, washed in ethanol and stored dry. Gonads were removed and fixed in Formaldehyde-Acetic Acid-Calcium Chloride (FAACC). One sagitta from each pair was weighed to the nearest 0.1mg. This was mounted on the edge of a glass slide in thermoplastic glue and ground to the core using 800 or 1200-grade wet and dry sandpaper. Subsequently, the glue was re-heated, the otolith placed with the core flat against the glass slide and the opposite end ground,

leaving a thin section through the core mounted in the glue on the glass slide. The thermoplastic glue was then spread thinly across the section to increase the clarity of the increments. Sectioned otoliths were examined under dissecting microscopes using transmitted and reflected light. Counts were made along a consistent axis following Choat & Axe (1996). Each otolith was read at least 2 times for annuli. Any discrepancy resulted in a 3rd reading. Any sagittae that were obviously 0+ age categories were polished further and counts of presumed daily rings made under high power microscopes using transmitted light.

Otolith increments can vary with respect to their readability between families, species, individuals, locations with which the samples were obtained, or any combination thereof. Therefore, a means by which we can measure the ease of interpretation is often desirable for comparative purposes. Beamish and Fournier (1981) recommended the use of an index of average percent error (IAPE), which was highlighted and further emphasised in Campana et al. (1995). The IAPE is calculated as:

$$IAPE = \frac{100}{N} \sum_{j=1}^{N} \left[\frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j} \right]$$

Where N is the number of fish aged, R is the number of times fish are aged, X_{ij} is the ith determination for the jth fish, and X_j is the average estimated age of the jth fish. As the IAPE is derived from an average across all individuals it becomes a means of assessing the ease to which the increments can be determined (Campana et al. 1995).

2.2.3 Marginal increment analysis:

Marginal increment analysis (MIA) requires fish to be collected at periodic intervals throughout the year and preferably over several years (two years in this study). Distances of the last complete incremental cycle, one opaque zone and one translucent zone, and those between the last opaque zone to the outside edge of the otolith were measured along the short axis from the primordium (nucleus or otolith centre) to the proximal surface using the free UTHSCSA ImageTool program (developed at the University of Texas Health Science Center at San Antonio, Texas and available from the Internet by anonymous FTP from ftp://maxrad6.uthscsa.edu). The marginal increment for each otolith was expressed as a proportion of the preceding

annulus (Fowler & Short, 1998). This was plotted against the time of year the individual was collected. The resulting graph should be sinusoidal with a frequency of 1 if the increments are annual (Campana, 2001). In addition, edge analysis was performed where the presence of an opaque or translucent zone was recorded. As with MIA the result should have a frequency of 1 if the increments were in fact annual.

2.2.4 Reproductive staging and sex specific size at age:

Gonads were weighed to four decimal places and reproductively staged using histological methods. Individual maturity was assessed based on the most advanced germ cell (oocyte or spermatocyte) present (West 1990; Table 2.1). Mature resting females were defined as those females that had completed spawning for a season. Identification of transitional (sex changing) individuals was based upon Sadovy & Shapiro (1987; Figure 2.2). All males sampled were observed to be mature and ripe, whereby the testis was undergoing active spermatogenesis with spermatozoa within sperm sinuses. The presence of transitionals, coupled with the observation of primary and secondary males demonstrated that the species is diandric (Shapiro & Rassotto 1993). Primary males (that did not undergo adult sex change) possessed a centralised duct and no ex-ovarian lumen within the testis. Sperm sinuses in secondary males were present in the ex-ovarian wall and were peripheral in nature. Furthermore, an ex-ovarian lumen was present in the testis of secondary males.

Frequency distributions of each age (years) and size (cm) class were plotted by sexual stage. In addition, gonadosomatic index (GSI) was calculated for each individual in which intact and complete gonads were collected by dividing gonad weight by body weight. This value was then plotted against the day of the year in which the individual was sampled. In order to obtain information regarding the seasonality of spawning, each mature female was further separated by the histological stage (i.e. just spawned, running ripe, ripe, ripening and resting) and again plotted against the time of the year in which the individual was sampled. Finally, to ascertain the relationship between size and age for each sex, each age class was divided by sex and stage and the mean size calculated accordingly.

Table 2.1: Reproductive stages of *T. lunare* based upon histological examination adapted from West (1990); Burton et al. (1997)[a]; Shapiro et al. (1993)[b]; Fennessy & Sadovy (2002)[c], and; Sadovy & Shapiro (1987)[d]. * The transitional individual was found in the Lizard Island Outer Reef region as no transitionals were found in the Palm Group of islands.

Developmental stage	Histological description
Immature	Ovary small and dominated by previtellogenic (primary growth phase) oocytes. Thin gonad wall[a]. No evidence of prior spawning, such as post ovulatory follicles (POF's), atretic vitellogenic oocytes or intralamellar muscular bundles[b].
Mature Resting Female	Ovary dominated by previtellogenic oocytes (as in immature female) but with a thick gonad wall[a]. Evidence of recent prior spawning indicated by intralamellar muscle bundles[b] and possibly POF's.
Undetermined Inactive Female	Ovary dominated by previtellogenic oocytes as in immature, yet larger in size. Insufficient morphological features such as a clearly thick gonad wall, degenerated vitellogenic oocytes and/or intralamellar scaring to determine maturity[c].
Ripening Female	Cortical alveolar stage oocytes most advanced stage present.
Ripe Mature Female	Ovary in active vitellogenesis with oocytes present in all stages of development. However, the most advanced oocyte stages present are the vitellogenic yolk globules and migratory nucleolus stages.
Running Ripe Mature Female	Ovary in active vitellogenesis as in ripe mature females, however, hydrated oocytes are the most advanced oocytes present.
Just spawned Mature Female	Ovary dominated by previtellogenic oocytes at times hydrated, however, POF's are abundant.
Transitional Phase[d] (Figure 2.2*)	Degenerating vitellogenic oocytes in the presence of proliferating (up to spermatids stage) spermatogenic tissue – and/or proliferating spermatogenic tissue in an ovary that has evidence of previous spawning.
Mature Ripe Males	Testis in active spermatogenesis whereby all stages of spermatozoa were present, and spermatozoa fills the sperm sinuses. Previtellogenic oocytes were present in the testis of some secondary males

2.3. Results:

2.3.1 Precision of age estimates:

The index of average percent error (IAPE) for incremental interpretation of *Thalassoma lunare* otoliths collected at the Palm Group was 6.34. This species is relatively short lived with longevity at this location not in excess of 7 years of age. Therefore any discrepancy in a single age class has a relatively large impact on the IAPE value. The value of 6.34 is therefore considered to be a relatively precise estimate, indicative of the ability to repeatedly read increments consistently due to clear visible rings.

2.3.2 Marginal increment analysis:

The marginal increment analysis considered all fish sampled across a time span of approximately 2 years. Nevertheless, the pattern is consistent with the predictions of a sinusoidal graph with a frequency of one (Figure 2.3). The graph shows an increasing proportion through time from February until mid April where a 1:1 ratio is reached between the last complete increment and the subsequent developing increment. Correspondingly several samples show opaque zones forming from April through to mid August. The highest proportion of opaque to translucent otoliths occurs in May to June. This pattern is consistent with the pattern of opaque zone formation in the winter months of May to July. The smallest proportion of the forming increment to the preceding full increment was found in mid August. Following this, the continuation of increment formation is through the summer months of November, and December. The sinusoidal frequency of 1 in conjunction with the edge analysis revealing only the months from April to August exhibiting otoliths with opaque margins is substantial evidence that the opaque rings are formed only in those winter months and therefore once a year.

2.3.3 Size and age structure:

The maximum size and age of *T. lunare* found at the Palm Group of islands was 184mm Standard Length (SL) and 7 years of age respectively (Figure 2.4). However, these estimates came from two separate individuals with the 184mm SL individual (at 6 years of age) found to be of an exceptionally large size and weight (165g). The next

sized fish was 174mm SL and weighing over 25% less at 123g. The range of sizes found in the population was 66 – 184mm SL, aged between 1 and 7 years, with the youngest/smallest and largest/oldest being female and male respectively. Size and age structures by sex and stage reveal that no females were found in the population beyond the age of 5 years or a size of 130mm SL, whilst males were only evident in the population from 2 years of age or a size of 90mm SL. A proportion of females were mature at the age of 1 year and size of 70 mm SL, however a small proportion of immature females remained in the population until the age of 3 years and size of 100mm SL. This pattern is typical of a sequential protogynous hermaphrodite, where individuals change sex from females to males. *Thalassoma lunare* generally exhibited sex change at an age of approximately 3 years and size of approximately 120 mm SL. However, whilst no transitional individuals were found at the Palm Group of islands, there was one found at another region sampled (Chapter 4).

    2.3.4 Gonadosomatic index:

    GSI values by sex were also indicative of a protogynous reproductive strategy, where female gonad weight was significantly higher for a given body weight compared to male gonads. The highest GSI values were evident in the months of February, November and December (Figure 2.5). Of the fish sampled throughout the two years, few mature females were collected in June and July, giving the GSI figure by months a concave shape and therefore the impression that spawning does not occur throughout the winter periods. However, in mid July 2000 a spawning aggregation was observed on the North side of Cattle Bay at the Western end of the channel between Orpheus and Pelorus Islands whilst performing underwater visual censuses. During this time several pairs were seen darting towards the surface before returning to the reef and subsequently swimming in separate directions. However, it cannot be certain as to whether spawning actually occurred during this display or not.

    By examining the GSI of stages of mature females by month, further evidence can be seen of potential spawning events outside that of summer months. Whilst no individuals were collected during June and July, in late April, early May, individuals were collected showing evidence of having just spawned in the form of postovulatory

follicles (POF's). Furthermore, one individual was found to be running ripe. However, a much larger proportion of resting females were found in these months. No other resting females were found in the months from August through to February. In December, the majority of individuals exhibited evidence of having just spawned. All fish except one, a running ripe female, were categorised into this stage. It appears therefore, that whilst spawning may occur throughout the year, it is possible that only a small proportion of individuals are spawning in the winter months, whilst all spawn during the summer months.

2.3.5 Sex specific size at age:

Mean size at age also shows typical protogynous traits, with the mean size of males exhibiting significantly larger size for any given age than those of the females (Figure 2.6). This is evident for all ages and all categories of females, be they immature, undetermined or mature. Furthermore, mature females were significantly larger than immature females at 2 and 3 years of age, but not at the age of 1 year. The male growth trajectory appears to continue increasing in size with increasing age, however, the increase in size with age for the females is markedly reduced in comparison. From the age of 3 to 5 years the increase in size for mature females is relatively small.

2.4. Discussion:

The periodicity of the incremental marks in the *Thalassoma lunare* otoliths from the Palm Group of islands was successfully determined to be yearly in formation. This is not particularly surprising due to the increasing evidence supporting annual formation of incremental marks in a mounting number of tropical species (Fowler & Doherty 1992, Cappo et al. 2000, Kalish 2002, Grandcourt 2002, Caldow & Wellington 2003). Marginal increment analysis and edge analysis have often been acknowledged as the least reliable of all validation techniques (Campana 2001), it is nonetheless useful for interpreting incremental marks as annual (or otherwise) with a minimum of logistic problems associated with re-capture (Fowler & Short 1998, Caldow & Wellington 2003). However, investigation into whether a validation technique returns an accurate age for the sample, as opposed to the determination of the periodicity of incremental formation (Francis 1995), has left marginal increment and edge analysis open to criticism in

comparison to the more expensive techniques (Campana 2001). Techniques such as the examination of bomb radiocarbon (Kalish 2002) or ^{210}Pb:^{226}Ra ratios (Cailliet et al. 2001). Whilst these techniques have their place in the accurate determination of fish ages for well funded national fisheries stock assessments, the utility of marginal increment and edge analysis should not be undermined. This is especially so for determination of age-based dynamics of a highly speciose group such as tropical reef fishes (Choat & Bellwood 1991). Historically, problems have stemmed from the use of marginal increment analysis to validate increments in scales or whole otoliths, both of which often underestimate the actual age in older fish (see Campana, 2001). However, opaque and translucent increments are often clearer in sectioned otoliths than their whole otolith counterparts and should therefore present a minimum of problems (Fowler 1990). Furthermore, marginal increment analysis of locally abundant, relatively short-lived fish is a cost effective and logistically possible exercise. In addition, this study showed that the ability to precisely estimate ages from sectioned otoliths was certainly indicative of repeatable estimates. Indicating that the incremental marks were readily identifiable. Whilst the utility of estimating ages using whole otoliths was not tested, Williams et al. (2003) showed that for *Lethrinus miniatus*, a relatively long-lived tropical reef associated species, age estimates for whole otoliths and sectioned otoliths were consistently matched, even at the older ages (21 years). However, this was not the case for *Lutjanus carponotatus* where whole otoliths significantly underestimated ages beyond 10 years (Kritzer 2002). It is unlikely that whole otoliths would underestimate the ages of *T. lunare,* as the oldest fish was 7 years of age. However, for labroid species the whole otoliths are generally small and semi-transparent (pers. obs.). Furthermore, with respect to marginal increment analysis its utility is reliant upon relatively accurate measurements of partial increments, which can be a limitation of the technique (Campana 2001). This would be made more difficult with whole otoliths. Therefore, for the purpose of estimating the age of this species sectioned otoliths were preferable and reliable.

Thalassoma lunare was found to be a relatively short-lived fish with a maximum age at the Palm Group of islands to be 7 years of age. However, few individuals were found to live beyond the age of 5 years. This is in strict contrast to the estimates of Eckert (1987) however, who used length-based estimates to establish longevities for *T.*

lunare. However, the differences in maximum ages between this study and Eckert's (1987) may simply be reflective of the different geographic regions sampled by the two studies. However, additional work at the same region in which Eckert (1987) assessed the longevity of this species reveals this not to be the case (Chapter 4). This highlights the problems associated with length-based analysis, especially for reef fish that live beyond three years (the nominal time scale of a PhD project), whose growth is reduced (or ceases completely) after maturity. Similarly, when length-based analyses were used to estimate growth trajectories of the Caribbean scarid, *Sparisoma viride*, van Rooij et al. (1995) estimated that 5% of all individuals would reach the age of 20 years. In contrast however, Choat et al. (2003), using age-based estimates derived from otoliths, found that it was unlikely they would live beyond 10 years of age.

The longevity estimate of 7 years for *T. lunare* is not unusual for a labroid of this size (i.e. < 20cm). The Caribbean bluehead wrasse *Thalassoma bifasciatum* is reported to live to approximately 2.5 years (Hoffman et al. 1985) and no more than 3 years (Warner 1998). However, *T. lunare* is significantly larger than *T. bifasciatum* and therefore it is not surprising that it lives to be at least three times older. Furthermore, several large species of labrid have been found to live in excess of 20 years. *Achoerodus viridis* has been found to be at least 20 years old (Gillanders 1995) and *A. gouldii* to be at least 25 years and possibly 50 years of age (Gillanders 1999). Cowen (1990) estimated that *Semicossyphus pulcher* reached maximum ages of 21 years, Choat et al. (in prep) found *Cheilinus undulatus* to be in excess of 30 years and Hostetter & Munroe (1993) in their analysis of the large temperate labrid, *Tautoga onitis*, found them to be at least 25 years of age. However, these species are all at least 5 times the size of *T. lunare* and therefore it is no surprise that they are almost 5 times as old.

The sexual size and age structure of *T. lunare* is typical of a sequential protogynous hermaphrodite (Shapiro & Rassotto 1993). Males were significantly larger and older than mature females as would be expected if all males entered the population via sex change from mature females. This result was certainly not unexpected as many families of coral reef fish exhibit patterns of sex change (Francis 1992), however it is especially prevalent in the labroids (Choat & Robertson 1975, Warner 1988). However, whether this species exhibits a diandric strategy was unresolved. Warner & Hoffman

(1980) found that, depending upon the population densities, some *T. bifasciatum* individuals may mature as males, rather than progressing through the female pathway. These smaller/younger males were categorised as 'sneaker males', in which they either spawned in large numbers or, by exhibiting the female colour pattern, made their way into a terminal (territorial) males territory and joined in with a spawning pair. Whilst there was little evidence for diandry at this region, as no primary male was collected, primary males have been sampled at other regions. This has occurred both within the Great Barrier Reef (GBR) and in other geographic locations where *T. lunare* live in higher densities (Chapter 4). Furthermore, it is unlikely that this species is monandric as the operational sex ratio was not significantly different from that of 1F:1M, which is unusual for a protogynous hermaphrodite (see Charnov 1993 and references therein). Charnov (1989) examined the prevalence of initial phase males in 27 species of labroid fish and found that for those exhibiting a large proportion of initial phase males, the sex ratio was likely be higher than those species that were 'purely protogynous' (very low proportions of initial phase males). However, he also highlights that the sex ratio for these species exhibiting a diandric nature was still female biased. With no species exhibiting a ratio of less than 2F:1M.

The even sex ratio found at this location however, may be influenced by the possibility of a sampling bias towards the males. Males are larger, more active and obvious compared to females and therefore possibly selected preferentially. There is some evidence for this as there were no females sampled in the July 2000 period. However, females were apparent during this period, as they were associated with a potential spawning aggregation in which the males were collected. In the congener *T. bifasciatum* evidence has been presented showing that the male of the species, in the presence of a reward, is more likely to take risks in the presence of a threat (Warner 1998). If this is the case for *T. lunare* females, they may be far less likely to take risks in the presence of a potential threat. The collection of females therefore, may be made more difficult in addition to their size differences. However, whilst sampling techniques are often species specific depending on the species size, mobility, or food preference (Russell et al. 1978, Cappo & Brown 1996), recent work on gear selectivity has shown that spear fishing better represents the population than some other techniques (Welch 2002).

Size at first maturity (i.e. 50% maturity) in *T. lunare* was estimated to occur at approximately 55% of the maximum size. This value is marginally less than those predicted for fishes in general. Charnov (1993) estimated the 'typical fish' to mature at approximately 65% of maximum size, although this can range from 50% to 90% between geographically separate populations. However, *T. bifasciatum* matures at a size approximately 30% of the maximum size (Warner 1998), and therefore the estimate is considerably high. However, mature females were initially evident in the population at a size approximately 38% of the maximum size, which is consistent with its congener. In addition, *T. lunare* females changed sex into terminal phase males at approximately 70% of the maximum size, similar to the proportion shown for *T. bifasciatum*, at 62% (Warner & Swearer 1991).

The age at maturity (50 % maturity) of *T. lunare* at this region however, is relatively late, occurring at approximately 28% of the maximum age. Choat & Robertson (2002) found that in relatively long-lived reef fishes, age at first maturity occurred at 5–6% of the life span. In contrast, walleye, *Stizostedion vitreum*, have been reported to mature at approximately 38% of the maximum age (Beverton 1987 in Charnov 1993). However, as with the size estimates, mature females were evident in the population at a relatively young age, 14% of the maximum age, which is much more consistent with the findings of Choat & Robertson (2002).

The GSI data throughout the year, in conjunction with underwater observations for this location, suggest that this species spawns all year round. Again this result was not entirely unexpected. Whilst most reef fish have been shown to spawn during the summer months, with surviving recruits subsequently returning to the reef system weeks or months later (see review by Doherty 1991), several studies have shown some families continuing to recruit to the reef not just over the summer months but throughout the entire year (Victor 1986; Thorrold et al. 1994). However, it is possible that these differences may be between oceanic systems as much as between species. As several Caribbean species have been reported to spawn all year around with some form of recruitment happening throughout the year (Doherty 1991). For example, the Caribbean congeneric, *T. bifasciatum*, spawns throughout the year (Warner 1998) and subsequently recruits sporadically throughout the year (Sponaugle & Cowen 1997, Wilson 2001).

Additional work regarding spawning occurrences in conjunction with evaluating settlement times of *T. lunare* recruits is necessary to further examine this possibility.

Males were significantly larger than females of the same age in *T. lunare*. Whilst this is not unusual in a protogynous hermaphrodite (Choat et al. 1996, Grandcourt 2002), there are three possible reasons for this result. Firstly, the females that change sex are those with historically large size at particular ages. In a study on *Plectropomus maculatus*, the protogynous serranid, Adams & Williams (2001), using back calculated age estimates, found that there was no evidence of a growth spurt after the age at which sexual transition occurred. Rather, the evidence suggested that mature females that obtained a large size early in life were more likely to be the ones that changed sex. This result was also obtained for two species of scarid, *Chlorurus sordidus* and *Scarus frenatus*, using a similar technique (Munday et al. 2004). In addition, the present results found mature females were significantly larger than immature females for the majority of age classes. Evidence that size plays a significant role in maturity and therefore possibly sex change schedules.

Secondly, those individuals that change sex do so then grow rapidly (Grandcourt 2002). If reproduction incurs a significant cost, either to growth or survival, a non-reproductive period may be selected (Reznick 1985). For protogynous hermaphrodites, this may occur between sex change. Therefore, whilst some individuals may exhibit what appears to be relatively early sex change, evident as small or young mature males, they may not in fact reproduce and therefore use this as an adaptive life history strategy (Rogers & Sargent 2001). Therefore, we would expect to see an increase in the growth rate of these newly sex-changed individuals. An occurrence that Warner (1984a) reported for newly sex changed individuals in *T. bifasciatum*, compared with that of the females. In addition to this circumstantial evidence growth spurt after sex change has been incorporated into the growth models for some species (Garratt et al. 1993). However, in this example the model was unable to account for the pre-sex-change growth trajectory as the size at age data for the males began at the age of five. Little empirical evidence supports the growth spurt hypothesis, however, further work on back-calculated size at age could potentially resolve the role of size in governing sex maturation and change (see Walker & McCormick 2004).

Finally, that size selectivity in sampling has targeted the larger males. However, there was a distinct overlap in size distribution between mature females and males. At least 30 mature females and 18 males were sampled in the size range between 100 and 120 mm SL. Therefore, unless the females exhibit risk avoidance (Warner 1998) in proportion to their size, this situation is unlikely. Warner (1998) reported that females of the bluehead wrasse, *T. bifasciatum*, whilst able to assess spawning site resource assessment, normally copy other females. Site location is a learned response. Therefore, it is possible that risk assessment is a learned response and may therefore be proportional to size if the younger/smaller females 'learn' from the larger/older females. However, in the two years of sampling at this region, no mature females (initial colour phase) were observed larger than that collected.

The presence of the 5-year-old mature female in the population suggests that not all females may change sex to become males. Rather, some may remain as females. Choat et al. (in prep) found a similar result with the large tropical reef fish, *Cheilinus undulatus*, where the oldest individuals in the population were found to be mature females, even though the males were significantly larger. This strategy would enable them to utilise their increased size to potentially increase fecundity (Fox 1994, Munoz & Warner 2003a). Advantages of changing sex at a small size and becoming a relatively small male may be reduced once a particular age is reached, due to the difficulties of obtaining a territory. This has been documented in a protogynous species that habituated seagrass beds in which small males had sufficient access to females (i.e. sperm competition). This in turn altered the pattern of sex change from that of the largest female to a subordinate female. Sperm competition strongly reduced the potential of paternity for a sex-changed male and therefore any expected benefits from sex change decreased (Munoz & Warner 2003b). In general, however, reef systems should allow terminal phase males to remain dominant (Robertson & Warner 1978). If this was the case for *T. lunare* at this region, mature females should be prevalent in the larger size classes, which was not the case. In addition, relatively few females were sampled in the 4- and 5-year age classes (N = 2 & 1 respectively) and none in the 6- and 7-year age classes.

The prevalence of identifiable yearly incremental marks in the otoliths of *T. lunare* has demonstrated that this reef fish species is unlikely to live beyond eight years of age. It is a sequential protogynous hermaphrodite that appears to spawn over an extensive temporal period in the Palm Group of islands. In addition, for any given age class the males are significantly larger than the mature females, which are generally larger than immature females. Supporting the assumption that size plays a fundamental role in the demography of this species. These baseline age and reproductive data will facilitate the examination of demographic variation amongst populations of *T. lunare* across both large regional spatial scales and local habitats.
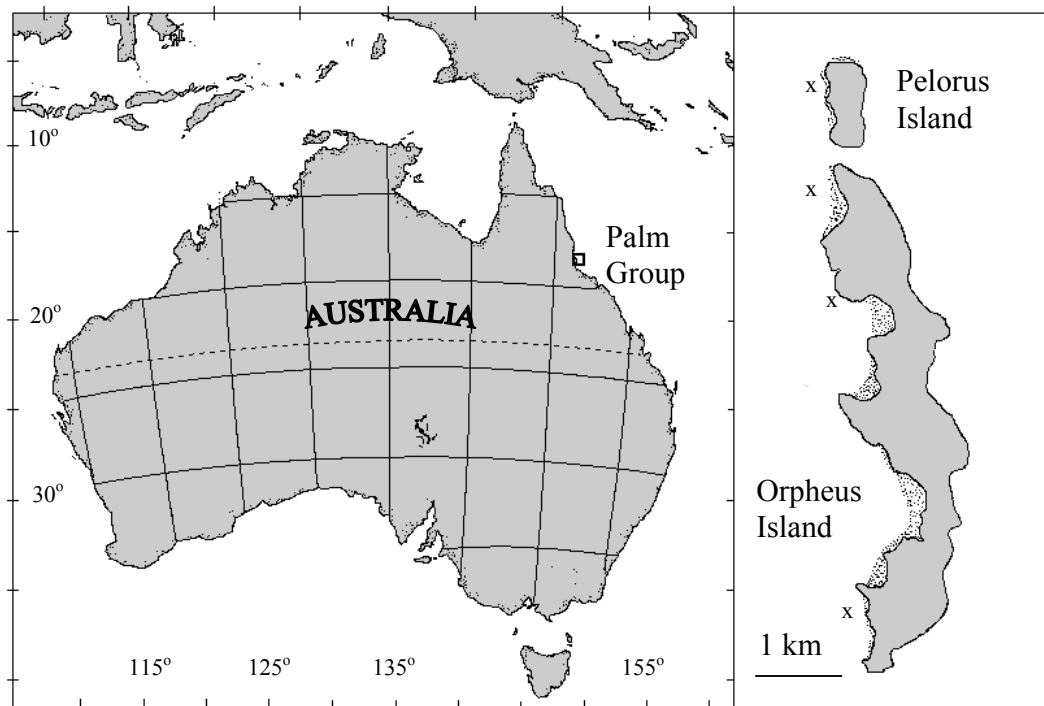
Figure 2.1: Sampling locality of the Palm Group of Islands in the Great Barrier Reef (GBR), along the east coast of Australia. Insert shows the leeward sampling sites (x) of Pelorus and Orpheus Islands.
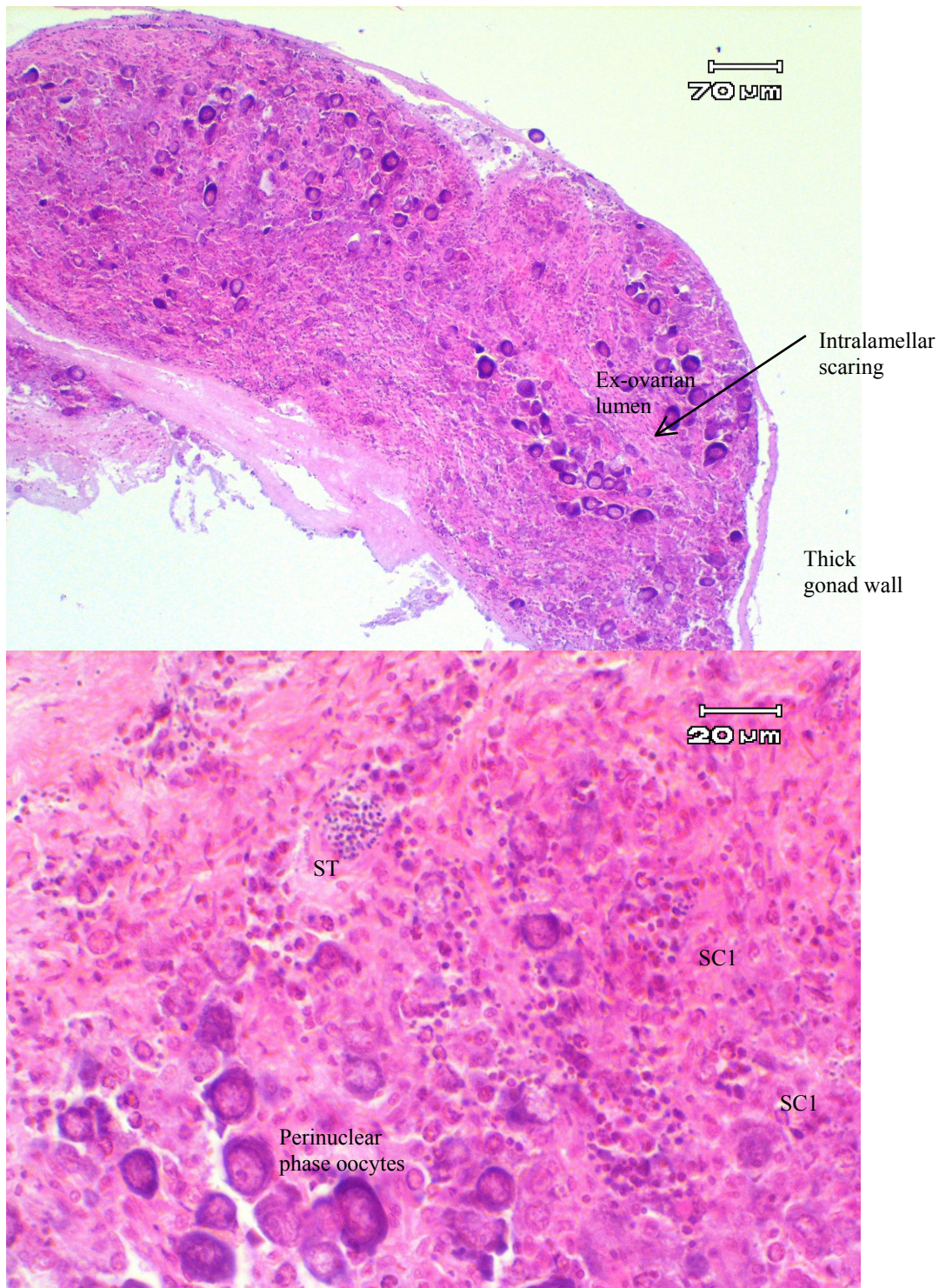
Figure 2.2: Histological section of an individual undergoing sexual transition. Proliferating spermatogenic material is indicated by the presence of spermatids (ST) and spermatocysts of primary spermatocytes (SC1). Evidence of historic reproduction as a female can be seen in the size of the ovary, presence of intralamellar muscle bundles and a thick gonad wall.
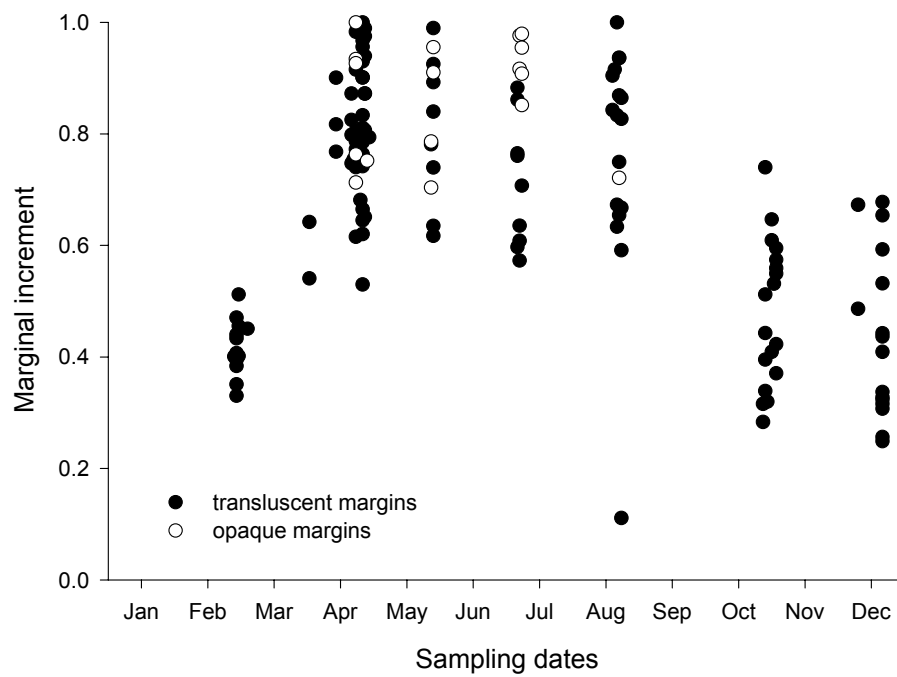
Figure 2.3: Marginal increment and edge analysis of the otoliths of *T. lunare* sampled at the Palm Group of islands over periodic intervals across two years. The marginal increment is shown as a proportion of the previous complete increment. Each symbol represents an individual with solid symbols indicating translucent margins, whilst open symbols indicate an opaque margin.
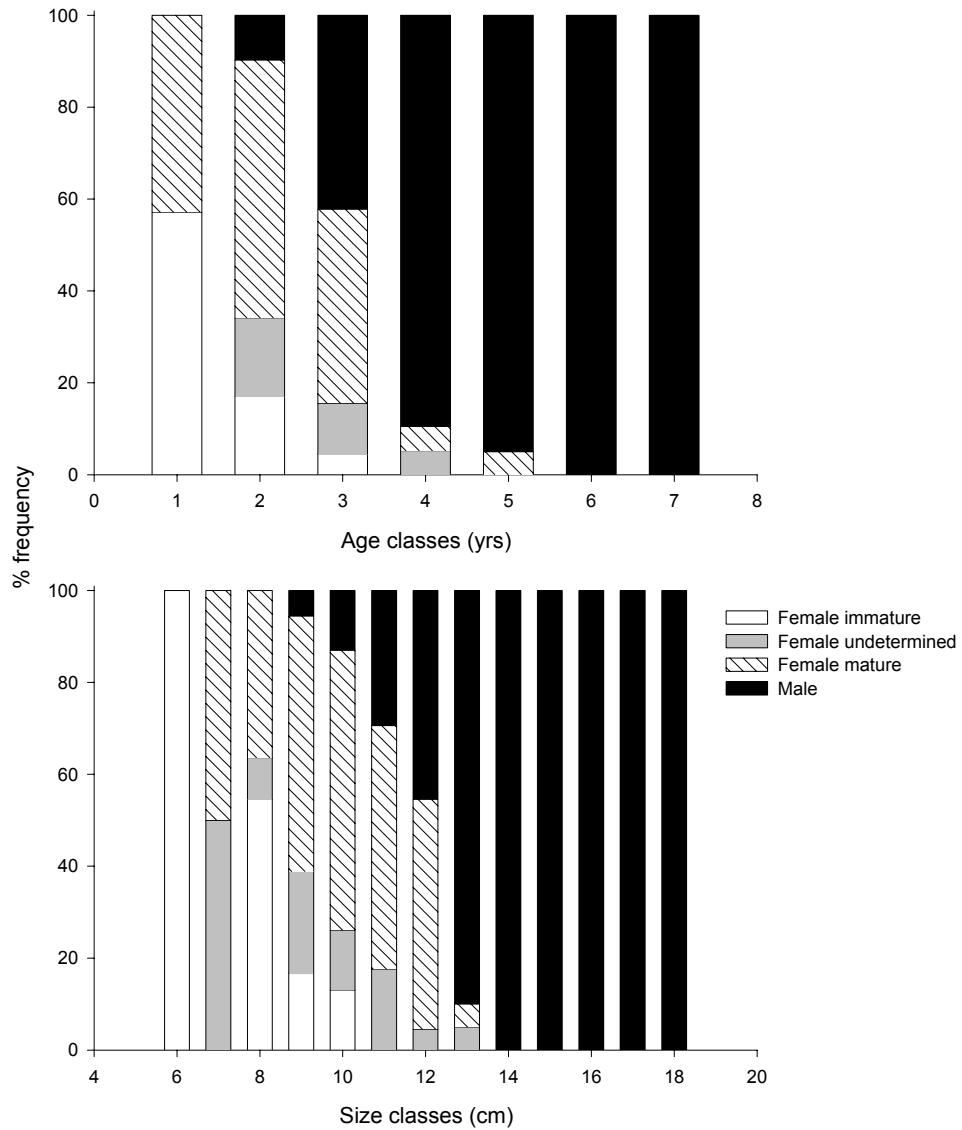
Figure 2.4: Frequencies of each size (cm) and age (years) class of *T. lunare* by sex and stage, sampled from the Palm Group of islands.
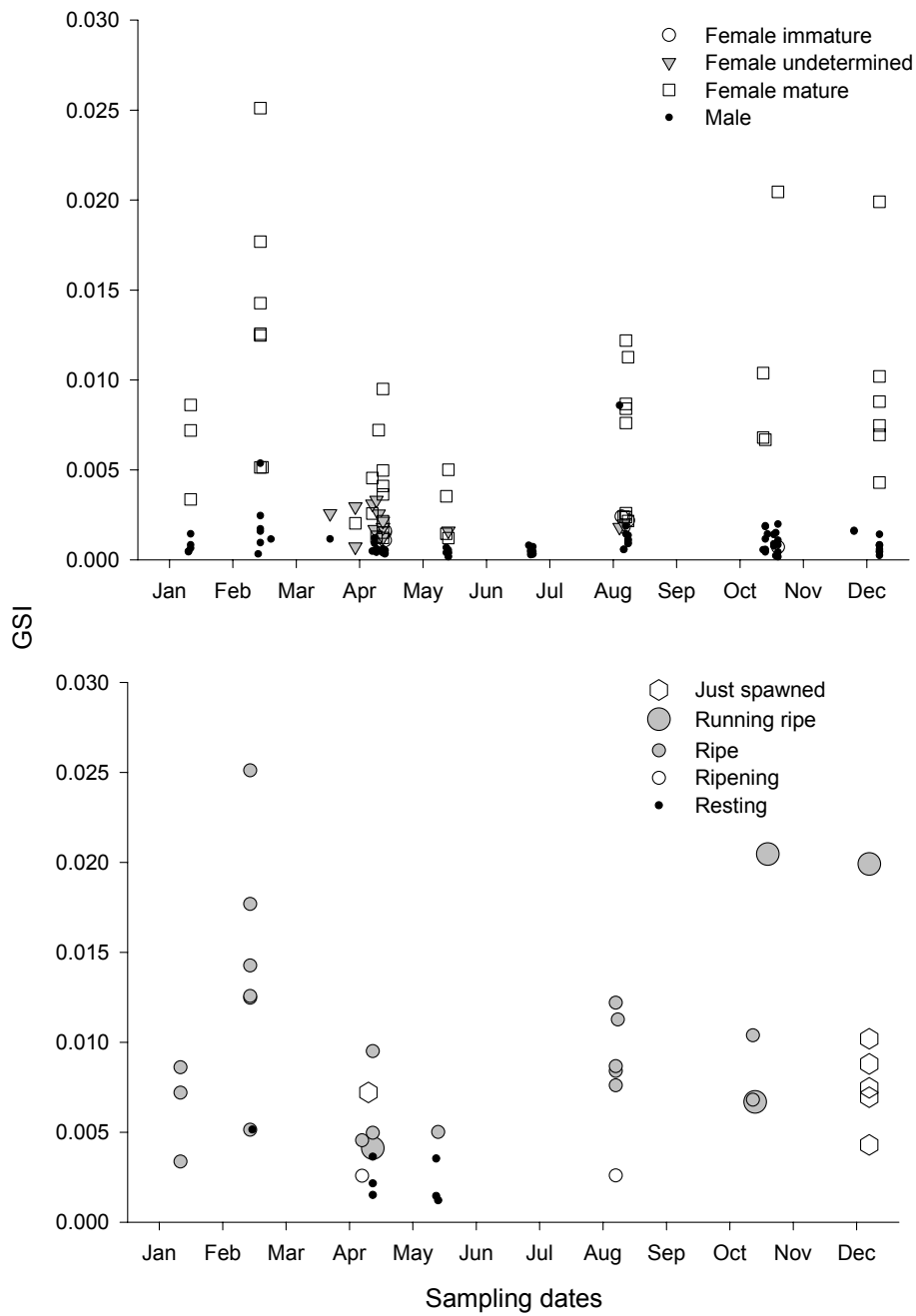
Figure 2.5: Gonadosomatic index (GSI) of a) all individual *T. lunare* by sex, and b) mature females by stage sampled at the Palm Group of islands over periodic intervals across two years.
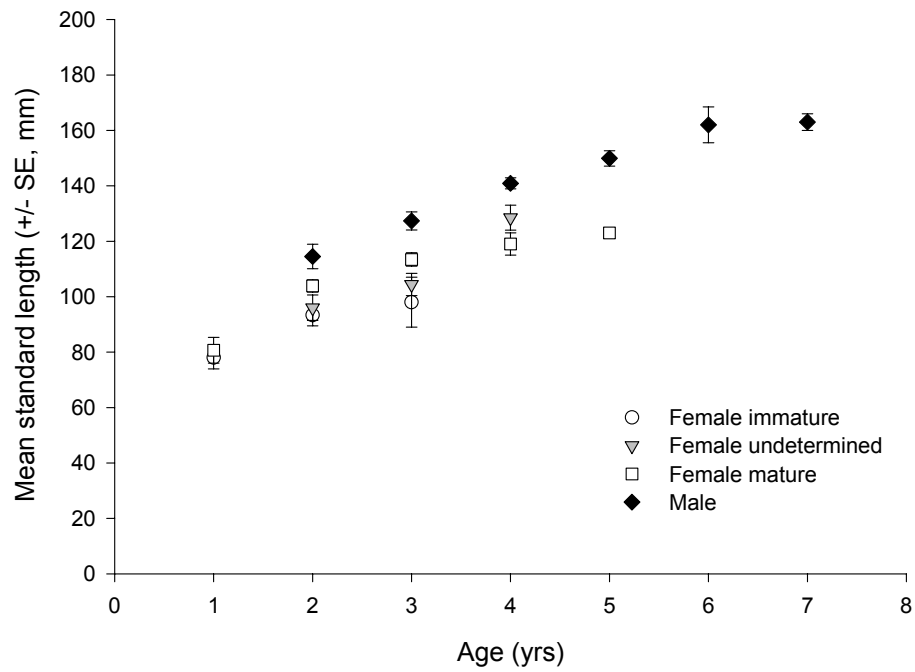
Figure 2.6: Mean standard length (± SE, mm) of *T. lunare* by sex at each age class (years).

