A multi-scale analysis of population dynamics and sexual size dimorphism in a widely distributed coral reef fish family (Acanthuridae)

Thesis submitted by

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General Abstract

There is a large amount of evidence that the demography and associated life history features of coral reef fish vary across a range of spatial scales. Many Indo-Pacific species are particular in that their geographical distribution extends over ocean basins, and there is increasing evidence that a number of coral reef fish display highly asymptotic growth trajectories. This thesis uses an age-based approach to examine the mechanisms and patterns of variation in the demography and associated life history features over broad geographical scales and in the context of asymptotic growth, exploring the nature of the trade-offs in life history traits associated with variation in growth in coral reef fish. Over 1500 individuals of three Acanthurid species, *Ctenochaetus striatus*, *Acanthurus nigricans* and *Acanthurus leucosternon*, were collected at 14 locations across the Indo-Pacific region. Three critical demographic parameters were examined: mean adult body size, growth rate and longevity, and the relationship between size, age and sex was established using the re-parameterised equation of the Von Bertalanffy Growth Function.

We found a longitudinal trend in life span, with Indian Ocean populations being shorter lived than those of the Pacific region, suggesting the presence of differences in population dynamics and recruitment patterns between ocean basins. In contrast, there was no predictable pattern in growth, which varied primarily across locations indicating a substantial effect on growth of local habitat conditions. There was a clear sex-specific structure in growth within all populations sampled. The mechanism underlying the variation in size among and within populations was a mechanism of fast initial growth, which was consistent across species, geographical scales, and across the sexes. This result indicates that adult body size is determined by the rate of growth during the early years of post-settlement life of all individuals, regardless of the nature of sexual ontogeny, suggesting the absence of a trade-off between reproductive and somatic growth in both males and females of the study species. The magnitude of the differences in size between the sexes increased in populations where large absolute adult size was favoured, suggesting an allometric relationship between sexual size dimorphism and the rate of growth of the larger sex. The direction of sex-specific size distributions of the study species varied with adult body size of males, providing evidence that female-biased sexual size dimorphism in acanthurid species is the result of selection for small body size in males.

This study illustrates the importance of early post-settlement life history in shaping the demography and life histories in coral reef fish with a highly asymptotic form of growth, and suggests that determinate growth is associated with: 1) a large potential for flexibility in growth, 2) constraints on the nature of the mechanisms underlying variation in size across geographical scales, and between the sexes, and 3) an evolutionary life history trade-off between juvenile survival and lifetime reproductive success overriding the costs of reproductive growth of females.

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STATEMENT ON SOURCES

DECLARATION

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

General Introduction

The demography of marine fish has been extensively documented, and latitudinal gradients in demographic features have been demonstrated for a wide range of temperate species. In most examples, populations living at low latitudes in warmer environments often grow to small sizes, and have comparatively reduced growth rates as compared to high latitude populations. These results have largely influenced the directions of research in the demography and associated life histories of tropical fish species, and a similar positive correlation with latitude of mean adult size, and in some cases longevity, has been demonstrated for an increasing number of coral reef fish (Meekan et al 2001, Choat and Robertson 2002, Choat et al 2003, Caldow & Wellington 2003).

Whilst the distribution of many Atlantic and Indo-Pacific coral reef fishes span a similar range of latitudes, the longitudinal distribution of some Indo-Pacific Ocean species differs in that it extends over ocean basins and water masses, which have often experienced diverging evolutionary histories. As fish are poikilotherms, we may expect the broad geographical distribution of a species to have substantial effects on its demography and associated life histories. In many temperate fish, large adult body size in colder waters is often achieved through a compensatory mechanism of fast growth associated with a reduction in the length of the growing season at high latitudes (Counter-gradient Variation Model, Conover 1990, Conover and Present 1990, Yamahira and Conover 2002). In tropical species, the possibility that small sizes are the result of reduced growth rates is significant in that it contradicts the generalisation that tropical waters generate faster rates of somatic growth (Pauly 1998).

Variation in size and growth may be influenced by a species' form of growth, and is often accompanied by variation in the underlying trade-offs in life history traits, which often shape the mechanisms associated with demographic variation among populations or individuals (Stearns 1992, Rochet 2000). Growth in fish is indeterminate in a majority of temperate marine species, whereby the continuous relationship between size and age is generally associated with a trade-off between reproductive and somatic growth, and on which most of general life history theory of fish has been largely based (Roff 1992). However, there is increasing evidence that a number of coral reef fish taxa undergo highly asymptotic growth patterns, in which the relationship between size and age is effectively decoupled, including a number of Lutjanidae (Newman et al 1996, 2000), Chaetodontidae (Berumen in press), and Acanthuridae (Choat and Axe 1996, Choat and Robertson 2002). In this case, the potential for growth, and hence for variation in growth, is restricted to the early life history stages of these species, and this has often been explained by a mutually exclusive relationship between reproductive and somatic growth, whereby all energy is allocated to growth during the first years of life, and thereafter switches entirely to the reproductive functions of an individual (Roff 1992).

Geographical variation along latitudinal gradients of temperature has been shown for a number of key life history traits, in a range of poikilotherm taxa. For example, the colder environments of high latitude populations have been associated with increased duration of gonad maturation (Pawson et al 2000), increased size at maturity and fecundity (Cardoso and Defeo 2003), increased rates of somatic energy storage (Schultz and Conover 1997), and increased reproductive output and reduced egg size (Kokita 2003). Consequently, the relationship between somatic and reproductive growth may vary substantially over broad geographical ranges, and we may expect this relationship to be of significance in understanding the mechanisms of variation in growth over broad latitudinal and longitudinal gradients (Arendt 1997). This thesis examines the mechanisms underlying variation in adult body size, growth rate and longevity in coral reef fish across geographical scales, investigating differences among and within populations and exploring the nature of the trade-offs in life history traits associated with an asymptotic form of growth.

Variation in life history trade-offs is most readily studied through examination of sex-specific variation in the relationship between size and age. Sexual size dimorphism is a common feature among coral reef fish species, and the direction of differences in size among males and females of reproductively active populations often varies with species identity. Male-biased sex-specific size distributions are common on coral reefs, and are found in a wide range of fish species, from small-bodied gobies (Lachner and Karnella 1980), to larger-bodied species including Lutjanids (Grimes 1987, Kritzer 2004), Scarids (Robertson and Warner 1978), Labrids (Warner and Robertson 1978), Acanthurids (Robertson 1985), and Serranids (Ferreira 1995). In contrast to most other coral reef fish families, acanthurids are relatively labile in terms of the direction of sexual size dimorphism, and include a number of female-biased and male-biased sexually dimorphic species (Robertson et al 1979, Robertson 1983, 1985). There are a number of reasons why Acanthuridae represent an excellent target group for such an analysis. Firstly, many acanthurid species have wide geographic distribution spanning significant latitudinal and longitudinal gradients across the Indo-Pacific region. Secondly, growth has been described for a number of species in previous publications, and is highly asymptotic (Choat and Axe 1996, Choat and Robertson 2002, Gust et al 2002). Thirdly, female-biased and male-biased sexually dimorphic species co-occur across the region, allowing for a comparative analysis of the mechanisms underlying variation in size among and within populations between the sexes and across geographical scales. Finally, age estimates can be extracted from the analysis of sectioned sagittal otoliths allowing for a size-at-age based approach of the demographic patterns and mechanisms (Choat and Axe 1996, Choat and Robertson 2002).

The general aim of this study is to explore the patterns and mechanisms of variation in the demography and associated life history traits over broad longitudinal and latitudinal geographical scales in widely distributed Indo-Pacific coral reef fish species. For this study I chose acanthurid species with contrasting patterns of sexual size dimorphism to examine the mechanisms and associated trade-offs underlying the variation in demography of these species. *Ctenochaetus striatus* (Quoy & Gaimard) is widely distributed and abundant across the Indo-Pacific region. In this species males are often larger than females. *Acanthurus nigricans* and *Acanthurus leucosternon* are two sister species living in the Pacific Ocean and the Indian Ocean, respectively. In these species, females often reach a larger mean adult body size than males. The asymptotic nature of growth in acanthurids is a key issue in the investigation of variation in the demography and associated life history features in these species. In contrast with slower growing species, acanthurids complete 85% of their somatic growth within the first 15% of their life span, which implies that they undergo a rapid early growth. Consequently, adult body size of males and females is achieved very early in life, and the mechanism responsible for the difference in size among populations and between sexes must act within the limited timeframe of the first years of a lifespan often exceeding 30 years. Therefore I chose three critical demographic parameters to describe growth in these species. These are mean adult body size, growth rate and longevity.

In Chapter 1, I determine the geographical patterns of variation in mean adult body size, growth rate and longevity for *Ctenochaetus striatus* across a range of spatial scales, and explore the relationship between growth rate and adult size along latitudinal and longitudinal gradients. Chapters 2 & 3 focus on the mechanism of variation in size in acanthurid species and examine the underlying trade-offs in reproductive and somatic growth in the context of asymptotic growth. In Chapter 2, I examine the mechanisms underlying large size in males in *Ctenochaetus striatus*, and in Chapter 3, I use a comparative approach of the mechanism underlying large size in females in *Acanthurus nigricans* and *A. leucosternon* with the results found for *C. striatus*.

Chapter 1: Spatial variation of life history features in a widely distributed coral reef fish across the Indo-Pacific region: the importance of early growth

Synopsis

This study examines the spatial patterns in growth and longevity, and the mechanism underlying variation in size across the Indo-Pacific region in a widely distributed species *Ctenochaetus striatus* (Acanthuridae). Size-at-age estimates were collected for over 1000 individuals from the Seychelles in the Indian Ocean to American Samoa in the western Pacific area, and along a latitudinal gradient from Papua New Guinea to the southern Great Barrier Reef. We found a general trend in longevity across the Indo-Pacific region, with shorter-lived populations in the Indian Ocean than in the Pacific region, suggesting differences in population dynamics and varying recruitment patterns between ocean basins. In contrast, there was no predictable pattern in growth across the Indo-Pacific region, and growth varied primarily among locations. These results suggested a large potential for flexibility in growth in the study species, and indicated a substantial effect on growth of local habitat conditions. The mechanism underlying the patterns of variation in size was a mechanism of faster growth, indicating that adult size is determined by the rate of growth during the first year of post-settlement life. This study illustrates the importance of early post-settlement life history in shaping the demographic patterns of a widely distributed species.