CHAPTER 3. TECHNIQUES FOR THE ANALYSIS OF GROWTH RATES OF AGE-BASED DATA.

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3.1. Introduction:

The von Bertalanffy growth function (VBGF) is easily the most widely used model to describe size at age in the field of fish biology (Ricker 1979, Roff 1984, Charnov, 1993). Its use in describing the indeterminate growth of fish has been widely accepted. In general, many species exhibit an increase in size with an increase in age approaching some mean asymptotic length. The widespread use of the VBGF has come about through not only its use in describing fish growth, but also through the comparison of growth between sexes (Choat et al. 2003), populations (Gust et al. 2002) and species (Meekan et al. 2001).

However, the VBGF has also been widely criticised. The detractors have not only criticised the model (Knight 1968), but also the misuse of the parameter estimates (Roff 1980, Francis 1995, Day & Taylor 1997). Critics of the model have highlighted the prevalence of an asymptote, assuming there is an upper limit to growth (Jensen 1996). Similarly, it has been mentioned that a VBGF fitted to data without a definitive asymptote will result in asymptotic sizes greater than the maximum size of any individual (Knight 1968, Gallucci & Quinn 1979). In addition, it ignores the physiological processes occurring at size and age at maturity (Day & Taylor 1997) and lacks a term with units of length per unit time, an important aspect when considering growth and growth rates (Ricker 1979, Jensen 1996). However, whilst the VBGF has been criticised, it is still a perfectly useful growth model (Schnute 1981), is a valid choice for many fish species (Kritzer et al. in prep), and if used carefully can be a useful tool (Essington et al. 2001). In addition, comparative analyses, which can only be of use if a common model is used, will likely keep the VBGF as the leading model to describe fish growth (Roff 1980). Critics of the misuse of parameter estimates have called for a more considered approach to the interpretation of the parameters (Francis 1995) and increased attention to the plausibility of the parameter estimates (Kritzer et al. in prep). This is especially so when correlations between the VBGF parameters and other life history variables are sought (Pauly 1980, Jensen 1996).

Correlations surrounding the VBGF parameter estimates and other life history parameters have been investigated thoroughly (Pauly 1980, Charnov 1993, Jensen 1996, Musick 1999a). This is not only to gain further insight into the life history attributes of fish, but also to determine whether the VBGF estimates, which are generally abundant throughout the literature, can be used to predict those parameters not so easily attained (Essington et al. 2001). More specifically, the k parameter, correctly defined as the rate at which the increase in size decreases, with units of time^{-1}, but often referred to as a growth rate, has received much attention. Correlations between k and estimates of mortality, age at maturity and even one of the other parameters within the von Bertalanffy model, the mean asymptotic size (L_∞) have been reported (Beverton & Holt 1959, Pauly 1980, Buesa 1987, Pilling et al. 2002). However, there can be a great deal of variation around the estimate of k. This is especially so for those species that grow fast initially, and asymptote for the majority of the life span (Choat & Axe 1996, Choat & Robertson 2002). This growth pattern can lead to relatively high estimates of k and potentially large confidence intervals surrounding this parameter estimate (Meekan et al. 2001). Therefore, the use of this parameter has limitations regarding the interpretation of other life history variables and certainly has limitations regarding its use as a growth rate, the least of which is the units. However, growth rate is a particular important characteristic of shaping life history attributes (Stearns 1992), and therefore it is of great importance to seek methods or techniques to allow the determination of growth rates at particularly pertinent age classes, such as those of juveniles compared with adults (Hutchings 1993).

Given the relative difficulties associated with obtaining growth rate data for reef fish it is essential to devise additional methods that utilise the limited information available (Essington et al. 2001). Here we describe a technique to further utilise the von Bertalanffy growth model to estimate and compare instantaneous growth rates at particular ages of interest beyond the simple (and incorrect) use of the k parameter as a growth rate (Cerrato 1991). We do this using size and age data of the labrid *Thalassoma lunare*, collected from the Palm Group of islands along the east coast of Australia. Additionally, we compare the

output of size and age frequency data, gathered from each iteration, with that of the re-parameterisation estimates following Francis (1988).

3.2. Methods:

Size at age data of *T. lunare* from the Palm Group of islands were calculated constraining the theoretical size at which length is zero (t_0) to age zero (Kritzer et al. in prep) using the von Bertalanffy growth function:

$$L_t = L_\infty(1 - \exp(-k^{(t-t0)}))$$

where L_t is the estimated standard length at age t, L_∞ is the mean asymptotic standard length, k is a curvature parameter and t_0 is the age at which fish have theoretical length of 0. This two-parameter version of the von Bertalanffy growth model has been reported as a reasonable strategy for parameter estimation (Gallucci and Quinn, 1979), which has the effect of improving the fit (Roff 1984).

3.2.1 Instantaneous growth rates:

Instantaneous growth rates at specific time periods were calculated through the use of bootstrapping methods. Periods in time can be defined for any age, however, were defined here as the age at settlement (52 days following Wilson & McCormick 1999), 3 monthly increments until 1 year of age, then yearly increments until the age of 5 years. Size-age data pairs were randomly chosen (with replication) n times. Where n represents the actual sample size in question. For each randomly chosen data set, the von Bertalanffy growth model was calculated according to the same constraints as mentioned above. Based upon the formula of Porch et al. (2002) the growth rate (mm.year^{-1}) at any given time t is calculated as:

$$dL_t/dt = k(L_\infty - L_t)$$

where L_∞ and k are as above and L_t is the expected size at age t. This was calculated for t equals 52 days, 3 monthly increments until 1 year of age, then yearly increments until the age of 5 years. This complete process was iterated 250 times for each population. The random size and age data pairs were saved for each iteration. Subsequently, estimates of mean size at each age class, for which there was data, were

calculated for each iteration and the mean of these estimates derived. Growth rates reported here are the bias adjusted growth rates where the bias is calculated as the mean of the iterations subtracted from actual growth rates (based upon the actual data and VBGF parameters for that data). This bias is then subtracted from the actual growth rates (Manly 1997).

3.2.2 Re-parameterisation:

Re-parameterisation of the VBGF followed Francis (1988), whereby three expected lengths were assigned at arbitrarily chosen ages for the parameters:

$$L = l_\tau + \{[l_\upsilon - l_\tau][1-r^{2(T-\tau)/(\upsilon-\tau)}]/(1-r^2)\}$$

Where

$$r = (l_\upsilon - l_\omega)/(l_\omega - l_\tau)$$

The parameters l_τ and l_υ are the mean lengths at ages τ and υ, the parameter l_ω is the mean length at age $(\tau + \upsilon)/2$. As *T. lunare* has a maximum age of 7 years at the Palm Group of islands and Cerrato (1991) advised against basing the expected value on the maximum age in a sample, the largest age class chosen (υ) was 6 years, the lowest age class (τ) chosen was 2 years (as ω would not be appropriate if $\tau = 1$) and therefore the third age (ω) was 4 years. Parameters were estimated by minimising the Maximum Likelihood Estimate (Kimura 1980).

Each data set was re-sampled 1000 times with replication maintaining original sample size (n) and age structure, where n represents the actual sample size within that age class. For each of the 1000 re-samples, a best-fit combination of the parameters l_τ, l_υ and l_ω was estimated by minimising the Negative Log of the Likelihood given a probability density function with a Poisson distribution (Haddon 2001). This generated 1000 combinations of best-fit parameter values, thereby producing confidence regions around the original parameters.

All confidence intervals were calculated as 1.96*stdev of the iterated estimates (Manly 1997).

3.2.3 Comparison:

Estimates of mean size at age between the re-parameterisation estimates and the output from the growth rate analysis were compared visually by plotting the bootstrapped estimates against each other and examining the 95% confidence intervals.

3.3. Results:

As expected the bootstrapped estimates of instantaneous growth rates showed a decline in the growth rate from the age at settlement until the final age class with which growth rates were calculated (Figure 3.1). Intuitively, the rate of decline decreased with increasing age, indicative of the general shape of the VBGF. However, the difference in growth rates between the age categories 5 and 4 years is significantly less than the difference between that of the 1 year and settlement categories. Although, growth rate declines at a constant rate of approximately 60% per year regardless of physiological processes, such as the age at which maturity occurs (Chapter 2). It should be noted that whilst there appears to be a significant decrease in the instantaneous growth rates after 1 year of age, this decline is simply reflective of the alteration in the age category scale.

Confidence intervals surrounding estimates of age-specific growth rates show that there are significant differences within a relatively short period within the first year. In general, growth declines significantly every 3-month period. These confidence intervals are therefore fundamental to making growth rate comparisons between populations at ages of interest.

Bootstrapped re-parameterisation estimates of size for the ages, 2, 4 and 6 years showed no difference between the mean size for the same age classes calculated from the output of each iteration used for the calculation of instantaneous growth rates (Figure 3.2). Confidence intervals overlapped between the two methods for each of the chosen age classes. Very little difference was evident between the actual values, with no age class showing differences between the two methods of more than 0.85 mm. As expected, the mean size at age increased with increasing age, with no overlap of 95% confidence intervals between any of the examined age classes, regardless of the technique. The output of mean size at each age class, from each iteration used in the calculation of instantaneous growth rates, is therefore comparable with the re-parameterisation technique of Francis (1988).

3.4. Discussion:

Using growth trajectories and bootstrapping methods the technique described enables growth rate estimates to be evaluated and compared at particular age specific periods from size-age data. These can be evaluated at ages of particular interest, such as those at settlement (Sponaugle & Cowen 1997, Jones 1997), age at maturity (Jones 1980a, van Rooij et al. 1995), age at sex change (Warner 1984a, Garratt et al. 1993) or simply compared between the juvenile and adult stages (Fox 1994). Furthermore, with a collection of age and size data from other regions, or other species, comparisons can be made between populations or phylogenetic groups.

Growth rate and its potential consequences is an extremely important aspect of understanding life history variation (Fox 1994, Gotthard et al. 1994). It has been shown that fast growth prior to maturation can lead to smaller final sizes (Atkinson 1994, Van Voorhies 1996; although see Stearns and Koella 1986), but earlier maturation (Roff 1984, Hutchings 1993), and potentially shorter life spans (Forsythe & Hanlon 1988, Metcalfe & Monaghan 2003). Therefore, our understanding of growth rates at age specific points is particularly important to understanding life history variation and the trade-off between life history traits. Nowhere is this more important than with fish where the curvature coefficient (k) has been used extensively as an estimate of growth rate (Francis 1996, but see Wang & Milton 2000). However, the use of this parameter as a growth rate has two particular problems. First, that it does not distinguish between pre- and post-maturation. We can make comparisons between populations with k as a component (i.e. confidence regions around both parameters of the 2-parameter VBGF; see Chapter 4); however, it does not allow for the determination of growth rate differences, or whether they exist prior to or post maturation. Nor does it allow us to determine any effects of fast or slow growth during the juvenile stage (Meekan & Fortier 1996), especially in comparison with the adult growth rate (Fox 1994). It merely expresses the rate at which the asymptote is reached, or the curvature of the complete growth trajectory of an average individual within a population. Secondly, in strict definition, k is not a growth rate with size per time units (Ricker 1979, Jensen 1996). Rather, it has units of time^{-1}, which in itself is difficult to interpret.

This technique of estimating age-specific growth rates appears to be sufficiently suited for any age class required, regardless of whether size data is available for that particular age category. However, caution must be taken as estimates of growth rates beyond the last age class within the data are likely to be defined by the existing size-age data, irrespective of the problems associated as to whether that age class exists. Furthermore, age-specific growth rates at very early ages have a similar problem. Estimates of growth rates at settlement using this technique are determined by juvenile and adult data and the VBGF for the population as a whole. However, it is possible that the growth rates of settling fish will be significantly different to those rates of juveniles or adults, due to processes operating whilst in the pelagic zone or during metamorphosis (McCormick et al. 2002). Estimates of growth of larval fish have shown that rates can alter significantly over a few days to weeks (Bergenius et al. 2002, Meekan et al. 2003). Furthermore, incorporating early size and age data has often revealed relatively slow initial growth prior to the recruitment phase (Searcy & Sponaugle 2001). Therefore, a sigmoidal curve over the entire lifespan is possible (Ricker 1979). This is a constraint of the VBGF (Gallucci & Quinn 1979), and one that will influence the estimate of age-specific growth rates of very early stage juveniles. An additional limitation to this technique, not surprisingly, is that the estimates rely heavily upon the VBGF. Therefore, it is necessary to ensure reliable estimates of VB parameters. This can only be achieved if size age data covers the smaller age/size classes (Kritzer et al. in prep). Furthermore, due to the bootstrapping methods, unless sufficient sample sizes are used, in the order of 8-10 samples per age class, then not only will confidence intervals around the estimates be large, but the utility of re-sampling with repetition will be questionable (Connolly pers com).

The comparison between Francis's (1988) re-parameterisation technique and the output from the iterations used to calculate instantaneous growth rates revealed little difference in the mean estimates of size at these three age classes. This leaves little doubt that the technique used here to calculate age-specific growth rates is, at the very least, comparable. However, in contrast to the re-parameterisation method, the output of age-specific growth rate analysis includes data for all age classes in the sample. This is one of the limitations of Francis's (1988) technique. With limited age classes (i.e. seven in this

case), the analysis can only be used on specific ages (i.e. 2, 4 and 6). Furthermore, in addition to the mean size at age data as a result of bootstrapping, the technique returns additional information such as age-specific growth rates and the variation surrounding them. This technique will allow age-specific growth rates to be estimated and compared between geographically distinct populations as a contribution to the examination of life history traits across spatial scales (Chapters 4 & 5).
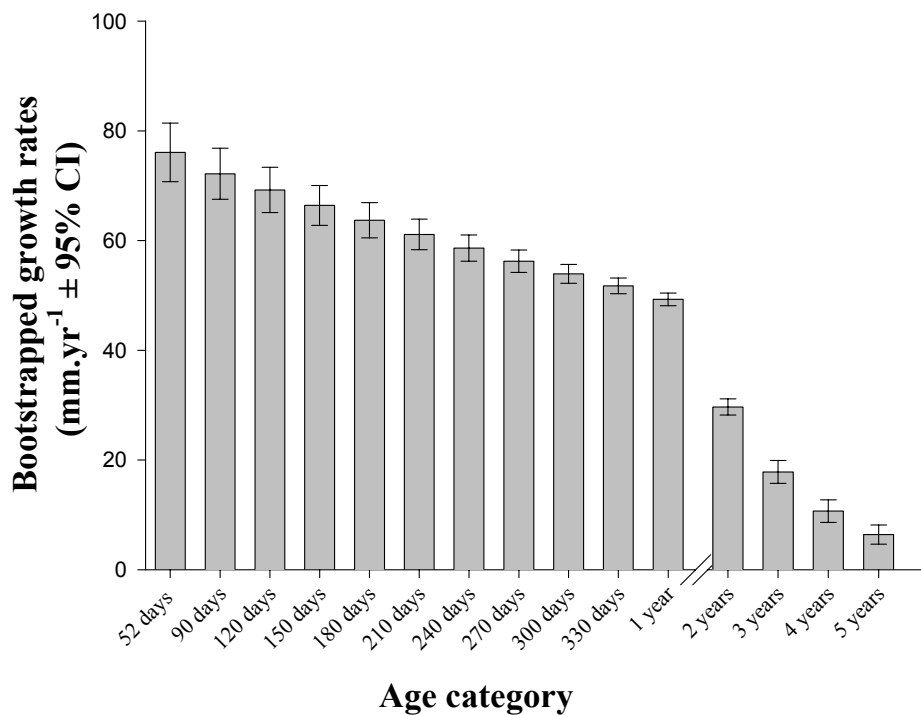
Figure 3.1: Bias adjusted instantaneous growth rates from the Palm Group of islands in the Pacific Basin, based upon bootstrapped estimates and the predicted VBGF for this region. Growth rates shown at age at settlement (52 days following Wilson & McCormick, 1999), 3 monthly increments until 1 year of age, then yearly increments until the age of 5 years. Confidence intervals calculated upon standard bootstrap methods using 1.96*SD (Manly 1997).
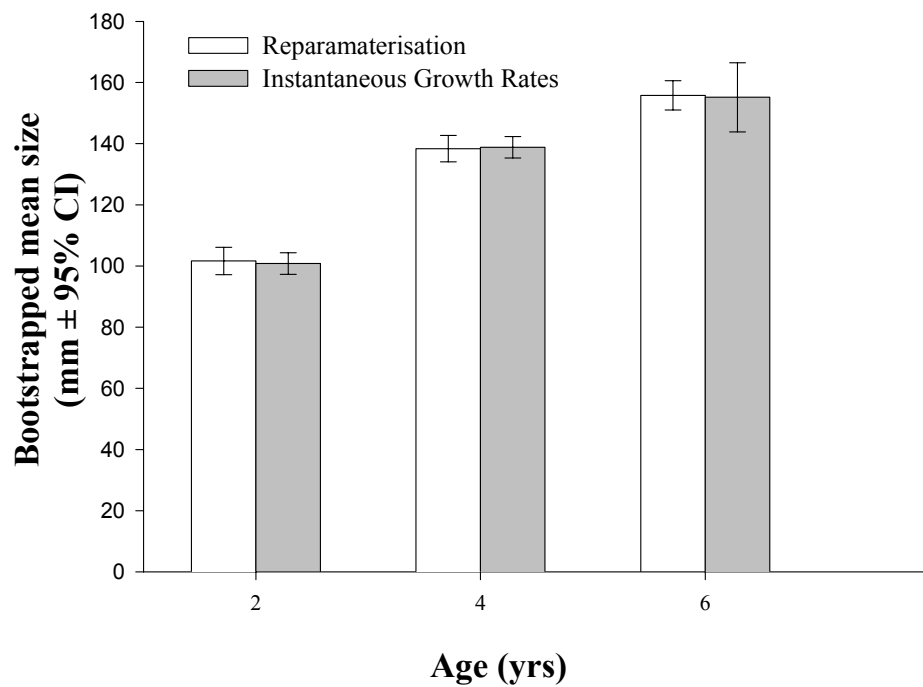
Figure 3.2: Bootstrapped estimates of mean size at age calculated through the re-parameterisation method of Francis (1988; white bars) and from the mean size at each age class for each iteration used in the calculation of instantaneous growth rates (grey bars). Confidence intervals calculated upon standard bootstrap methods using 1.96*SD (Manly 1997).

CHAPTER 4. VARIATION IN THE AGE-BASED DEMOGRAPHY OF *THALASSOMA LUNARE* I. LATITUDINAL VARIATION WITHIN 2 OCEANIC BASINS.

4.1. Introduction:

Life history traits of populations have been found to vary over large geographical ranges, especially those involving a latitudinal or altitudinal gradient (Atkinson, 1994). In most cases, individuals show larger body sizes, greater longevity and yet slower growth rates with an increase in latitude. Additionally, several studies have shown similar life history alterations along altitudinal gradients with populations at higher altitudes exhibiting similar traits with those at higher latitudes (Stalker & Carson 1948; Berven 1982). Several factors may contribute to this variation; however, temperature is likely to be important over large geographic scales for ectotherms (Sebens 1987). There have been many experimental examples, especially with *Drosophila*, exhibiting life history alterations to an increase or decrease in temperature (Partridge et al. 1994, Partridge & French 1996). Results show that an increase in temperature during the rearing phase increases both metabolic rates and growth rates (Brett, 1979; Rilling & Houde, 1998; Wood & O'Dor, 1999). Furthermore, studies of larval reef fish have shown that individuals settling onto a reef during years exhibiting cooler water temperatures grow slowly compared with those settling during warmer water temperatures (Meekan et al. 2003). However, much of the variation in life history traits over large spatial scales has focused upon terrestrial organisms. Few studies have attempted to examine life history variation in tropical reef fish (Caley, 1998; but see Meekan et al. 2001, Choat et al. 2003).

General life history theory predicts that at higher latitudes (lower temperatures) coral reef fish would exhibit larger final body sizes but smaller size at age (i.e. slower growth). With slower growth there is likely to be a trend towards later maturation (Roff 1984). With later maturation (at larger sizes) reproductive effort is delayed and therefore possibly decreased, however there is the potential for greater fecundity due to increased body size (but see Fox 1994) and reduced mortality and increased longevity (Stearns &

Koella, 1986). We have yet to determine whether these fundamental life history trade offs are applicable to coral reef fish. Furthermore, in their recent work on freshwater fishes, Belk & Houston (2002) called for further empirical field analyses of latitudinal gradients in body size for ectotherms, as their results showed that the expected size cline, larger individuals at higher latitudes did not exist. However, an increase in maximum age was evident at higher latitudes in some instances. The examination of this variation (or lack of it) in reef fishes is therefore an essential step towards resolving ectothermic responses in life histories to broad scale environmental variation.

Examination of tropical reef fish can make a significant contribution to our understanding of life history theory (Munday & Jones 1998). They invariably have a bipartite life cycle in which the fertilized eggs are swept off the reef and the subsequent larvae spend days to weeks in the pelagic or blue water (Wilson & McCormick 1999). Upon their return to the reef they settle into the population, with some larvae undergoing a metamorphic alteration in body shape and structure (McCormick et al. 2002). In addition, some reef fish undergo adult sex change, a rare phenomenon in terrestrial organisms (Rogers & Sargent 2001). These introduce additional variables to be considered when examining life history models over large spatial scales (Charnov, 1993). Moreover, whilst traditional life history theory predicts an increase in age with an increase in body size, some reef fish families have shown the opposite (Munday & Jones 1998, Mosse 2001, Choat & Robertson 2002). In addition, further complexities are introduced by recent findings that have shown reef fish can vary in age-based demographics across small spatial scales with large exposure gradients (< 30 km, Gust et al. 2002).

Density dependent effects upon fish demography have been examined numerous times, with emphasis placed upon mortality estimates, settlement of juveniles into the reef system, or recruitment into adult populations (Jones 1990, Doherty 1991, Booth 1995, Shima 2002). Furthermore, effects of higher densities on survivability (Bjornstad et al. 1999) and on growth rates (Doherty 1982) have also been reported (see Jones 1991 and references therein). Evidence suggests that adult densities may alter growth and ultimately, final body size (Kritzer 2002), but it is likely that this will only be evident once densities reach a certain level (Jones 1991, Kritzer 2002). However, whilst density

dependent effects upon growth and mortality have been examined in many site attached reef fish, rarely have studies examined the effect across a suite of age-based demographic traits and environmental gradients.

Thalassoma lunare is an ideal study species to identify some of the effects of latitudinal gradients on age-based demographics. They are abundant and widely distributed across both regional and local spatial scales. They occur throughout tropical and temperate regions, found along both the west and east coasts of Australia. Therefore, any variation in age-based demographic parameters can be examined across large latitudinal gradients in two oceanic basins. Furthermore, the widespread dispersal of pelagic larvae reduces the opportunity of local genetic differentiation (Schultz & Warner, 1991; Shulman, 1998). Therefore any variation in life history parameters across these large spatial scales is likely to be caused by environmental conditions.

The main objective of this study therefore, was to examine the demographic variables of size, age and density and their subsequent interactions of geographically distinct populations of *T. lunare* in both the East Indian Ocean and West Pacific Basin. Specifically, the interaction of these variables across latitudes will determine whether *T. lunare* populations found at higher latitudes would fit the traditional predictions of 1) slower initial growth rates, 2) larger final body sizes, 3) greater maximum lifespans, 4) decreased mortality estimates, and 5) delayed maturity and sex change. The number of variables analysed combined with the spatial scales examined makes this study the first of its kind to answer questions of age-based dynamics of reef fish on several spatial scales including a large geographic range and two oceanic basins. In addition, reef exposure and density estimates will be incorporated into the analysis to determine whether exposure and density dependent effects contribute to life history variation observed in populations of *T. lunare*. Specifically, the exposure gradient, from regions of low to high exposure (i.e. from inshore to outer reefs) is expected to increase initial growth rates, reduce the maximum size and age of individuals, increase mortality and promote early maturation and sex change (Gust et al. 2002). Furthermore, in populations exhibiting high density estimates, it is expected that size and age will be reduced, mortality will be greater and maturity and sex change schedules will be earlier than those populations exhibiting lower estimates of abundance. In addition, sexual strategies are

likely to be altered, with a greater prevalence of primary males in those populations with higher densities (Warner & Hoffman 1980). Interactions between these variables will provide us with an insight into potential trade-offs within the age-based demography of a widespread coral reef fish.

4.2. Methods:

4.2.1 Regional sites:

In the South East Indian Ocean *T. lunare* is found from equatorial regions ranging to approximately 32°S. Within this basin 5 latitudinal regions were chosen along approximately 113 ^{o}E to 122 ^{o}E, ranging from 14°S to 32°S, including; Scott Reef (14°S), Tantabiddi, Ningaloo Reef North (22°S), Coral Bay, Ningaloo Reef South (23°S), Beacon Island, the Houtman Abrolhos Islands (29°S) and Rottnest Island (32°S) (Figure 4.1). Reynolds Sea Surface Temperature data provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA, from their Web site at http://www.cdc.noaa.gov/ displayed temperature ranges from 25.5–31°C at Scott Reef to 18.0–24.5^{o}C at Rottnest Island (Table 4.1).

In the South West Pacific *T. lunare* is found from equatorial regions ranging to 36°S. Within this basin 6 distinct regions were chosen along approximately 155 ^{o}E ranging from 5°S to 32°S, including; Kimbe Bay, Papua New Guinea (PNG; 5°S), Roviana Lagoon, Solomon Islands (8°S), Lizard Island (14°S), the Palm Group of islands (19°S), One Tree Island Lagoon (23°S) and Cabbage Tree Island, Port Stephens (32°S), an exposed island off the mid coast of New South Wales (Figure 4.1). In addition, two exposed outer shelf reefs were sampled along this gradient. One at 14°S (approximately 30km east of Lizard Island), the other at 23°S (the exposed outer shelf reef surrounding the One Tree Island Lagoon). These additional outer shelf reefs were sampled to examine variation caused by exposure as large demographic differences have been reported for reef fish across this environmental gradient (Gust et al. 2002). Variation of demographic variables in the Pacific Basin will therefore be examined at two scales; regional and cross-continental shelf. Overall sampling covered approximately 3000kms in the Pacific Basin and over 1900km's in the Indian Ocean. Temperature ranges

exhibited in the Pacific Basin were from 27.0–30.5^{o}C at Kimbe Bay to 18.0–25.5^{o}C at Port Stephens (Table 4.1).

4.2.2 Sampling procedure:

Individual fish within each regional site were collected by hand-spears. Attempts were made to collect as many fish as possible within varying, but often restrictive, time frames. Collections of fish were through a 'haphazard' sampling protocol, allowing for an unbiased representative sample of each size class following Choat et al. (2003). Fish were weighed and measured for fork and standard length (FL and SL respectively) to the nearest mm. Sagittae were removed, cleaned, washed in ethanol and stored dry. Gonads were removed and fixed in Formaldehyde-Acetic Acid-Calcium Chloride (FAACC). One sagitta from each pair was weighed to the nearest 0.1mg and processed according to the methods of Chapter 2. Increments at all locations were considered to be annuli, as they were consistent with validated annuli from the Palm Group of islands (Chapter 2). As yearly increments are produced at particular times throughout the year, yet spawning episodes were observed throughout the year at two regions and therefore recruitment was assumed to be an ongoing process, ages were assigned half years if an opaque (or translucent) band was found at both the outer edge and close to the sagittal core. However, where analyses relied upon frequency distributions any individual assigned a half-year was rounded up to a whole year class. Gonads were weighed to four decimal places and reproductively staged through histological methods (a full description of the staging can be found in Chapter 2).

4.2.3 Sagittal growth:

To determine any discrepancy in age determination the relationship between sagittal weight and age was examined for each region using least squares linear regression. Slopes of the otolith weight-age regression between regions were compared using Analysis of Covariance (ANCOVA) where the assumption of heterogeneity of slopes was tested according to the procedures of Zar (1999).

4.2.4 Longevity:

With relatively small sample sizes a single individual has the potential to influence estimates of longevity based upon maximum ages (T_{max}). Therefore, longevity estimates at each location within each region were compared based upon the mean age of the oldest 20 % of individuals sampled, rather than the maximum age. The arbitrary figure of 20% was chosen as Gust et al. (2002) found little difference between estimates based upon the oldest 20% compared with those based upon the oldest 10%. A one-way ANOVA was performed on the mean 20% longevity estimates to determine any regional differences. Following significant differences, a Tukeys multiple comparison test was performed. However, in cases where the assumption of homogeneity of variances was violated (following a Bartletts C test according to Zar (1999)) a Dunnett C multiple comparison test was used to determine differences.

4.2.5 Growth:

Size at age data was plotted with growth parameters estimated by fitting the von Bertalanffy growth function:

$$L_t = L_\infty(1 - \exp(-k^{(t-t_0)}))$$

where L_t is the estimated standard length at age t, L_∞ is the mean asymptotic standard length, k is a curvature parameter and t_0 is the age at which fish have theoretical length of 0. Because VBGF parameter estimates can be sensitive to the range of ages and sizes used (for empirical examples see Ferreira and Russ 1994, Craig 1999), t_0 was constrained to 0 for all regions (Kritzer et al. in prep) as it is often small and has little effect (Roff 1984). Ninety-five percent confidence regions around the parameters k and L_∞ were plotted to compare growth estimates between regions (Kimura 1980, Meekan et al. 2001).

4.2.6 Growth rates:

The examination of growth rates at particular ages is imperative to the proper understanding of life history variation. Initial growth rates can affect longevity, age at maturity and maximum size. However, contrary to popular use, the k parameter in the von Bertalanffy growth model cannot be effectively used as a measure of growth rate. This is because it is neither a growth rate (with units of size.time^{-1}), nor a parameter

enabling the examination of age-specific life history stages. However, a method of utilising the von Bertalanffy growth model to examine age-specific growth rates has been developed (Chapter 3). Therefore, it was possible to examine and compare growth rates of each geographically separated population, pre- and post-maturation.

Instantaneous growth rates at settlement, sub yearly and yearly time periods were calculated through the use of bootstrapping methods. This was calculated for t equals 52 (approximate settlement times of *T. lunare* following Wilson & McCormick 1999), 180 and 270 days and years 1 through to the maximum age for that region. This process was iterated 250 times for each region. Growth rates reported here are the bias adjusted growth rates. Confidence intervals are calculated as 1.96*stdev of the iterated estimates (see Chapter 3 for a full description of the methods).

4.2.7 Mortality:

Age-based catch curves described by Pauly (1984), were used to estimate the instantaneous rate of total mortality (M expressed as year^{-1}) for *T. lunare* populations at each region. These methods assume that there is no systematic trend in annual recruitment rates at each site and involve calculation of the natural logarithm of the number of fish sampled from each age class, plotted against their corresponding age. Any year classes to the left of the age-frequency mode were excluded since sampling procedures may have under-estimated numbers of smaller fishes. Regression slopes of each region were compared using ANCOVA where the assumption of heterogeneity of slopes was tested. Significant differences were evaluated using a multiple comparison test among slopes following Zar (1999). Survivorship (S expressed as %.year^{-1}) for each region was calculated from the above estimates of mortality following $S = e^{-M}$.