1.1. Introduction

Many species of reef fish have broad geographical distributions, and thus span a wide range of environmental conditions (Jones et al 2002). As fish are poikilotherms, we might expect this to have substantial effects on their body size, growth rate and associated life-history traits. Previous studies have primarily focused on the relationship between life history and environmental gradients, and patterns of spatial variation in demography have recently been established for a number of coral reef fish species. These suggest that populations of a given species grow to smaller adult sizes and have shorter life spans at low latitudes than those living at high latitudes (Meekan et al 2001, Choat et al 2003, Choat and Robertson 2002, Caldow & Wellington 2003). However, the Indian and the Pacific Oceans have distinct evolutionary histories, and there is increasing evidence that this is associated with a clear genetic structure in a number of coral reef fish species separating populations from the Indian and the Pacific regions (Bay et al 2004, Bernardi et al 2001). Here we examine the spatial patterns of variation in growth and longevity on an evolutionarily significant geographical scale across the Indian and the Pacific Oceans.

The mechanism underlying variation in body size in fish has primarily been examined in temperate species, and small body sizes at low latitudes are often the result of a reduction in the rate of growth (Conover 1990, Conover and Present 1990, Conover et al 1997, Yamahira and Conover 2002). For tropical species, the possibility that small sizes at low latitudes may be associated with reduced growth rates is significant in that it contradicts the generalisation that tropical waters favour higher growth rates than colder temperate environments (Pauly 1998). Two general hypotheses can be invoked to explain how differences in body size may occur. These include growth-based and age-based mechanisms, and involve combinations of evolutionary, environmental and demographic processes (Partridge and Sibly 1991, Arendt 1997). Under conditions of high mortality rates in adults, growing fast to increase body size may enhance juvenile survival and augment chances to produce large numbers of offspring before mortality occurs (Arendt and Wilson 1999). However, large size does not necessarily imply fast growth, and may be achieved through a relatively long period of slow growth. The relationship between slow growth and larger size involves a trade-off between the benefit of being large and the cost of growth, and may favour individuals in situations of unpredictable and limited resource availability (Arendt 1997). Alternatively, larger body size may be the result of an increase in the length of life. In habitats where environmental conditions generate low and irregular recruitment levels, natural selection may have favoured longer life spans to insure population replenishment (Victor 1983, Warner and Chesson 1985). Combinations of these mechanisms may also occur, and increased longevity may be associated with variation in the rate of growth when maturity is delayed (Stearns and Koella 1986).

The general aim of this study is to explore the spatial patterns of variation in growth and longevity on a broad geographical scale and investigate the mechanisms associated with variation in growth. The relationship between initial size, adult size and longevity will be determined on a range of geographical scales across the Indo-Pacific region in the widely distributed coral reef surgeonfish *Ctenochaetus striatus* (Acanthuridae). The bristletooth surgeonfish is abundant across the Indo-Pacific, and its growth trajectory is highly asymptotic (Choat and Axe 1996, Choat and Robertson 2002, Gust et al 2002). This form of growth implies that the potential for growth, and hence the potential for variation in growth, is restricted to a relatively small proportion of the life span. Consequently, an age-based mechanism in the study species appears unlikely, as mortality in the populations achieving relatively smaller sizes would occur before maturity is reached (Figure 1A). For *C. striatus*, we expect that variation in size will be associated with a growth-based mechanism. In the case of a mechanism of faster growth, we expect a positive relationship between initial size and adult size (Figure 1B). Alternatively, in the case of a mechanism of relatively slow growth, we expect that initial size and adult size will be negatively correlated (Figure 1C). Exploring demographic processes on evolutionary significant geographical scales has broad implications for our understanding of the evolution and the mechanisms shaping life histories in coral reef fish.

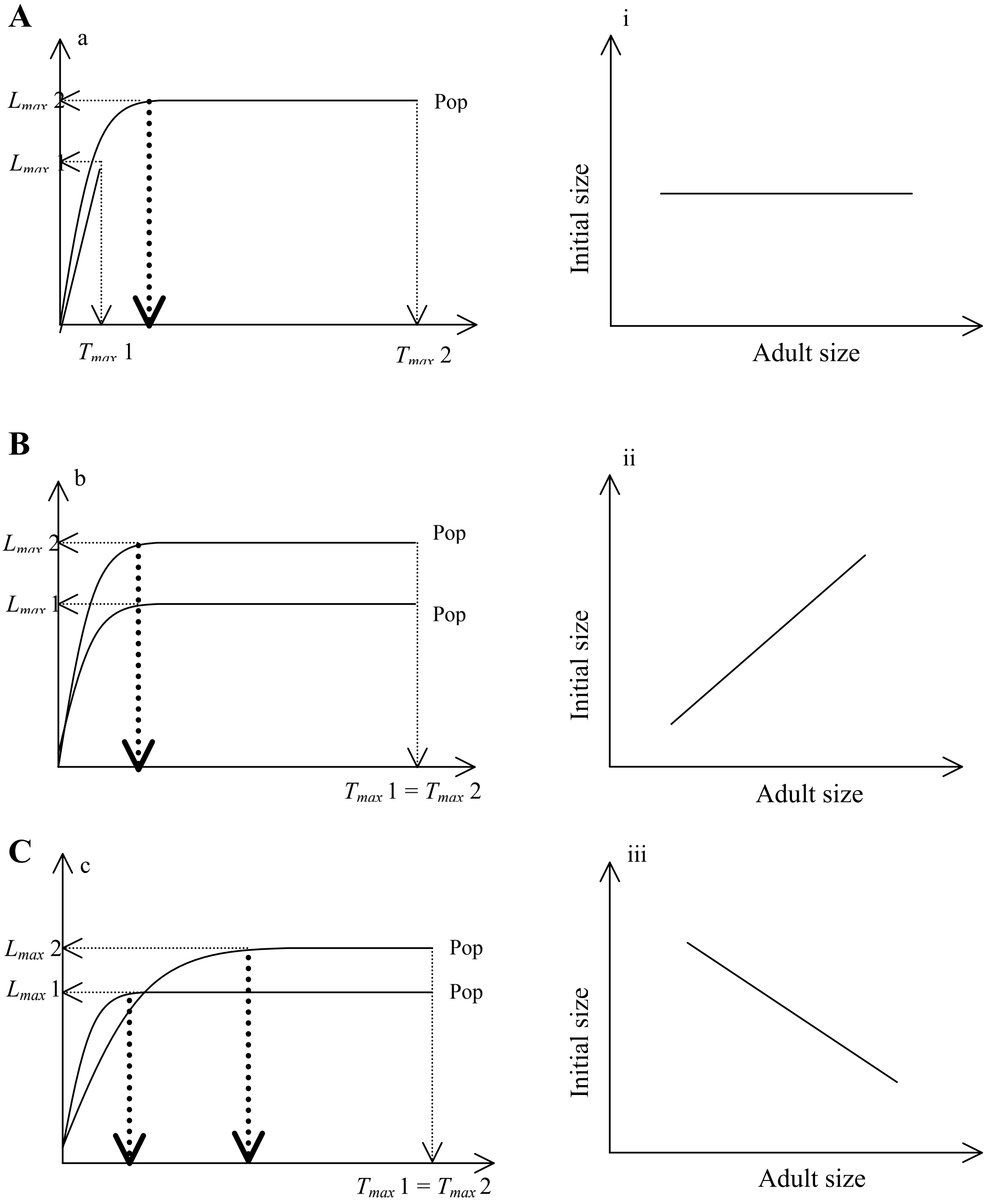


Figure 1. Diagram illustrating the hypotheses explaining the alternative mechanisms underlying variation in growth when growth is asymptotic and the relationship between size and age is decoupled.

Diagrams a – c: lines represent theoretical growth trajectories for hypothetical populations pop 1 and pop 2. Age is presented on the *x*-axis, maximum age achieved is T_{max}, and size is presented on the *y*-axis, L_{max} is mean maximum size achieved. Dashed arrows represent theoretical age at sexual maturity.

Diagrams i – iii: lines represent theoretical relationship between adult body size and initial size underlying hypotheses a, b and c respectively.

Theoretical scenarios A (figures a & i), B (figures b & ii) and C (figures c & iii) explain the three alternative hypotheses for variation in growth in the context of asymptotic growth. Scenario A explains the age-based hypothesis. Scenario B represents the mechanism of faster growth. And scenario C corresponds to the mechanism of slower growth associated with an increased proportion of the life span allocated to growth.

1.2. Materials and methods

1.2.1. Data collection, sampling locations and spatial scales

Samples were collected in the Indian Ocean, the west South Pacific Ocean, and the central South Pacific Ocean. In the Indian Ocean, fish were sampled at four locations: on the reefs fringing the granitic inner islands of the Seychelles (55.4^{o}E, 4.35^{o}S), on the reef edges of the coralline islands of the Amirantes Island group (53.1^{o}E, 6^{o}S), which lie 230 to 1150 km southwest of the Seychelles, in the granitic reefs of Al Halaaniyaats in Oman (57^{o}E, 21^{o}N), which are a highly productive region of cold water up-welling, and at Cocos Keeling Island (96.5^{o}E, 12.3^{o}S). In the western South Pacific Ocean, samples were collected from Papua New Guinea (PNG) in Kavieng (152.5^{o}E, 3.7^{o}S) and Kimbe Bay (151^{o}E, 5^{o}S), and along the Great Barrier Reef (Australia) (GBR) from Lizard Island at the northern end of the GBR (145.27^{o}E, 14.4^{o}S), including the fringing reefs surrounding Lizard Island and the exposed reef fronts of the outer shelf, from the mid-shelf reefs off Townsville in Central GBR (146.48^{o}E, 19.13^{o}S), and from One Tree Island at the southern end of the GBR (152.3^{o}E, 23.42^{o}S). Independent samples were collected from the reef crest and the lagoonal areas at Cocos Keeling and One Tree islands, and at Lizard Island samples were collected on along a cross-shelf gradient from the mid-shelf reefs of Lizard Island and the outer-shelf reefs of No Name, Day and Hicks reefs. In the central South Pacific Ocean, samples were collected in American Samoa (170^{o}W, 14.2^{o}S), from the fringing coral reefs of Ofu, Olosega, Ta'u and Tutuila. Sampling locations and scales are summarised in Figure 2.