4.2.8 Density:

Density estimates were taken at all regions excluding Ningaloo South in the Indian Ocean. All observations were conducted on SCUBA at a location and depth in which fish were to be collected on subsequent dives. The size of each visual strip transect was 50m by 4m following Green (1996). Size (FL) of each *T. lunare* sighted within the area was estimated whilst simultaneously unwinding the 50 m transect tape (initial counts). In all regions each strip transect was repeated at least four times.

Thalassoma lunare is a diver positive fish and therefore to account for possible erroneous overestimations of individual abundance due to fish swimming in from outside the defined area through an initial attraction to the diver (see Bellwood & Wainwright 2001), counts were also performed upon winding in the transect tape (return counts). A paired t-test was performed on all visual strip transects to determine whether there was any difference between the initial counts and the return counts.

To ensure size estimates were accurate, underwater estimates of inanimate objects (shaolin wooden fish) were performed in conjunction with estimating the size of several live fish preceding their collection. The actual vs estimated size was analysed using linear least squares regression to test whether the slope and origin deviated from that of 1 and 0 respectively.

A one-way ANOVA was performed on the density estimates to determine any regional differences. Following significant differences, a Tukeys multiple comparison test was performed. However, in cases where the assumption of homogeneity of variances was violated (following a Bartletts *C* test according to Zar (1999)) a Dunnett *C* multiple comparison test was used to determine differences.

4.2.9 Age- and size-based reproductive parameters:

Age-based reproductive traits were recorded for all regions in both oceanic basins. In addition, *T. lunare*, as is the case with most wrasses, have been found to be a protogynous hermaphrodite, (change sex from females to males, Chapter 2) and therefore they offer a unique opportunity to study an additional life history characteristic, not common in general life history studies. Individuals were histologically classified into reproductive categories following Chapter 2. *Thalassoma* spp. are known to contain primary (or sneaker) males in their populations, where smaller fish, with female colour patterns, are reproductively active males. These smaller males often have disproportionately large testis, compared with the larger territorial males, and are therefore easily identifiable upon dissection. Females were classified as immature, undetermined or mature. Female maturity and sex change ogives were calculated through the minimisation of the sums of squares, following:

$$\text{Age}_{predicted} = 1/(1 + e^{mx + b}),$$

where *m* and *b* are coefficients of the sigmoidal function and *x* represents the observed age or size frequency. The predicted proportions of mature females were calculated for each age or size class from the observed proportion of mature females compared with the total number of females found in each age or size class. Predicted sex change ogives were calculated for each age or size class as a proportion of all terminal phase mature males compared with the total number of fish in that age or size class. For each region both female maturity and sex change ogives were superimposed over the frequency distribution of the sex specific age and size structure. Reproductive traits are reported as the size and age at which 50% of individuals are mature and size and age at which 50% of individuals change sex following Rochet (2000).

4.3. Results:

4.3.1 Sagittal growth:

Sectioned sagittae from all regions and exposures showed consistent opaque and translucent incremental bands (Figure 4.2). Even with large geographical ranges, and potentially variable sea surface temperatures, it was not considered any more difficult to interpret incremental bands at lower latitudes compared with those samples from higher latitudes. Increasing age showed the same general linear increase in sagittal accretion at all sites (Figures 4.3 & 4.4). However, the ANCOVA results returned significant differences between regions within each of the oceanic basins (Indian Ocean, $F_{4, 312}$ = 8.54, p << 0.001; Pacific Basin, $F_{7, 730}$ = 13.58, p << 0.01). In the Indian Ocean multiple comparison tests revealed no significant difference between the two most southern regions, Abrolhos Islands and Rottnest Island. However, these two were significantly different from Scott Reef and Ningaloo South. Ningaloo North was also significantly different to Ningaloo South, however, as there was no difference between Scott Reef and either Ningaloo South or Ningaloo North, any differences between these latter two sites need to be made with caution. In the Pacific Basin, multiple comparison tests revealed no significant difference between the Palm Group of islands and PNG, but significant differences between these two and all other sites.

4.3.2 Longevity:

In no population did the maximum age reach those suggested by Eckert (1987). The oldest fish from any region (in either basin), an 8 year old, was found at the One Tree Island Lagoon. A general pattern of increasing longevity with increasing latitude was evident in both the Indian Ocean and Pacific Basin, with significant differences between the regions within both basins (Indian Ocean ANOVA $F_{4, 62}$ = 17.49, p << 0.001; Pacific Basin ANOVA $F_{7, 146}$ = 24.74, p << 0.001; Figure 4.5, Table 4.1). Mean 20% longevity estimates from regions in the Indian Ocean were highest for the populations at Rottnest Is and the Abrolhos Is, being significantly greater than those estimates from Ningaloo South and Scott Reef. However, the Pacific Basin revealed a more complex pattern. Whilst there was a general increase in longevity estimates with increasing latitude from PNG to One Tree Island, Port Stephens in the far south exhibited relatively low estimates of longevity. In general, the lowest estimates of longevity were found at regions that are best described as exposed environments being the exposed Outer Reef and the most southern region sampled in the Pacific Basin, Port Stephens. However, the region with the lowest 20% longevity estimate (1.9 years ± 0.1 SE), and correspondingly the lowest maximum age (in either the Indian Ocean, or Pacific Basin) was PNG, the most northern regional site, yet also one of the most sheltered regions. A Dunnett *C* multiple comparisons test showed that there was a significant difference between this region and all other regions in the Pacific. In addition, One Tree Island Lagoon was significantly different to the most southern region, Port Stephens. There was little statistical difference between all other regions.

4.3.3 Growth:

In general, size at age plots for populations in most regions showed similar patterns of initial rapid increases followed by a tapering growth trajectory (Figures 4.6 & 4.7). The exceptions to this were the populations sampled at Ningaloo South and PNG in the Indian Ocean and Pacific Basin. At these two regions, size increased throughout life, clearly demonstrating indeterminate growth (Calder 1983). However, at PNG, maximum age and size were much smaller than those found at all other regions, with no fish found living beyond 2 years of age or 104 mm SL (Table 4.1).

In the Indian Ocean, 95% confidence ellipses around the VB parameter estimates revealed similar growth parameters between the populations at Ningaloo North, Abrolhos Islands and Rottnest Island (Figure 4.8A). Large differences were evident between these 3 regions and Ningaloo South and Scott Reef. However, this was not illustrated as a decline from north to south. Rather populations in the Abrolhos Islands and Ningaloo South (middle of the sampling range) had the largest mean asymptotic lengths compared with that of population at the extreme latitudes sampled. In addition, there was no evidence of a latitudinal gradient in VB parameters across the Pacific Basin (Figure 4.8B). Instead, growth parameters varied to a greater extent across exposure gradients. Relatively sheltered sites, Lizard Island, the Palm Group of islands and One Tree Island Lagoon were areas in which populations exhibited larger mean asymptotic sizes, whilst populations found at exposed sites, the two outer shelf reefs and Port Stephens, exhibited smaller mean asymptotic lengths. Although, populations at PNG showed the smallest mean asymptotic length, little difference was evident between this site and populations at Port Stephens, two regions separated by the greatest distance (Figures 4.1 & 4.8B). Whilst the confidence regions around the VB parameter estimates at One Tree Island Outer Reef is large due to relatively small sample sizes, individuals in the 4, 5 and 6 year old age classes are much smaller compared with those found in the lagoon (Figure 4.7). Additionally, individuals in the younger age classes are generally smaller at the former location compared with the latter. The regions with populations exhibiting the largest values of mean asymptotic length were, in descending order, the Palm Group of islands, One Tree Island Lagoon and the Lizard Island region. However, differences were evident between the population at the Palm Group of islands and the population at Lizard Island. Growth parameters of these three populations were all significantly different compared with all other regions.

4.3.4 Growth rates:

Instantaneous growth rates throughout the life of *T. lunare* did not display a cline from higher to lower latitudes consistent with the prediction that higher latitudes (colder waters) would exhibit slower initial growth rates compared with lower latitudes (Figures 4.9 & 4.10). In the Indian Ocean the slowest growth rates upon settlement were found for populations in the mid-latitudinal region, Ningaloo South (Figure 4.9). Furthermore,

slow initial growth rates were not indicative of extended longevity, as Ningaloo South was one of the shortest-lived populations in the Indian Ocean. In the Pacific Basin, slower initial growth rates were also discovered in the mid-latitudinal regions whereas, PNG, Solomon Islands and Port Stephens at the equatorial and most extreme southern region exhibited relatively fast initial growth rates (Figure 4.10). These differences, again, appear to be driven by exposure, as the significantly slower initial growth rates were evident at Lizard Island, the Palm Group of islands and One Tree Island Lagoon. In contrast, fast initial growth rates were found not only at the northern regions, but also the exposed sites of One Tree Island Outer Reef the outer shelf reef off Lizard Island and Port Stephens in the south. This pattern was reversed by 2 years of age in both oceanic basins. In contrast to the Indian Ocean however, slow initial growth rates were indicative of increased longevity in the Pacific Basin populations, as One Tree Island Lagoon, the Palm Group of islands and Lizard Island were all regions with individuals exhibiting ages beyond 6 years.

4.3.5 Mortality:

There was a general trend of reduced mortality estimates with an increase in latitude calculated from catch curves following Pauly (1984). However, deviations existed with this pattern in both oceanic basins. In the Indian Ocean, Ningaloo South, in the centre of the sampling range, exhibited the highest estimate of mortality, followed by Scott Reef in the north, Ningaloo North, Rottnest Is, at the extreme south, and lastly the Abrolhos Is (Figure 4.11; Table 4.1). However, ANCOVA results revealed there were no significant differences between regions (Table 4.2). In the Pacific Basin there was a general decline in mortality from PNG, through Lizard Island and the Palm Group of islands to One Tree Island (Figure 4.12; Table 4.1). However, populations in the exposed reefs off Lizard and One Tree Islands both exhibited relatively low estimates of mortality, as did the Solomon Islands, one of the most northern regions (Figure 4.12; Table 4.1). However, again there was no significant difference between regions (Table 4.2); although, PNG was removed from any statistical analysis, as there were too few age classes to return a statistically meaningful result. It should be noted however, that the two most northern regions sampled, PNG and the Solomon Islands exhibited vastly

different estimates of mortality. Intuitively, estimates of mortality for PNG must be high due to the reduced longevity.

4.3.6 Density:

The mean estimates of *T. lunare* density at each site were slightly higher for the initial counts than the return counts; however, this difference was not found to be significant (t = $_{0.05 (2), 91}$ = -4.58, p < 0.0001). Density estimates reported will therefore be the return counts to provide a more conservative estimate. Underwater estimates of size did not deviate more than a 1:1 ratio with the actual estimates (n = 25), with the slope and intercept not significantly different to that of one and zero respectively (slope = 1.01 ± 0.10; intercept = 4.66 ± 23.61).

In both the Indian Ocean and Pacific Basin estimates of abundance did not increase consistently with either increasing or decreasing latitude (Figure 4.13). In the Indian Ocean, the most southern and northern regions exhibited the lowest estimates of density, whilst Ningaloo North exhibited the highest estimates. However, ANOVA results revealed no significant difference between the regions sampled in this oceanic basin ($F_{3, 13}$ = 1.49, p = 0.26). Whilst there was no formal density estimate taken for Ningaloo South, this region had a greater number of individuals per square metre than other regions (pers obs). In only 3-4 hours of sampling, approximately 50 individuals were collected, which exceeded the collection rate in any other population.

The abundance of individuals at PNG was significantly greater than all other regions in the Pacific Basin, with the exception of the Solomon Islands and One Tree Island Lagoon (ANOVA; $F_{5, 38}$ = 6.63, p = 0.0002; Figure 4.13). Furthermore, the Solomon Islands exhibited greater density estimates than both Lizard Island and Port Stephens. Whilst Port Stephens, Lizard Island and the Palm Group all exhibited relatively low numbers of individuals it should be noted that the Outer Reef regions, off Lizard Island and One Tree Island, potentially had the least number of individuals (pers obs). Whilst there was a substantial amount of time spent sampling these two regions, few individuals were collected.

Maximum size appeared to follow mean size in both the Indian Ocean and Pacific Basin following underwater estimates of length. In addition, underwater estimates of size

appeared comparable with the maximum size of individuals collected at each region (Figure 4.13; Table 4.1). With the exclusion of Rottnest Island in the Indian Ocean there was a general trend for increasing size with increasing latitude. However, the underwater estimates at Rottnest Island in the Indian Ocean appear to be slightly underrepresented. This pattern was repeated in the Pacific Basin to some extent, with the exclusion of the exposed southern most region, Port Stephens. Furthermore, the three regions in the middle of the sampling range appeared to have similar maximum sizes. There was no apparent association between mean or maximum length with density. However, PNG showed the smallest mean and maximum lengths in the Pacific in conjunction with the highest densities. In addition, the largest individuals at Ningaloo South were relatively small; mean size was as small as those found in the Scott Reef population, yet the population exhibited relatively high densities (see above). Furthermore, across the range of regions, there was little evidence of a negative relationship between density and maximum age, with the exception of the populations at PNG and Ningaloo South, in the Pacific Basin and Indian Ocean respectively. At these two regions, populations exhibited relatively low maximum ages, yet high densities.

4.3.7 Age-based reproductive parameters:

For the majority of regions, female fish were mature by the age of 1 year, and few mature females remained in the population beyond the age of 4 years (Figures 4.14 & 4.15). In addition, the majority of regions had males evident in the population by 2 years of age and a substantial proportion by the age of 4 years. Aside from the different age-based reproductive stages found at PNG, likely due to reduced longevity, exceptions to these patterns were evident at Rottnest Island in the Indian Ocean and One Tree Island Lagoon in the Pacific Basin. At these two regions, females were evident in the population up to the age of 5 years and in the case of One Tree Island Lagoon 7 years of age, which appeared to be uncharacteristic of this species given the results at all other regions. It was difficult to evaluate the presence of a latitudinal cline in the age at which 50% female maturity occurred, because mature females were evident in the population at the age of 1 year, the lowest age class in the sample. Therefore, in some instances ogives were at 100% by this age. However, maturity ogives for regions in the Indian Ocean show that 50% female maturity was highest for Rottnest Island, the most southern region

(Figure 4.14; Table 4.3). Unfortunately, no female gonads were collected from the Abrolhos Islands and therefore maturity values for this region are lacking.

Excluding Port Stephens and the Solomon Island populations, a general latitudinal cline in the 50% maturity estimates was observed across Pacific populations (Figure 4.15; Table 4.3). This was illustrated by increasing estimates of maturity, gained from maturity ogives, from the northern population, PNG, to the southern populations of the Palm Group of islands and One Tree Island Lagoon. In contrast however, the Solomon Islands exhibited relatively late ages at maturity, whilst females at Port Stephens matured relatively early. In conjunction with a general latitudinal cline, exposed offshore regions exhibited reduced age estimates at which 50% of females matured, compared with regions of similar latitude. The lowest ages at which 50% female maturity occurred were at One Tree Island Outer Reef, Port Stephens and PNG, whilst the highest values occurred at the Palm Group.

Not surprisingly, a similar general pattern as that described for female maturity was found for the age at which 50% of individuals changed sex from females to males. In the Indian Ocean the lowest age at which 50% sex change occurred was at the Abrolhos Island, followed by Ningaloo South and Scott Reef (Figure 4.14; Table 4.3). Correspondingly the highest ages occurred at Rottnest Island. In the Pacific Basin evidence of a latitudinal cline in sex change was more pronounced than maturity estimates would predict. Populations at the most northern regions sampled, PNG and the Solomon Is, showed the earliest age at which 50% sex change occurred, whilst the population at Port Stephens, in the south, showed much later ages (Figure 4.15; Table 4.3).

In both oceanic basins there was a general trend of steep female maturity ogives in populations exhibiting lower maximum ages. In those populations with a maximum age of 7 or 8 years, female maturity ogives were much more inclined to be gradual. In general, 50% female maturity occurred at approximately 10 to 30% of a population's maximum age, whilst 50% sex change occurred at approximately 25 to 80% of a population's maximum age (Table 4.3). Furthermore, those sites exhibiting relatively high densities, and/or located in sheltered exposures, such as Ningaloo South, OTI

lagoon, Solomon Is and PNG, returned smaller time periods between the age at which 50% female maturity occurred and the age at which 50% sex change occurred compared with those regions exhibiting lower densities. Additionally, the exposed reefs and/or those with relatively low densities exhibited much larger age differences between maturity and sex change.

Primary males were evident in the majority of populations sampled in the Indian Ocean and half of the populations sampled in the Pacific. With the exception of the Solomon Is, areas of high density were more than likely to have primary males in the population. The high-density regions of Ningaloo North, Ningaloo South, PNG and One Tree Island Lagoon, all had at least 5% of the population as sexually mature primary males.

4.3.8 Size-based reproductive parameters:

Variation in the size at maturity and size at sex change across latitudinal populations were similar to that seen in the age-based reproductive parameters. For most regions, female fish were mature by the size of 60 mm SL, and few mature females remained in the population beyond the size of 110-120 mm SL (Figures 4.16 & 4.17). In addition, the majority of regions had males evident in the population by 80-100 mm SL and a substantial proportion by the size 120 mm SL. Including the size-based reproductive stages found at PNG, due to smaller maximum sizes, exceptions to the general patterns of size-based maturity and sex change were evident at Rottnest Island and One Tree Island Lagoon. In a similar manner to the age-based reproductive stages at these two regions, females were evident in the population up to the size of 140 mm and 160 mm SL respectively. Size-based maturity ogives for regions in the Indian Ocean show that 50% female maturity was largest for Rottnest Island, the most southern region (Figure 4.16; Table 4.4). In the Pacific Basin difficulties in estimating reliable estimates of size at maturity also arise from the absence of particularly small size classes. However, for those regions with reasonable ogives, size at maturity (50% maturity) was generally at a size of 60 mm SL (Figure 4.17; Table 4.4). The exception to this was the Palm Group of islands with an estimated size at which 50% maturity occurs at approximately 90 mm.

Not surprisingly, the size at which 50% of individuals changed sex was similar to that described for female maturity. In contrast to the age-based reproductive schedules, the size at which 50% sex changed occurred was on average 50 mm larger than size at maturity (Figures 4.16 & 4.17; Table 4.4). This appeared to be regardless of latitude, density or exposure gradients. Correspondingly, the largest size at which 50% sex change occurred was at Rottnest Island in the Indian Ocean and the Palm Group of islands in the Pacific Basin. In general, 50% female maturity occurred at approximately 40% of a population's maximum size, ranging from 25 to 50%. Likewise, 50% sex change occurred between 50 to 90% of a population's maximum size with the majority at approximately 70% (Table 4.4).

4.4. Discussion:

Variation in age- and size-based parameters of *Thalassoma lunare* populations throughout both the East Indian Ocean and West Pacific Basin were not consistent with the broad predictions of 1) slower initial growth rates, 2) larger final body sizes, 3) greater maximum lifespans, 4) decreased mortality, and 5) delayed maturity and sex change from lower to higher latitudes. Fast initial growth rates were found at both high and low latitude regions irrespective of final age or size. Evidence suggested that regional populations deviated from the predicted latitudinal pattern in each basin under high densities or those on exposed reefs. Only when these regions were excluded was there a general gradient of increasing maximum size in populations from lower to higher latitudes. However, unlike size, an increase in maximum age with an increase in latitude was only evident in Indian Ocean populations. Whilst there appeared to be a general increase in longevity from northern to southern populations in the Pacific Basin, this was not statistically different. Likewise mortality estimates for populations were not observed to be significant from lower to higher latitudes in either Basin. Evidence suggests that whilst there may be a trend of increasing size at maturity (but not age at maturity) with increasing latitude, which may be expected considering its relationship with maximum size and to some degree maximum age. However, density and latitude had a significant role in affecting the size and age at sex change, whereby populations in regions of high density changed sex at smaller sizes and younger ages. Furthermore, evidence suggested

that density might play a role in shaping numerous life history parameters, but only once above a critical level.

Reef exposure appeared to play a significantly large role in shaping life history parameters of *T. lunare*. Populations residing in sheltered regions exhibited slow initial growth rates compared with those populations in exposed regions. Additionally, gradients from exposed outer shelf reefs through to sheltered inshore reefs were just as likely to cause an increase in body size. However, the reduced body size in populations under exposed conditions (i.e. the outer reefs) did not always reflect reduced maximum age, nor reduced mortality estimates. Exposure therefore, appears to play a role in influencing *T. lunare* life histories, but not in a predictable fashion.

In addition to latitudinal and exposure differences in the life history traits of *T. lunare*, density appeared to play a significant role in shaping life history parameters. Populations exhibiting a high abundance of conspecifics displayed smaller body sizes, reduced longevities and extremely high mortality estimates. These included; Ningaloo South in the East Indian Ocean and PNG in the Pacific Basin. Therefore, density may have an effect on size, maximum age and mortality, however; only once it reaches a critical level. For the purpose of clarity, the spatial variation displayed in the individual life history parameters will be discussed separately.

4.4.1 Sagittal growth:

Sagittal growth of *T. lunare* varied between several regions. Sagittae from northern regions in both basins were found to be significantly smaller at age compared with most other regions. It is possible that this may be caused by inaccurate estimation of increments. However, the marks in *T. lunare* otoliths were relatively easy to identify, regardless of the region in which they were collected. Increments in sagittae from most populations exhibited little difference with that of the Palm Group of islands, which had marks that were easily interpretable and validated as forming yearly (Chapter 2). This is consistent with Francis et al. (1993) who found that fish exhibiting relatively fast growth, as was evident in northern populations, tend to exhibit smaller otoliths (Francis et al. 1993). Decreasing clarity with a decreasing temperature range has been reported for reef fish otoliths (Caldow & Wellington 2003), with the focus upon those from low latitudes.

However, if the particularly small ages at PNG were an artefact of under-representing age classes (i.e. missing increments) the oldest age, based upon otolith weight alone would still not exceed 3-4 years of age. Likewise, the examination and interpretation of otoliths from geographically separate populations of the tropical scarid, *Sparisoma viride*, even those from low latitudes, was not found to be particularly difficult (Choat et al. 2003).

4.4.2 Growth rates:

Growth rates and body size, particularly in ectotherms have been found to alter over latitudinal gradients (Atkinson 1994). Temperature is the likely cause as it has been demonstrated that increasing the rearing temperature of fish increases the initial growth rates but reduces final size (Atkinson 1996). This was consistent with populations residing in low latitudes. However, initial growth rates of *T. lunare* in southern populations were not reduced, nor were final sizes necessarily increased (e.g. Port Stephens in the Pacific Basin). For reef fish therefore, it appears that temperature is not the only factor affecting these demographic traits as fast initial growth rates were found at both low and high latitudes. However, populations exhibiting fast initial growth rates in high latitudes can, in part, be explained by their location in areas of high exposure. The results of fast initial growth rates in populations residing in outer reef exposed locations were consistent with the results of Gust et al. (2002). These differences in growth rates between sheltered and exposed locations could be a response to increased predation in the latter regions. Experimental work has shown that in areas of increased predator abundance growth rates tend to be rapid, and individuals are inclined to mature earlier and at smaller sizes (Reznick & Endler 1982, Bertschy & Fox 1999; but see Connell 1998a). This appeared to be the case for those populations on exposed outer shelf reefs.

Habitat structure and increased complexity has been shown to reduce predation in coral reef fish (Caley & St John 1996; Beukers & Jones 1997). Furthermore, exposed, outer shelf reefs have been suggested to be less complex in comparison with areas of inshore, sheltered reefs (Gust et al. 2002). Therefore, in regions exhibiting increased exposure individuals may be more susceptible to predation events. In addition, turbidity has been cited as a potential reason for resulting in reduced predation events (Fiksen et al. 2002). Turbid waters are more prevalent at inshore reefs compared with those further

offshore, due to their proximity to the coast. Therefore, these turbid, complex inshore environments may offer greater protection for reef fish populations from predation. However, whilst high abundances of predators on outer reefs have been suggested (Williams & Hatcher 1983), and juvenile reef fish mortality has been attributed to predator abundance (Holbrook & Schmitt 2003), a direct link to the abundance of predators with that of actual predation patterns is difficult to evaluate (Connell 1998b, Forrester & Steele 2000).

Exposure and predation alone cannot explain fast initial growth rates exhibited in all populations. If exposure and predation were key factors in increasing growth rates, the Solomon Islands would likely exhibit significantly slower initial growth rates than those observed. The difference between this location and all others is that the human population of the region is heavily reliant on subsistence fishing (Aswani & Hamilton 2004). Therefore, densities of many large predators are significantly reduced. Furthermore, this region was relatively sheltered. Therefore, the results suggest that early growth rates in regions positioned in low latitudes (warmer waters) are still likely to exhibit fast initial growth rates regardless of exposure and predator abundance.

Faster initial growth rates at certain regions may also be due to the availability of food resources. Intuitively, increased resources can increase growth rates (Thresher 1983, Booth & Alquezar 2002). In addition, the allocation of resources to growth can be beneficial as reproductive output is often correlated with size (Roff 1984, Fox 1994, Rogers & Sargent 2001). But if fast growth were the outcome of greater resources, size at maturity would likely be at a larger size due to the benefits, but not necessarily an older age (see Stearns & Koella 1986 and Reznick et al. 2000). This is likely the case for the population at Rottnest Island. This region has sheltered bays with extensive sub-tidal beds of *Sargassum* spp. and a fringing limestone reef (Kendrick & Brearley 1997). Therefore, it is not considered to be an exposed region, without shelter from predation, nor is it located at a low latitudinal position. The population at Rottnest Island, in conjunction with fast initial growth rates, exhibited large size at maturity and an age at maturity that was similar to the populations in the Palm Group of islands and the One Tree Island Lagoon. Therefore, an increased amount of energetic resources at this location is a likely explanation for fast initial growth rates. However, an increased

amount of food is unlikely the explanation for those populations in exposed or low latitudinal regions that exhibited fast initial growth rates. The existence of relatively small final body sizes in these populations, yet fast initial growth rates, suggests that if greater food resources were available, individuals at these regions are not allocating it to growth beyond maturity. Furthermore, size at maturity was at relatively small sizes. Therefore, the availability of food resources is unlikely to be an important cause of the differences between growth rates across exposure and latitudinal gradients, but it cannot be ruled out entirely (see Thresher 1983).

It has been suggested that growth in the early stages is more likely to be controlled by density dependent effects (Cushing 1975). However, Pitcher (1992) found little difference between growth rates of juvenile fish at different densities, although, this is contrasted against the findings of Jones (1984). If density of conspecifics were an influence over initial growth rates, then both PNG and Ningaloo South, the regions with the highest densities, would be predicted to have similar early growth rates. This was not the case, and whilst it is likely that density dependence structures several life history attributes in particular populations (Jones 1991), again, the effect of low latitude on initial growth rates cannot be ruled out in the PNG region. However, to gain a more comprehensive understanding of initial growth rates it may be necessary to examine daily incremental marks in the otoliths of juveniles.

It could be argued that reduced growth rates in sheltered regions are an artefact of large asymptotic sizes. However, if this were the case, the populations at the Abrolhos Is and Ningaloo South would display similar initial growth rates. Whilst these populations have similar mean asymptotic sizes, the non-overlapping confidence intervals surrounding the VBGF parameters between these two regions indicate that growth is significantly different (Meekan et al. 2001). The examination of age-specific growth rates highlighted that these growth differences between the populations began early in life. At early ages, Ningaloo South exhibited significantly lower growth rates than the Abrolhos Islands. Between the ages of 2 and 3 years growth rates were similar between the two regions, but by the older age classes Ningaloo South displayed significantly faster growth rates. Therefore, the calculation of age specific growth rates is not simply a

reflection of VB parameters, but rather they offer a significant contribution to understanding reef fish life histories.

4.4.3 Size and age:

There was evidence of a general gradient of increasing maximum size from lower to higher latitudes. Whilst it was similar in both oceanic basins, it was not described by latitude alone. In the Indian Ocean, southern regions exhibited larger final body sizes, but this was not the case in the Pacific Basin. For example, adult fish in the most southern region sampled, Port Stephens, appeared to be relatively small. The difference between this region and the southern region in the Indian Ocean in final adult size is likely explained by their different exposure. Cabbage Tree Island (Port Stephens) in the southern Pacific Basin is a small coastal island, with a highly exposed reef, mainly comprised of large rocky boulders. Average wave energy is considered to be similar to that found on outer shelf reefs in the Great Barrier Reef (Fulton & Bellwood 2004). In contrast however, Rottnest Island in the southern Indian Ocean is relatively sheltered (Kendrick & Brearley 1997). Similarly, Gust et al. (2002) found variation in life history parameters in both scarid and acanthurid populations across an exposure gradient along the continental shelf at 14° latitude. As in this study, populations on exposed reefs were found to have smaller size at age than those populations inhabiting sheltered regions. However, the relatively sheltered region of PNG and the Solomon Islands was an anomaly, as it had a relatively small size for its age, in comparison to the other sheltered regions. The smaller size at age of the populations at PNG and the Solomon Islands was likely due to increased water temperatures as a result of their low latitude. Excluding regions with high exposures, the pattern of increasing size with increasing latitude becomes detectable.

Density of conspecifics also appeared to play a role in shaping final body sizes of *T. lunare*. Those regions exhibiting high abundances also returned relatively small final body sizes. These included; Ningaloo South in the East Indian Ocean and PNG in the Pacific Basin. However, there is likely a critical level of conspecific abundance, below which it has little effect upon final body size. Density estimates at the Solomon Islands and One Tree Island Lagoon were larger than other regions in the same oceanic basin, but

insignificantly smaller than those of PNG. Yet, whilst small body sizes were found in the population at the Solomon Islands, large final sizes were found in the population at One Tree Island. Kritzer (2002) found circumstantial evidence that high densities of conspecifics result in smaller asymptotic sizes in his examination of *Lutjanus carponotatus* demography across several populations. However, as in this study, it was not always consistent as again populations with similar densities returned large final sizes. Furthermore, it has been reported that an increase in body size occurs in conjunction with an increase in density, once a no-take coral reef marine reserve has been instigated (Russ & Alcala 1998, Chapman & Kramer 1999). Therefore if density does affect body size, it is likely that it will only evident once a critical level of abundance has been reached.

However, it remains unclear what is driving the high densities at Ningaloo South and PNG considering they are characterised by life history variables that would dictate low densities. For example, Ningaloo South is a sheltered region that has slow growth, delayed size and age at maturity, and reduced final body sizes and maximum ages. PNG is a region of greatly reduced size and age. Both regions have characteristics that should reduce lifetime reproductive output. However, these regions may have high recruitment rates. There is evidence that numbers of adult fish increase with an increase in recruitment (Jones 1984). Locations such as Coral Bay at Ningaloo South and Kimbe Bay at PNG may be subject to increased recruitment events, compared with other regions despite having a relatively closed nature. Increasing evidence suggests that recruitment to natal reefs (self-recruitment) is more common than previously thought in reef fishes (Swearer et al. 1999, Jones et al. 1999). This may be facilitated by larval retention within these relatively closed systems (Leis et al. 1998). However, the link between high self-recruitment and higher associated survivorship of pelagic stage larvae is yet to be examined (but see Swearer et al. 1999). Therefore, future work focusing upon these two regions may be beneficial to not only understanding these patterns further, but to understanding larval, juvenile and adult stages of reef fish.

The existence of the Leeuwin Current bringing warm nutrient-poor water southward along the edge of the West Australian continental shelf is likely to explain, in part, the body size differences between populations located in the southern regions of the

Pacific and Indian Oceans. Temperature has been shown to affect growth of larval reef fish above the effects of productivity, often accounting for approximately 30% of the variation in growth between cohorts (McCormick & Molony 1995, Meekan et al. 2003). Whilst size and growth differences have been shown to vary accordingly with variable food quality and quantity (Booth & Hixon 1999, Cardona 1999, Booth & Alquezar 2002) temperature is likely to play a significant role. In addition, the Leeuwin current has been shown to have a positive effect on settlement of lobster larvae, likely through increased growth and survivability due to warmer waters (Caputi et al. 2001). This is especially so during periods of higher water temperatures associated with a stronger Leeuwin current. Therefore, the effect that this warm water current has upon the southern Indian Ocean populations is likely to be significant.

Populations in the Port Stephens area are likely to be an artefact of the regions high exposure. In addition to this, fish settling in summer at this region, may be subjected to winter temperatures beyond their range of growth or survivability. Fish have an optimal range of temperatures in which to grow, above and below this range growth tends to slow (Brett 1979). The lack of warm waters at Port Stephens may lead this population to exhibit high rates of mortality over winter. Winterkill of fish populations would be expected to cause life history differences similar to those populations in fluctuating environments (i.e. small size and faster generations; Blanckenhorn 1998, Roff 2002). *Thalassoma lunare* have been observed further south of Port Stephens in the Pacific Basin, at Montague Island beyond 36°S, in which individuals were much smaller than those of any location (pers obs). At this region these individuals are likely summer recruits with extremely high mortality levels over winter ($\approx$100%). However, survivability over winter appears not to be problematic for the Port Stephens population, as the age structure indicates individuals are at least surviving several winters. In addition, Fox & Keast (1991) examined populations of fish subjected to major levels of winterkill and found that whilst individuals matured earlier and at smaller sizes, size was not necessarily reduced compared with populations living in an adjacent water-body without winterkill. Life history parameters in the Port Stephens region, therefore, are likely to be driven by factors associated with an exposed environment rather than the effect of a colder climate.

Longevity tended to increase with an increase in latitude in the Indian Ocean, which is consistent with life history predictions. However, with the exception of PNG, there was little significant variation amongst these estimates in the Pacific Basin. Similarly, Choat et al. (2003) found that whilst differences in final body size between four *Sparisoma viride* populations in the Caribbean were evident, differences in longevity between the populations was minimal. This could be explained, in part, by recent evidence suggesting that maximum age may be intrinsically driven. Recent work on birds and fish has demonstrated that genome length is correlated with longevity (Monaghan & Metcalfe 2000, Griffith et al. 2003; but see Morand & Ricklefs 2001). Therefore, extrinsic variables, such as temperature or exposure, may not alter the length of life to any great degree. However, this does not explain the significantly reduced life spans at the PNG *T. lunare* population in the Pacific Basin. Likewise, Meekan et al. (2001) found at least a three-fold difference in maximum ages between two geographically separate populations of *Stegastes flavilatus*. However, the short life span of PNG is possibly the result of extremely high densities. In addition, density is a likely explanation for the significantly reduced longevity estimates at Ningaloo South. Similarly, density is a potential explanation for the significant differences in longevity estimates of two species of Scarid found between reefs of different exposure, as Gust et al. (2001) reported significantly higher abundances on those reefs with shorter life spans. Therefore, longevity estimates and reasons for differences between populations may be driven by the abundance of conspecifics, again once they have reached particular, but critical levels.

Whilst high abundances may reduce maximum age, it does not explain why populations in particular regions exhibited relatively low maximum ages. For example, the population at Scott Reef does not exhibit high abundances, yet this population exhibits relatively small maximum ages. However, reduced ages at this population may be due to the reduced coral cover and increased coral rubble (pers. obs.) as a result of several bleaching events in recent years (L. Smith pers. comm.). Recruits of *T. lunare* are reported to prefer live branching coral (Eckert 1985 in Green 1996) and therefore processes acting during the settlement period may have additional consequences later in life. Reduced resources (food and shelter) and potentially increased predation, either

directly due to the isolated location of Scott Reef, or indirectly as a result of the reduced habitat through extensive coral bleaching, may be affecting the age-based parameters at this region (see Thresher 1983). Whilst it is evident that coral bleaching can have an effect upon the coral reef fish community (Booth & Beretta 2002), the effect bleaching has upon age-based demography of reef fishes has yet to be determined.

Similarities in growth parameters existed between populations separated by 1,000's of kilometres in both oceanic basins, which is inconsistent with traditional life history theory. For example, populations of *T. lunare* at Port Stephens, One Tree Island outer reef, Outer shelf reef off Lizard Island, Solomon Islands and PNG all exhibited similar, if not overlapping, confidence regions around the von Bertalanffy growth parameters. Similarly, confidence regions surrounding growth parameters overlapped between the populations in sheltered regions. This was evident between populations at One Tree Island Lagoon and the Palm Group of islands and between this latter region and Lizard Island. Numerous studies have demonstrated that increased temperature induces fast growth, evident through low latitude populations exhibiting fast initial growth rates (Ray 1960, Atkinson 1996, Nunney & Cheung 1997). This, however, does not explain how fish living in cool, exposed environments achieve similar growth trajectories, such as Port Stephens. Two explanations are possible for the anomaly. Firstly, that fish in generally cool environments (high latitudes) are adapted to the temperature ranges most frequently encountered by them. Therefore, they can grow at similar rates as those fish in lower latitudes, although the temperatures which they can achieve similar growth rates are reduced, assuming that fish do in fact grow at these reduced temperatures (Conover & Present 1990). Alternatively, fish located in cooler, more seasonal environments, can exhibit compensatory growth (Conover 1990, Schultz et al. 2002). Fish in southern populations (higher latitudes) may experience faster growth periods during the summer months, however, a reduced period with which to do so (Conover et al. 1997, Yamahira & Conover 2002). In contrast, fish in northern regions (lower latitudes) may experience year round growth, however, slower annual growth rates overall. Experimental evidence suggests that fish under restricted rations are able to compensate for reduced growth periods, sometimes beyond the normal growth rate, once conditions are returned to normal (Schultz et al. 2002).