A total of 1367 individuals were speared on scuba and snorkel. On collection, individuals were immediately placed in an ice-slurry on the boat until return to the laboratory for processing on the same day. Fork Length (FL) was measured to the nearest millimetre for each individual, and the sagittal pair of otoliths was removed through sectioning of the skull, cleaned and stored dry in trays.

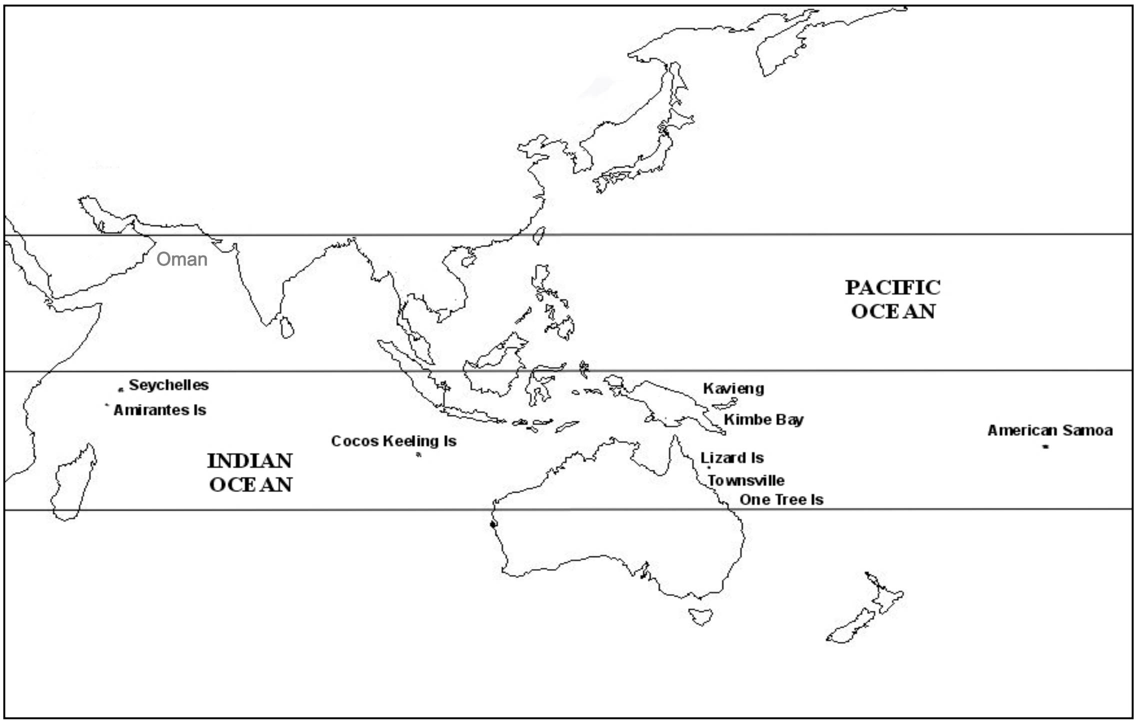


Figure 2: Map illustrating the 14 sampling locations of *Ctenochaetus striatus* across the Indo-Pacific region. Three islands were sampled in American Samoa: Ofu / Olosega, Ta'u and Tutuila. At Lizard Island we sampled in the inner reefs surrounding the island, and on the outer shelf reefs northeast of Lizard Island.

1.2.2. Otolith preparation and determination of age

All age estimates were based on sectioned sagittal otoliths (Choat and Axe 1996, Hart and Russ 1996). The annual pattern of increment formation has been validated for a number of acanthurid species including *Ctenochaetus striatus* (Choat and Axe 1996). Daily ring formation has been previously validated for juvenile acanthurids of the same Genus (*Ctenochaetus binotatus*, Lou and Moltschaniwskyj 1992).

One sagitta of each pair of otoliths was chosen randomly and weighed, in grams, to the nearest 1x10^{-4} for adults, and to the nearest 1x10^{-5} for juveniles to establish the relationship between otolith weight and age. Site-specific regressions of otolith weight on age allowed checking precision of reading of the number of annuli and daily increments (Boehlert 1985, Choat and Axe 1996). A transverse section was obtained by grinding down both rostral and distal ends of the otolith using 400-1200 grade wet & dry sandpaper, resulting in a thin transverse section containing the nucleus. First, each sagitta was ground mounted on a glass slide and positioned so that the upper limit of the nucleus was sitting just below the edge of the slide and the distal-rostral axe was oriented perpendicularly to the edge of the slide. The half sectioned otolith was then mounted ground-face down, allowing for the distal end to be ground down until rings could be distinguished between the nucleus and the outer margin of the otolith. The section was then covered with Crystalbond^{TM} thermoplastic cement for reading. Annual increments were counted under a stereo dissector with transmitted light, and daily rings were counted under a high-power microscope at 400x magnification with transmitted light. Age was estimated as the mean of three separate readings provided that the three counts did not differ more than 10% from each other. When readings deviated by more than 10%, the second otolith if available was processed, or else the individual was not included in the age-based analyses.

1.2.3. Modelling of somatic growth and estimation of initial size

Estimating initial size and comparing growth trajectories between populations: limitations of the VBGF equation

Growth in fish is traditionally described using the generalised equation of the Von Bertalanffy growth function (VBGF), which often adequately describes growth in fish

(Cerrato 1990, Chen et al 1992). However, the biological interpretability of the VBGF parameters L_{inf}, K and t_0 has often been questioned, and many uncertainties have been raised as to the statistical properties of the parameters when comparing them between populations (Knight 1968, Roff 1980, Ratkowsky 1986, Moreau 1987, Cerrato 1991, Mulligan and Leaman 1992, Craig 1999). Additionally, the "curvature" parameter K is not a true growth rate (Cerrato 1991). K is a measure, as a reciprocal of time, of the time taken before the asymptote is (or would be) reached, and a high value of K does not necessarily imply a high rate of growth. These limitations to the VBGF equation were of primary concern for two key aspects of this study, the assessment of early somatic growth, and the statistical comparison of demographic parameters among populations. Therefore, the VBGF equation was re-parameterised as proposed by Francis (1988), and as seen in Moulton et al (1992) and Ewing (2003).

Re-parameterised version of the VBGF equation

The re-parameterised version of the VBGF equation (rVBGF) is based on three parameters $L(\tau)$, $L(\omega)$ and $L(\mu)$, which are estimated from the average body size at arbitrary ages τ, ω and μ. As a result, the biological significance of the parameters allows for a direct comparison of mean size-at-age data between populations. Ages τ and μ are chosen arbitrarily within the range of the data set so as to represent the general form of growth, and ω is determined by the average age of τ and μ. The re-parameterised equation of the VBGF is described as follows:

$$L(t) = L\tau + \frac{(L\mu - L\tau)(1 - r(2\frac{t-\tau}{\mu-\tau})}{1 - r^2}$$

Where $r = \frac{L\mu - L\omega}{L\omega - L\tau}$, and *L(t)* is average size at age *t* to be predicted by the model, provided that:

1) $L(\tau) < L(\omega) < L(\mu)$
2) $(L\mu - L\omega) \neq (L\omega - L\tau)$

which are limitations of both the generalised and the re-parameterised VBGF.

The focus of this study being the comparison of initial and adult body size between populations sampled, τ and μ were chosen to represent mean size-at-age during both the fast growing and plateauing components of the asymptotic growth trajectory of *Ctenochaetus striatus*. Consequently, age τ was set at 1 year old as a measure of initial size *L(1)*, and age μ at 5 years old for an approximation of adult size *L(5)*. Age ω was calculated to be 3 years old. Thus the parameters for the rVBGF model in this study were *L(1)*, *L(3)* and *L(5)*. Here we will focus primarily on the parameters *L(1)* and *L(5)*. Parameter *L(1)* also provided an estimate of the amount of somatic growth realised between age 0 and age 1 and was considered as an average measure of the initial rate of post-settlement growth of the study species.

The rVBGF model was fitted through the observed size-at-age data of each sample, and the best-fit model describing each data set was determined by minimising the negative Log of the Maximum Likelihood Estimate (Kimura 1980, Haddon 2001). As the rVBGF model has been relatively rarely used to describe growth in fish, expected trajectories generated by the rVBGF were visually compared with the generalised VBGF predictions.

1.2.4. Spatial variation in initial size, adult size and longevity across ocean basins in the Indo-Pacific region

A principal component analysis (PCA) was performed on the parameter values of *L(1)* and *L(5)* and on mean maximum age. Mean maximum age, *mean* T_{max}, was calculated as the average age of the older 5% individuals of each sampled population (modified from Choat and Robertson 2002 for larger sample sizes). The main purpose for using this data exploration technique was to explore the patterns of spatial variation in initial size, adult body size and longevity across the Indo-Pacific region. The Principal Component and Classification Analysis module in the statistical package STATISTICA 6.2 (StatSoft, Inc., Tulsa, Okla.) was used for the analysis.

Confidence regions were generated around the rVBGF parameters *L(1)*, *L(3)* and *L(5)* for all sampled populations using a bootstrapping technique. Each data set was re-sampled 1000 times with replication, maintaining sample size *N* and population age structure (Haddon 2001). For each of the 1000 re-samples, a best-fit combination of the parameters was estimated by minimising the negative Log of the Likelihood given a probability density function with a Poisson distribution (Kimura 1980, Haddon 2001). This generated for each population 1000 combinations of best-fit parameter values thereby producing confidence regions around the original parameters. Confidence intervals were estimated in a similar fashion for assessment of longevity. Each population was re-sampled 1000 times and, for each re-sample, mean maximum age *mean* T_{max} was calculated as the average age of the 5% oldest individuals. Bootstrapping for variance in longevity estimates was performed with replication and maintaining sample size, and resulted in 1000 values of mean maximum age for each population sampled.

Separate analyses of variance (ANOVA) were performed on the bootstrap estimates of *L(1)*, *L(5)* and *mean* T_{max} to test for differences in initial size, adult size and longevity among ocean basins. Ocean was treated as a fixed factor, and locations, nested within each level of ocean, were treated as a random factor. In order to compare samples on a longitudinal gradient, locations at equivalent latitudes were included in the analysis. These were the Seychelles, the Amirantes group and Cocos Keeling reef crest in the Indian Ocean, and Lizard Island, Townsville and Ofu in the Pacific Ocean. These spanned longitudes from the western Indian Ocean to the central South Pacific region. The General Linear Models module in STATISTICA was used for the analyses.

Variance components were then calculated for *L(1)*, *L(5)* and *mean* T_{max} to estimate the proportion of the overall variation that could be explained by each spatial scale (Hughes et al 1999). Mean parameter values of *L(1)*, *L(5)* and *mean* T_{max} were plotted with 95% confidence intervals to illustrate the direction of the differences in initial size, adult size and longevity. Means of parameter values were bias-corrected for the difference between the original parameter value and the mean of the bootstrap estimates of the parameter (Bias-adjusted mean = original value – bias) (Haddon 2001). Confidence intervals were calculated as: $CI = 1.96 * SE$ of the bootstrapped estimates (Haddon 2001).

1.2.5. Spatial variation in initial size, adult size and longevity along a latitudinal gradient in the West Pacific region

A linear regression analysis was used to examine the relationship between latitude and respectively initial size, adult body size and longevity within the West Pacific region.

Bias-adjusted means of the bootstrap estimates of parameters *L(1)*, *L(5)* and *mean* T_{max} were examined for the analysis, and locations included were Kavieng (3.7°S) and Kimbe Bay (5°S) in Papua New Guinea, and Lizard Island (14.4°S), Townsville (19.13°S) and One Tree Island (23.42°S) along the GBR. The null hypothesis tested was that there was no linear relationship between latitude and each dependent variable (slope of zero). Adjusted R^2 values were used to indicate the proportion of the variance explained by the regression model. The analysis was performed using the General Regression Models module in STATISTICA.

1.2.6. Relationship between initial size and adult body size

The relationship between early growth and adult body size (Figure 1) was tested using a bi-variate Correlation Analysis on the bias-adjusted mean bootstrap estimates of *L(1)* as a measure of initial size and of mean maximum size *mean* L_{max} as a measure of adult size. *Mean* L_{max} was calculated from the average size of the 5% oldest individuals and bootstrapped as described in paragraph 1.2.4 for calculation of mean maximum age *mean* T_{max}. The nature of the relationship between the two variables was assessed using Pearson's correlation coefficient. All locations sampled from both ocean basins were included. Mean parameter values of *L(1)* and *mean* L_{max} for each location sampled were plotted with 95% confidence intervals, calculated as: $CI = 1.96 * SE$ of the bootstrapped estimates (Haddon 2001). The Correlation Matrix module in Basic Statistics and Tables in STATISTICA was used to perform the analysis.

1.3. Results

Analysis of the relationship between size and age in fourteen populations of *Ctenochaetus striatus* from the Indian Ocean (5 populations), the west Pacific Ocean (6 populations) and the central Pacific Ocean (3 populations) revealed an asymptotic form of growth that was consistent across locations and geographical scales (Figure 3). In all sampled populations, there was a fast initial growth, which reduced sharply within the first 10 to 40% of the life span before reaching mean asymptotic size. When adult size was achieved there was comparatively little or no change in size over the remaining 60% to 90% of the life span. As a result, size and age are decoupled for most of the species' reproductively active life. This form of growth coincides with that found for *C. striatus* in previous publications (Choat and Axe 1996, Choat and Robertson 2002), and is consistent with the general form of growth of many Acanthurid species (Choat and Axe 1996, Hart and Russ 1996, Craig et al 1997, Choat and Robertson 2002, Gust et al 2002). Growth trajectories plotted using the re-parameterised equation of the Von Bertalanffy Growth Function (rVBGF) resulted in trajectories similar to the generalised VBGF, thus the rVBGF model adequately described growth of the study species.

Whilst all populations sampled displayed a consistent form of growth, there was a large amount of variation in the relationship between size and age among locations. Shifts among populations could be observed along both the *x*- and *y*-axes of the size-at-age relationships, and resulted in variation in longevity, mean maximum size, and steepness of the ascending part of the growth trajectory (Figure 3). This suggested substantial differences among populations in the parameters of longevity, adult size and initial size.

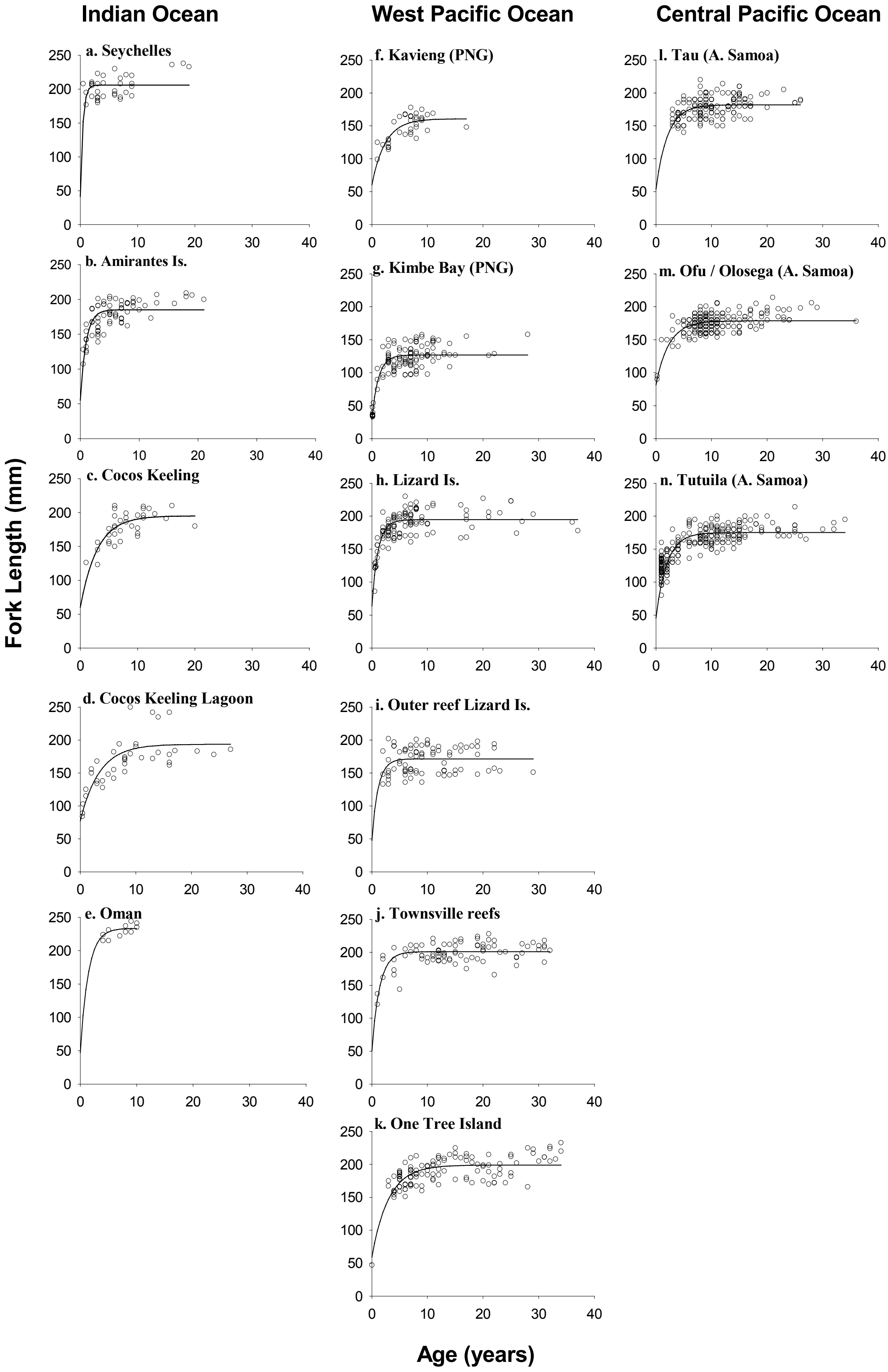


Figure 3. Size-at-age relationships for *Ctenochaetus striatus* across the Indo-Pacific region. Circles present observed size-at-age of individual fish sampled and lines represent best-fit rVBGF growth trajectories from which model parameters L(1), L(3) and L(5) were estimated.

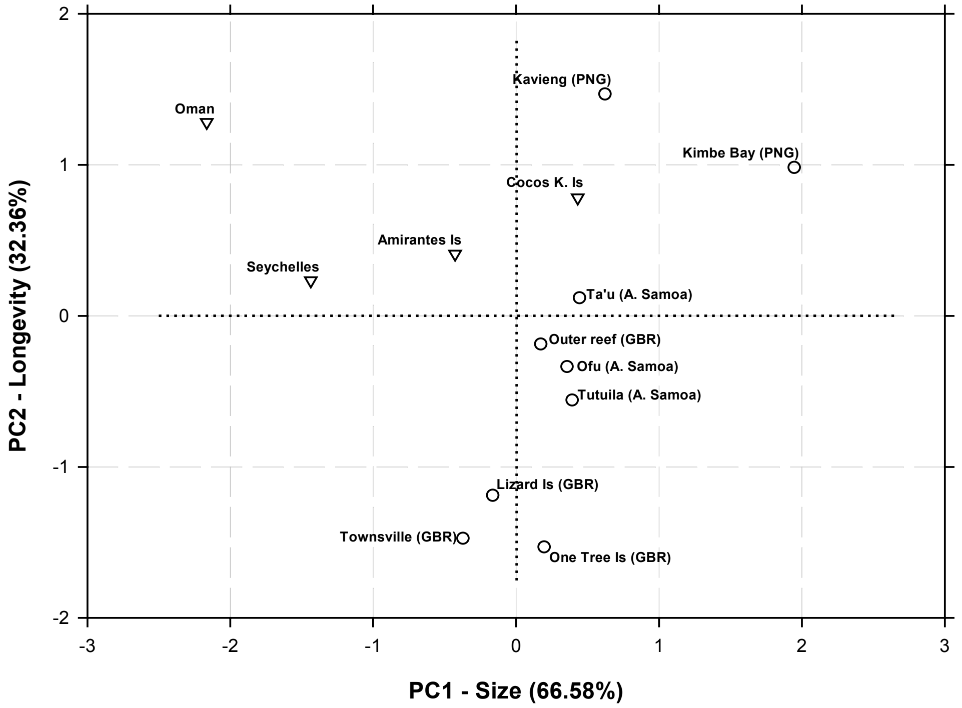


Figure 4. Ordination of the variables *L(1)* for initial size, *L(5)* for adult size, and longevity mean *Tmax* exploring the demography of *Ctenochaetus striatus* across the Indo-Pacific region using principal components analysis (PCA). PC1 explained 66.58% of the variance and was correlated with both variables describing size *L(1)* and *L(5)*. PC2 explained 32.36% of the variance and was correlated with longevity. Triangles illustrate samples from the Indian Ocean and circles from the Pacific Ocean.