These two theories, temperature adaptation or temperature compensation, assume a certain level of genetic variability between populations. Findings by Conover & Schultz (1995, reviewed by Arendt, 1997) have shown that genotype by environment interactions can play a significant role in the shaping of size and age variables. Individuals from populations found at higher latitudes do exhibit faster growth rates than those individuals from lower latitudes when temperature is controlled (i.e. counter-gradient variation). These differences can come about through differences in resting metabolic rates and higher efficiencies at lower temperatures for the populations in colder environments (Clarke 2003). However, for reef fish with a dispersive larval phase, genetic differences are not necessarily the explanation to demographic differences. Dudgeon et al. (2000) found that there was relatively high gene flow between spatially separate populations of Scarids, even though large demographic differences (e.g. growth) existed (Gust et al. 2002). However, genetic differences may be evident when examining large geographic ranges, such as those examined here (Bernardi et al. 2001). This is especially so across oceanic basins, where strong genetic subdivision has been reported for populations of the reef fish, *Chlorurus sordidus* (Bay et al. 2004). Further work is necessary to determine the level of gene flow between populations of reef fish across these large spatial scales to determine the level of genetic diversity that can account for demographic differences.

As Belk & Houston (2002) point out, predictions regarding temperature effects on size are based largely upon laboratory rearing experiments where temperature is altered whilst all other factors are controlled. Under these circumstances growth will vary between individuals under different temperature regimes, even though they come from the same population. However, it is difficult, if not impossible to re-create the complexities of a natural environment in strictly common-laboratory experiments. Therefore, variation found in the field, even with widespread dispersive larvae, is likely a combination of many factors, either genetic or environmental, and the interactions between them.

4.4.4 Mortality:

Mortality estimates of *T. lunare* populations did not decrease with increasing latitude as would be expected. For example, the population at the Solomon Island region displayed extremely low estimates of mortality, despite its low latitude. Although there was little statistical difference between the estimates across regions, it is possible that low estimates of mortality at the Solomon Islands was due to the reduced abundance of predators (see above). Links between predator abundance and mortality have been made (Reznick et al. 1996, Connell 1998a) especially for juvenile reef fish (Holbrook & Schmitt 2003). However, the effect of increased mortality on adult fish due to predation is likely reduced size at maturity and consequently, reduced body sizes (Reznick & Endler 1982, Abrams & Rowe 1996, Reznick et al. 1996). Therefore, the lack of predation on the Solomon Islands population does not explain the relatively small sizes of individuals at this region. However, the low latitude of the Solomon Islands, and therefore increased temperatures, is the likely cause of small body sizes. Therefore predation (or the lack of it) may influence mortality, but increased temperatures will still play a role in reducing the final size of reef fish.

An additional influence on mortality may be high densities of conspecifics. Two regions, Ningaloo South and PNG, were estimated as having relatively high densities in conjunction with high estimates of mortality. Whilst environmental effects confound the pattern, density dependent effects upon mortality have been examined more closely than other age-based demographic traits (Caley 1998, Shima 2002; but see Hixon 1998). However, Scott Reef and Lizard Island also exhibited relatively high estimates of mortality, although insignificant, yet low estimates of abundance. For the same reason Scott Reef exhibited relatively low maximum ages and small size, the consequence of coral bleaching may also be increased mortality. Effects of refuge availability upon mortality has been examined (Beukers & Jones 1997), however, it has been shown that with few refuges, prey species are more likely to exhibit density dependent mortality compared to when refuges are in abundance (Forrester & Steele 2004). Contrastingly, the high estimates of mortality at Lizard Island may be explained due to the existence of a single 7-year-old individual in the sample. This single fish has a disproportionate effect on the slope of the catch curve and consequently the mortality estimate, as it increases the gradient of the regression. However, it was an outlier, as it was a particularly large size,

yet exhibited female colouration patterns and little evidence of reproductive tissue (see Chapter 5). Therefore, whilst circumstantial evidence exists for the effect density has upon size, maximum age and mortality, it is likely that the density dependent effects will only be evident once it reaches a particular, yet critical level.

Whilst estimates of mortality exhibited little difference between regions, the method used to determine these estimates (catch curves) is reliant upon a number of assumptions (Pauly 1984). In addition, they return a single estimate of mortality, regardless of age, and therefore the lack of significant differences between most regions needs to be treated with caution (Meekan et al. 2001). Even though mortality is an important aspect of understanding reef fish life histories, it is one of the most difficult parameters in which to obtain precise estimates (Kritzer et al. 2001). Furthermore, single estimates of mortality for the entire life span of a species has limited utility (Jones 1991). Rates of mortality on juvenile fishes has been shown to be age-dependent, with the majority of individuals (25%) disappearing in the first 5 days of settlement, after which survivorship increases (Doherty and Sale 1985, Searcy & Sponaugle 2001, McCormick & Hoey 2004). However, mortality of *T. lunare* between the older ages is unlikely to exhibit such disproportionate estimates. Furthermore, without following cohorts through time, age specific estimates of mortality are difficult to obtain. In addition, one of the assumptions of mortality estimates based upon age frequencies is constant recruitment through time (Pauly, 1984). As longevity is often correlated with recruitment fluctuations through time (Meekan et al. 2001, Longhurst 2002), it is unlikely that *T. lunare* would exhibit significant differences across years due to the relatively short life span. However, variation cannot be ruled out. Low numbers of 3 year olds at Rottnest Island indicate that there may have been a period of recruitment failure in 1997/1998; a year in which cooler waters were reported at the North West Cape of Western Australia (Meekan et al. 2003). In addition, Eckert (1984) found significant differences in the abundance of *T. lunare* juveniles across several reefs between two years. However, actual recruitment to the reefs was not measured as surveys were performed once early mortality of the recruits was presumed to have taken effect. To gain a more comprehensive understanding of mortality between regions, survivability between age classes would need to be examined independently. Typically this would involve

following cohorts through time (van Rooij & Videler 1997). Alternatively, estimates of mortality between adults and juveniles (i.e. the juvenile/adult mortality ratio) would possibly clarify whether mortality differences exist between regions and whether mortality differences between life history stages play a role in shaping reproductive schedules (see Reznick et al. 1996).

4.4.5 Maturity and sex change:

There was a general trend of increasing size at maturity with increasing latitude in populations of *T. lunare*. However, size at maturity is likely a reflection of the maximum body sizes at these regions as a result of the latitudinal gradient in maximum size. In contrast however, there was little evidence of a latitudinal gradient in the age at maturity, even though some populations exhibited a tendency to have increased longevity estimates with increasing latitude. This is surprising, as age at maturity is often positively correlated with maximum age (Charnov & Berrigan 1990, Fox 1994). However, the resolution associated with identifying differences in age at maturity is likely to be limited given they tend to mature at relatively young ages and over what appears to be relatively small age ranges. Furthermore, it may be a result of little significant difference amongst longevity estimates in the Pacific. It does suggest however, that final body sizes have a strong influence on maturity schedules. Jones (1980a) found a similar result in the temperate labrid *Pseudolabrus celidotus* and evidence exists that demonstrates *Labroides dimidiatus* and *T. bifasciatum* in the Pacific and Caribbean respectively, are socially controlled, facilitated by size class hierarchies (Robertson 1972, Warner & Swearer 1991). This is not unexpected, as size at maturity is often positively correlated with mean asymptotic size or maximum size (Charnov 1993, Jensen 1996, Rochet 2000). Furthermore, with the exception of Rottnest Island, regions exhibiting high initial growth rates also exhibited relatively reduced size and age at maturity. This has the potential to reduce reproductive output due to the positive correlation between fecundity and size (Roff 1984). However, maturing earlier has the potential of increasing the number of spawning events and potentially reducing generation times (Stearns & Koella 1986)

Regional variation in maturity schedules of fish is not uncommon (Jones 1980a, Adams et al. 2000, Adams 2002) and has been attributed to temperature, and/or

demographic differences between populations (Jones 1980a, Conover & Heins 1987, Cowen 1990). This is consistent with the results in this study as latitudinal variation appeared to create differences in size and consequently in size at maturity. Furthermore, the relationship between maturity and final body size is consistent with social inhibition of smaller immature females by the larger mature females (Jones 1980b)

Additional to the latitudinal gradient in size at maturity, both size and age at sex change appeared to increase with increasing latitude. Whilst this is also likely a reflection of the maximum sizes, density estimates played a significant role in schedules of sex change. In regions of increased conspecific abundance, size and age at sex change was found to be at smaller sizes and at earlier ages. However, increased abundance of conspecifics tended to result in reduced body sizes (discussed below). Therefore, abundance may alter the size and age at which sex change occurred either directly or indirectly as a result of affecting maximum body size. The fact that sex change is related to final body sizes is not entirely unexpected. In their recent review of 52 species of fish exhibiting sequential hermaphroditism, Allsop & West (2003) found that the ratio between size at sex change and maximum size was consistently in the order of 80%. Whilst the majority of regions in this study exhibited slightly lower estimates, the ratio was generally predictable at approximately 70% on average.

Age at sex change exhibited an increase in age with an increase in latitude even though age at maturity did not. However, for those regions with reliable estimates of age at maturity, it appears that females change sex, on average, at approximately 2.4 times their age at maturity. Although the values ranged from 1.4 to 3.5, it is in accordance with the dimensionless value of 2.5 estimated by Allsop & West (2003). However, due to the size/age relationship in reproductive schedules, it is likely that age at sex change, like size at maturity and size at sex change, is related to the overall sizes reached in the population. This is expected, as reproductive traits are often a function of size, whilst survival is often a function of age (Rogers & Sargent 2001).

Reproductive strategies in protogynous fish can be driven by conspecific abundances. Evidence has been presented that demonstrates *T. bifasciatum* may alter its male reproductive strategy when population densities are increased (Warner & Hoffman

1980).   Increased densities within local populations often result in an increased proportion of initial phase males. However, this result was not necessarily the case amongst the regions sampled here.   Those regions exhibiting extraordinarily high estimates of abundance showed evidence of alternate male strategies.   However, in regions of relatively low densities, such as Port Stephens, Lizard Island and Rottnest Island, primary males were also evident in the population. Furthermore, Port Stephens exhibited a relatively large proportion of primary males in comparison to these other regions. The number of primary males within each population has been shown to be a function of reef size, the number of spawning territories within it, and the ability of the territorial males to defend their sites from the primary males (Warner & Hoffman 1980). An anomaly exists at Cabbage Tree Island (Port Stephens) whereby primary males dominate despite the low densities. This is inconsistent with the findings of Warner & Hoffman (1980).   It could be that because Cabbage Tree Island is a relatively small exposed island, in comparison to Lizard and Rottnest Islands, there may be limited or no preferred spawning sites (Samoilys & Squire 1994).   Therefore, opportunities for territorial males to set up and defend preferred sites is removed. Furthermore, if this region does exhibit an increased risk due to predation, females may be more apprehensive to spawn with displaying males (Warner & Dill 2000).   Therefore a primary male strategy at this region may be advantageous, despite the low densities.

4.4.6 Conclusion:

Gradients of life history patterns along latitudinal clines have been reported for many ectotherms due to the external temperature having a greater effect on their physiology. However, it appears that the variation in coral reef fish life histories cannot be solely explained by traditional theories based upon predominantly terrestrial studies. Environmental factors that are associated with exposure have a significant capacity to confound any examination of latitudinal variation of life history parameters in the Indo-Pacific.   Furthermore, particular environmental conditions such as high or low temperature (latitudinal), exposure (sheltered or exposed), and/or density thresholds (< 1 fish.10m^{-2} vs > 1 fish.10m^{-2}) translate into variations in *T. lunare* life history traits. However, the ability to control for this factor in the field is extremely difficult because of the natural variation in the marine environment at these spatial scales. One approach

however, would be to focus upon habitat specialists (Munday 2002). However, this will not necessarily be indicative of life history traits seen in coral reef fishes.

The variation of life history variables observed here suggest that populations in some regions may be more important than others in their contribution to larval supply and therefore the meta-population (James et al. 2002). Growth trajectories of *T. lunare* are typical of indeterminate growth where initial growth rates appear to have little effect upon maximum size or maximum age. There is evidence of a strong relationship between size and age at maturity and maximum size, but not necessarily maximum age. Therefore, it seems that life history aspects of *T. lunare* are driven largely by size, not necessarily by age. For *T. lunare*, in sheltered regions exhibiting relatively low to medium abundance of conspecifics at medium to high latitudes, initial growth will tend to be slow and maturity will be slightly delayed. However, in these regions large sizes will be attained and therefore slightly older ages. This has the potential of disproportionately increasing reproductive output at these regions through the relationship of increased fecundity with increased body size in conjunction with a potentially greater reproductive lifespan. Therefore, if spawning frequency is similar between regions, these populations may be disproportionately important in ensuring the continuation of the meta-population.

Table 4.1: Life history and demographic variables for the regions sampled along latitudinal gradients in both the East Indian Ocean and West Pacific Basin. Temperature range based upon 1° latitude x 1° longitude grid.

Ocean / Region	Temp range (°C)	n	Age range (yrs)	Size range (mm)	L_∞ (mm)	k (yr^{-1})	r^2	M (yr^{-1})	S (%.yr^{-1})
Indian Ocean									
Rottnest Is	18.0 – 24.5	79	0.63 - 6.5	63 - 180	151.52	0.76	0.89	0.49	61.26
Abrolhos Is	19.0 – 25.5	27	1 - 5.5	86 - 176	153.59	0.86	0.78	0.44	64.40
Ningaloo Sth	21.5 – 28.5	47	1 - 4.5	64 - 142	158.34	0.47	0.68	1.09	33.62
Ningaloo Nth	22.0 – 29.5	77	0.55 – 6	58 - 163	145.78	0.76	0.72	0.75	47.24
Scott Reef	25.5 – 31.0	92	0.52 - 4.5	41 - 142	121.57	1.04	0.75	0.93	39.46
West Pacific Basin									
Port Stephens	18.0 – 25.5	51	0.47 – 5	50 - 122	107.64	1.22	0.62	0.73	48.19
One Tree Island Outer Reef	21.0 – 28.5	14	1 – 6	82 - 130	116.99	1.10	0.47	0.41	66.37
One Tree Island Lagoon	21.0 – 28.5	81	0.47 – 8	48 - 172	151.75	0.57	0.75	0.55	57.70
Palm Group	22.0 – 29.5	182	1 - 7	66 - 184	161.42	0.49	0.71	0.64	52.73
Outer Reef	24.0 – 29.5	37	0.55 - 5.5	54 - 127	106.09	1.29	0.71	0.53	58.86
Lizard Is	24.0 – 29.5	283	0.28 - 7	23 - 166	137.66	0.71	0.78	0.98	37.53
Solomon Is	26.5 – 30.5	46	0.47 – 6	45 - 122	113.77	1.17	0.74	0.37	69.07
PNG	27.0 – 30.5	53	0.44 – 2	41 - 104	99.63	1.20	0.61	1.46	23.22

Table 4.2: Summary of ANCOVA comparisons of mortality rates of *T. lunare* populations within the two basins.

Ocean	K	df	F	p
Indian Ocean	5	4, 17	2.017298	0.13757
Pacific Ocean*	7	6, 23	1.844242	0.13453

*PNG was removed from the analysis of mortality due to insufficient age classes. The initial multiple comparison test between PNG and the Lizard Island Lagoon returned a non-significant result. However, there is no residual mean square as there were only 2 age classes at PNG.

Table 4.3: Age (years) and proportion at which 50% female maturity and 50% sex change occurred according to the ogives (see methods) in both the East Indian Ocean and Pacific Basin.

Indian Ocean	50% Female maturity (years)	% of max age	50% Sex change (years)	% of max age
Rottnest Is	1.77	27.30	4.83	74.28
Abrolhos Is	No data		1.63	29.61
Ningaloo Sth	0.36*	7.99	1.90	42.33
Ningaloo Nth	0.11*	1.84	2.70	44.94
Scott Reef	0.39*	8.67	1.94	43.04
Pacific Basin				
Port Stephens	0.39*	7.80	3.94	78.82
One Tree Island Outer Reef	Insufficient data		2.40	39.97
One Tree Island Lagoon	1.58	19.71	2.84	35.55
Palm Group	2.02	28.91	3.12	44.57
Outer Reef	0.84	15.30	2.96	53.80
Lizard Is	0.81	11.61	2.84	40.57
Solomon Is	0.94	15.59	1.39	23.09
PNG	0.41*	20.43	0.93	46.33

Table 4.4: Size (cms) and proportion at which 50% female maturity and 50% sex change occurred according to the ogives (see methods) in both the East Indian Ocean and Pacific Basin. * denotes estimates that may be considered unreliable, as mature females were already prevalent in the youngest age categories.

Indian Ocean	50% Female maturity	% of max size	50% Sex change	% of max size
Rottnest Is	9.66	53.68	14.25	79.17
Abrolhos Is	No data		9.32	52.94
Ningaloo Sth	Insufficient data		9.18	64.65
Ningaloo Nth	Insufficient data		10.86	66.60
Scott Reef	Insufficient data		9.53	67.14
Pacific Basin				
Port Stephens	Insufficient data		10.95	89.76
One Tree Island Outer Reef	6.11	46.99	9.07	69.75
One Tree Island Lagoon	6.58	38.28	7.98	46.37
Palm Group	8.65	47.04	11.86	64.46
Outer Reef	5.49	43.24	9.40	74.00
Lizard Is	5.76	34.69	10.64	64.12
Solomon Is	2.91	23.82	8.08	66.22
PNG	Insufficient data		5.95	57.23
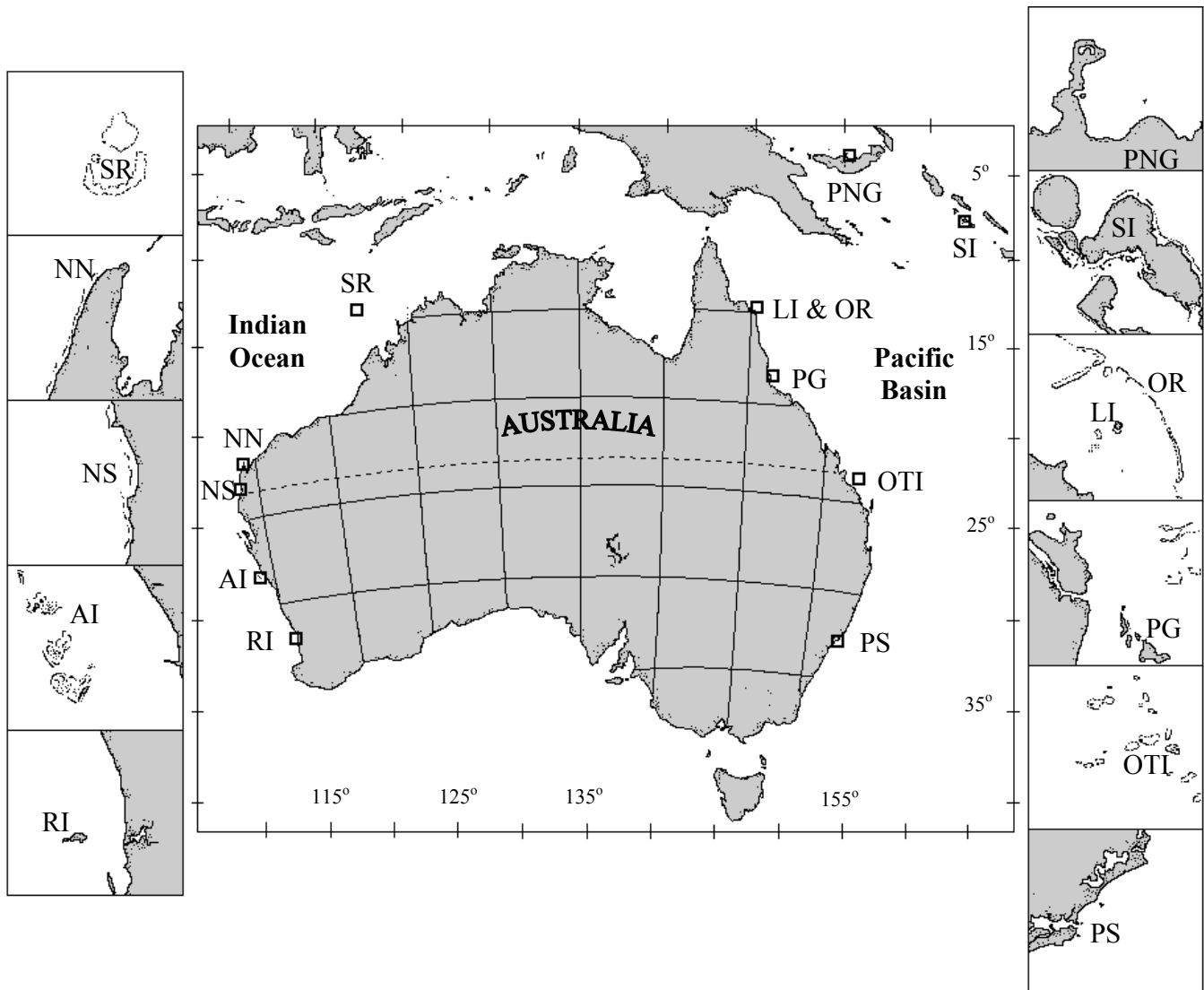
Figure 4.1: Sites of sampling regions within the Pacific Basin and Indian Ocean. SR = Scott Reef; NN = Ningaloo North; NS = Ningaloo South; AI = Abrolhos Islands; RI = Rottnest Island; PNG = Papua New Guinea; SI = Solomon Islands; LI = Lizard Island; OR = Outer Reef; PG = Palm Group; OTI = One Tree Island; PS = Port Stephens. Insets represent approximately 1° of latitude and longitude.
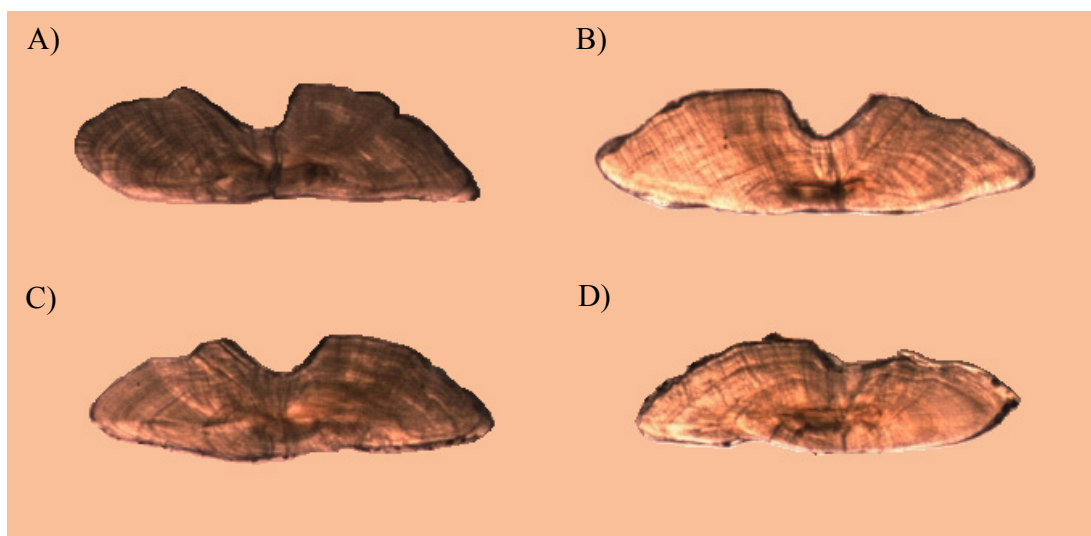
Figure 4.2: Sectioned sagittae of adult *T. lunare* from sampling sites in the West Pacific Basin. Represented sites range in latitude and habitat. A) PNG (5°S) 97 mm SL, 2 years of age; B) Outer Reef (14°S) 107 mm SL, 4 years of age; C) Palm Group (19°S) 93 mm SL, 3 years of age; D) Port Stephens (32°S) 110 mm SL, 3 years of age.
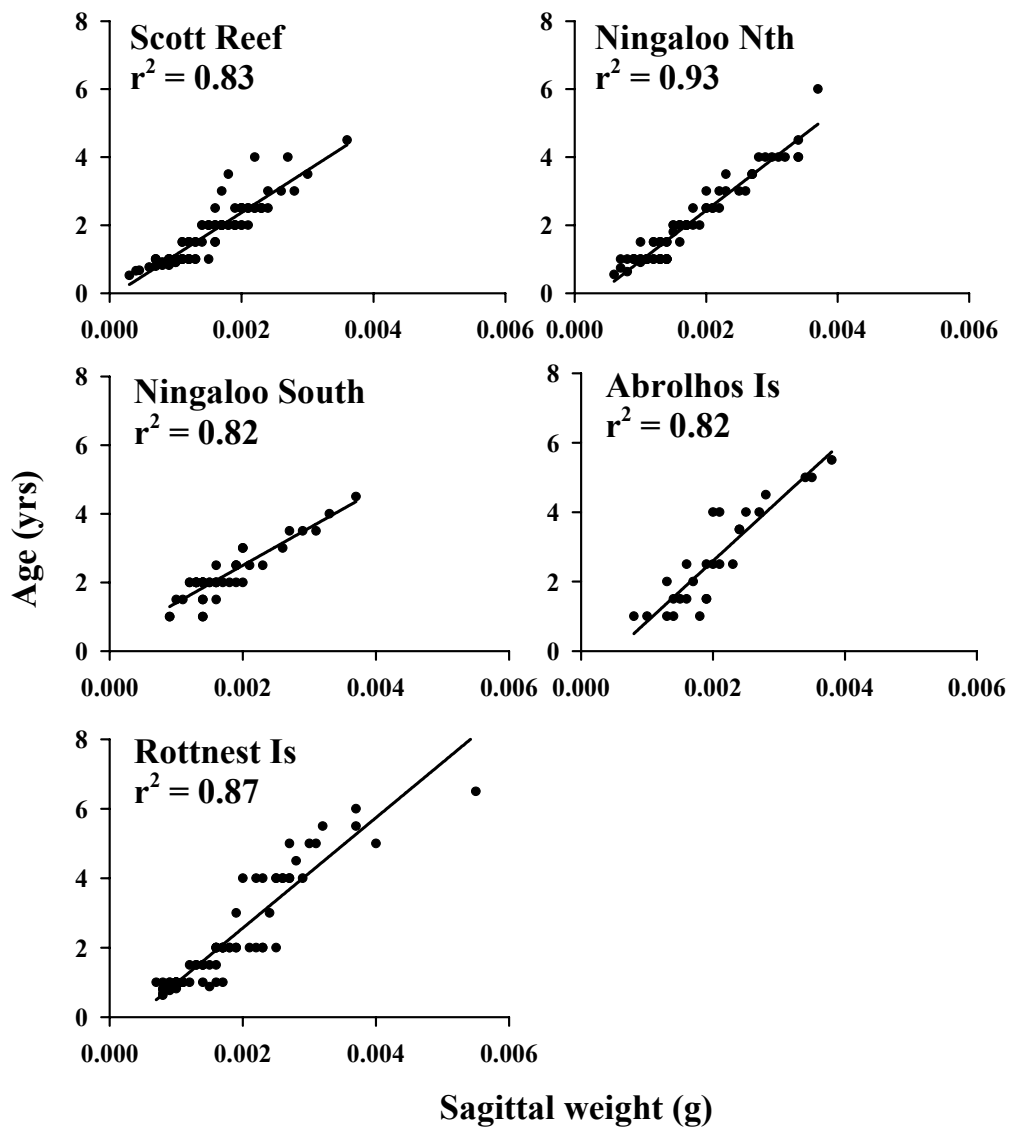
Figure 4.3: Linear relationships of sagittal increments (age in years) on sagittal weights (grams) of 5 *T. lunare* populations sampled from along the west coast of Australia. Scott Reef: y = 1244.78x – 0.12, n = 92; Ningaloo North: y = 1490.32x – 0.54, n = 77; Ningaloo South: y = 1091.85x + 0.31, n = 47; Abrolhos Islands: y = 1744.15x – 0.89, n = 27; Rottnest Island: y = 1588.41x – 0.61, n = 79.
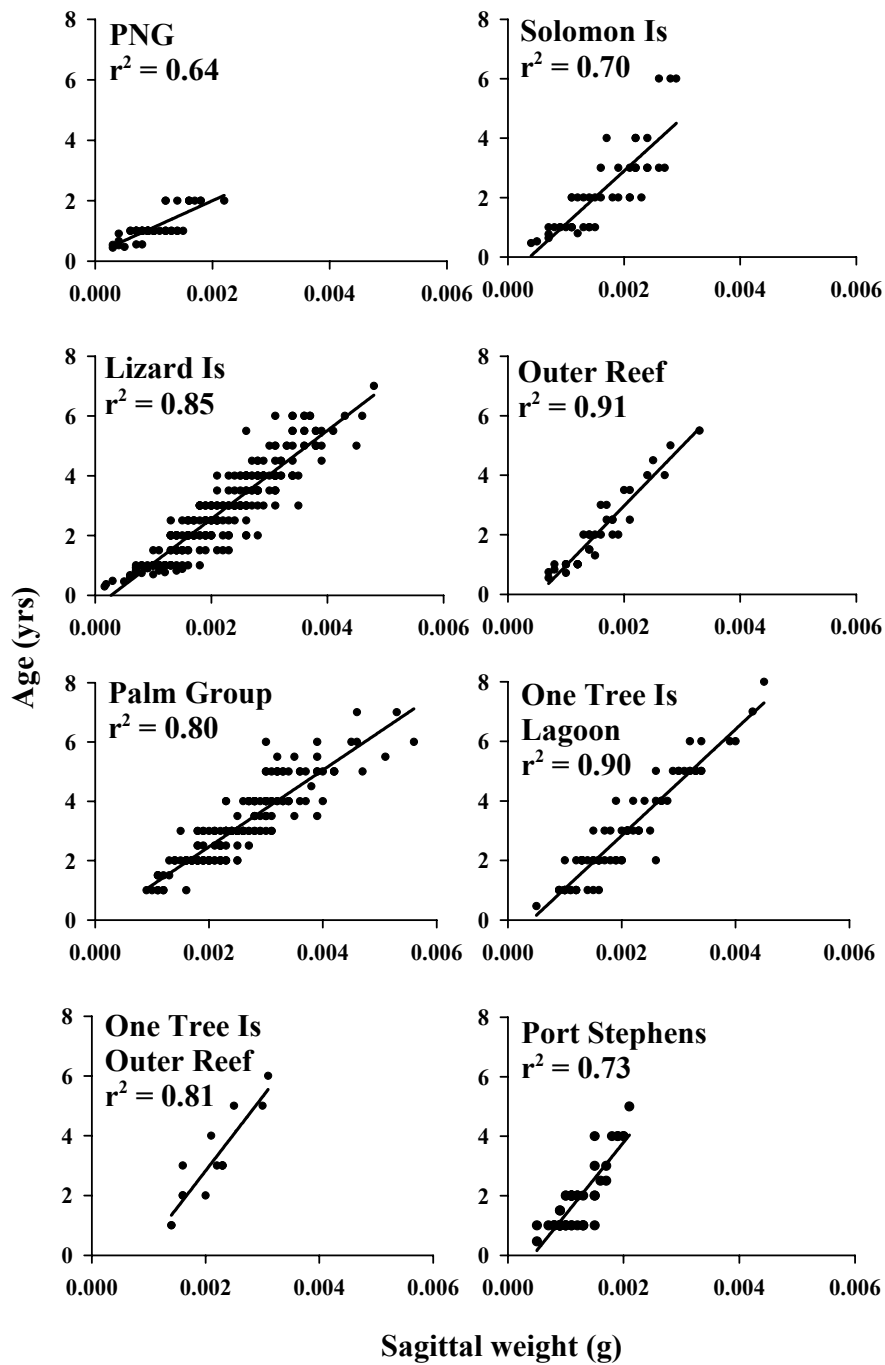
Figure 4.4: Linear relationships of sagittal increments (age in years) on sagittal weights (grams) of 8 *T. lunare* populations sampled from within the Pacific Basin. PNG: y = 878.49x + 0.24, n = 53; Solomon Islands: y = 1782.40x – 0.67, n = 46; Lizard Island: y = 1480.43x – 0.41, n = 283; Outer Reef: y = 2009.15x – 1.05, n = 37; Palm Group: y = 1292.22x – 0.12, n = 182; One Tree Island Lagoon: y = 1784.11x – 0.73, n = 80; One Tree Island Outer Reef: y = 2473.96x – 2.12, n = 14; Port Stephens: y = 2424.32x – 1.05, n = 51.
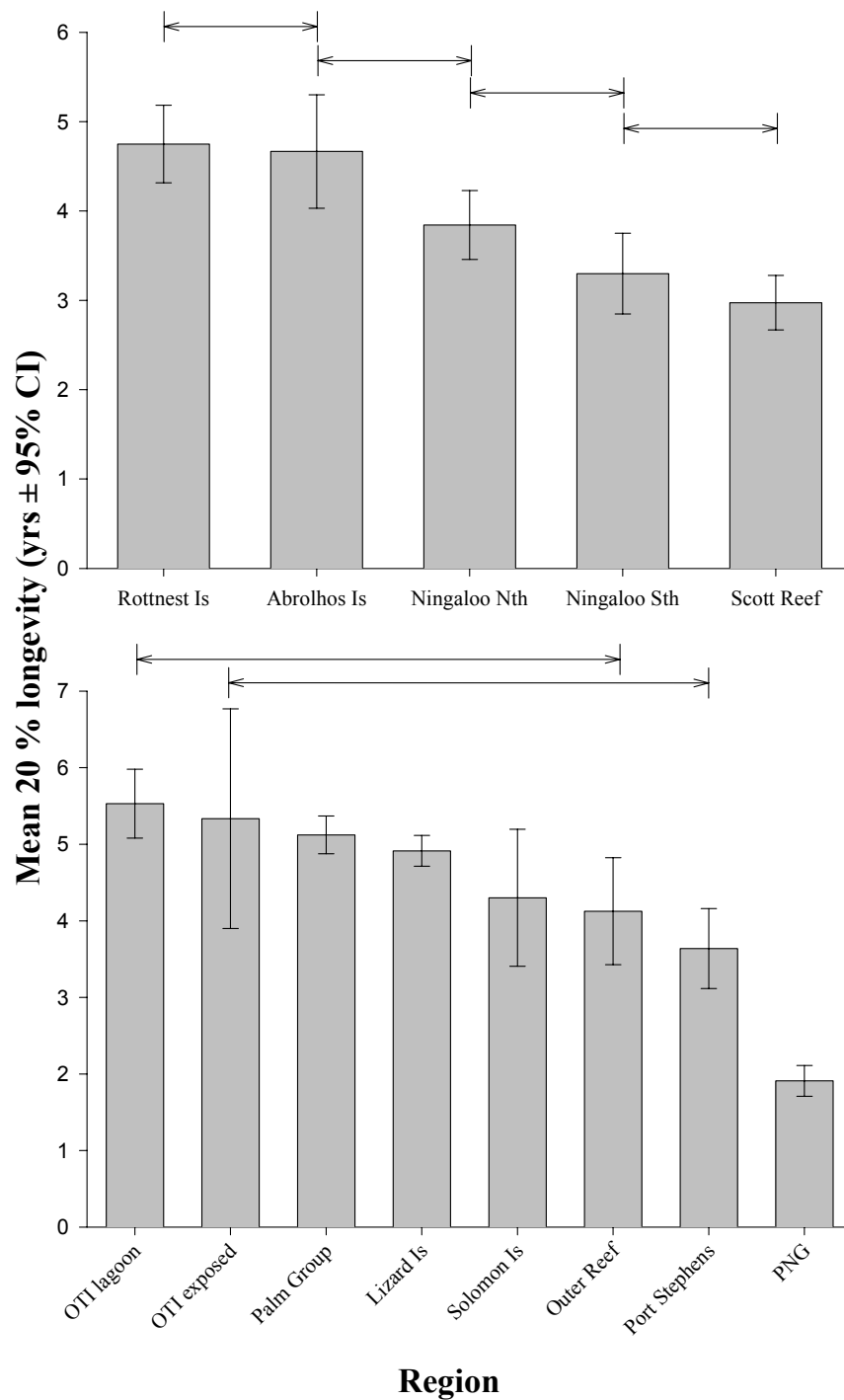
Figure 4.5: Mean *T. lunare* longevity (± 95% CI) based upon the oldest 20 % of individuals sampled within each region in the A) Indian Ocean, and B) Pacific Basin. Continuous arrows above locations indicate non-significant differences between means following the results of the multiple comparison Dunnett *C* test. ANOVA results in text.
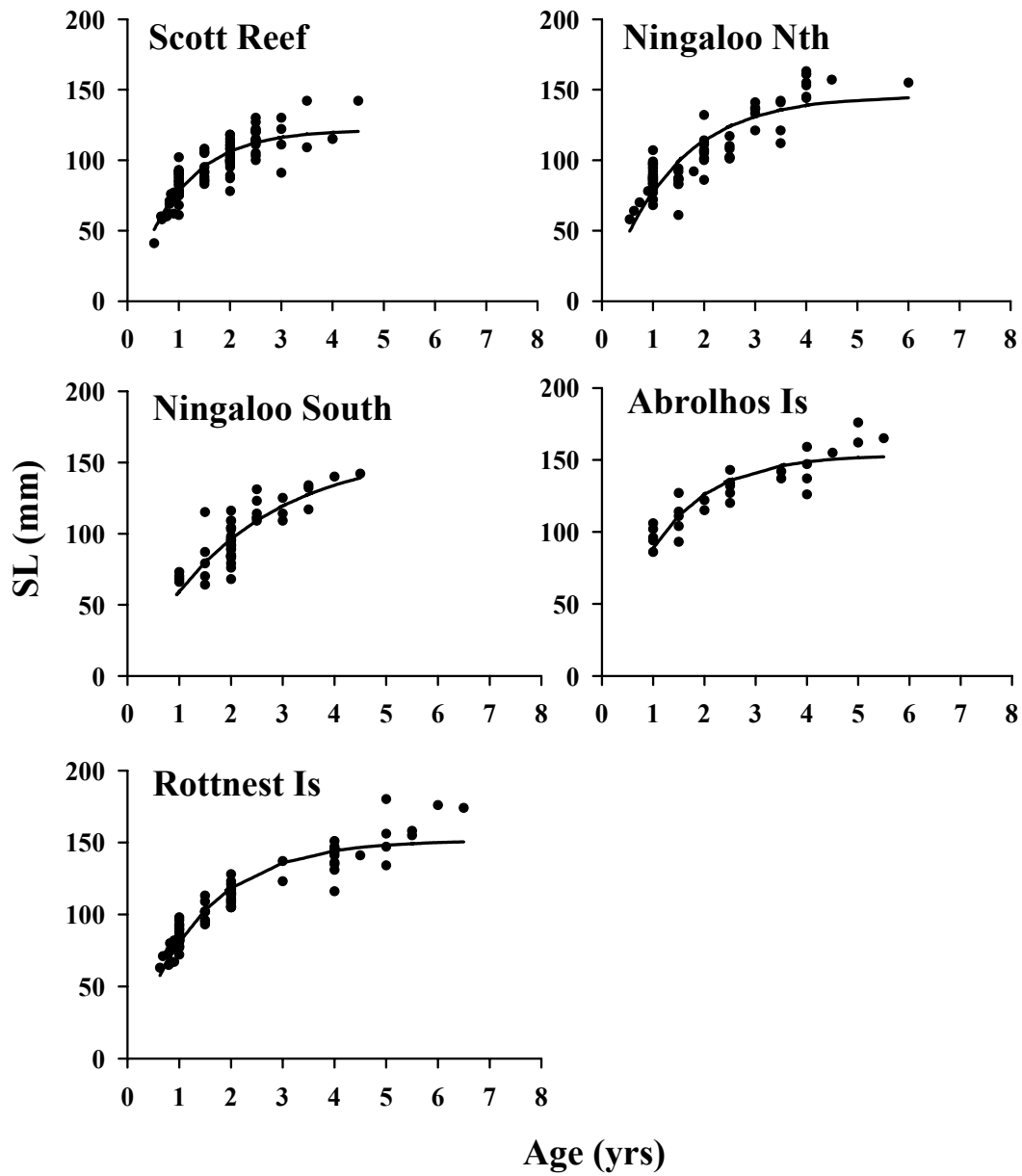
Figure 4.6: Size at age plots with constrained VBGF at 5 localities along the west coast of Australia. VBGF parameters as in Table 4.1.
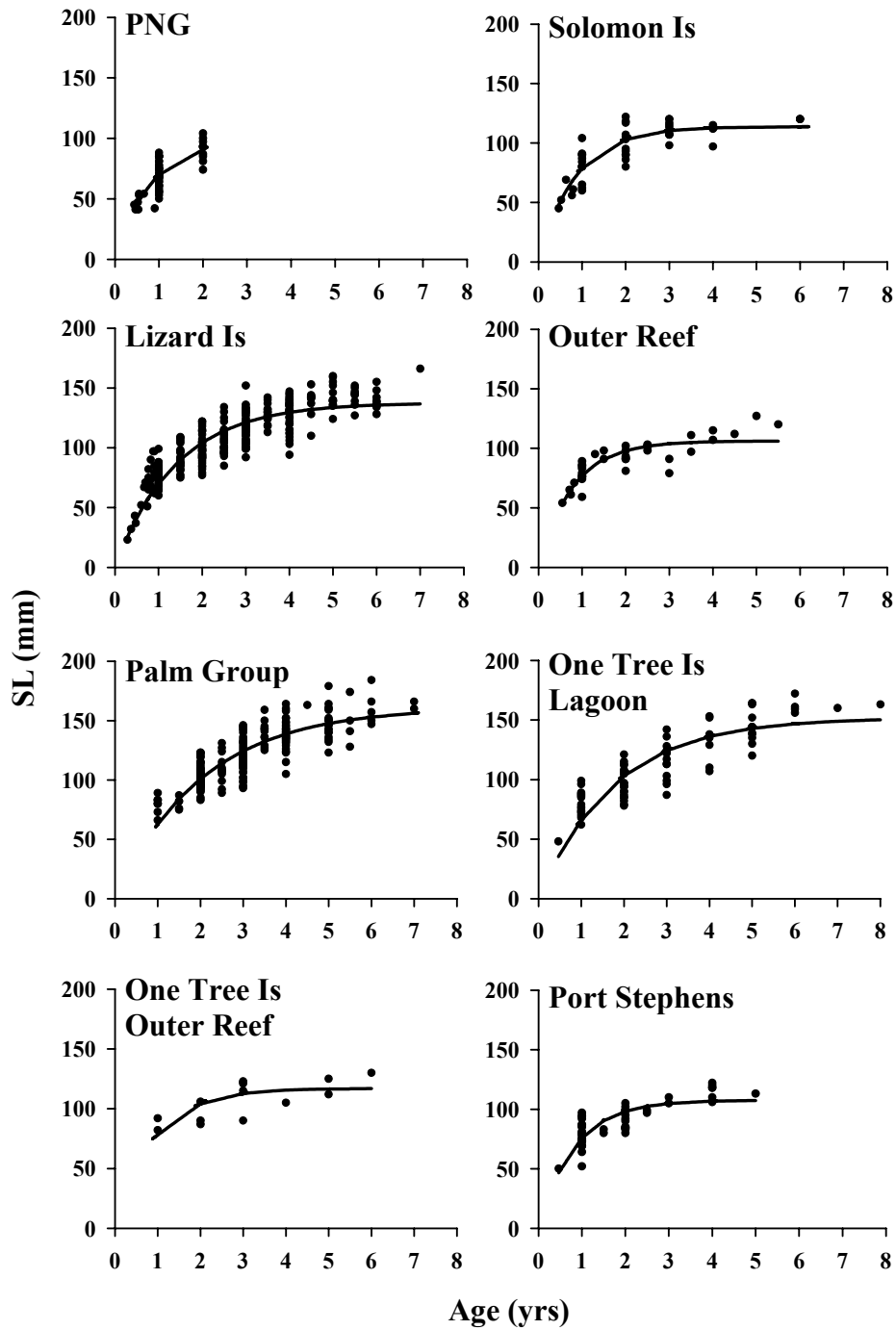
Figure 4.7: Size at age plots with constrained VBGF at 8 localities within the Pacific Basin. VBGF parameters as in Table 4.1.
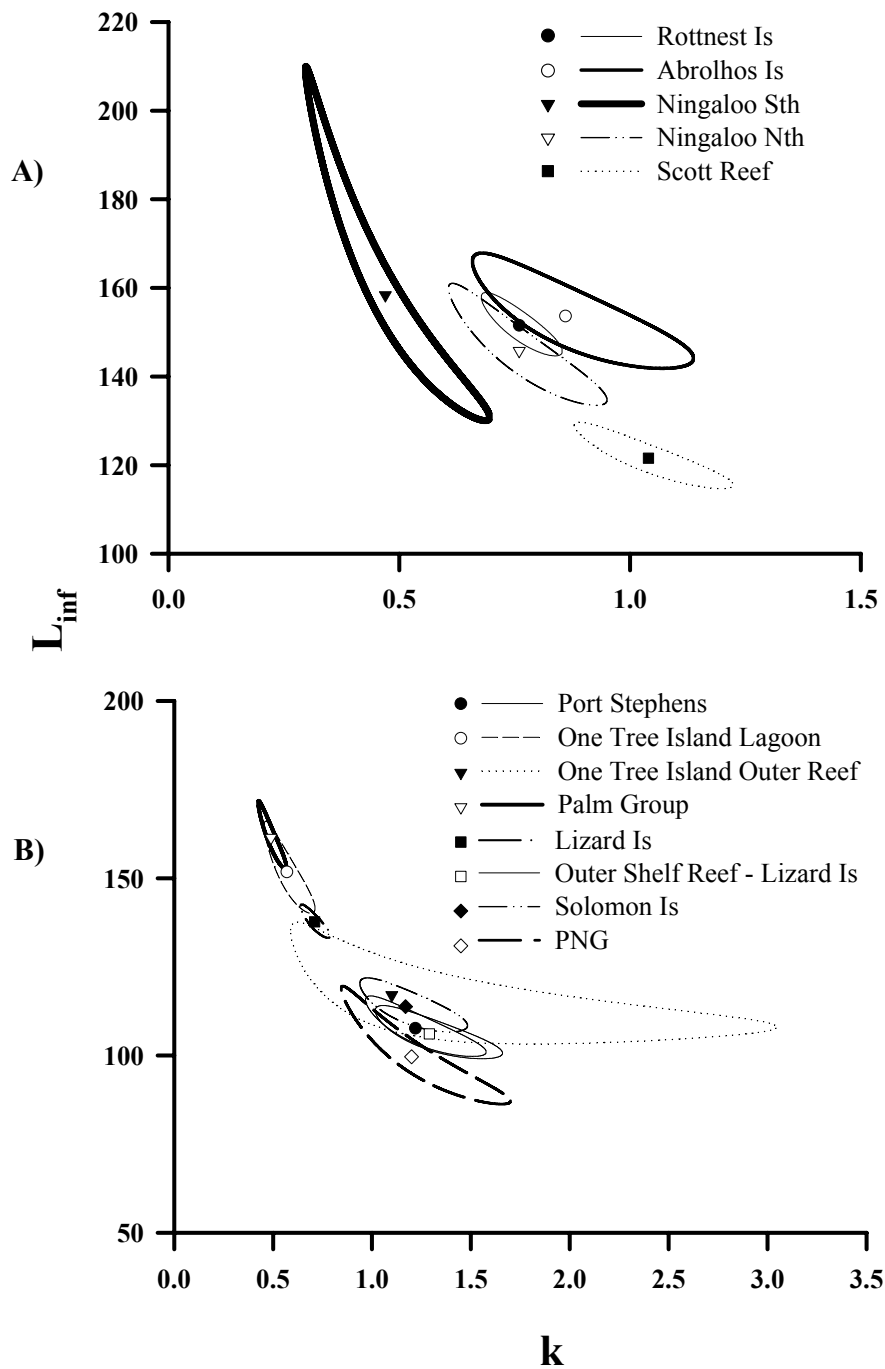
Figure 4.8: Comparison of VBGF parameters for regional populations of *T. lunare* in the A) Indian Ocean and the B) Pacific Basin showing 95 % confidence regions around least square estimates of *k* and L_∞. Symbols represent parameter estimates; lines represent 95 % confidence regions.
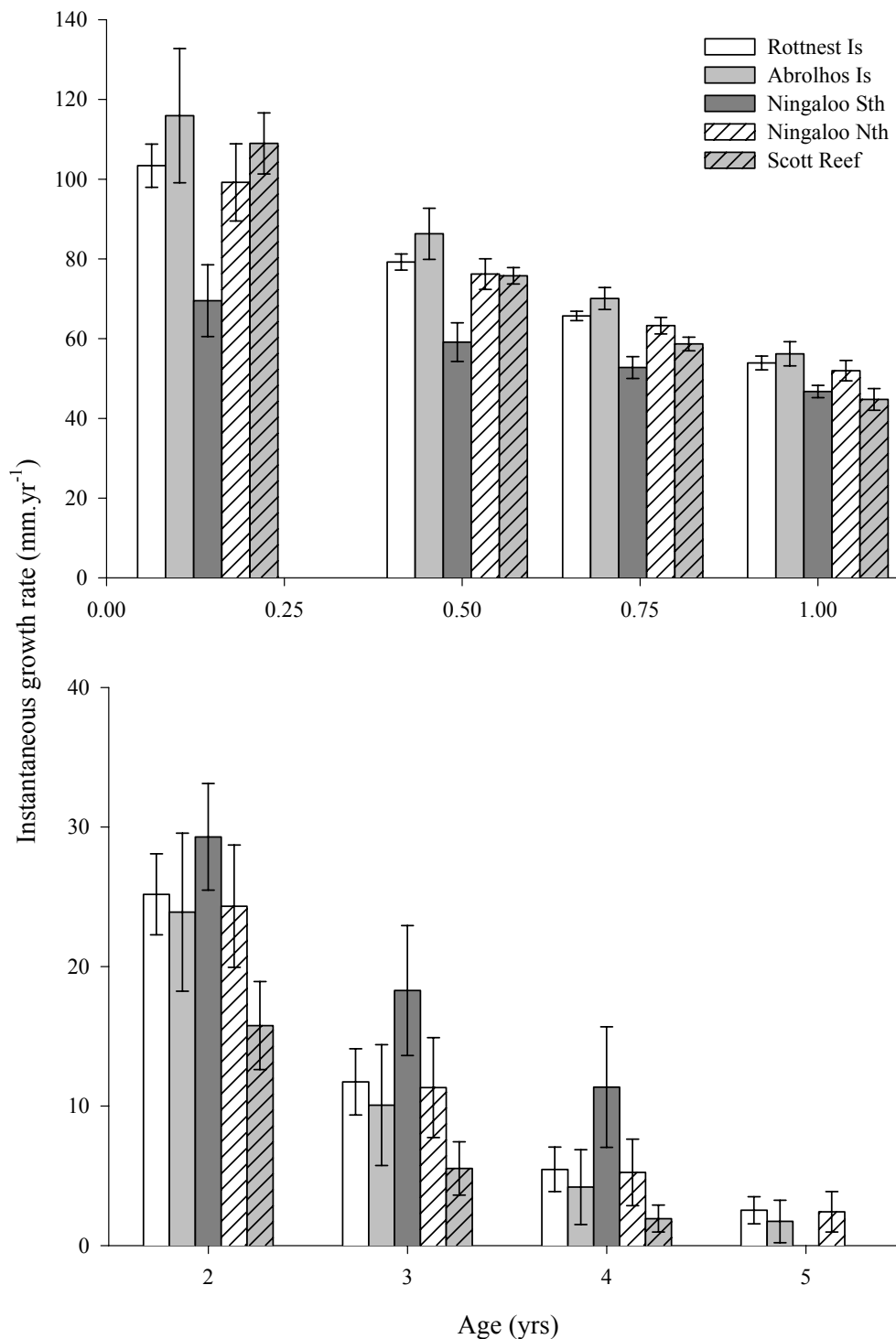
Figure 4.9: Bias adjusted instantaneous growth rates at the 5 regional locations in the Indian Ocean, based upon bootstrapped estimates and the predicted VBGF for each region. Growth rates shown at settlement (based upon Wilson & McCormick, 1999), sub yearly and at yearly increments. Confidence intervals calculated upon standard bootstrap methods using 1.96*SD of the iterations (Manly 1997).
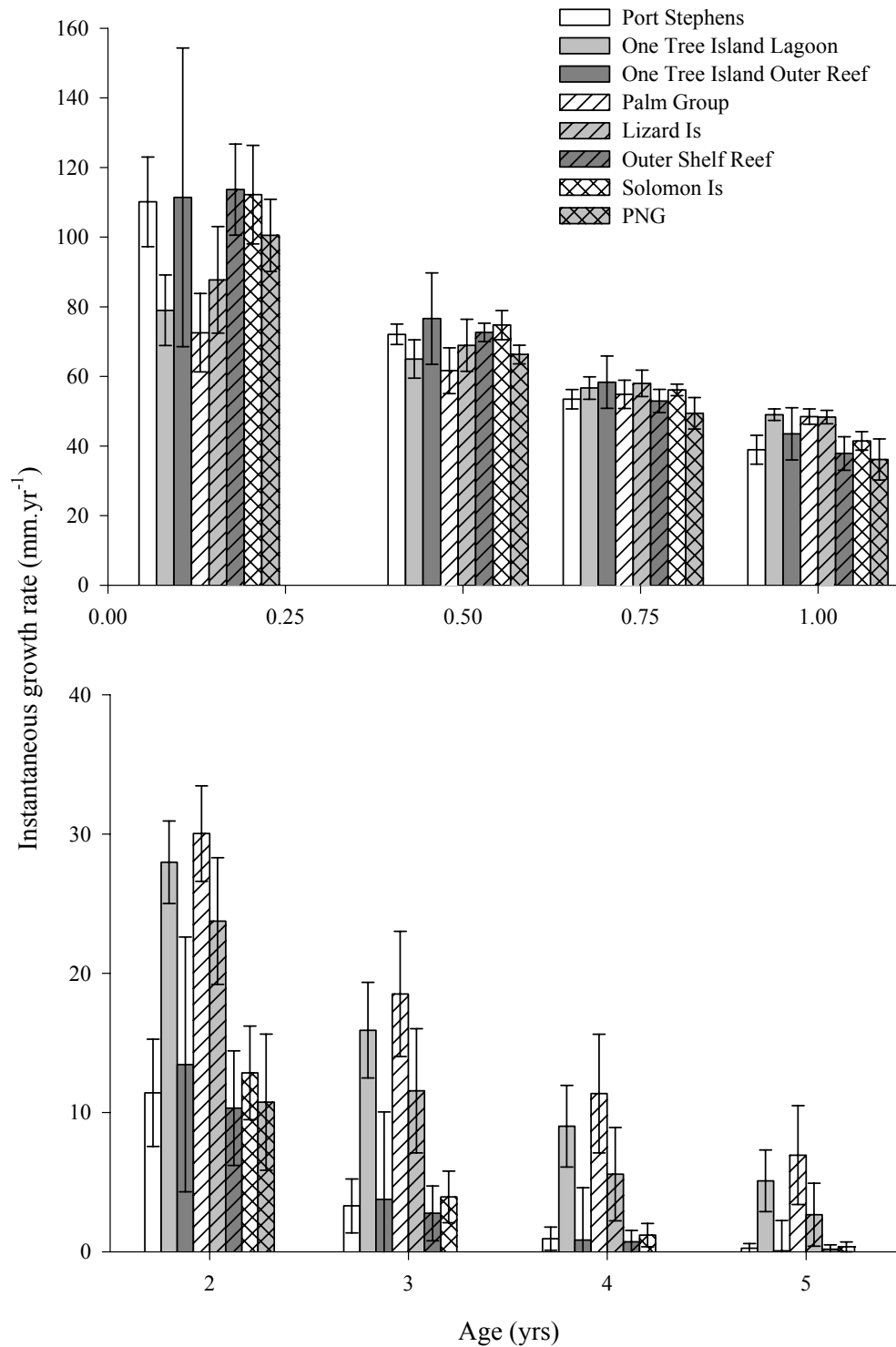
Figure 4.10: Bias adjusted instantaneous growth rates at the 8 regional locations in the Pacific Basin, based upon bootstrapped estimates and the predicted VBGF for each region. Growth rates shown at settlement (based upon Wilson & McCormick, 1999), sub yearly and at yearly increments. Confidence intervals calculated upon standard bootstrap methods using 1.96*SD (Manly 1997).
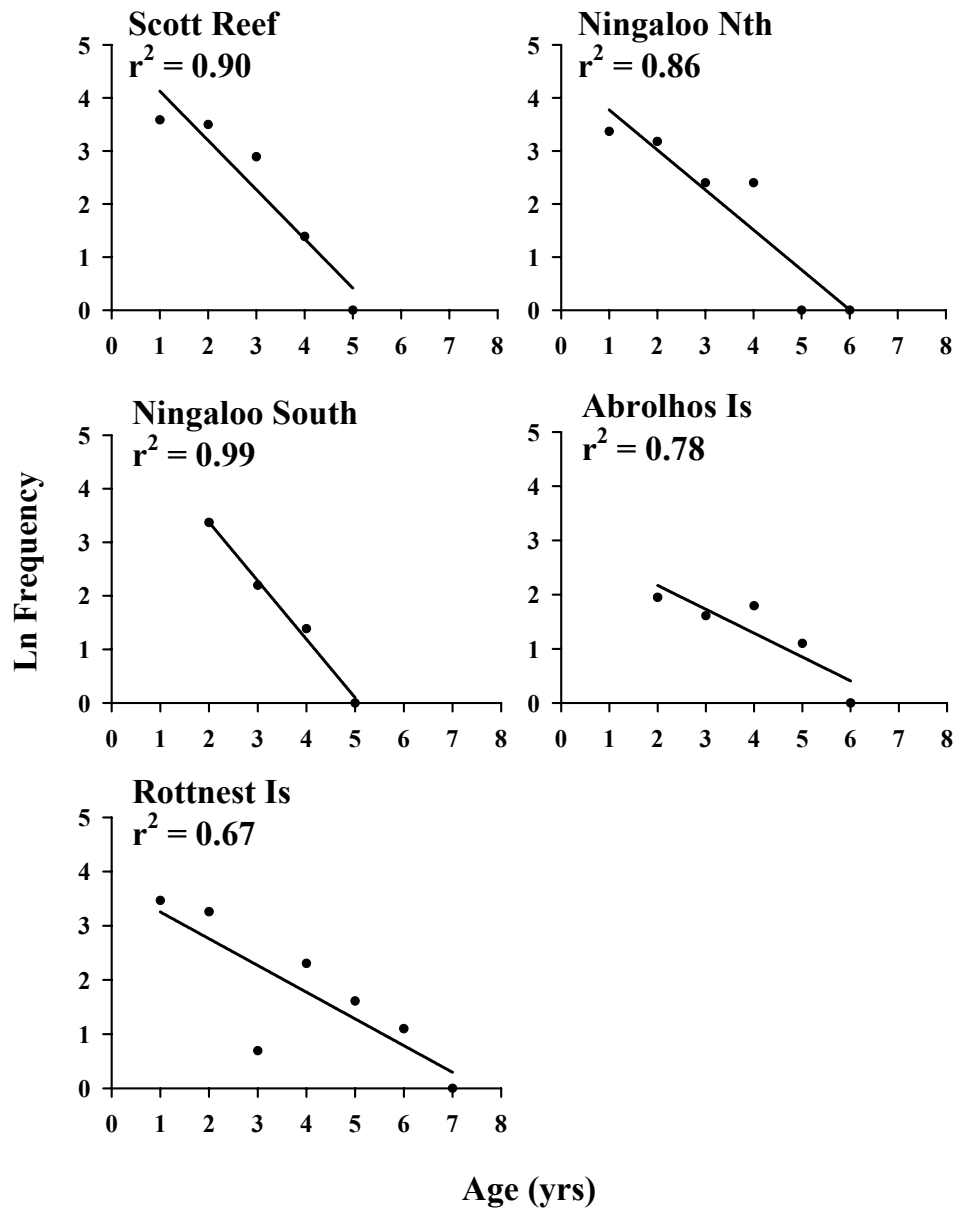
Figure 4.11: Estimates of mortality from catch curves at 5 locations in the Indian Ocean. Scott Reef: y = -0.93x + 5.05; Ningaloo North: y = -0.75x + 4.53; Ningaloo South: y = -1.09x + 5.56; Abrolhos Islands: y = -0.44x + 3.05; Rottnest Island: y = -0.49x + 3.75. Mortality and survivability estimates recorded in Table 4.1. ANCOVA analysis of regression slopes shown in Table 4.2.
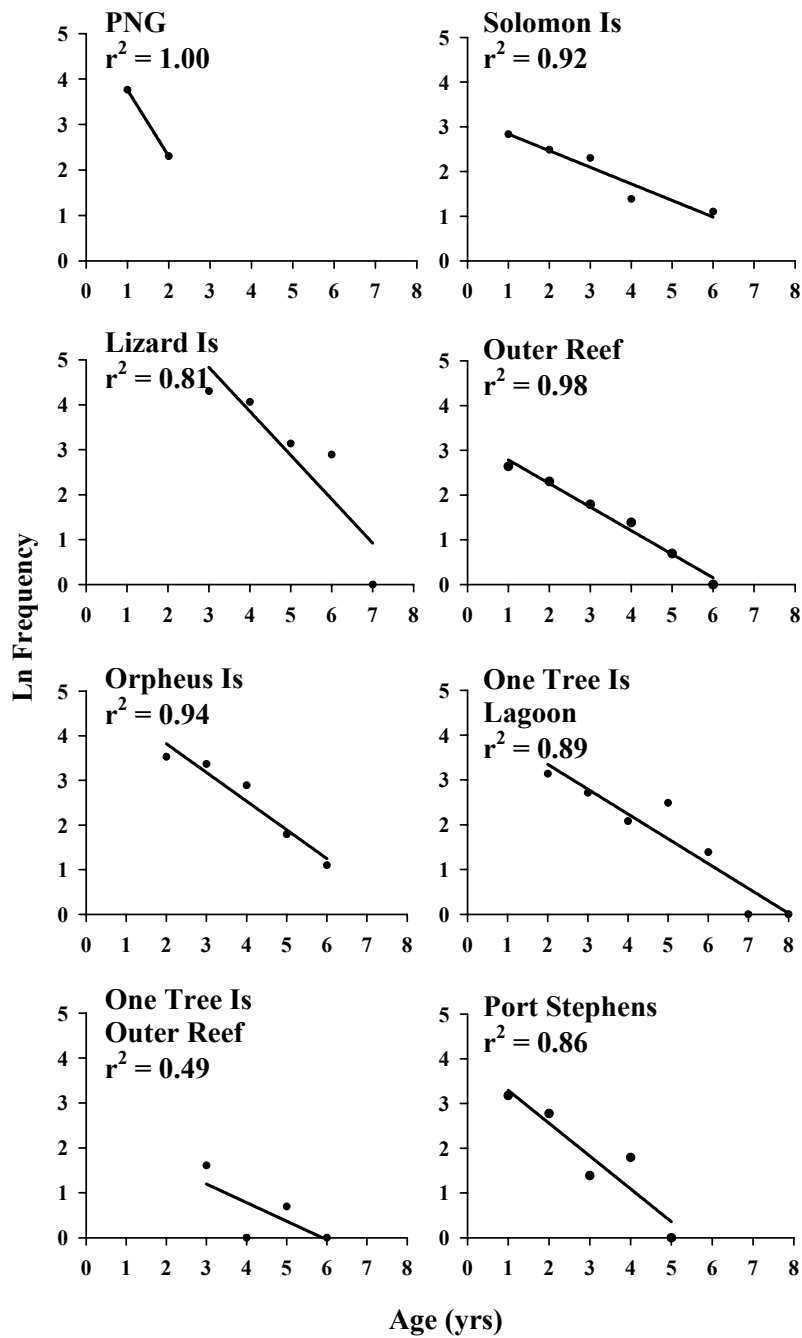
Figure 4.12: Estimates of mortality from catch curves at 8 locations within the Pacific Basin. PNG: y = -1.46x + 5.22; Solomon Islands: y = -0.37x + 3.21; Lizard Island: y = -0.98x + 7.77; Outer Reef: y = -0.53x + 3.31; Palm Group: y = -0.64x + 5.11; One Tree Island Lagoon: y = -0.55x + 4.46; One Tree Island Outer Reef: y = -0.41x + 2.44; Port Stephens: y = -0.73x + 4.03. Mortality and survivability estimates recorded in Table 4.1. ANCOVA analysis of regression slopes shown in Table 4.2.
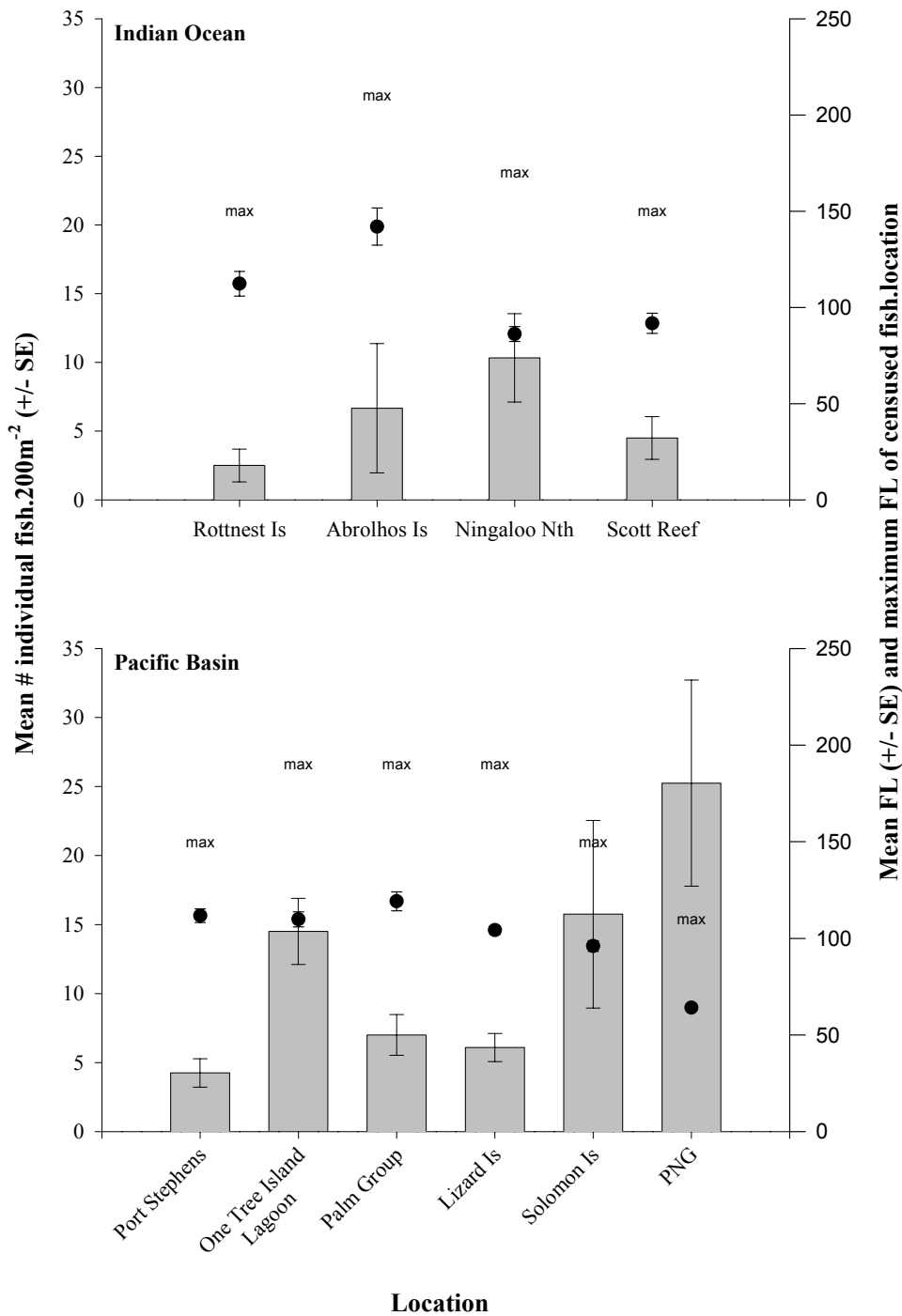
Figure 4.13: Estimates of mean abundance (± SE), mean size (FL ± SE) and maximum size (FL) of *T. lunare* obtained from repeated visual belt transect counts (50 x 4m) made prior to the collections at various sampling localities in the Indian Ocean and the Pacific Basin. Bars represent mean abundance, filled circles represent mean size and max represents the maximum size observed.
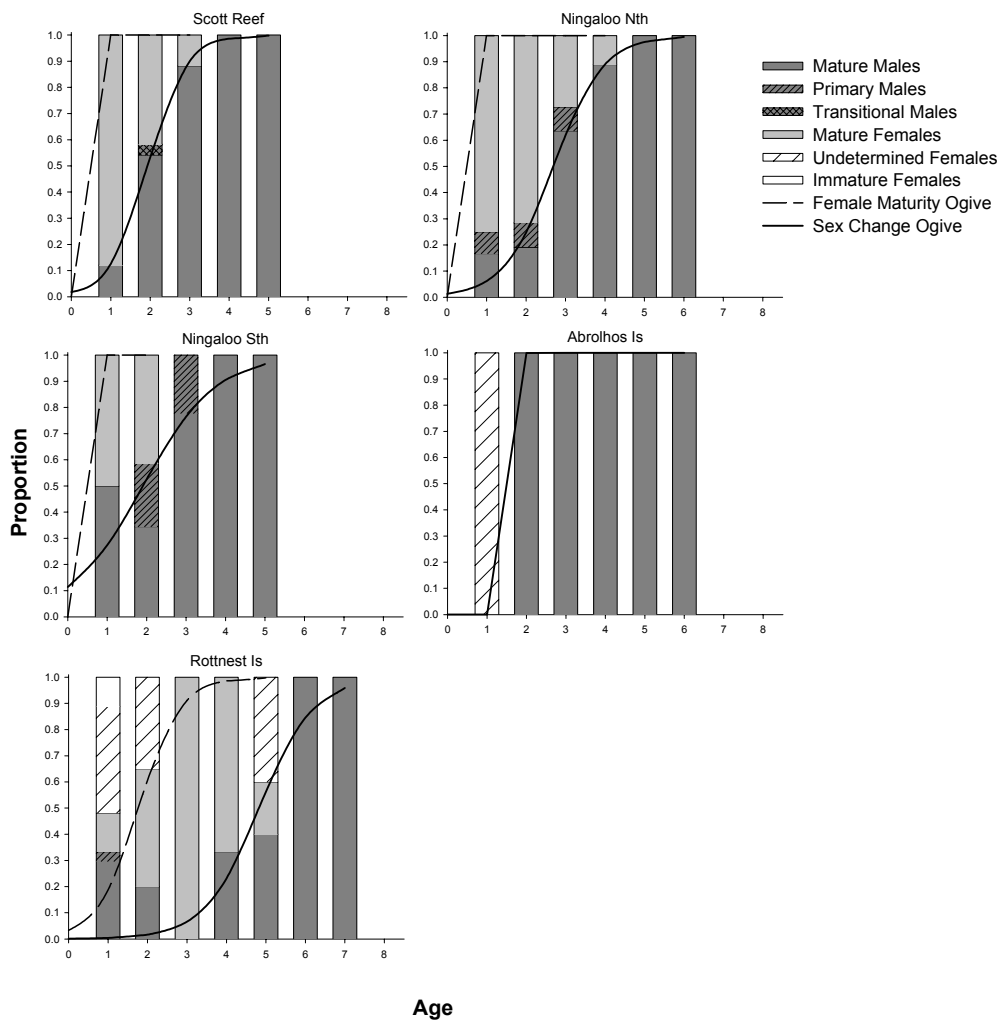
Figure 4.14: Frequency distribution of the sex specific age structure at each region sampled within the Indian Ocean. Dashed line represents the female maturity ogive, calculated from the proportion of mature females observed within each age class compared with all females in that age class. Solid line represents the sex change ogive, calculated from the proportion of terminal phase males observed within each age class compared with all individuals found within that age class.
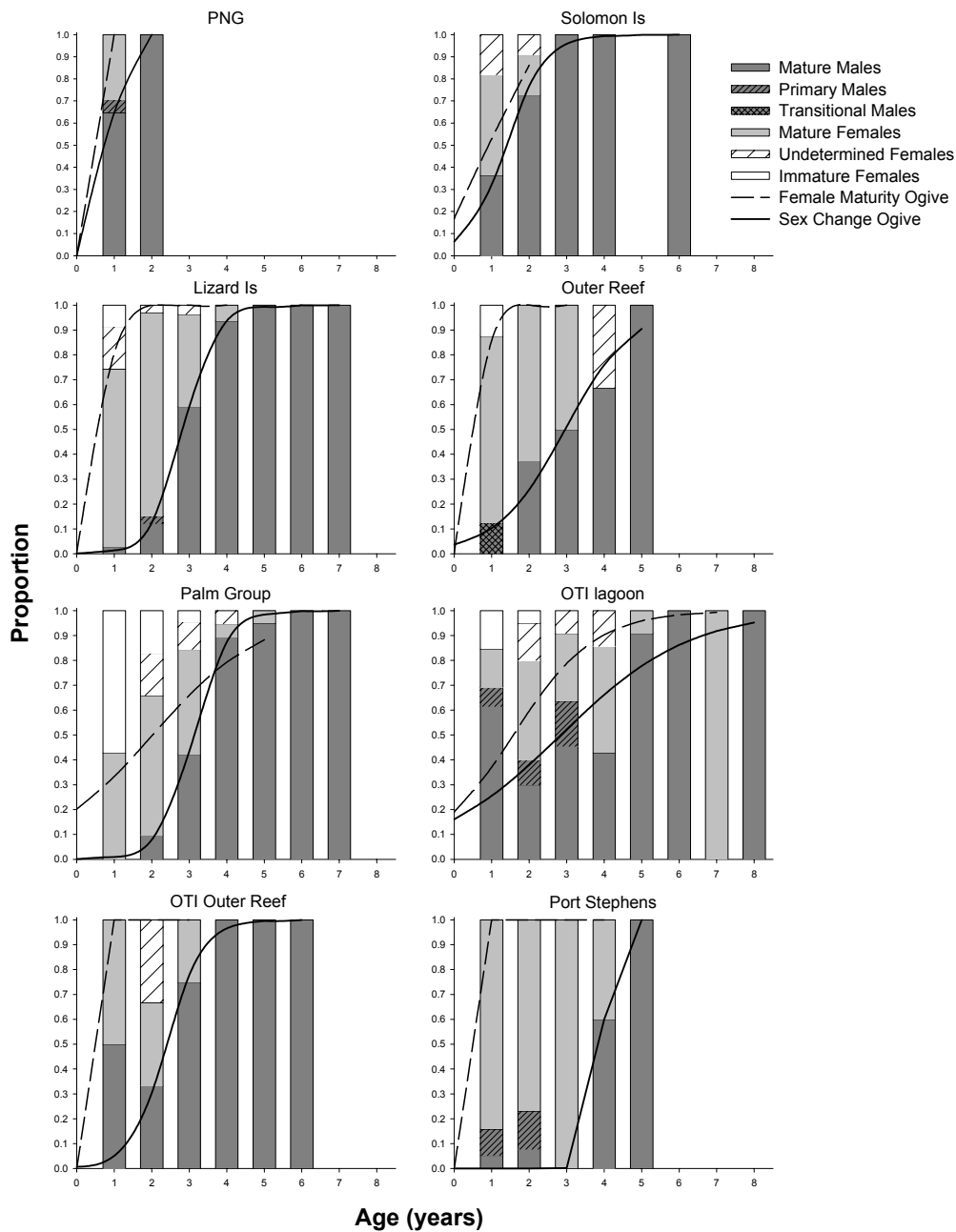
Figure 4.15: Frequency distribution of the sex specific age structure at each region sampled within the Pacific Basin. Dashed line represents the female maturity ogive, calculated from the proportion of mature females observed within each age class compared with all females in that age class. Solid line represents the sex change ogive, calculated from the proportion of terminal phase males observed within each age class compared with all individuals found within that age class.
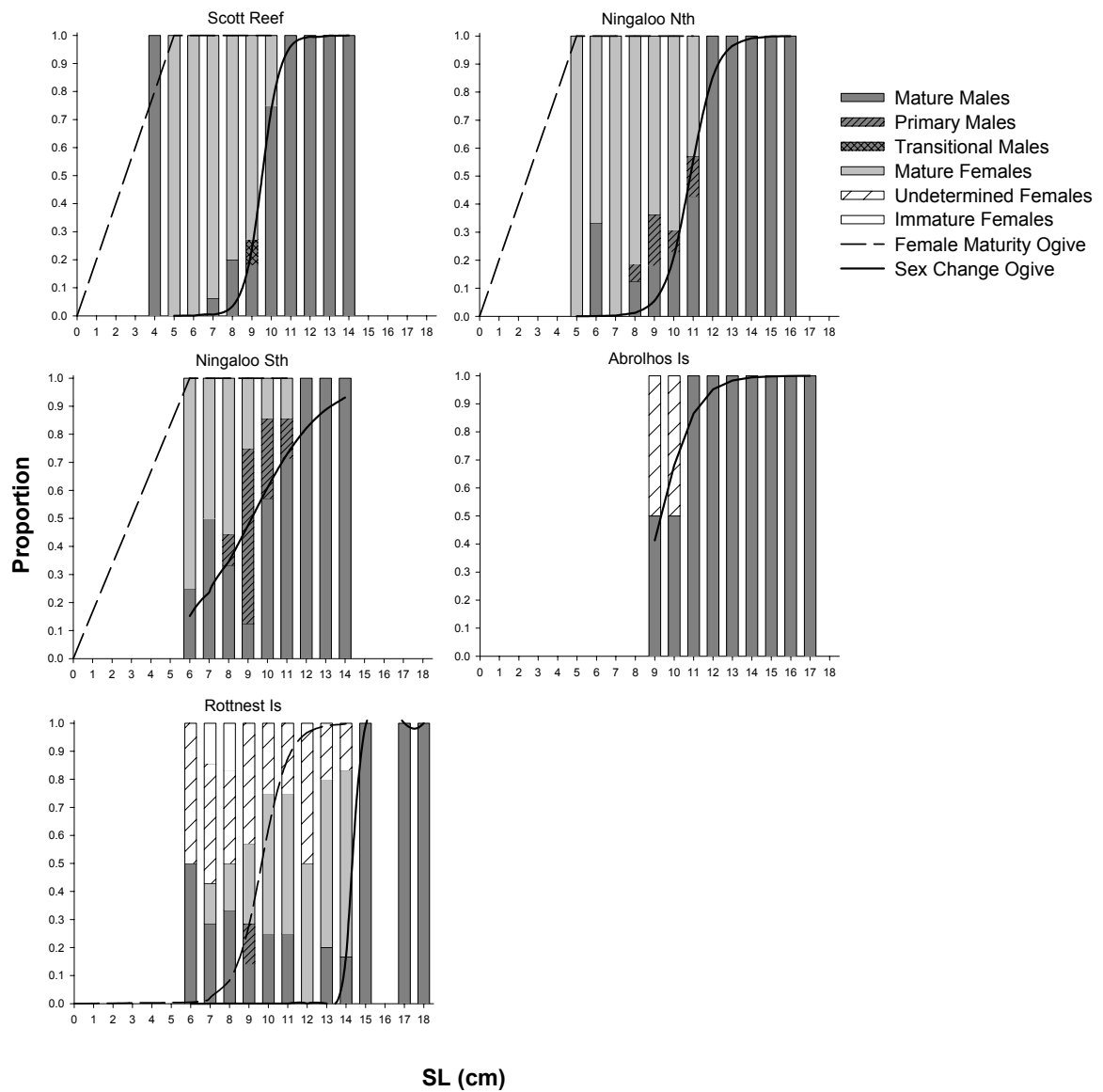
Figure 4.16: Frequency distribution of the sex specific size structure at each region sampled within the Indian Ocean. Dashed line represents the female maturity ogive, calculated from the proportion of mature females observed within each size class compared with all females in that size class. Solid line represents the sex change ogive, calculated from the proportion of terminal phase males observed within each size class compared with all individuals found within that size class.
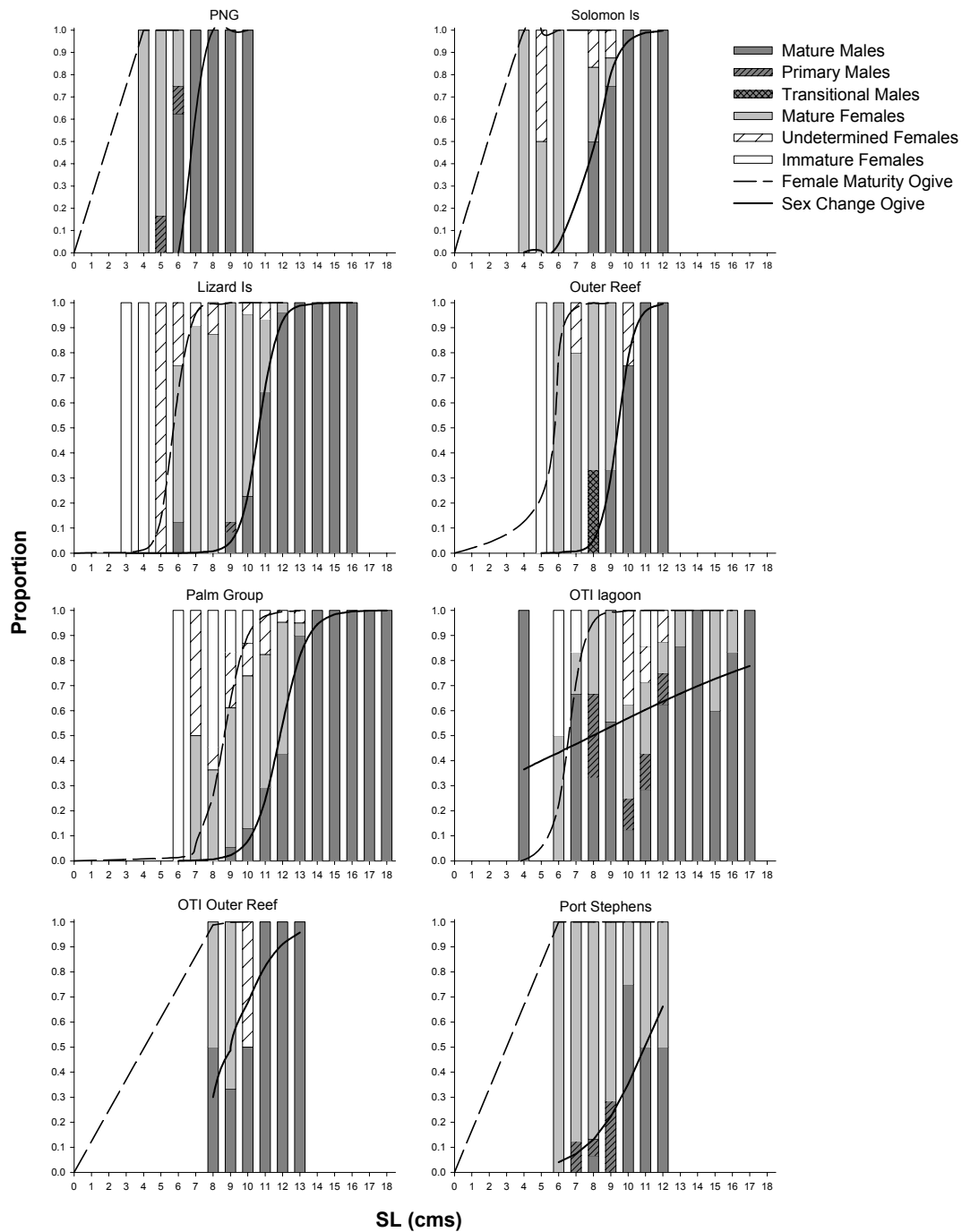
Figure 4.17: Frequency distribution of the sex specific size structure at each region sampled within the Pacific Basin. Dashed line represents the female maturity ogive, calculated from the proportion of mature females observed within each size class compared with all females in that size class. Solid line represents the sex change ogive, calculated from the proportion of terminal phase males observed within each size class compared with all individuals found within that size class.