Preliminary ordination of mean estimates of asymptotic size, initial size and longevity revealed clear structure in the data (Figure 4). Principal Component Analysis resulted in two principal components PC1 and PC2, which together accounted for 98% of the variation. Both variables of size at age 1 and at age 5 (initial size *L(1)* and adult size *L(5)*) were correlated with PC1, which explained 63% of the variation, and PC2 was correlated with longevity and contributed to explain a further 32% of the variation in demography among the locations sampled. Groupings observed were as follows: i) PC1 and PC2 separated the Indian and the Pacific Ocean populations Indian Ocean populations overall showed larger asymptotic sizes, larger initial sizes and shorter life spans than populations living in the Pacific areas. In contrast, fish living in the Pacific area were generally smaller and longer lived. ii) Among the Pacific Ocean populations, locations appeared to follow a latitudinal trend, with populations in the low latitude locations of PNG displaying smaller adult and initial sizes and reduced life spans, as opposed to the larger and longer-lived populations of the GBR. Central Pacific populations and the outer reefs of Lizard Island showed intermediate sizes and longevities relative to PNG and the GBR. However, even though general trends appeared to structure the demographic data, there remained a considerable amount of variation among locations in all three parameters examined.

Dependent variable	Source of variation	*df*	*MS*	*F*	*p*
L(1)	Ocean	1	241330	0.29	>0.05
	Location	4	837509	43390.42	***<0.001***
	Residual	5994	19		
L(5)	Ocean	1	19	0.00	> 0.05
	Location	4	315626	40031.20	***<0.001***
	Residual	5994	8		
T_{max}	Ocean	1	241140	19.898	***<0.05***
	Location	4	12119	3513.914	***<0.001***
	Residual	5994	3		

Table 1: Results of analyses of variance testing variation in initial body size, adult body size, and mean longevity in *Ctenochaetus striatus* across the Indo-Pacific region. Two geographical scales were examined: 1) between ocean basins, and 2) among locations. Analyses were performed on bootstrap estimates of rVBGF parameters *L(1)* and *L(5)*, and of mean maximum age *mean* T_{max}. Variables tested were initial size *L(1)*, adult size *L(5)*, and mean longevity T_{max}, and categorical predictor variables were Ocean (Indian and Pacific), and Location. Three locations within each ocean basin were included in the analyses; these were the Seychelles, Amirantes Islands and Cocos Keeling in the Indian Ocean, and Lizard Island, Townsville and Ofu in the Pacific Ocean. Significant results are highlighted in bold.

Analysis of variance confirmed the presence of significant differences in longevity among ocean basins (Table 1). Indian Ocean populations were significantly shorter lived than those in the Pacific region (Figure 5). The differences in *mean* T_{max} between ocean basins contributed to explain 48% of the variation. Longevity also varied significantly among locations, which accounted for 30% of the variation in longevity. However, these results suggested an overall trend in longevity on a broad geographical scale across the Indo-Pacific region.

In contrast, analysis of variance of adult size *L(5)* and initial size *L(1)* revealed no significant differences between ocean basins. Variation across locations of both size estimates were explained primarily by differences among locations, which explained 61 to 66% of the variation (Figure 5). This suggested there was no general pattern in size between the Indian and the Pacific Oceans, and that growth in the study species varied substantially on a local scale.

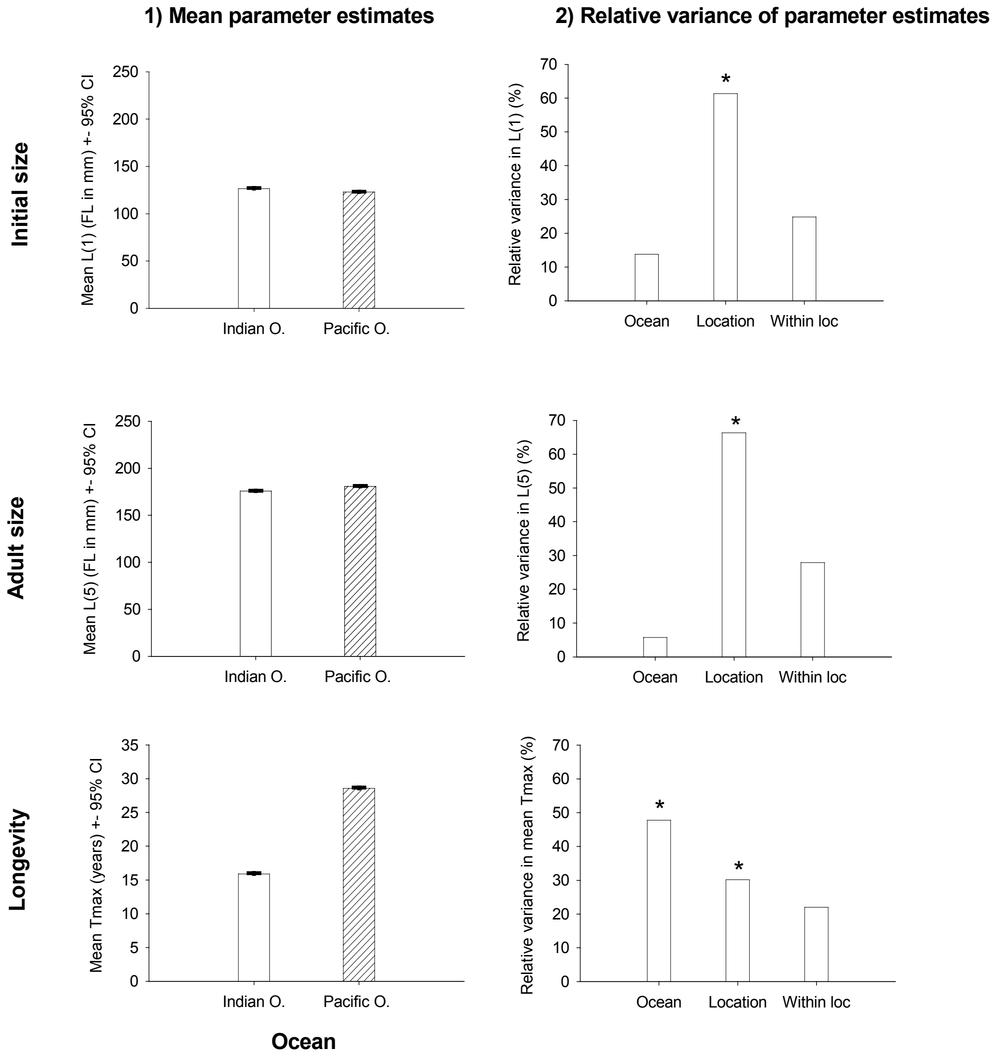


Figure 5. *Ctenochaetus striatus.* Patterns of spatial variation in initial size L(1), adult size L(5) and longevity (mean Tmax) across the Indo-Pacific region. 1) Comparison of mean estimates between ocean basins. Histograms show bias-adjusted mean values of bootstrap estimates for parameters L(1), L(5) and mean Tmax with 95% CI. 2) Variance Components were calculated and plotted for three geographical scales: between ocean basins, among locations and within locations sampled. * show significant results.

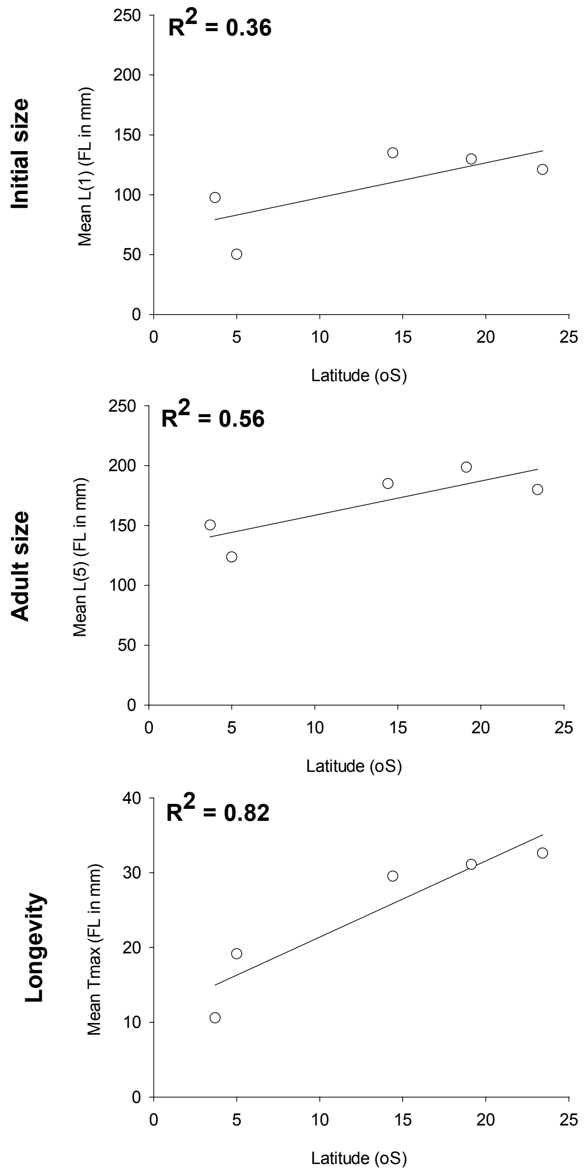


Figure 6. *Ctenochaetus striatus.* Latitudinal variation in initial size *L(1)*, adult size *L(5)* and longevity (*mean Tmax*) in the West Pacific region. Scatterplots show bias-adjusted mean values of bootstrap estimates of parameter estimates *L(1)*, *L(5)* and *mean Tmax* with least-squares regression line. R^2 values indicate the proportion of the variance explained by a latitudinal trend for all 3 parameters examined. Locations plotted were sampled in Papua New Guinea (2) and along the Great Barrier Reef (3).