CHAPTER 5. VARIATION IN THE AGE-BASED DEMOGRAPHY OF *THALASSOMA LUNARE* I. HABITAT VARIATION WITHIN 3 SPATIALLY SEPARATED REGIONS.

5.1. Introduction:

At the habitat level, numerous studies have focused upon community structure (Roberts & Ormond, 1987; Green 1996; Munday et al. 1997) or juvenile growth rates (Pitcher 1992, Sogard 1992), however, little work has been done on small-scale habitat differences in the age-based demographics of adults (but see Pitcher 1992 & Stunz et al. 2002). Yet, habitat differences can have a profound effect upon an organism's life history. In general, these stem from the availability of nutritional resources (Paperno et al. 2000; Schafer et al. 2002) and protection from predation (Beukers & Jones 1997). Furthermore, interactions between these can have an additional influence. For example, habitats with increased food availability can mediate a decrease in foraging behaviour and therefore minimise the risk to predation (Biro et al. 2003). Life history variables directly affected by these factors include, amongst others, body size (Choat et al. 2003), growth (Munday, 2001), longevity (Gust et al. 2002) and survivorship (Beukers & Jones, 1997). Furthermore, habitat structure can influence the abundance and composition of individuals and species (Jenkins & Wheatley, 1998; Syms & Jones, 2000, Robertson & Winemiller, 2003). In their examination of labrid distribution, Bellwood & Wainwright (2001) reported that whilst differences were evident across the continental shelf, within reef habitat differences caused the greatest source of variation. Furthermore, during 1997/1998 it was reported that increased sea surface temperatures, and subsequent widespread coral bleaching, altered reef fish communities (Lindahl et al. 2001; Booth & Beretta, 2002). An alteration in community structure (Reznick & Endler 1982, Reznick et al. 1996) or population density, in turn, can alter life history profiles of populations (Jones 1991, Booth 1995, Kritzer 2002), further complicating the examination of life history variables. Therefore, the habitat that an organism lives in can either directly or indirectly affect the way in which it grows, reproduces and survives. Coral reef habitats are no exception.

Coral reef habitats can vary depending on current strength and direction (Thresher 1983, Wolanski & Deleersnijder 1998, Harlan et al. 2002), substrate complexity (Luckhurst & Luckhurst, 1978), food availability (Crossman et al. 2001),

predation (Kingsford 1992, Connell & Kingsford 1998), turbidity (Fabricius & De'ath 2001) and wind and/or wave exposure (Choat & Bellwood 1985, Fulton & Bellwood 2004). Each of these factors, or their interactions, can affect the way a fish inhabits the area (Bellwood & Wainwright 2001, Eagle et al. 2001, Fulton & Bellwood 2004). More mobile species, of course, have the ability to move into more suitable habitats and therefore they may not exhibit life histories attributable to small-scale habitat differences (Williams et al. 2003). However, this can be up to several kilometres away and therefore more site-specific species are likely to be affected. Individuals that settle into substandard habitat will find it difficult to reach maximum potential, however optimal strategies are likely through trade-offs between various life history traits (Kozlowski 1992). This may be smaller final body size, but earlier maturity and increased generation times, possibly caused by limited resources (Blanckenhorn 1998) or delayed maturity but increased body size and fecundity (Roff 1984, Stearns & Koella 1986), caused by predatory avoidance (Rodd & Reznick, 1997).

Age-based life histories of *T. lunare* populations over large regional scales in two oceanic basins exhibited variation in accordance with exposure differences across the continental shelf that were often in excess of the variation found over 1,000's of kilometres (Chapter 4). Additionally, age-based demographics have been shown to vary between reefs separated by no more than 30 km (Gust et al. 2002, Kritzer 2002). Gust et al. (2002) specifically examined cross-shelf differences, where outer shelf reefs returned higher recruitment rates, smaller mean adult body sizes, faster initial growth rates and reduced longevities than mid shelf reefs. If habitat differences less than 30km apart can have marked differences in age-based demographics then what is the minimum spatial scale that reef fish exhibit variable age-based traits. Whilst Gust et al. (2002) inspected within reef variation the sites examined were of similar exposure. Exposure differences within reefs, such as windward, leeward or lagoonal habitats may also drive differences in life history profiles. This is unlikely a concern for those species that move between reefs (Williams et al. 2003). However, for those species that are relatively site attached, yet recruit to significantly different habitats, these differences could significantly affect life history traits. Pitcher (1992) examined juvenile growth rates between a leeward and windward habitat within one reef, highlighting that the former habitat produced faster growing individuals compared with the latter. However, how this translates into adult size and age is unknown. It is

therefore important to determine how habitat differences drive variation in age-based demographics following cross continental shelf variation, which is potentially greater than that found on large regional scales.

Some general expectations can be made based upon the results of a large geographic study using *Thalassoma lunare* (Chapter 4) and Gust et al. (2002), being a gradient of increasing size, and longevity and decreasing mortality from exposed habitats through sheltered to lagoonal habitats. Exposed habitats often have higher wave exposure, greater number of predators, limited food resources (Crossman et al. 2001) and potentially less structure than protected, sheltered habitats. Differences between lagoonal and sheltered habitats are a little more difficult to predict. However, increased turbidity levels in the lagoon, compared with the sheltered habitats, may offer individuals greater shelter from predation. Furthermore, lagoonal habitats are often protected from any form of wave exposure. In contrast, although infrequent, sheltered habitats may still be subjected to wind and wave patterns, creating conditions similar to exposed habitats.

Following the results of a larger study looking at life history variation in *Thalassoma lunare* (Chapter 4), further work was necessary to determine the extent that habitat variation had on age-based parameters at small spatial scales within geographic regions. *Thalassoma lunare* is found throughout inshore, midshelf and outer shelf reefs on the Great Barrier Reef, and exposed, sheltered and lagoonal sites throughout its range. It is unlikely to move substantial distances and therefore it is an ideal study organism to look at small-scale habitat effects within larger regional scales. The objective of this study therefore was to examine age-based parameters of *T. lunare* populations between variable habitats across geographically distinct regions. Comparisons of populations located in a combination of exposed, sheltered or lagoonal habitats were examined at three geographically separate locations. Following age-based demographic differences found in *T. lunare* populations across exposure gradients, the following expectations were predicted:

1)   Longevity would increase from exposed through sheltered to lagoonal reefs;

2)   Growth trajectories would return differences between habitats, with exposed sites exhibiting smaller mean asymptotic sizes and increased curvature coefficients;

3)   Mortality would decrease from exposed through sheltered to lagoonal reefs.

5.2 Methods:

5.2.1 Sampling locations:

Sampling of *Thalassoma lunare* begun in December 1999 through to May 2002 with collections occurring throughout the year. Three regional locations were chosen, two within the Great Barrier Reef (GBR) and one in the Indian Ocean (Figure 5.1). These were chosen in order to sample separate populations living under heterogeneous and homogeneous environmental conditions within similar regions. These included the Lizard Island Region and Palm Group of Islands within the GBR and Scott Reef in the Indian Ocean. At Lizard Island, a midshelf continental island, individual fish were sampled from 3 habitat types identified following Choat & Bellwood (1985); an exposed reef, a sheltered reef and a lagoon. Furthermore, within this region 2 further midshelf sites were sampled; the sheltered side of North Direction Island, a continental island located approximately 9 km SE of Lizard Island, and the sheltered habitat of MacGillivaries Reef (Mac's Reef), a small sand cay located approximately 2 km NE of Lizard Island. These two sites were situated on these reefs in a similar leeward manner as the sheltered reef at Lizard Island and therefore they were considered to be similar habitats.

The Palm Group of islands, an inner shelf group, consisted of 4 sites, 3 of which are located along the leeward side of Orpheus Island, the 4th along the leeward side of Pelorus Island. The Orpheus Island localities consisted of Harrier Bay, Pioneer Bay and Cattle Bay, located at the southern, central and northern ends of the island respectively (following Kritzer 2002). All four sites are defined as sheltered habitats at this region. Finally, Scott Reef, located more than 300 km off the West Australia coast in the Indian Ocean, consisting of a large U-shaped reef spanning more than 25 km across, with an additional sandy cay at the top of the western arm. The 3 sites chosen were; an outer reef site on the eastern arm of the U-shaped reef, considered to be an exposed habitat; a site on the inside and bottom of the U, considered to a sheltered

habitat; and the eastern (leeward) side of the sandy cay, also considered to be a sheltered habitat. Topography of the sites was consistent with their exposed and sheltered classifications.

5.2.2 Sampling procedures:

Individual fish within each site were collected using hand-spears. Fish were weighed and measured for fork length (FL) and standard length (SL). Sagittae were removed, cleaned, washed in ethanol and stored dry. Subsequently, one sagitta from each pair was weighed and sectioned according to Chapter 2. Sectioned otoliths were read along a consistent axis following Choat & Axe (1996). For a detailed description of the methodological techniques refer to Chapters 2 and 4.

5.2.3 Analysis:

The relationship between sagittal weight (grams) and age (years) was examined using least-squares linear regression analysis. As with Chapter 4 longevity analysis was performed on the oldest 20% of individuals sampled. The von Bertalanffy (VB) growth function [VBGF; $L_t = L_\infty(1 - \exp(-k^{(t-t0)}))$] was modelled to size at age data. The VBGF parameter t_0 was constrained to 0 for all habitats within each region (Kritzer et al. in prep). Growth parameters were compared by plotting 95% confidence regions around the K and L_∞ estimates at each habitat by region combination.

Age-based catch curves were used to estimate the instantaneous rate of total mortality (M) in each habitat at each of the 3 geographic locations. Any year classes to the left of the age-frequency mode were excluded. In the event that habitat sites exhibited only 2 age classes to the right of the age-frequency mode the 1st age class to the left of the mode was included. Whilst this has the effect of erroneously reducing mortality estimates, as they incorporate age classes that are potentially underrepresented, the alternative of comparing a slope with only 2 data points was deemed unacceptable. Comparisons of mortality rates were made using analysis of covariance (ANCOVA; Zar, 1999).

5.3. Results:

5.3.1 Size and age:

The oldest fishes collected in any habitat in the Lizard Island Group were 7 years of age. These were collected from the exposed habitat around Lizard Island and

the sheltered habitat at MacGillivaries Reef (Table 5.1). Maximum ages in all other habitats reached at least 6 years of age. Maximum body size at this region ranged from 145 mm SL collected from the population at Nth Direction Island to 166 mm SL from the population at the exposed habitat. Populations from the three remaining sites, two sheltered habitats and the lagoon, displayed similar maximum size as the exposed habitat. In the Palm Group of islands differences in maximum size and age appeared to be more prevalent, even though all sites were considered to be sheltered habitats (Table 5.1). The population at Pelorus Island exhibited the largest and oldest fish, whilst the population at Cattle Bay had the smallest and youngest maximum size and age for this region. As described in Chapter 4, fish at Scott Reef were relatively short-lived, and exhibiting small maximum sizes compared with other regions. However, the population located at the sheltered habitat of the Inner Reef returned the largest and oldest fish for this region (Table 5.1). Fish in the exposed outer reef habitat of this region exhibited comparatively younger and smaller maximum age and size.

5.3.2 Sagittal growth:

In all habitats at all regions sagittal weight and age showed strong linear relationships indicating that the interpretations were, at least, consistent (Figures 5.2, 5.3, & 5.4). No significant differences were found between habitat types within any region. However, surprisingly, significant differences were found between the sheltered sites of the Palm Group of islands (Table 5.2). Following a multiple comparisons test, the populations found at the two sheltered sites of Pioneer and Harrier Bays were found to exhibit differences in sagittal growth (Table 5.3).

5.3.3 Longevity:

Mean longevity estimates for the oldest 20% of individuals sampled across all regions ranged between 2.25 ($\pm$ 0.11 SE) and 5.60 ($\pm$ 0.40) years at the exposed site at Scott Outer Reef and the sheltered site at MacGillivaries Reef respectively (Figure 5.5). Differences between habitats (within regions) were only evident at the Palm Group of islands and Scott Reef regions (Table 5.4). The Lizard Island region exhibited little difference between mean 20% longevity across sites, irrespective of the different habitats (Table 5.4). In the Palm Group of islands, the Pelorus Island population returned significantly greater longevity estimates compared to populations at both Harrier and Cattle Bays, regardless of the sites being located in similar habitats (Table

5.5). Differences in longevity estimates were also evident in the Scott Reef region. Populations located at the Inner Reef site, a sheltered habitat, were significantly longer lived compared with the other two Scott Reef sites, the sandy cay, also considered to be a sheltered habitat, and the exposed outer reef site (Table 5.5).

5.3.4 Growth:

Von Bertalanffy growth parameters fit to the size at age plots showed consistent growth trajectories, with the majority of locations showing continuous growth over a large proportion of the lifespan (Figures 5.6, 5.7, & 5.8; Table 5.1). The size at age plot from the exposed site at the Lizard Island region highlights the reason for this site returning one of the largest and oldest fishes, despite it being an exposed habitat. One individual, a relatively large 7-year-old fish was collected at the Lizard Island exposed reef (Figure 5.6). However, regardless of this individual, differences between growth trajectories of populations at two sheltered sites with that of the exposed site were evident. Confidence regions around the VB parameter estimates show similarities between MacGillivaries Reef and the sheltered site at Lizard Island; but differences between these two sheltered habitats and the exposed site (Figure 5.9A). However, whilst the population in the lagoon returned a higher mean asymptotic size (L_∞) compared with the population located in the exposed habitat, the 95% confidence regions surrounding the estimates overlapped. In addition, the lagoon population returned lower estimates of L_∞ than the sheltered site at Lizard Island, however the confidence regions also overlapped, highlighting the lack of differences in growth between the lagoon and the other two habitats. At the Palm Group of islands differences in growth trajectories were only evident at the Harrier Bay site. Confidence regions around the parameter estimates for this population did not overlap with any other population (Figure 5.9B). However, estimates of L_∞ for this site are higher than the largest fish collected. No differences were evident in VB parameter estimates at the three Scott Reef sites, regardless of habitat differences, as confidence ellipses were overlayed (Figure 5.9C).

5.3.5 Mortality:

The frequency data for age classes at each location provided estimates of mortality based upon age-based catch curves (Figures 5.10, 5.11 & 5.12, Table 5.1). The highest estimate of mortality (lowest rates of survivability) was found in the

population at the exposed site of Lizard Island. Furthermore, of the three regions sampled only the Lizard Island region exhibited any significant differences between mortality estimates amongst habitats (Table 5.6). These were between the exposed site and the sheltered habitat of MacGillivaries Reef, with this latter site exhibiting the lowest estimate of mortality of any site in any region (Table 5.7). To allow comparisons of mortality estimates between habitats within the Scott Reef region the 1-year-old frequency data was incorporated into the analysis at the Sandy Cay habitat as it exhibited only 2 data points from the mode to the oldest age class. Whilst this has the effect of reducing the mortality estimate (from 0.69.year^{-1} to 0.16.year^{-1}), there remained no statistical difference between the three habitats within this region.

5.4. Discussion:

There was significant variation in the age-based demographic parameters of *T. lunare* populations between sites within regions. However, the variation was not always consistent with predictions of increased longevity, significantly different growth trajectories and reduced mortality from exposed through sheltered to lagoonal habitats. Furthermore, age-based demographic differences occurred amongst populations within regions residing in similar habitats. For example, estimates of longevity amongst populations within regions were different between similar habitats, and similar between different habitats. In contrast however, growth trajectories and mortality estimates were more likely to follow predictions as populations within regions residing in vastly different habitats exhibited the largest variation in both growth and mortality. However, again there were contradictions as regions with populations living in similar habitats were found to have growth differences (Table 5.8). Whilst the variation in age-based demographic traits at this spatial scale was not always consistent, a number of general statements can be made regarding age-based demographic traits across small spatial scales. Firstly, that subtle differences in age-based demographics are likely within regions, even amongst habitats of apparently similar physical conditions. However, if differences in population demographics between exposed and sheltered habitats are evident, they are likely to be expressed as predicted. Namely, exposed habitats exhibiting slightly reduced maximum ages, reduced growth and increased mortality.

Exposed habitats did not consistently alter longevity estimates between local populations, even with potentially variable physical conditions. An increased

maximum age was evident in the sheltered habitat of the inner reef at the Scott Reef region. However, little difference was evident between sites and habitats at the Lizard Island region irrespective of three well defined habitats (Choat & Bellwood 1985, Fulton et al. 2001). The inconsistencies between these two regions may be in the potential of *T. lunare* to move away from the exposed sites. In their work on the locomotion of labrids, Bellwood & Wainwright (2001) described the swimming abilities of wrasse in relation to their habitat association. The genus *Thalassoma* was reported as having characteristics indicative of fast swimmers which was correlated with their use of exposed habitats. However, the species *T. lunare* whilst maintaining relatively fast swimming attributes was more often found in sheltered environments. Whether this is due to competitive exclusion or habitat preference is unknown. Although, sheltered regions appear to offer *T. lunare* a greater suite of resources with which to increase size and potentially age. The result of which would be a greater potential lifetime reproductive output (Roff 1984, Stearns & Koella, 1986). Green (1996) described a similar result in her work on the distribution of labrids at a smaller spatial scale, which was further supported by Fulton et al. (2001). *T. lunare* preferred the reef base, rather than the more dynamic reef crest. Spatial scales of this small magnitude are unlikely to affect this species life history, simply through their ability to move over these distances. In fact, an ontogenetic shift from the reef slope to the deeper reef base has been reported for this species (Green 1996), highlighting their vantage regarding wave exposure.

If *T. lunare* can move from regions of exposure, why are they found in exposed regions at all? Encounter rates at Lizard Island were much lower in the lagoon compared with the exposed site. However, spawning aggregations were observed in this latter habitat. Spawning sites for labrids are generally traditional, in areas exhibiting outgoing currents (Warner 1984a, 1990), which the exposed reefs are likely to offer. It is possible therefore, that this species uses the exposed habitats as spawning sites, yet resides in more sheltered conditions, even if this is at the base of the exposed reefs or in the lagoon. This could explain the lack of differences in longevity, growth and mortality between the lagoon and the exposed sites at Lizard Island, as they could be the same population. The distance between the two habitats in which fish were sampled was less than 1km. It has been observed in other regions that this species may move up to 500 metres along a contiguous reef during periods of strong tidal movement

for spawning purposes (pers. obs.). Movement was observed from areas of minimal water flow to areas in which the tidal flow was increased in an off reef direction. These latter conditions would be difficult to find within a lagoon and therefore movement may be necessary to enhance reproductive capabilities. Warner (1995) reported that the smaller congeneric, *T. bifasciatum,* can migrate to spawning sites over 1.5 kilometres away. The lagoon may represent a preferential habitat in which to reside, however, it may lack the resources associated with preferential spawning sites (Warner 1990, Samoilys & Squire 1994).

Thalassoma lunare populations displayed variation in longevity between sites of similar habitats. In the Palm Group of islands all three sheltered sites at Orpheus returned similar estimates of longevity, however, an additional site with similar habitat structure on an adjacent island, Pelorus Island, exhibited significantly increased longevity estimates. Two possible reasons exist for this discrepancy. Firstly, that there are in fact small habitat differences that benefit those individuals located at Pelorus Island. However, differences in longevity were marginal across larger spatial scales, including oceanic basins, latudinal gradients and cross-shelf exposures (see Chapter 4). Therefore, an indistinguishable difference between the habitats at Orpheus and Pelorus Islands is unlikely to create significant differences in this trait. The second reason for the significant differences between these sites is predatory differences. Pelorus Island and the southern end of Orpheus Island, Harrier Bay, are open to fishing and therefore the abundance of larger predatory fish is likely to be reduced at these two sites. Whilst there was no evidence of older *T. lunare* at Harrier Bay, the close proximity of this site to an adjacent non-fished bay may allow large predatory fish to remain in significant abundance (Russ & Alcala 2003). Kritzer (2002) in his analysis of age-based demographics of a lutjanid, found little difference in maximum ages between populations located at these two sites. However, Pelorus Island exhibited larger fish in higher densities, of which was partially attributed to fishing pressure on the larger predatory species. Whilst habitat similarities between sites are expected to return similar life history traits, the effect of anthropogenic boundaries may cause variation.

Populations at Lizard Island exhibited significantly different growth trajectories between the exposed habitat compared to populations residing in several sheltered habitats. These differences were exhibited as smaller mean asymptotic sizes, but not necessarily different curvature coefficients. Exposure to increased wave action, or

different coral communities and therefore variable refuge availability are likely to have an effect on growth. However, this is likely only when it is difficult for individuals to move into preferential habitat. Whilst differences in growth were found between several sheltered habitats and the exposed habitat at Lizard Island, little difference was found between the lagoon and the exposed reef. However, recent work by Fulton & Bellwood (in review) has shown that the movement of water through the lagoon, caused by wave action can be greater than the sheltered location at this region. Similarities in demography between the lagoon and the exposed sites may therefore be due to movement of fish between the two sites. Alternatively, it may be because the lagoon is a habitat with greater wave exposure than originally thought and therefore, it may not be beneficial as first predicted.

Abundance did not support the theory that the Lizard Island lagoon may be a beneficial habitat for *T. lunare*. Low abundance of this species was observed throughout this site compared with other habitats (pers. obs.). However, this may be driven largely by greater recruitment to the slope of the exposed habitat. Although larval fish have been shown to settle in preferential habitats (Booth et al. 2000), the rate of recruitment does not necessarily reflect any advantage in growth (Pitcher 1992). Furthermore, recruitment events have been shown to be higher for outer reef sites compared with lagoonal regions, likely due to settlement as they appear from the water column (Booth et al. 2000). The exposed reef, which surrounds the lagoon, may offer settling individuals not only a greater area in which to settle, but the first opportunity. In comparison, larvae settling into the lagoon would do so via the relatively small entrance into the lagoon or across the reef flat, which would involve passing over the exposed site. Therefore adult abundance in the lagoon may reflect limited recruitment events. Furthermore, any ontogenetic shift from the exposed site is likely to be to deeper waters (Green 1996) as the lagoon is unlikely to offer *T. lunare* the reduced wave exposure they appear to prefer (Fulton & Bellwood in review).

In contrast to Lizard Island, there was little difference in growth between the exposed outer reef habitat of Scott Reef and either of the other two sites, which were more sheltered, even with little potential for movement. Resource limitation is a possible explanation for growth similarities within this region. Coral bleaching at this region has been extensive (discussed in Chapter 4). The resultant rubble associated with the decrease of coral cover may alter this species foraging abilities and therefore

resource acquisition. Furthermore, refuge availability is likely to have been significantly altered. It has been reported that preferential settlement of *T. lunare* recruits is often to live branching coral (Eckert 1985 in Green 1996). Therefore, settling larvae, juveniles and adults may all be affected to some extent at this region, regardless of the local scale habitat to which they have settled. This may affect and limit growth in all habitats. Assessment of growth trajectories over a temporal scale would need to be assessed to determine whether there has been an alteration of size at age due to this environmental influence.

As with longevity, the Palm Group of islands exhibited differences in growth between populations, regardless of similar habitats. Pelorus Island exhibited older fish, yet it was the southern bay of Orpheus Island, Harrier Bay, which exhibited significantly different growth trajectories, displaying larger mean asymptotic sizes. This could be because the habitat at Harrier Bay is conducive to increased growth. This habitat is adjacent to an island with an extensive mangrove lined bay and is therefore prone to additional turbidity above the other bays which are all similarly affected by the Herbert River opposite Orpheus Island. It has been surmised that turbidity may incur additional costs due to extra activity (Sweka & Hartman 2001). However, any impairment of vision by increased turbidity has been shown not to affect the ability of juvenile trout to feed (Rowe et al. 2003). If this is the case with *T. lunare*, the additional siltation may increase interstitial organisms on which to feed and consequently additional resources for growth. An alternative explanation than subtle habitat differences causing growth variation is that the lack of fish in the older age classes may drive the increased mean asymptotic sizes. This is likely, as the largest fish was actually found at Pelorus Island, although, Harrier Bay also exhibited at least one individual of similar size. Additionally, the mean asymptotic size at Harrier Bay is greater than the largest fish found at this site. Therefore, the pattern observed of differential growth trajectories at this site compared with the others at this region, may in fact be an artefact of the significantly reduced life spans.

In contrast to the larger spatial scale analysis of demographic differences, mortality estimates were found to differ among habitats at one region. Significantly increased mortality estimates were found at the exposed habitat of Lizard Island in comparison with the sheltered habitat of MacGillivaries Reef. Populations in exposed habitats may be more prone to mortality, either directly through predation (Connell

1998a) or indirectly through wave exposure (see Fulton & Bellwood 2004), reduction in habitat complexity (Beukers & Jones 1997) or reduced food resources (see Thresher 1983, Booth & Hixon 1999). As mentioned, sheltered regions appear to offer *T. lunare* with a greater suite of resources with which to increase size and potentially age. Therefore, if size is potentially increased, mortality due to predation may be reduced, especially if there is a size threshold to which predatory events are significantly precluded (Reznick et al. 1996). This is likely the case immediately following settlement (Doherty and Sale 1985, Searcy & Sponaugle 2001, McCormick & Hoey 2004). However, it is unknown whether size specific differences in mortality (see Sogard 1997) remain once adulthood is reached. Furthermore, if settlement is greater at the exposed site, and mortality at settlement is particularly high, then mortality will naturally be greater at this site.

The high mortality estimates at the exposed site of Lizard Island may be an artefact of the method used to calculate this demographic trait. The steep decline of the number of individuals in each age class may be an artefact of the increased settlement rates at this site in conjunction with the inclusion of a particularly old and large individual fish. This 7-year-od fish was coloured in a similar manner to a juvenile/female/primary male; a drab olive-green with a transparent caudal fin and little colouration of the pectoral fins and head. However, it was extraordinarily large, especially for a fish in an exposed habitat. The second largest individual collected in the exposed habitat was approximately 2 cm (10%) smaller than this individual. Furthermore, upon dissection of this animal, there was no evidence of any discernable gonad tissue. For a fish of this size, this was extremely unusual. Two possible scenarios may account for this anomaly. Firstly, that this fish exhibited evidence of senescence, in which gonad material degenerated and the terminal/territorial colour phase was lost. Whilst senescence has been examined in fish (Bryant & Reznick 2004), usually in relation with extrinsic mortality (Reznick et al. 2002), little work has involved reproductive senescence. This is likely due to the concept that few individuals in the wild will survive to an age in which senescence can be measured. However, the question of why this fish should be a much larger size than other individuals in the same habitat remains unanswered. Unless the apparent deterioration of the gonad enabled the individual an extraordinary growth spurt at this latter stage of life. Whilst a growth spurt during sex change has been reported (Warner 1984a,

Walker & McCormick 2004), a growth spurt coinciding with the complete breakdown of all gonad material is unknown. The second possibility is that this fish has been reproductively inert its entire life, and this has enabled it to put resources into growth and survivorship. In either case, evidence exists of a reproductive/growth – survivorship trade-off.

In contrast to Lizard Island, no significant differences in mortality estimates were found between sites at the Scott Reef region. However, mortality estimates based upon age frequencies are obviously driven, to some extent, by the number of age classes exhibited. Therefore, the lack of age classes at this region, compared with other regions, may be an explanation behind insignificant differences in mortality estimates. In addition, the relatively small sample sizes at each site may prevent significant power to examine differences. As described previously, mortality estimates are heavily reliant on larger sample sizes, as they are based upon frequencies (see discussion in Chapter 4). Precision decreases in mortality estimates when fewer than 8 individuals per age class are present (Kritzer et al. 2001).

Habitat associations of reef fish have been studied extensively, however, the use of otoliths in examining reef fish life histories facilitates the assessment of habitat induced differences. It is evident that differences in age-based parameters can be found over small distances within reefs. However, between habitat differences in life history parameters of *T. lunare* were not always consistent with predictions. These inconsistencies were both across regions and across parameters. The *a-priori* interpretation of habitats was possibly subjective, and therefore may explain why some results did not fit expectations. However, even without any ambiguity associated with habitat definition, there were two generalisations that came of this work. Differences in life history traits are likely to be evident amongst sites within regions, even between habitats of apparently similar physical conditions. Furthermore, demographic differences between exposed and sheltered habitats are likely to exhibit subtly reduced age, growth and survivability. Any examination of age-based demography of reef fish over large spatial scales will therefore need to incorporate or acknowledge the possibility of small-scale differences. As even these small scale differences may have implications regarding total reproductive outputs of populations.

Table 5.1: Sample sizes (n), age ranges, size ranges, VBGF parameters (L_∞ and k) and coefficient of determination (r^2), estimates of mortality (M) and estimates of survivability (S) for different sites and habitats within three spatially separated regions of populations of *T. lunare*. Intercepts of the growth functions constrained to the origin (0 mm).

Region Location - habitat	n	Age range (yrs)	Size range (mm)	L_∞ (mm)	k (yr^{-1})	r^2	M (yr^{-1})	S (%.yr^{-1})
Lizard Island Group								
Lizard Is – Exposed	106	0.74 - 7	51 - 166	130.54	0.74	0.76	0.81	44.49
Lizard Is – Lagoon	61	0.60 - 6	52 - 160	134.70	0.74	0.76	0.39	67.71
Lizard Is – Sheltered	116	0.28 - 6	23 - 159	142.53	0.72	0.82	0.41	66.37
Mac's Reef – Sheltered	19	1 - 7	75 - 165	152.82	0.62	0.84	0.32	72.61
Nth Direction Is – Sheltered	17	0.71 - 6	72 - 145	129.49	0.76	0.62	0.53	58.86
Palm Group								
Harrier Bay - Sheltered	31	1 - 5.5	83 - 179	192.28	0.40	0.73	0.73	48.19
Pioneer Bay – Sheltered	34	1 - 6	73 - 164	154.46	0.55	0.74	0.56	57.12
Cattle Bay – Sheltered	34	1 - 5	66 - 163	174.09	0.39	0.82	0.61	54.34
Pelorus Island – Sheltered	76	1 - 7	80 - 184	161.4	0.48	0.70	0.81	44.49
Scott Reef								
Sandy Cay – Sheltered	35	0.52 - 3	41 - 130	119.25	1.11	0.69	0.69	50.16
Inner Reef – Sheltered	32	0.79 - 4.5	62 - 142	123.32	0.96	0.73	0.55	57.70
Outer Reef – Exposed	25	0.66 - 2.5	58 - 122	125.04	1.00	0.86	0.80	44.93

Table 5.2: Summary of ANOVA comparisons of otolith weight vs age of *T. lunare* populations within three regions. *A multiple comparison test returned no differences.

Region	K	df	F	P
Lizard Island Group	5	4, 309	1.264711018	0.283819466
Palm Group	4	3, 167	2.909341682	0.036191318
Scott Reef*	3	2, 86	3.477312686	0.035300446

Table 5.3: Summary of significant differences following a multiple comparison between otolith weight and age at the Palm group.

Location	df	q	q critical
Pioneer Bay vs Harrier Bay	4, 167	4.038723499	3.685

Table 5.4: Summary of ANOVA comparisons of mean 20% longevity of *T. lunare* populations within three regions.

Region	K	df	F	P
Lizard Island Group	5	4, 63	1.711421346	0.15858927
Palm Group	4	3, 35	11.63287728	1.93466E-05
Scott Reef	3	2, 18	15.21079046	0.000135551

Table 5.5: Summary of significant differences following a multiple comparison between mean 20% longevity estimates at the Palm group and Scott Reef regions.

Location	df	q	q critical
Pelorus Is vs Cattle Bay	4, 35	6.968130129	3.845
Pelorus Is vs Harrier Bay	4, 35	6.575567347	3.845
Scott Reef Inner vs Outer Reef	3, 18	7.555144248	3.609
Scott Reef Inner vs Sandy Cay	3, 18	5.432649104	3.609

Table 5.6: Summary of ANCOVA comparisons of mortality rates of *T. lunare* populations within three regions. * 1-year-old data was added to the Sandy Cay location within the Scott Reef region for the slopes comparison as the original mortality estimates for this location contained only 2 points.

Region	K	df	F	P
Lizard Island Group	5	4, 15	3.425101	0.03527
Palm Group	4	3, 9	0.566644	0.650671
Scott Reef *	3	2, 5	1.260336	0.360399

Table 5.7: Summary of significant differences following a multiple comparison between mortality estimates at the Lizard Island region.

Location	df	q	q critical
Mac's Reef vs Exposed Reef	5, 15	5.014038868	4.333

Table 5.8: Predictions and observed relationships of age-based parameters of each site within each region. Site names are often representative of the habitat type. Bold type represents observed conditions that meet predictions.

Age-based Parameters	Lizard Island	Palm Group	Scott Reef
PREDICTIONS			
Longevity	Exposed < Sheltered = Mac's = Nth Direction < Lagoon	Harrier = Pioneer = Cattle = Pelorus	Outer < Cay < Inner
Growth	Exposed ≠ Sheltered = Mac's = Nth Direction ≠ Lagoon	Harrier = Pioneer = Cattle = Pelorus	Outer ≠ Cay ≠ Inner
Mortality	Exposed > Sheltered = Mac's = Nth Direction > Lagoon	Harrier = Pioneer = Cattle = Pelorus	Outer > Cay > Inner
OBSERVED			
Longevity	Exposed = **Sheltered = Mac's = Nth Direction** = Lagoon	**Pioneer** = [**(Harrier = Cattle)** < Pelorus]	(Outer = Cay) **< Inner**
Growth	**[(Exposed ≠ (Sheltered = Mac's)]** = Nth Direction = Lagoon	Harrier ≠ **(Pioneer = Cattle = Pelorus)**	Outer = Cay = Inner
Mortality	**(Exposed > Mac's)** = **Sheltered = Nth Direction** = Lagoon	**Harrier = Pioneer = Cattle = Pelorus**	Inner = Cay= Outer

SR PG LI

SC OR IR

10 km

PI CB PB HB

1 km

MR S L E

AUSTRALIA

SR LI PG

ND

1 km
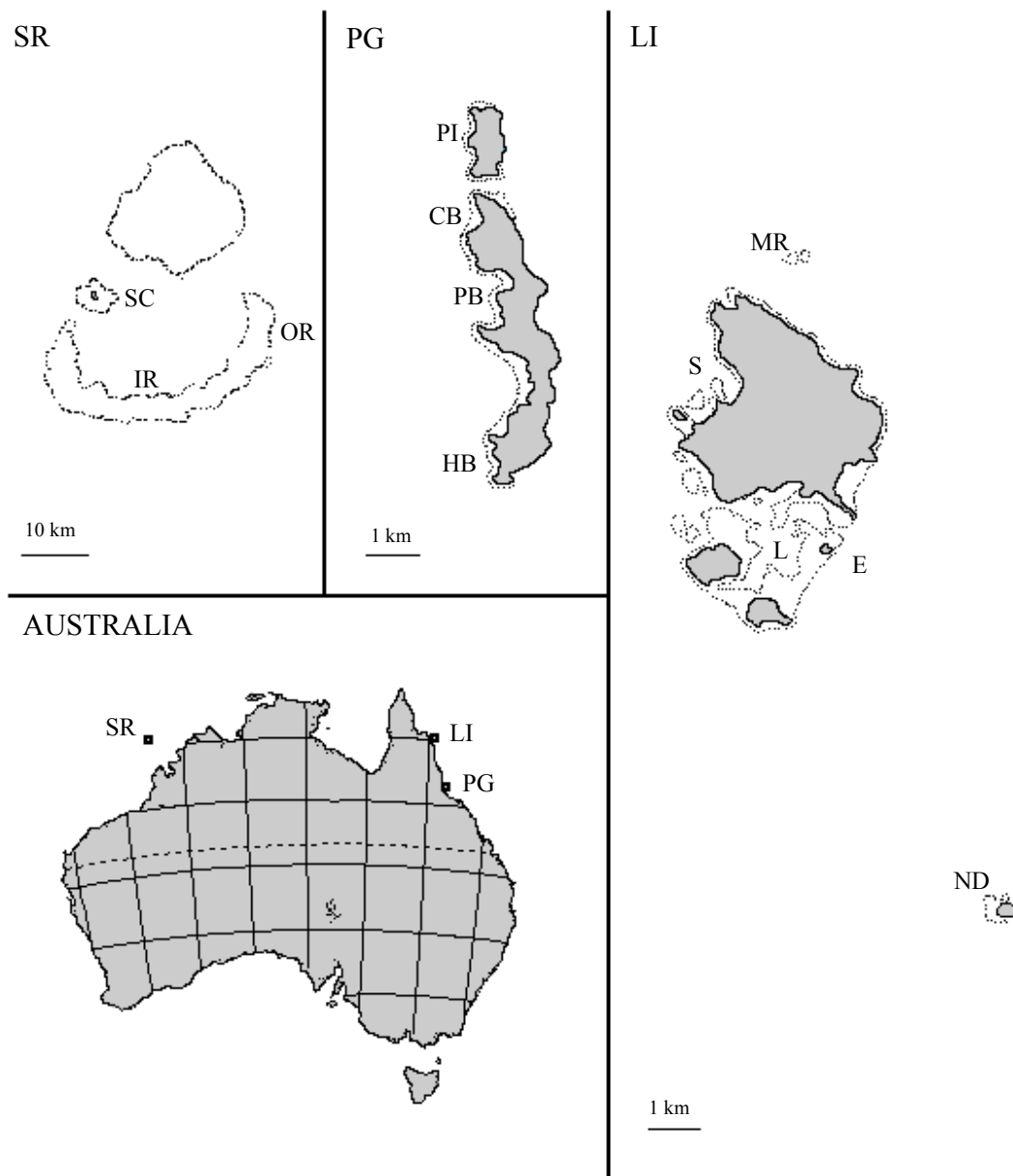
Figure 5.1: Sampling habitats and localities within the three regions, two in the GBR along the east coast of Australia, the third in the Indian Ocean. Inserts show the habitat localities for Lizard Island (LI), Palm Group (PG) and Scott Reef (SR). Locations within each region are marked. E = Exposed Reef, S = Sheltered, L = Lagoon, ND = North Direction Island, MR = MacGillivaries Reef, PI = Pelorus Island, CB = Cattle Bay, PB = Pioneer Bay, HB = Harrier Bay, OR = Outer Reef, SC = Sandy Cay, IR = Inner Reef.
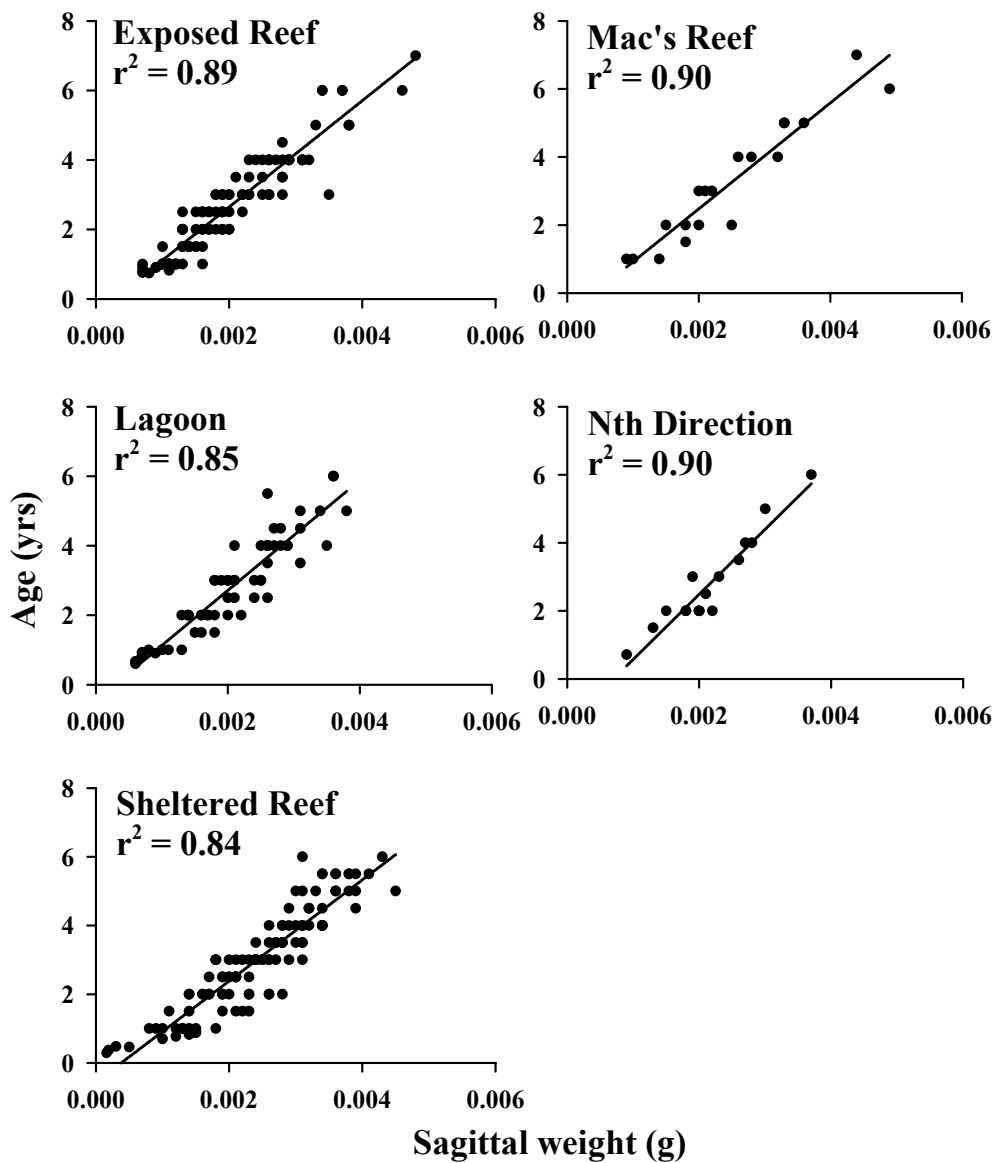
Figure 5.2: Linear relationships of sagittal increments (age in years) on sagittal weights (grams) in *T. lunare* populations sampled from five localities within the Lizard Island region. Exposed Reef: y = 1530.07x – 0.42, n = 106; Lagoon: y = 1584.26x – 0.45, n = 61; Sheltered Reef: y = 1471.55x – 0.56, n = 116; Mac's Reef: y = 1556.63x – 0.64, n = 19; Nth Direction Island: y = 1912.18x – 1.34, n = 17.
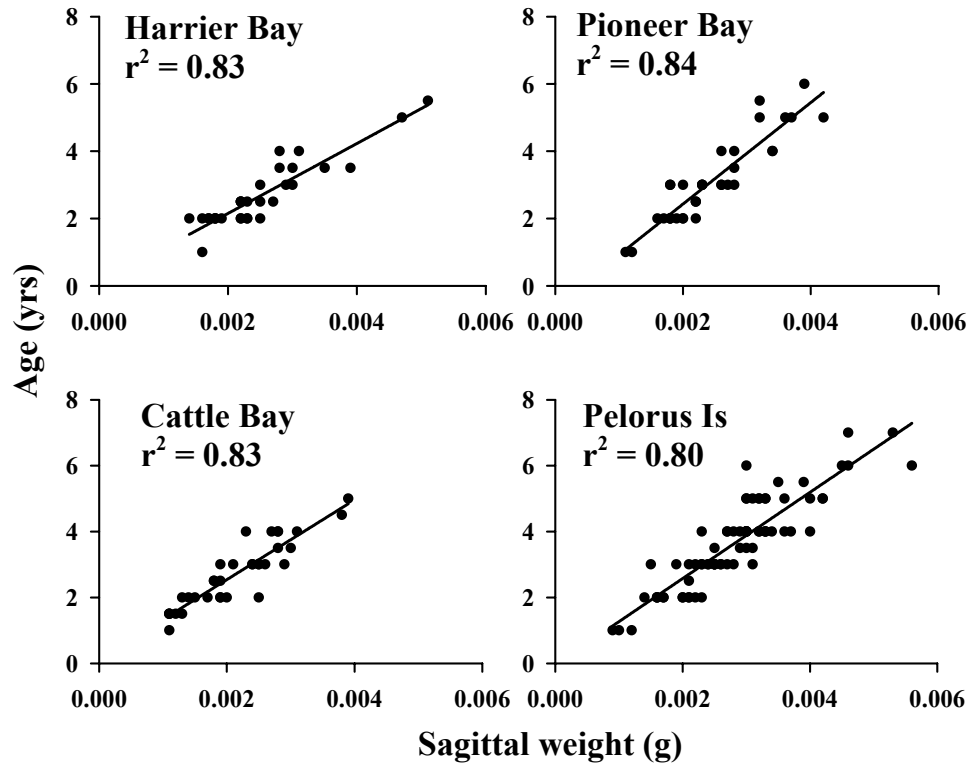
Figure 5.3: Linear relationships of sagittal increments (age in years) on sagittal weights (grams) in *T. lunare* sampled from four localities within the Palm Island region. Harrier Bay: y = 1039.04x + 0.07, n = 31; Cattle Bay: y = 1210.95x + 0.12, n = 34; Pioneer Bay: y = 1507.25x – 0.58, n = 34; Pelorus Island: y = 1308.15x – 0.04, n = 76.
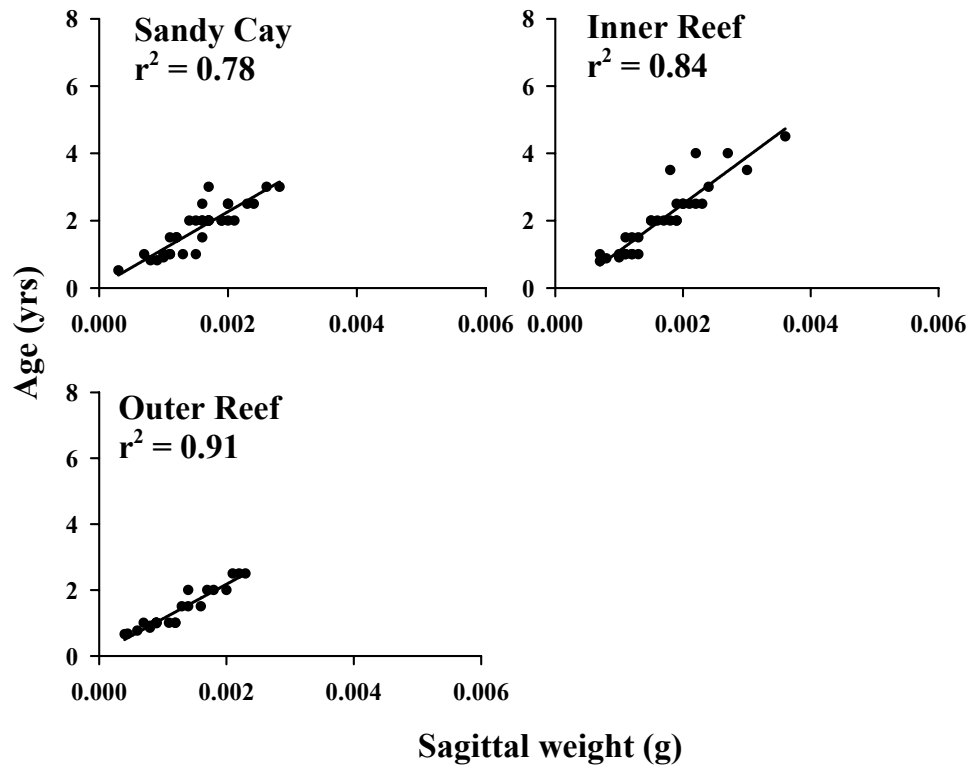
Figure 5.4: Linear relationships of sagittal increments (age in years) on sagittal weights (grams) in *T. lunare* sampled from three habitats within the Scott Reef region. Sandy Cay: y = 1108.30x + 0.05, n = 35; Outer Reef: y = 1049.73x + 0.08, n = 25; Inner Reef: y = 1396.81x – 0.30, n = 32.
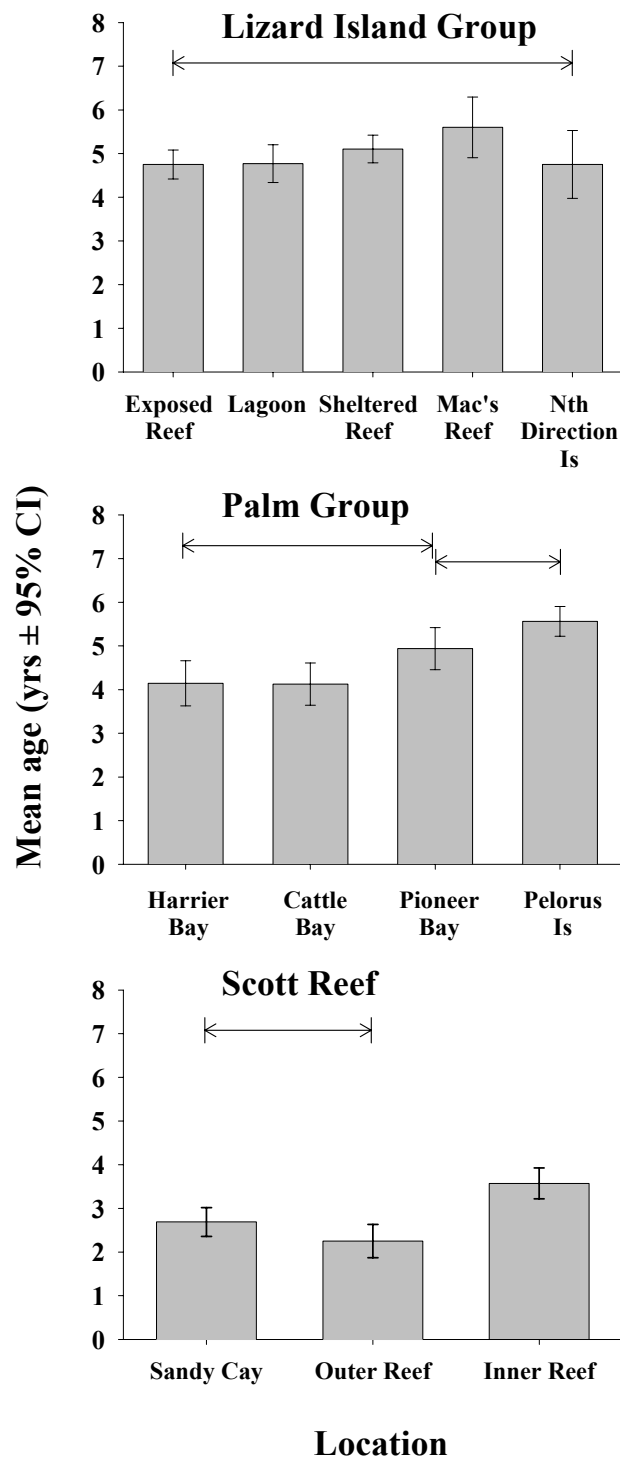
Figure 5.5: Mean *T. lunare* longevity (± 95% CI) based upon the oldest 20 % of individuals sampled within each location from each region. Continuous arrows above locations indicate non-significant differences between means following results of multiple comparison Tukeys test. ANOVA results in Table 5.4.
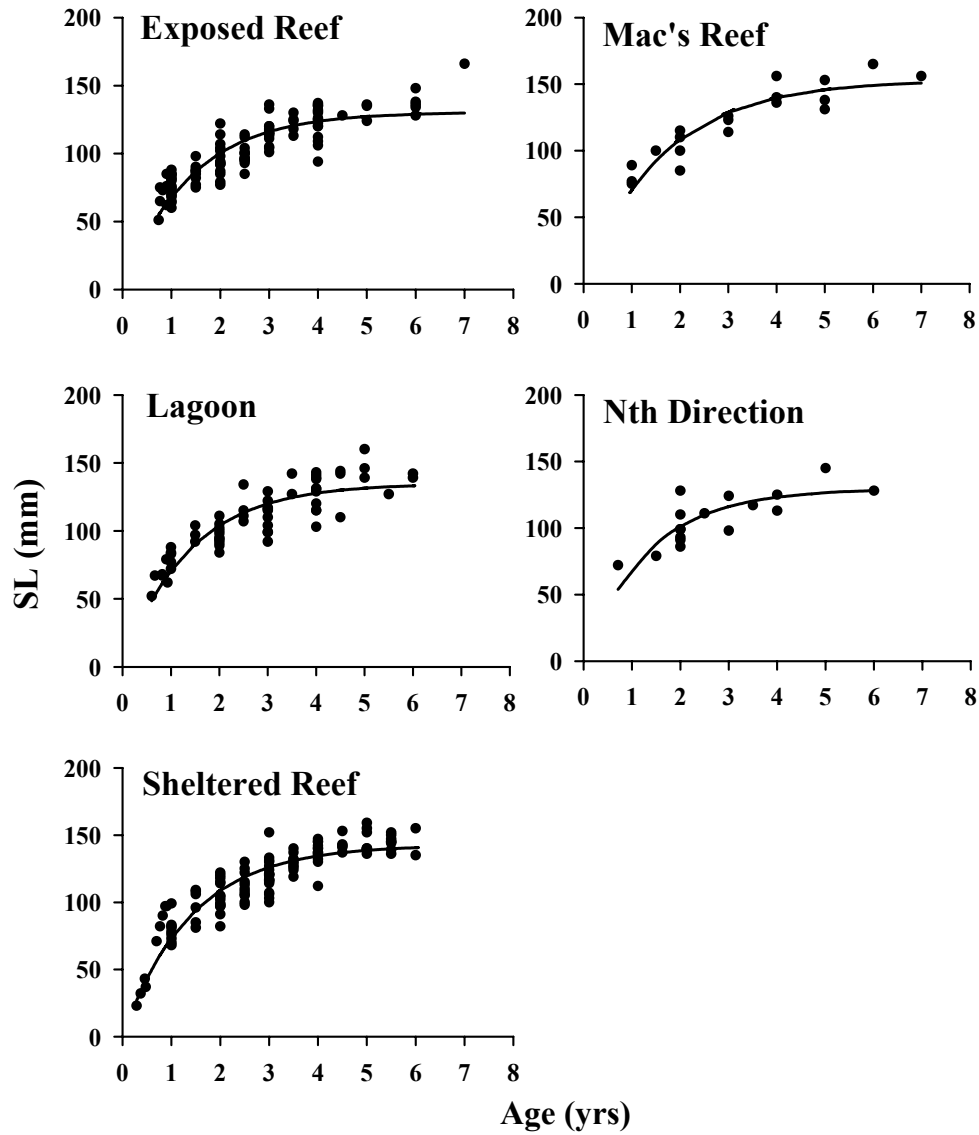
Figure 5.6: Size at age plots with constrained VBGF at 5 localities surrounding the Lizard Island region. VBGF parameters in Table 5.1.
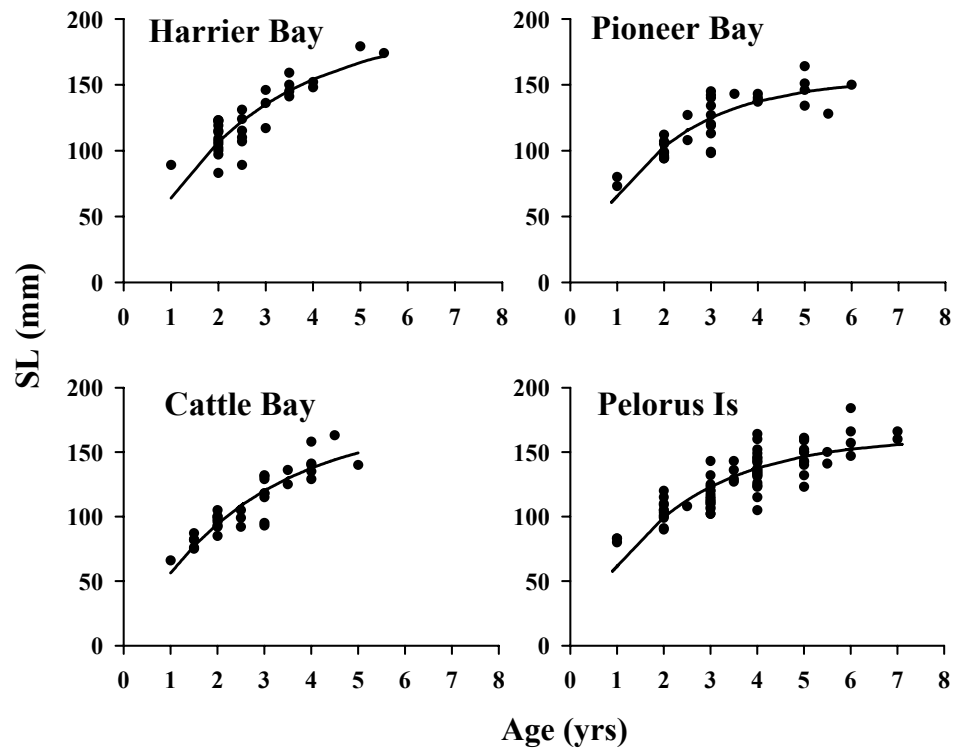
Figure 5.7: Size at age plots with constrained VBGF at 4 localities surrounding the Palm Island region. VBGF parameters in Table 5.1.
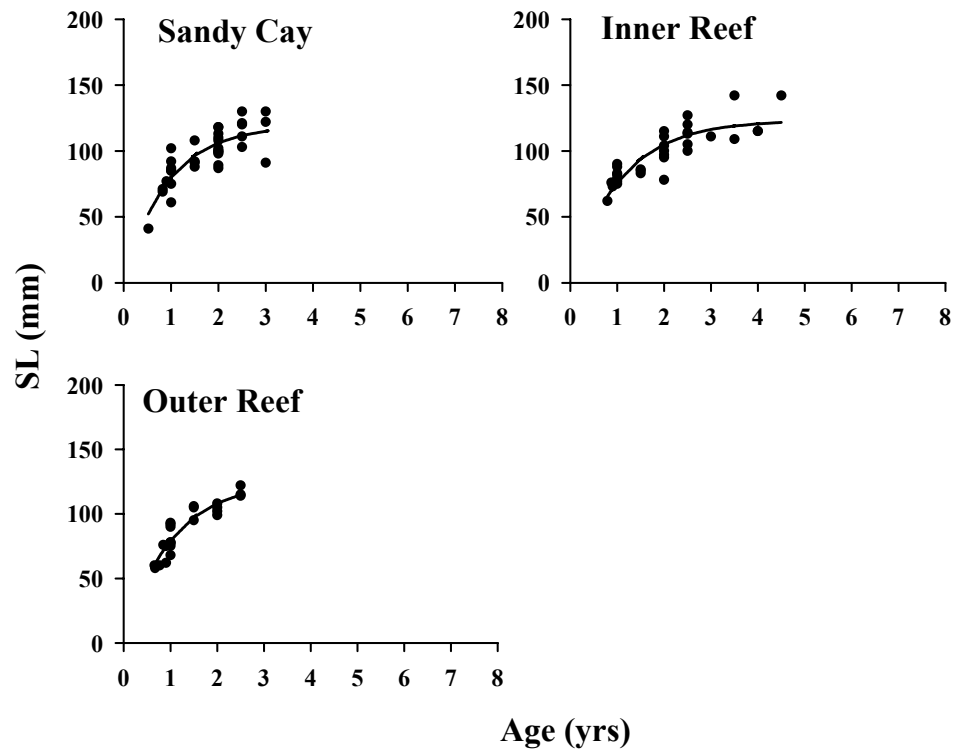
Figure 5.8: Size at age plots with constrained VBGF at 3 habitats surrounding the Scott Reef region. VBGF parameters in Table 5.1.
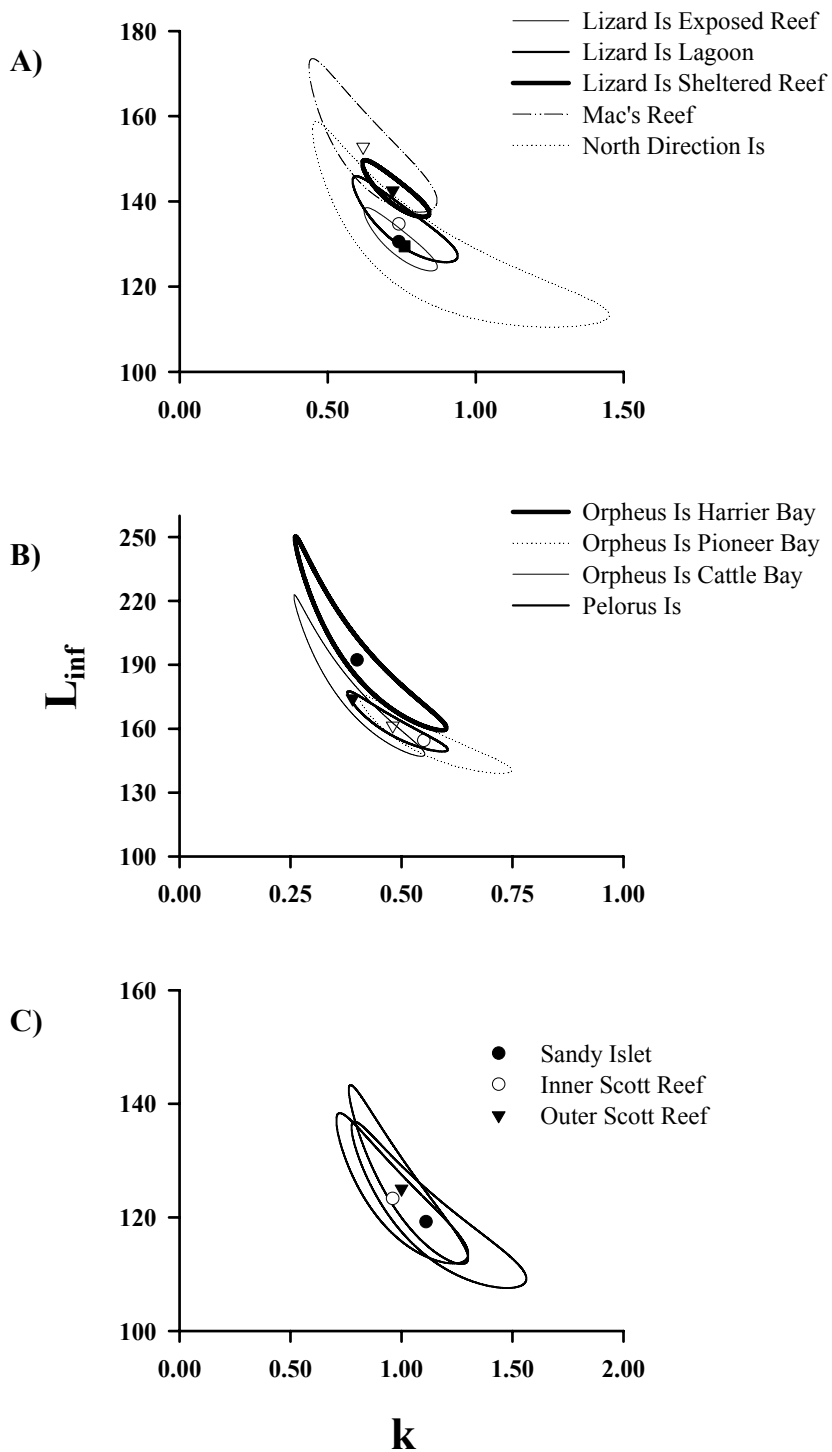
Figure 5.9: Comparison of VBGF parameters for local populations of *T. lunare* at the A) Lizard Island region, B) Palm Island region and C) Scott Reef region showing 95 % confidence regions around least square estimates of k and L_∞. Symbols represent parameter estimates; lines represent 95 % confidence regions.
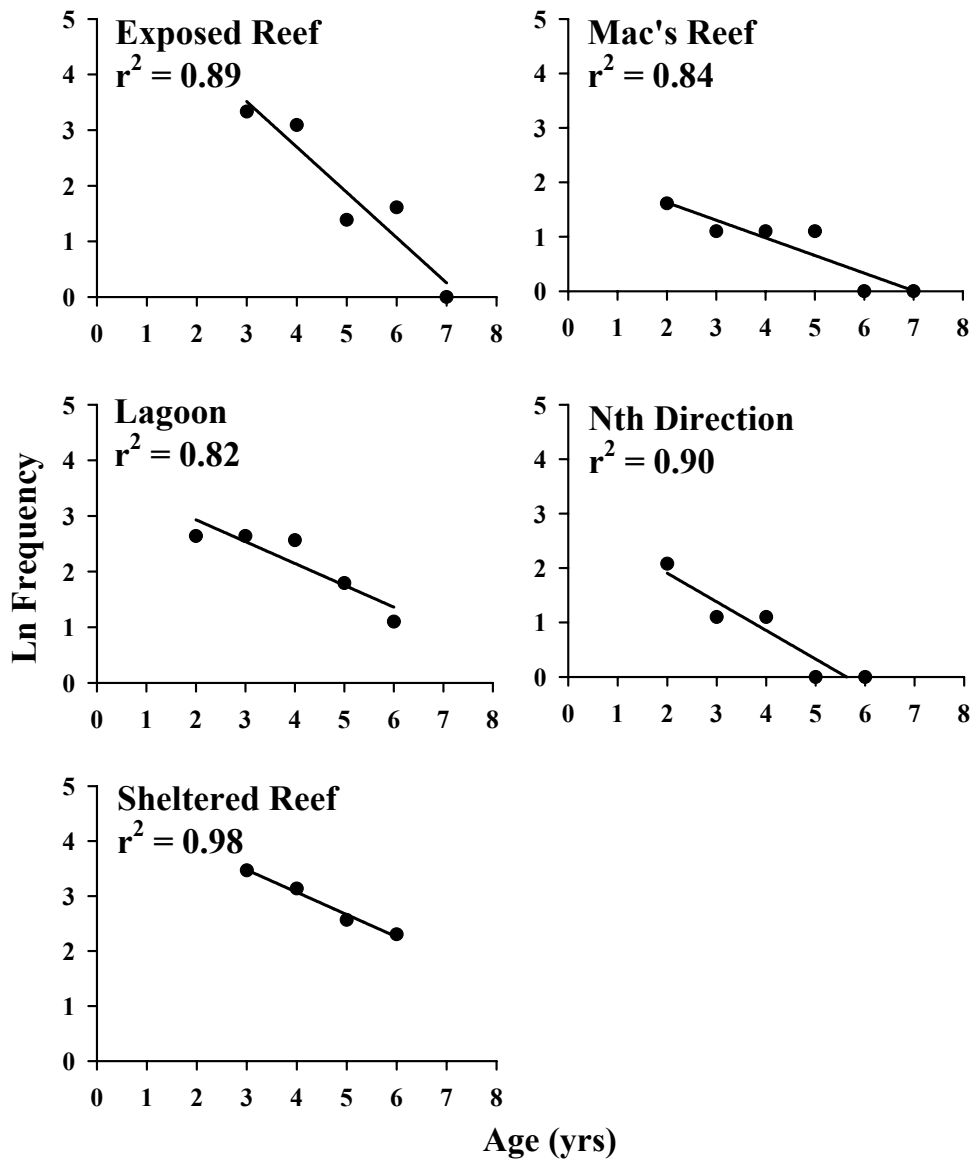
Figure 5.10: Estimates of mortality from catch curves at 5 locations surrounding the Lizard Island region. Exposed Reef: y = -0.81x + 5.96; Lagoon: y = -0.39x + 3.72; Sheltered Reef: y = -0.41x + 4.69; Mac's Reef: y = -0.32x + 2.28; Nth Direction Island: y = -0.53x + 2.96. Mortality and survivability estimates recorded in Table 5.1. ANCOVA analysis of regression slopes shown in Table 5.6. Multiple comparison analysis shown in Table 5.7.
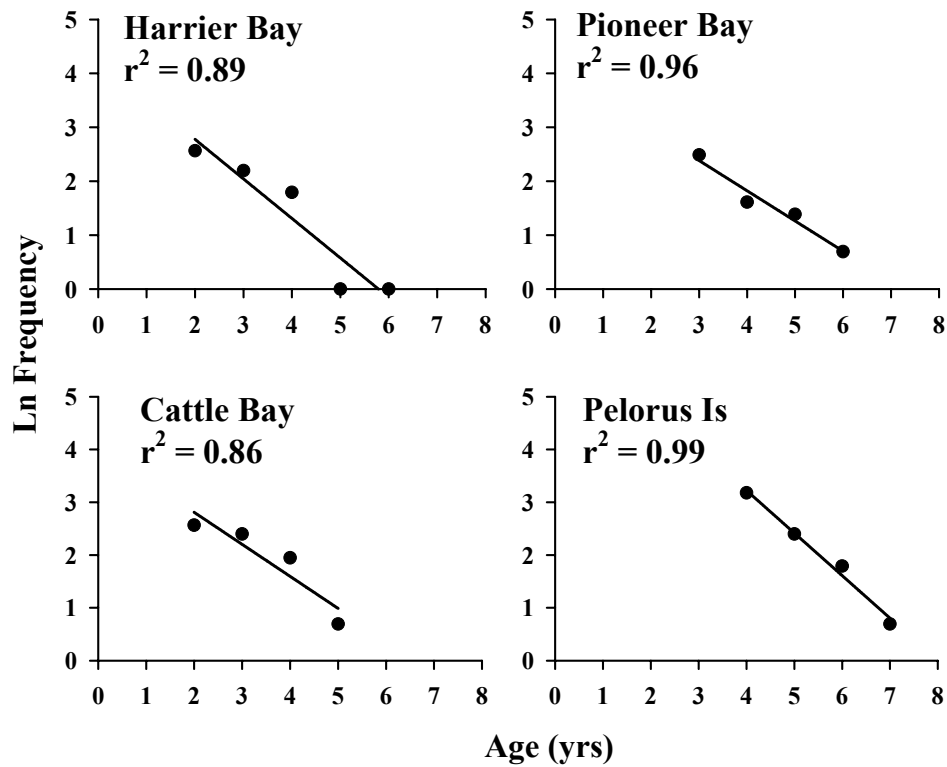
Figure 5.11: Estimates of mortality from catch curves at 4 locations surrounding the Palm Island region. Harrier Bay: y = -0.73x + 4.24; Cattle Bay: y = -0.61x + 4.02; Pioneer Bay: y = -0.56x + 4.06; Pelorus Island: y = -0.81x + 6.45. Mortality and survivability estimates recorded in Table 5.1. ANCOVA analysis of regression slopes shown in Table 5.6.
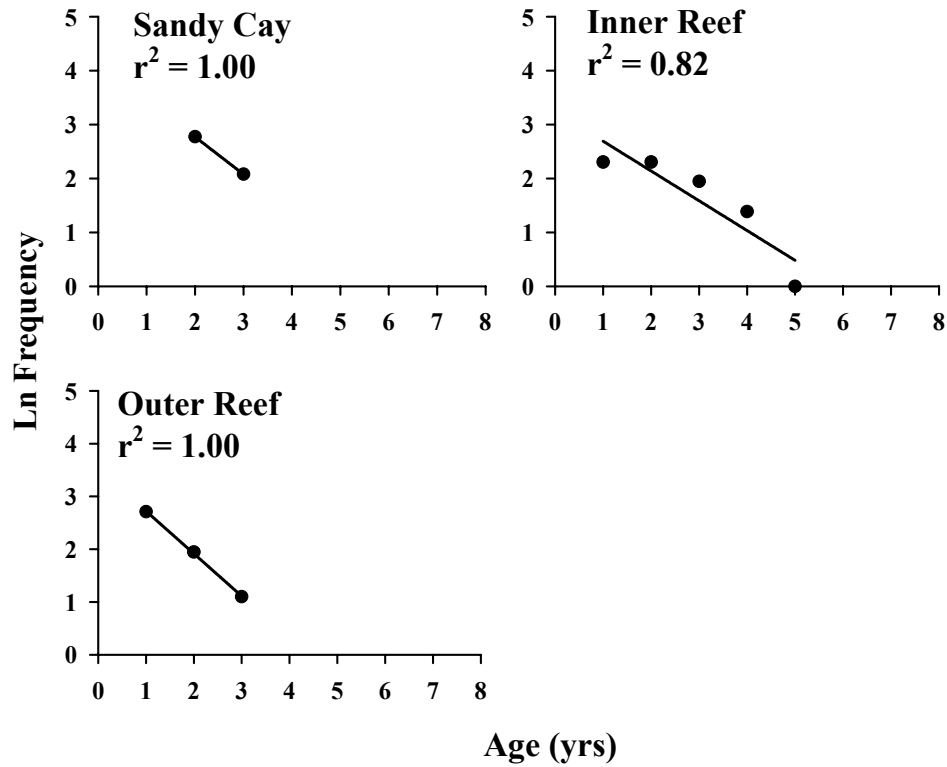
Figure 5.12: Estimates of mortality from catch curves at 3 locations surrounding the Scott Reef region. Sandy Cay: y = -0.69x + 4.16; Outer Reef: y = -0.80x + 3.53; Inner Reef: y = -0.55x + 3.24. Mortality and survivability estimates recorded in Table 5.1. ANCOVA analysis of regression slopes with 1 year old data incorporated for the Sandy Cay shown in Table 5.6.