There was a general latitudinal trend in the three demographic parameters examined. Initial size, adult size and life span overall increased from the low latitudes of PNG to the higher latitudes of the southern GBR, constituting a gradient spanning 20^o of latitude (Figure 6). However, whilst analysis of the relationship of these three variables with latitude within the west Pacific region revealed a significant relationship between longevity (*mean* T_{max}) and latitude, there was no significant relationship of mean initial size (*L(1)*) and mean adult size (*L(5)*) with latitude (Table 2). These results suggested that: 1) there was an increase in the mean length of life of the sampled populations with latitude, whereby populations living at low latitudes experienced shorter life spans than those of higher latitudes, 2) there was a large amount of variation in size at age 1 and 5 among locations sampled. However, populations living in the low latitudes of PNG achieved smaller sizes than those living in the higher latitudes of the GBR region (Figure 6), suggesting that an overall latitudinal trend may be overridden by variation in growth on a local habitat scale.

Dependent variable	Source of variation	*SS*	*df*	*MS*	*F*	*p*
L(1)	Latitude	2520.417	1	2520.417	3.30	*>0.05*
	Locations	2291.339	3	763.780		
	Total	4811.756	4			
L(5)	Latitude	2453.004	1	2453.004	6.15	*>0.05*
	Locations	1196.200	3	398.733		
	Total	3649.204	4			
T_{max}	Latitude	309.429	1	309.429	19.81	***<0.05***
	Locations	46.864	3	15.621		
	Total	356.293	4			

Table 2: Results of linear regression analyses examining latitudinal variation in initial body size, adult body size and mean longevity in *Ctenochaetus striatus* within the West Pacific region, from Papua New Guinea (2 locations) to the Southern Great Barrier Reef (3 locations) (Australia). Analyses were performed on bias-adjusted means of bootstrap estimates of rVBGF parameters *L(1)* and *L(5)*, and of mean maximum age *mean* T_{max}. Continuous dependent variables were initial size *L(1)*, adult size *L(5)* and longevity *mean* T_{max}, and continuous predictor variable was latitude (^{o}S). Significant results are highlighted in bold.

Finally, we examined the relationship between initial size and adult size to determine the mechanism underlying the observed variation in body size among locations by testing the predictions presented in Figure 1. Correlation analysis revealed a significant positive relationship between initial size *L(1)* and mean maximum size *mean* L_{max} (Figure 7). This showed that populations that achieve a larger mean adult size were also larger at age 1, and suggested that adult size is determined by initial size. This corresponds to the hypothesis of a mechanism of fast initial growth.

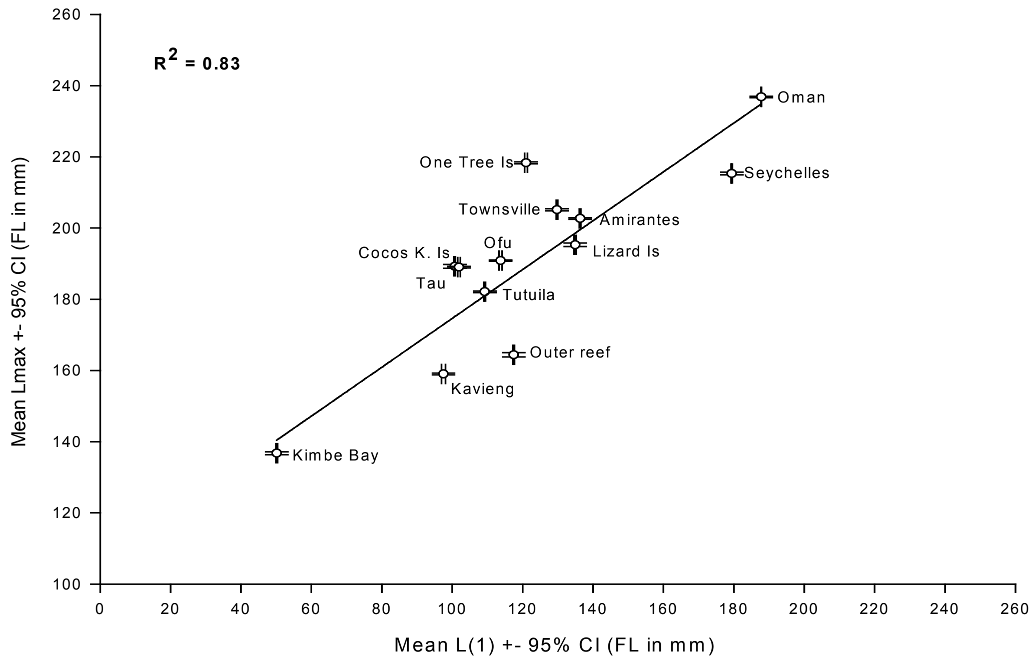


Figure 7. Relationship between mean initial size and adult size of *Ctenochaetus striatus* across populations sampled in the Indo-Pacific region, illustrating the mechanism underlying the spatial variation in size in the study species across the Indo-Pacific region. Means were bias-adjusted values of rVBGF parameter estimate L(1) and mean maximum size L_{max} and are presented with 95% confidence intervals.

1.4. Discussion

Major findings

Examination of the demography of *Ctenochaetus striatus* across the Indo-Pacific region suggests a general trend in longevity across the Indo-Pacific region, and that populations living in the Indian Ocean have shorter life spans than those of the Pacific region. In contrast, this study revealed no general patterns in both initial size and adult size for *C. striatus* across the Indo-Pacific region, and growth in the study species varied primarily on a local habitat scale. Larger adult size is associated with a larger initial size, suggesting that the mechanism underlying variation in size is a mechanism of faster growth. These results have a number of implications. 1) Differences in life span across the Indo-Pacific region suggest distinct population dynamics between ocean basins such as differences in recruitment levels. 2) There is a high potential for variation in size, even though growth is limited to early life history. The first two points suggest different evolutionary mechanisms determining longevity and growth. 3) Adult size is determined by early growth. This implies that the conditions experienced by an individual during early life history will be critical in determining adult size and associated life history features.

Patterns in longevity across oceans

Analysis of the variation in longevity across the Indo-Pacific region revealed substantial differences in life span between the two ocean basins, with Indian Ocean populations being shorter lived than their Pacific Ocean counterparts. Longer life spans are often observed in conditions of low and unpredictable recruitment levels, as it enhances the probability that the reproductively active population survives through a number of reproductive events (Victor 1983, Warner and Chesson 1985, Longhurst 2002). In this case, the presence of shorter life spans in Indian Ocean populations suggests higher recruitment levels and predictability in the Indian Ocean than in the Pacific region. In terms of evolution, an increase in the life span of a population is unlikely to be the result of a short time-scale process and to vary across successive cohorts. This indicates that natural selective pressures may play a role in the evolution of populations' life spans. However, estimation of recruitment levels in both the Indian and the Pacific Ocean basins will be necessary to examine this hypothesis, and its potential influence of the life spans of widely distributed coral reef fish species.

Patterns in growth across oceans

In contrast with longevity, examination of the demography of *Ctenochaetus striatus* on a broad geographical scale revealed no predictable pattern in growth across the Indo-Pacific region. Rather, growth in the study species varied primarily among locations suggesting high levels of variation in growth at a local habitat level. This suggests that growth in *C. striatus* may be determined by local adaptation, or alternatively that there is a high potential for plasticity in growth in the study species. There is increasing evidence that a number of coral reef fish families show a clear genetic structure separating populations from the Indian and the Pacific Oceans (Bernardi et al 2001, Bay et al 2004), and that this may be associated with variable demographic traits and dispersal abilities (Bay et al 2004). Within ocean basin, many highly dispersive species show no clear genetic structure among populations across the Pacific except for a separation with the Hawaiian populations (Bay et al 2004). Furthermore, no genetic structure was found for the study species in the West Pacific region (Doherty et al 1995). However, there is very little information available on the genetic structure of Indian Ocean populations of coral reef fishes. The loose genetic structure within ocean basins and the clear pattern that separates Indian and Pacific populations tend towards the hypothesis of a high potential for plasticity in growth in the study species to explain the large amount of variability in growth found across the Indo-Pacific region. It will prove interesting to further examine the genetic structure of the widespread *C. striatus* across the Indo-Pacific region and within both the Indian and the Pacific Ocean basins.

Demographic patterns within oceans

Our results suggest that local environmental conditions and habitat structure strongly affect the rate of growth and the resulting adult size achieved. When examining variation in growth within the West Pacific region, our results show no significant latitudinal gradient in both initial and adult size among the populations sampled, suggesting a large amount of variation in growth on a local habitat scale within a given ocean basin. This contradicts the pattern found for a number of coral reef and temperate fish species, and may imply that among location variation such as habitat structure and local environmental conditions may contribute to obscuring an overall latitudinal pattern in growth. In contrast, there was a significant trend in longevity increasing with latitude, with populations of low latitudes being shorter-lived than their high latitude counterparts. This result coincides with the emerging patterns found for a number of coral reef fish species, and supports the hypothesis that length of life varies along latitudinal gradients of temperature. Low latitude populations are also associated with higher species diversity and abundance (Meekan and Choat 1997), which may suggest that shorter life spans may be the result of increased intra- and inter-specific competition levels (Choat and Robertson 2002). However, while our results are confined to the West Pacific region, further investigation will be needed to explore variation in size and longevity within the Indian Ocean to determine whether latitudinal gradients in size and longevity are consistent across broad geographical scales.