CHAPTER 6. GENERAL DISCUSSION

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6.1. General life history patterns

Life history theory predicts slower initial growth rates, maturation at larger sizes and later ages, increased longevity and reduced mortality at regions of high latitude in comparison with those populations found at low latitudes. However, these predictions are founded upon terrestrial animals exhibiting an increase in final body sizes with an increase in latitude, which has been related to temperature (Atkinson 1994). At lower temperatures, organisms tend to exhibit slower growth (Ray 1960, Brett, 1979, Wood & O'Dor, 1999). However, this study showed that factors affecting variation in reef fish life history parameters are more complex. For example, exposure differences were shown to alter initial growth rates, maturity and sex change schedules, final body sizes, longevity and mortality. This can occur at spatial scales either across the continental shelf or within reef systems across variable habitats. Those reefs exhibiting increased wave exposure displayed general life history attributes of faster initial growth rates, early maturation, significantly different growth trajectories, smaller final body sizes and insignificantly reduced longevities. Additionally, density of con-specifics significantly altered life history traits of populations. Those populations residing in areas of high abundance were likely to exhibit smaller final body sizes and significantly reduced maximum ages.

There are four general patterns exhibited by *T. lunare* populations associated with regions of 1) sheltered, inshore reefs; 2) exposed outer shelf reefs; 3) high latitude exposed regions, and; 4) low latitude regions of high density. Whilst there are slight variations to these generalised patterns, examples of these four were found at the Palm Group of islands, the One Tree Island Outer Reef, Port Stephens and PNG respectively. These four regions exhibited particular traits regarding initial growth rates, size and age at maturity, size and age at sex change (even with similar maturity schedules), final body sizes and maximum age (Figure 6.1).
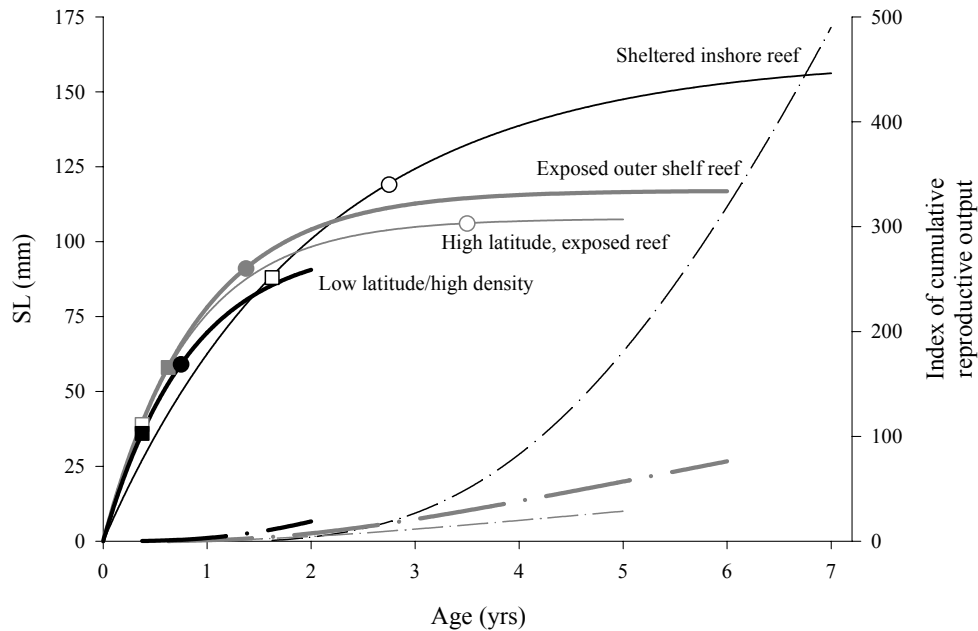
Figure 6.1: Growth trajectories and the corresponding index of reproductive output of *T. lunare* populations from regions exhibiting different exposures, latitudes and conspecific densities. Solid lines represent von Bertalanffy growth functions up to the maximum age for each represented region. Dot-dash lines are representative of an index of cumulative reproductive output calculated from growth trajectories, incorporating abundance, and based upon the exponential relationship between gonad weight and size in *T. lunare*. Thick black lines and filled black symbols represent the PNG region; thin grey lines and open grey symbols represent the Port Stephens region; thick grey lines and filled grey symbols represent the One Tree Island Outer Reef, and; thin black lines and open black symbols represent the Palm Group of islands. Squares and circles correspond to size at maturity and size at sex change for each region respectively. See text for calculations and further discussion.

Sheltered regions exhibited slow growth rates, which resulted in relatively large sizes and generally greater maximum age. Consequently, size and age at maturity were delayed (Figure 6.1). In contrast, populations residing in regions of low latitude were generally short lived and of small final body sizes. This was accentuated in areas exhibiting relatively high densities of conspecifics. Correspondingly, size and age at maturity was small and young respectively. Intermediate to these life history patters, populations on exposed reefs exhibited final body sizes midway between these two and insignificantly younger maximum ages compared with sheltered regions. Furthermore, exposed populations exhibited maturity schedules at a generally small size and young age compared with the sheltered populations. For most populations size and age at sex change was generally related to size and age at maturity. However, size and age at maturity of most regions was generally related to their final body size. Therefore the fundamental trait driving maturity appears to be final body size. Jones (1980b) also reported size as the trait most likely to define maturity in the protogynous temperate wrasse, *Pseudolabrus celidotus*, predominantly through social inhibition by the larger females towards immature fish. In support of this, Bertschy & Fox (1999) found that growth, and therefore size, was the driving force regarding the timing of maturity in sunfish populations, more so than mortality (see Reznick et al. 1996). However, age specific mortality may have a larger impact on reproductive effort, rather than age at maturity (Charnov & Schaffer 1973, Bertschy & Fox 1999). In contrast to the other general life history models, the population at Port Stephens, a high latitude region of extreme exposure, which exhibited similar traits to the exposed outer shelf regions, displayed particularly large size and correspondingly late age at sex change, irrespective of the size and age at maturity. However, whilst this may appear to be unusual, the existence of a large proportion of primary males and relatively large, old females at this region suggests that there may be an alternative mating strategy in place.

With significantly altered life history strategies in place for separate populations, depending upon the latitudinal position and/or the exposure of the reef, the consequences of such altered maturity schedules, sizes, longevity and density may be of great significance. For *Thalassoma lunare* to attain a large size an individual must reach an old age, there were relatively few small, old individuals. For individuals residing in

habitats where survivability is low, reaching a large size (and therefore older age) is unlikely. In these regions, where maximum size and age is reduced, the compensatory mechanism for increasing reproductive output is smaller size and younger age at maturity. If individuals delay maturity they may increase survivability and increase their fecundity, however, if they mature earlier they may increase generation times (Stearns & Koella 1986). Unless other mechanisms are operational however, (e.g. increased spawning frequency or increased abundance to facilitate similar comparative biomass), lifetime reproductive output may be significantly reduced compared to other regions in which older ages and larger sizes are reached. As Cole (1954) highlighted, selective advantages of extended life spans must be evaluated against the benefits that accrue due to small increases in reproductive effort (or to small reductions in the age at first reproduction). However, age specific mortality rates need to be taken into account (Charnov & Schaffer 1973). High adult to juvenile survival ratio expends the least reproductive effort, delays reproduction and experiences the lowest survival cost of reproduction (Hutchings 1993). Furthermore, if mortality is constant then lifetime reproductive output will increase with indeterminate growth.

An index of potential reproductive output for each population can be modelled following each general life history alternative exhibited by *T. lunare* (Figure 6.1). Assuming the age at maturity is the first age at reproduction, size at each age class is predicted as:

$$L_t = L_\infty(1 - \exp(-k^t))$$

where L_t is the estimated standard length at age t, L_∞ and k are the estimates for the population mean asymptotic standard length and curvature coefficient respectively. Fecundity is a function of body size at each age (L_t) where:

$$f(L_t) = 0.001e^{0.0518L_t}$$

based upon the relationship between gonad weight and body size of approximately 300 mature female *T. lunare*. Then the index of reproductive output can be calculated for each age class as:

$$IRO_t = d \exists f(L_t)$$

where IRO_t represents the index of reproductive output at each age class and d is the estimate of abundance found at the region under examination. By plotting the cumulative value against age for the region, a representative value of lifetime reproductive output can be estimated (Figure 6.1). It is evident that populations able to achieve large sizes and relatively old ages, even with slower initial growth rates and delayed maturity, are those with a disproportionately large overall reproductive output. However, those populations with a significantly reduced final size and life span are able to increase their potential lifetime reproductive output due to exceptionally high abundances and earlier maturity. Those populations living under relatively low abundances, similar ages at first reproduction, marginally increased sizes but significantly longer-lived individuals do not appear to gain any significant advantages. However, these populations may have an advantage simply due to the existence of older individuals. It is now becoming evident that not only do larger females produce more offspring with a greater chance of survival, but older females produce faster growing larvae with a greater resilience to starvation (Palumbi 2004). A certain level of caution is necessary regarding the interpretation of this index of reproductive output, as the existence of sex changing individuals may significantly alter the estimates. However, if this is the case, the reproductive output for each region is still likely to be relative to the maximum size in the population, as the larger terminal males are generally those with a significantly disproportionate mating frequency (Robertson & Warner 1978, Warner & Schultz 1992). Therefore, those populations that are able to reach a large size are potentially able to contribute disproportionately to the meta-population as a whole.

6.2 Relationships between traits

The mechanisms behind the variation in life history aspects of populations of reef fish have been discussed previously (chapters 4 and 5); however, the relationships between the variables are an additional point of interest. Following the examination of Pearson Correlation Coefficients between latitude, density and life history traits of *T. lunare* populations, growth rates were only related to the VBGF parameters (Table 6.1). Populations of *T. lunare* with fast initial growth rates were no more likely to exhibit reduced total mortality, early maturation, or reduced body sizes than those exhibiting slow initial growth rates. In addition, populations exhibiting slow initial growth rates

Table 6.1: Pearson correlation coefficients between latitude, density and life history traits of estimates from *T. lunare* populations throughout two oceanic basins. Only significant correlations are presented. Dimensionless numbers are denoted *. Actual life history values are presented in Chapter 4.

	Latitude	Density	Age_{max}	$Long_{20}$	$Size_{max}$	M	L_{∞}	k	Gr_{ini}	Age_{mat}	$Size_{mat}$	Age_{sex}	$Size_{sex}$
Latitude	—				0.55		0.54				0.84	0.66	0.64
Density		—				0.57						-0.66	-0.69
Age_{max}			—	0.93	0.71	-0.68	0.55			0.65			
$Long_{20}$				—	0.64	-0.77				0.75*			
$Size_{max}$					—		0.89	-0.79		0.65	0.81		0.62
M						—							
L_{∞}							—	-0.94	-0.64		0.76*		0.47
k								—	0.85				
Gr_{ini}									—				
Age_{mat}										—	0.82		
$Size_{mat}$											—	0.90	0.82
Age_{sex}												—	0.85
$Size_{sex}$													—

may mature relatively early (e.g. the Lizard Island population). This is in contrast to those studies on pomacentrids, where individuals exhibiting slower growth rates or smaller size displayed a reduction in survivorship (Jones 1997). Increased growth rate is an important factor in life history models as it is through growth that fish increase fecundity (Fox 1994). However, whilst fitness advantages have been shown for individuals that mature and reproduce early due to faster growth (Hutchings 1993), slow growth may be a sufficient when large final sizes are reached. Furthermore, high growth rates have been linked with reduced survivability (Metcalfe & Monaghan 2003). For example, butterflies with a high growth rate lost significant amounts of weight due to starvation during periods of limited resources, which was then associated with lower survivability when resources were again available (Gotthard et al. 1994). For this protogynous species it appears that final body size, rather than growth rate per se, plays a significant role in the determination of maturity.

Final body size and maximum age were related to age and size at maturity respectively (Table 6.1). Therefore, any peculiarities regarding initial growth rates is likely due to the inter-relationship between other parameters, such as density and mortality. For example, Ningaloo South exhibited relatively slow initial growth rates, yet, early age at maturation. However, this population also exhibited smaller final body size and significantly reduced life spans, partially explained by the positive relationship between density and mortality (Table 6.1). Therefore, whilst a slow initial growth rate was evident, the early maturation at smaller sizes is likely due to the smaller maximum size and younger final ages of this population. Similar results of an increase in size at maturity with an increase in mean asymptotic or maximum size have been reported numerous times (Charnov 1993, Jensen 1996, Rochet 2000). In the presence of strong competition and limited resources, individuals have been shown to mature earlier and at smaller sizes, even with stable growth rates (Blanckenhorn 1998). However, contrasting results have been reported for reef fish as to whether density does in fact alter growth rates (see Pitcher 1992 c.f. Jones 1984).

There may be additional, untested, trade-offs associated with fast growth rates. These trade-offs are often not evident in fish that are annual spawners with short life

spans. However, for *T. lunare* in high latitudes, exhibiting similar growth rates as those from lower latitudes, reduced spawning events throughout the year may be one possibility. In their examination of growth rates of *Menidia menidia* from populations of different latitudes, Billerbeck et al. (2001) discovered no apparent trade-offs in life history parameters when faster growth rates were evident. Nor did they find costs associated with maintenance, tissue synthesis or routine activity. However, they noted that faster growth rates appeared to be related to reduced endurance and/or slower sustained or burst swimming speeds. Therefore, whilst little evidence exists of a trade-off between initial growth rates and other life history variables, energetic costs associated with fast growth rates may need to be examined.

An increase in mortality estimates did not have any apparent trade-off with other life history traits amongst populations of *T. lunare*. Although there was a negative relationship with maximum age and/or longevity, the estimates of mortality based upon catch curves are automatically dependent upon these traits. Life history theory would predict however, that mortality would be high for populations with faster growth or lower mean asymptotic sizes. However, mortality rates estimated for *T. lunare* populations were not significantly different between the majority of regional and local populations. This is despite variation in growth models between regions, habitats and sites. The data therefore suggests that there was no trade-off to larger (or smaller) size with regards to mortality. This is despite the significant correlation reported between size and natural mortality (Pauly 1980).

A correlation between the curvature coefficient (*k*) and mortality was not evident (Table 6.1), despite the attention this relationship has received in the past (Beverton & Holt 1959, Pauly 1980, Charnov 1993). A plausible explanation for this is the lack of a relationship between the curvature coefficient and longevity (Table 6.1). The curvature coefficient describes the rate at which the increase in length decreases (Ricker 1979); it has little relationship with maximum age, especially in reef fish (see Choat & Robertson 2002 c.f. Pauly 1980). However, there is a negative relationship between maximum age and mortality (Table 6.1). Despite this, the curvature coefficient has often been proposed as an indication of mortality or an index of vulnerability (Pauly 1980, Musick 1999a). Species with a curvature coefficient of less than 0.10 have been proposed as particularly

vulnerable with a low resilience to additional levels of mortality (Musick 1999b). Whilst no population of *T. lunare* exhibited curvature coefficients lower than 0.47, the results within this study exemplify the problem with k as a determinant variable to predict mortality. The palm Group of islands exhibited one of the lowest estimates of k, yet according to the maximum size, growth trajectories, maturity schedules, and density, the population at this region exhibited the highest reproductive potential (Figure 6.1). Therefore additional mortality may reduce the age and size structure (Adams et al. 2000, Adams 2002) potentially reducing reproductive output to similar levels exhibited in other populations. Whilst the above traits in a population should not advocate intensive fishing practices, rather the opposite, it highlights the lack of credibility that estimates of k have in determining vulnerability. Instead biomass, longevity and age at maturity need to be taken into account.

6.3. Future directions:

Including this work, there is now a substantial database of age-based demographics for labroid fish (Jones 1980a, Choat et al. 1996, Gillanders 1997, Choat & Robertson 2002, Choat et al. 2003). Furthermore, pomacentrids have received additional interest regarding age-based dynamics (Pitcher 1992, Meekan et al. 2001), in conjunction with a great deal of attention regarding ecological processes that affect population dynamics (see Jones 1991). It is now necessary to broaden the objectives of age-based studies to determine what degree of variation exists between phylogenetic groups. Future work is necessary to couple life history attributes with phylogenetic information (Hutchings & Morris 1985). Furthermore, an examination needs to be performed focusing upon the environmental conditions under which potential differences may exist. Patterns surrounding demographic differences across phylogenetic groups and environmental variation will allow for the generation of hypothesis encompassing a broad range of reef fish. Therefore, it will strengthen our understanding of the processes affecting life histories of the reef fish community as a whole.

It is interesting to note the relative lack of differences regarding longevity estimates. As mentioned, there are several examples in which a range of spatial scales has returned significant differences between the maximum ages of separate populations

(Meekan et al. 2001, Gust et al. 2002). However, examples are becoming increasingly prevalent, including this study, where little difference was found between apparently separate populations (Kritzer 2002, Choat et al. 2003, Williams et al. 2003). Furthermore, recent evidence suggests that fundamental life history theory, such as larger animals live longer, cannot always be applied to reef fishes (Munday & Jones 1998, Mosse 2001, Choat & Robertson 2002). Since Cole (1954) focused attention on the demographic consequences of variable life spans, there have been numerous studies devoted to the determination of longevity (Monaghan & Metcalfe 2000; Norry & Loeschcke 2002). However, few of these studies have applied a multidisciplinary approach and therefore resolution over this pertinent question remains elusive. Demographic analysis of life history traits can provide a framework for comparative studies, especially the apparent trade-offs between shifts in the age at first reproduction versus increases in the reproductive life span (see Roff 1992 & Stearns 1992). Research is therefore necessary to determine the factors affecting longevity, so that informed predictions about potential consequences for increased longevity in reef fish can be made.

Additional to estimates of longevity, mortality is potentially one of the most important parameters when examining life history traits (Pauly 1980). However, it is also one of the most difficult to obtain in fish (Jones 1991, Kritzer et al. 2001). It has been stated extensively that mortality differences play a large role in establishing demographic differences (Kozlowski 1992, van Rooij & Videler 1997, Reznick et al. 2001). However, the lack of differences in mortality between populations in this study was against all predictions. Furthermore, they were in contrast with the results of other traits, such as longevity even though these demographic traits are inherently linked. Greater resolution regarding mortality estimates is therefore essential to increase our understanding of the role survivorship plays in age-based dynamics. Age-specific mortality rates are likely to be an important component, especially with the increased survivorship reported within a few days for settling reef fishes (Doherty and Sale 1985, Searcy & Sponaugle 2001, McCormick & Hoey 2004). Age selective mortality is more difficult to evaluate than single estimates, especially if faster growing fish are subjected to greater mortality, either through natural mortality or fishing mortality or a combination of both (Ricker 1979). However, age-specific mortality rates could be estimated using catch rates of cohorts

from a year-to-year basis with sufficient annual sampling programs (Russ et al. 1998), or through mark recapture programs (Reznick et al. 1996). Regardless of the technique, research is needed to determine intrinsic and extrinsic forces of mortality rates in these populations. The source and rate of mortality may be a significant component to understanding alterations in life history traits and whether these estimates differ between populations (Bertschy & Fox 1999).

Modelling the extent to which phenotypic flexibility exists amongst traits between genetically similar populations would make a valuable contribution to understanding reef fish life histories. Whilst the level of gene flow between the populations examined in this study is unknown at this stage (another avenue of research), the variation in size and growth amongst these populations was extensive. Even between those on a relatively small spatial scale, which are certainly unlikely to exhibit genetic differences (Dudgeon et al. 2000). One problem that was encountered with this study was the potential for confounding habitat and cross-shelf gradients with that of latitude, or oceanic basins. However, for a habitat generalist with a large geographic range, this is always going to be the case. The level of plasticity evident in life history traits of *T. lunare* suggests that it has evolved strategies to account for habitat heterogeneity. Modelling the amount of phenotypic variation evident at present may be one way to discern resilience in the face of global climate change and increased anthropogenic effects.

6.4. Summary:

Thalassoma lunare can be described as a sequential protogynous hermaphrodite with indeterminate growth. In general, this species lives to approximately 6 years of age, however, few individuals may live to be as old as 8 years of age, depending upon the location and habitat. Females mature before the age of one year and change sex at approximately two and a half years of age. Few females remain in the population beyond the age of four, although one 7-year-old female was collected in the One Tree Island Lagoon. Growth is rapid as a juvenile; however, once maturity is reached growth slows, but does not stop, with individuals exhibiting larger size with increasing age. With a maximum size of approximately 180mm SL, the longevity of approximately six years of

age was not unexpected, as age appears to be in proportion to the maximum size compared with most labrids examined to date (see Chapter 2).

Age- and size-based parameters of *Thalassoma lunare* populations throughout both the East Indian Ocean and West Pacific Basin were not consistent with the predictions of 1) slower initial growth rates, 2) larger final body sizes, 3) greater maximum lifespans, 4) decreased mortality, and 5) delayed maturity and sex change from lower to higher latitudes (Figure 6.1). Instead:

- Fast initial growth rates were found at both high and low latitude regions irrespective of final age or size

- Fast initial growth rates appeared not to affect the size or age at maturity.

- Only when populations in exposed regions or under high conspecific densities were excluded did a general increase in maximum body size with an increase in latitude become evident.

- Unlike size, an increase in maximum age with an increase in latitude was only evident in Indian Ocean populations.

- Mortality estimates for populations were similar between regions from lower to higher latitudes in both oceanic basins.

- The relationship between size at maturity and maximum size appeared to drive maturity schedules rather than latitude.

- There was little evidence of age at maturity following a latitudinal cline.

- Density and latitude had a significant role in affecting the size and age at sex change, whereby populations in regions of high density changed sex at smaller sizes and younger ages.

- Evidence suggested that density might play a role in shaping numerous life history parameters, but only once above a critical level.

Additionally, reef exposure played a significantly large role in shaping life history parameters of *T. lunare*, especially along a cross continental shelf gradient. For the most part:

- Populations residing in sheltered regions exhibited slow initial growth rates compared with those populations in exposed regions.

- Populations residing on exposed outer shelf reefs exhibited significantly smaller final body sizes compared with populations on sheltered inshore reefs. These cross-shelf differences were likely to be as large or larger than any latitudinal gradient in size.

- Reduced body sizes of populations under exposed conditions (i.e. the outer reefs) did not always reflect reduced maximum age, nor reduced mortality estimates.

In addition to latitudinal and exposure differences in the age-based demography of *T. lunare*, density appeared to play a significant role in shaping life history parameters:

- Populations exhibiting a relatively high abundance of conspecifics displayed smaller body sizes, reduced longevities and insignificantly high mortality estimates.

- However, it appears that density may only have an effect on size, maximum age and mortality only once it reaches a critical level.

The results of this project highlight the multifactorial nature affecting life history attributes. Clearly, scales of 100's of metres can have a profound effect upon the demography of local populations. These effects can be in the form of differences in longevity, asymptotic mean size and/or mortality. However, these differences do not follow predictions entirely, nor are they similar between regions:

- Estimates of longevity amongst populations within regions were different between similar habitats, and similar between different habitats. However, if

differences were evident, longevity was reduced for populations in regions of high exposure compared with sheltered habitats.

- In contrast, growth trajectories and mortality estimates were more likely to follow predictions as populations within regions residing in vastly different habitats exhibited the largest variation in both growth and mortality. Again, populations in exposed habitats were likely to exhibit reduced growth trajectories and increased mortality.

To predict evolutionary change, life-history theory needs details about the trade-offs that constrain it. Gasser et al. (2000) highlighted that "despite much work on *Drosophila melongaster* in evolutionary research, we do not yet know what trade-offs to expect under which environmental conditions". Reef fish have received significantly less attention, especially in this field. However, an overview from a diversity of reef fish is essential as a first step to evaluating general life history variation and to developing hypothesis regarding the processes affecting life history traits. The lack of consistently strong patterns in demographic variation along both a latitudinal gradient and across oceanic basins in this work highlights one problem of simplicity faced by field-based studies. Natural populations live in heterogeneous environments where habitat variation often drives the evolution of phenotypic plasticity. *Thalassoma lunare* appears to be a perfect example of this. They exhibit variable life history characteristics in response to environmental variation that is more complex than large-scale latitude would predict. With an increased number of studies examining age-based demography over large and small spatial scales it is becoming evident that this is not unusual. However, as a consequence, optimal life history strategies are likely to be different for each environment. This may be evident as earlier maturation at younger ages due to smaller final body size and potentially reduced longevities. However, even with the ability to alter life histories to increase optimality for a particular environment, the reduction in size alone may have significant consequences to the reproductive output of the population. Therefore, these populations may not be contributing to the gene flow in proportional

amounts as those populations in environments that are conducive to large size and increased maximum ages, even with delayed maturity.

Habitat generalists such as *T. lunare* are not unusual amongst coral reef fish. Yet their vulnerability may be similar to those species with strict habitat requirements. The nature of *T. lunare* as a habitat generalist may give it the appearance of a ubiquitous and abundant coral reef fish, however, if the habitats in which it can attain a large size are detrimentally affected, it may have negative impacts for the species as a whole. With reef systems in danger of increased anthropogenic effects it may be necessary to define those environments that are likely to increase reproductive output for a majority of reef fish species so that they can be conserved for the general protection of reef fish populations as a whole.

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