Mechanism of variation in size

We found a positive relationship between initial size and adult body size indicating that the large amount of plasticity in growth found for *C. striatus* across the Indo-

Pacific region is driven by a mechanism of faster growth. A corollary of this is that large adult body size is the result of increased growth during the first year of life of the fish. This coincides with the Counter-Gradient Variation Model, which explains the mechanism of variation in size in many temperate species (Conover 1990, Conover and Present 1990, Conover et al 1997, Yamahira and Conover 2002). However, this also suggests that high temperatures in tropical waters are not necessarily associated with higher rates of somatic growth, and points to the presence of compensatory mechanisms in growth to environmental factors such as the length of the growing season or colder water temperatures, as demonstrated for many temperate species (Arendt and Wilson 1999, Conover and Present 1990, Schultz et al 1996). This implies that the conditions experienced by an individual from settlement and during their first year of life are crucial in determining the size at which this individual will spend the rest of its life. In coral reef species, asymptotic growth is found primarily in Acanthuridae and Lutjanidae (Choat and Axe 1996, Newman et al 1996, 2000, Choat and Robertson 2002, Kritzer 2002). However, there is increasing evidence that a number of other coral reef fish taxa show similar asymptotic growth patterns (*Scarus frenatus*: Choat et al 1996, Chaetodontidae: Berumen in press). This suggests that similar mechanisms may explain variation in growth in a number of coral reef fish species. The present results also suggest that the restricted potential for variation in size associated with asymptotic growth in *C. striatus* does not appear to prevent highly variable growth patterns.

Conclusion

Our results suggest differences in population dynamics and recruitment levels in the Indian and the Pacific Ocean basins associated with predictable patterns in longevity across the region. In contrast, growth is highly flexible and appears to be largely influenced by local conditions, and early growth plays a critical role in determining adult size. These results have substantial consequences for our understanding of flexibility in growth in highly asymptotic species, and suggest that asymptotic growth does not limit the potential for plasticity in growth in widely distributed species. Furthermore, this study illustrates the importance of modelling early growth for highly asymptotic species. Further investigation is needed in several areas: assessment of recruitment levels in the Indian and the Pacific Oceans, examination of the genetic structure of *Ctenochaetus striatus* across the Indo-Pacific region, and exploration of these hypotheses in other asymptotic coral reef fish species.

Chapter 2. Demographic analysis of sexual size dimorphism in a widely distributed coral reef fish: fast initial growth as the mechanism underlying large size in males

Synopsis

Whilst the evolution of sexual size dimorphism has been largely documented, little is known as to how differences in body size may occur between the sexes. Here we examined two general hypotheses explaining comparatively large size in males, and tested for differences in initial size, adult size, and growth rate between the sexes of a widely distributed coral reef fish. Over 1000 individuals of *Ctenochaetus striatus* (Acanthuridae) were collected across the Indo-Pacific region. We found a significantly greater adult size, initial growth and growth rate in males for each population sampled, but Tutuila. Results of this study suggest that: 1) The mechanism underlying large adult size in males in the study species is the result of a mechanism of fast initial growth, 2) The magnitude of male-biased sex-specific size distributions increased with male size across populations sampled, suggesting the presence of an allometric relationship between sexual size dimorphism and growth of males, and 3) The absence of sex-specific growth patterns in Tutuila (American Samoa) may be the result of size-selective removal through artisanal fishing of larger and faster growing males.

2.1. Introduction

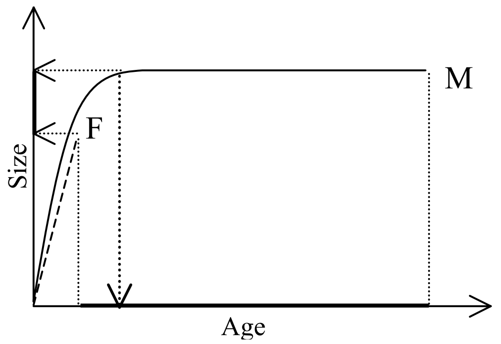
Sexual size dimorphism is defined as a difference in mean body size between sexually mature males and females of a population (Fairbairn 1997). It is a widespread phenomenon among plants and animals, and occurs in a wide range of fish (Parker 1992). The evolution of sexual size dimorphism has been widely documented, and differences in adult body size between the sexes of a reproductively active population are often associated with the distinct reproductive roles of males and females within a given mating system (Guiselin 1969, Warner 1984, Shine 1989, Fairbairn 1997). For example, large male size is often found to increase mating success in polygynous mating systems. However, little is known as to how differences in body size may occur between the sexes, and especially how males and females undergo distinct developmental processes as a result of sex-specific responses to common selective pressures (Badyaev 2002). Here we examine the mechanisms underlying large adult body size in males, in a widely distributed coral reef surgeonfish *Ctenochaetus striatus* (Acanthuridae) across the Indo-Pacific region.

There are two general mechanisms that may explain how males may achieve a larger adult body size than females, and these may be growth-based or age-based (Nylin and Gotthard 1998). In the case of a trade-off between reproductive and somatic growth, males may reach a larger size than females through a mechanism of faster growth when sexual maturation of males is associated with lower costs of reproduction than that of females. Depending on the schedule of sexual ontogeny and the relationship between growth and sexual identity, males may reach a larger size than females through consistent differences in growth established early in the life history, which corresponds to the hypothesis of fast initial growth (Francis and Barlow 1993, Adams and Williams 2001, Munday et al 2004). Alternatively, males may achieve a larger size through sex-specific changes in post-maturational growth patterns, which coincides with the hypothesis of a growth spurt after sexual maturation or sex change (Shine 1994, Choat et al 1996). The key difference between these two growth-based hypotheses lies in the relationship between growth and sexual identity. In the case of fast initial growth, an increased rate of growth may lead to the development of male sexual identity, while in the example of a growth-spurt, fast growth may be the result of sexual maturation as a male. In order to distinguish between these hypotheses, estimates of initial size of males and females and sex-specific growth rates will be necessary, and require an age-based approach.

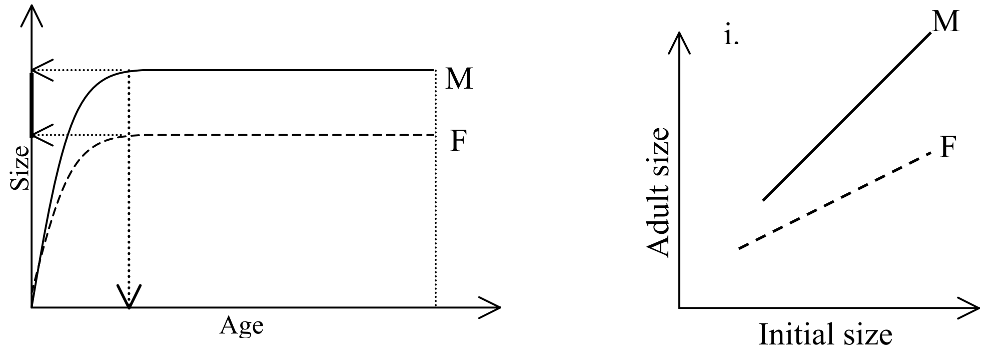
Alternatively, local environmental conditions or physiological requirements may result in sex-specific mortality rates, in which instance males may grow to a larger size than females because they live longer and continue to grow. This age-based hypothesis assumes that growth is continuous throughout life in both sexes. In coral reef fish, the mechanisms underlying variation in size have been most readily observed in species with indeterminate growth, where the potential for flexibility in growth is present throughout the life of the fish. However, there is increasing evidence that growth in many coral reef fish species is highly asymptotic, including a number of Lutjanidae (Newman et al 1996, 2000), Chaetodontidae (Berumen in press), and Acanthuridae (Choat and Axe 1996, Choat and Robertson 2002). In this case, a decoupled relationship between size and age implies that the potential for growth is restricted to the early stages of life history, and that the mechanisms underlying sex-specific size distributions in fast growing species may differ substantially from those underlying sexual size dimorphism in species with continuous growth trajectories.

The general aim of this study is to examine the mechanisms underlying large adult body of males associated with an asymptotic form of growth, in a widely distributed coral reef fish. The relationship between size, age and sex will be determined across geographical scales in the coral reef surgeonfish *Ctenochaetus striatus* (Acanthuridae). Males are often larger than females in this species (Robertson et al 1979, Robertson 1983, 1985, Fouda et al 1988), and growth in *C. striatus* has been described in previous publications (Choat and Axe 1996, Gust et al 2002, Choat and Robertson 2002). As a result of the form of growth, an age-based mechanism underlying the differences in size observed between the sexes in *C. striatus* appears unlikely, as mortality in females achieving relatively smaller sizes would occur before maturity is reached (Figure 1A). We expect that larger size in males will be the result of a growth-based mechanism. In the case of fast initial growth, we expect a positive relationship between initial size and adult size in both sexes, and that growth rate in males will be higher than that of females (Figure 1B). Alternatively, in the case of a growth spurt associated with sexual maturation, we expect to find no correlation between the rate of initial growth and adult size achieved in both males and females of a population (Figure 1C). First we determine the mechanism associated with large male size, and secondly, we examine the mechanisms of variation in the magnitude of sexual size dimorphism in the study species. Understanding how males and females achieve different body sizes will provide insight to the evolutionary mechanisms underlying sexual size dimorphism, and into the trade-offs in life histories associated with variation in growth in asymptotic coral reef fish.

A. *Hypothesis of an age-based mechanism*



B. *Hypothesis of a mechanism of fast initial growth*



C. *Hypothesis of a growth spurt after sexual maturation*

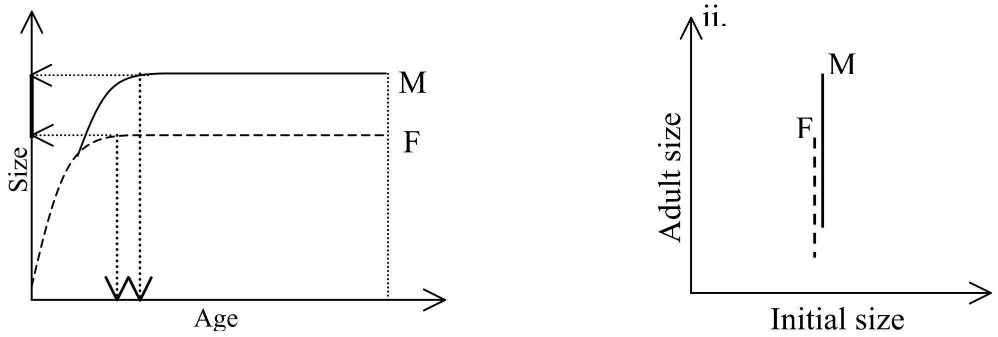


Figure 1. Diagram illustrating the hypotheses for the mechanism underlying sexual size dimorphism in the case where males achieve a larger adult size than females for a species with an asymptotic growth trajectory.

On each graph, males are represented by a continuous line and females are represented by a dotted line.

In the left column are presented theoretical sex-specific growth trajectories: age is presented on the *x*-axis, and size is presented on the *y*-axis. Dashed arrows represent theoretical age at sexual maturity.

Diagrams i & ii: lines represent theoretical relationship between adult body size and initial size in males and females underlying hypotheses b and c respectively.

Theoretical scenarios A (figure 1), B (figures 2 & i) and C (figures 3 & ii) explain the three alternative hypotheses for variation in growth in the context of asymptotic growth. Scenario A explains the age-based hypothesis. Scenario B represents the mechanism of fast initial growth. And scenario C corresponds to the mechanism of a growth spurt associated with the ontogeny of gonad maturation.

2.2. Materials and methods

2.2.1. Study species

Ctenochaetus striatus Quoy & Gaimard is commonly known as the stripped britletooth surgeonfish (Lieske and Myers, 1994). Its distribution extends from the Red Sea and western Indian Ocean to French Polynesia in the central south Pacific region. Spawning of adult *C. striatus* has been observed within polygynous mating units, in which one male dominates over a number of females, and in spawning aggregations of several thousands of individuals, where one female spawns with several males (Robertson 1983).

2.2.2. Data collection and sampling locations

A total of 1162 individuals were speared on scuba and snorkel from the western Indian Ocean to the Central South Pacific region, spanning 135° of longitude and 9° of latitude over the species' range. Approximately 50 to 200 fish were sampled from each location: in the Seychelles (55°E, 5°S), the Amirantes Islands group (53.1°E, 6°S), along the Great Barrier Reef (Australia) from Lizard Island and the exposed reef fronts of the outer shelf (145.27°E, 14.4°S), the mid-shelf reefs off Townsville (146.48°E, 19.13°S), and from One Tree Island (152.3°E, 23.42°S), and in the fringing coral reefs of Ofu/Olosega, Ta'u and Tutuila in American Samoa (170°W, 14.2°S). Sampling locations are summarised in Figure 2.

On collection, individuals were immediately placed in an ice slurry in the boat, until return to the laboratory for processing on the same day. For each individual, Fork Length (FL) was measured to the nearest millimetre, the sagittal pair of otoliths was removed through sectioning of the skull, otoliths cleaned and stored dry in trays, and gonads were dissected. Gonad samples were preserved in FAACC for a subsample of the populations sampled including Lizard Island, Townsville and One Tree Island. At all locations, sex was determined from macroscopic aspect of the gonads (Fishelson et al 1985, 1987, Fouda et al 1988).

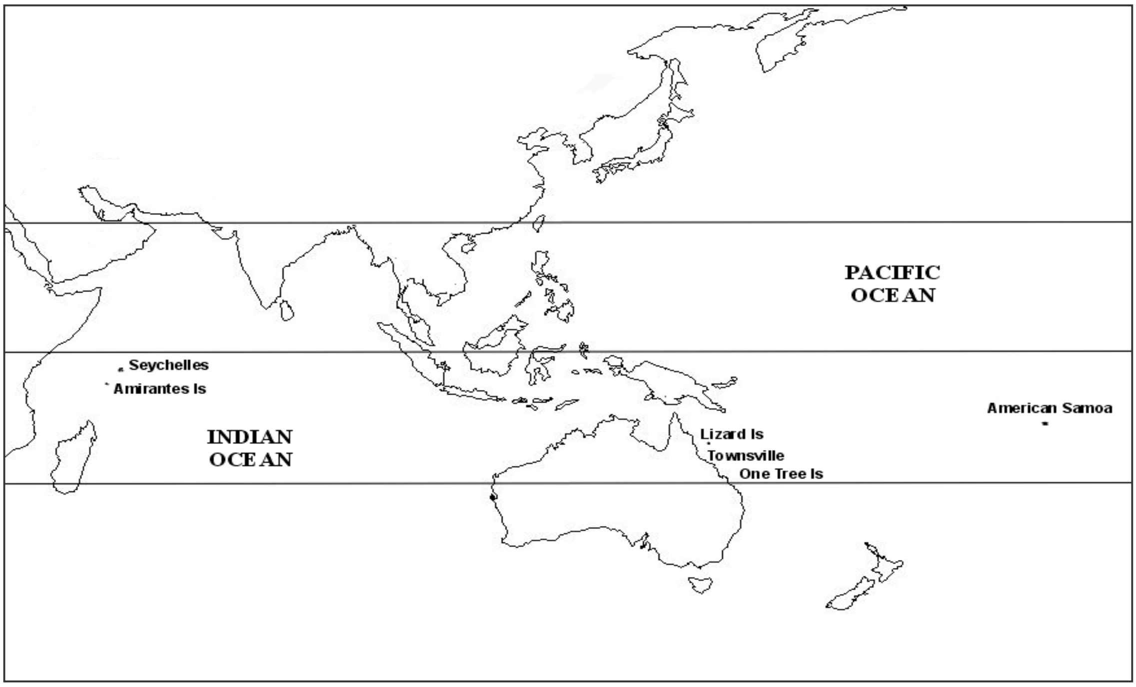


Figure 2: Map illustrating the 9 sampling locations of *Ctenochaetus striatus* across the Indo-Pacific region. Three islands were sampled in American Samoa: Ofu / Olosega, Ta'u and Tutuila. At Lizard Island we sampled in the inner reefs surrounding the island, and on the outer shelf reefs northeast of Lizard Island.

2.2.3. Otolith preparation and determination of age

All age estimates were based on sectioned sagittal otoliths (Choat and Axe 1996, Hart and Russ 1996). The annual pattern of increment formation has been validated for a number of acanthurid species including *Ctenochaetus striatus* (Choat and Axe 1996). Daily ring formation has been previously validated for juvenile acanthurids of the same Genus (*Ctenochaetus binotatus*, Lou and Moltschaniwskyj 1992).

Preparation of sagittal otoliths and estimation of age are described in Chapter 1, section 1.2.2.

2.2.4. Modelling of somatic growth and estimation of initial growth

Growth was modelled separately for males and females of each sample using the re-parameterised equation of the Von Bertalanffy Growth Function (rVBGF) (Francis 1988). The rVBGF equation is described in Chapter 1 section 1.2.3. The model parameters $L(\tau)$, $L(\omega)$ and $L(\mu)$ are based on average body size at three arbitrary ages τ, ω and μ (with $\omega = \frac{\mu + \tau}{2}$). Age τ was chosen at 1-year-old, and age μ at 5-years-old. Age ω was calculated to be 3-years-old. Consequently, the parameters used for this study were *L(1), L(3)* and *L(5)*. However, for the purpose of this study we focused on two of the three parameters including *L(1)* as a measure of initial size and *L(5)* as an estimate of adult size. As the parameters generate expected mean size at age, *L(1)* was also considered as an estimate of the average amount of growth undergone during the first year of life of the fish.

Parameters were estimated for males and females by minimising the negative Log of the Likelihood given a probability density function with a Poisson distribution (Kimura 1980, Haddon 2001), and sex-specific growth trajectories were plotted through observed size-at-age estimates of both sexes at all locations sampled.

2.2.5. Pattern of sexual size dimorphism of the study species across the Indo-Pacific region

Confidence regions were generated around the rVBGF parameters *L(1)*, *L(3)* and *L(5)* for males and females of all sampled populations using a bootstrapping technique, as described in Chapter 1 section 1.2.4. Briefly, for each sampled location sex-specific size-at-age estimates were re-sampled 1000 times with replication, maintaining sample size *N* and population age structure (Haddon 2001). This generated for males and females of each population 1000 combinations of best-fit parameter values thereby producing confidence regions around the original parameters *L(1)*, *L(3)* and *L(5)*.

To test for the presence and direction of sexual size dimorphism in *Ctenochaetus striatus* across the Indo-Pacific region, a two-way factorial analysis of variance (ANOVA) was performed on the bootstrapped estimates of *L(5)* to compare adult size of males and females across locations sampled. Sex was treated as a fixed factor and location as a random factor. All locations sampled were included in the analysis. The General Linear Models module in STATISTICA 6.2 (StatSoft, Inc., Tulsa, Okla.) was used for the analyses. Mean adult size of males and females across populations sampled was plotted with 95% confidence intervals to illustrate the direction of sexual size dimorphism in the study species across the Indo-Pacific region. Means of parameter values were bias-corrected for the difference between the original parameter value and the mean of the bootstrapped estimates of the parameter (Bias-adjusted mean = original value – bias) (Haddon 2001). Confidence intervals were calculated as: $CI = 1.96 * SE$ of the bootstrapped estimates (Haddon 2001).

2.2.6. Mechanism underlying sexual size dimorphism in *Ctenochaetus striatus* across the Indo-Pacific region

To investigate the mechanism underlying larger male size in the study species, we compared initial body size and growth rate between males and females.

Analysis of variance (ANOVA) was performed on the bootstrap estimates of *L(1)* to compare initial size of males and females across locations sampled. Sex was treated as a fixed factor and location as a random factor. All locations sampled were included in the analysis. The General Linear Models module in STATISTICA was used for the analyses. Bias-adjusted mean initial size of males and females across all sampled populations was plotted with 95% confidence intervals to illustrate the direction of the differences.

Sex-specific growth rates were estimated from the slope of the relationship between *L(1)* and *L(5)* independently for males and females across all populations sampled. These represented the average amount of growth achieved between age 1 and age 5 for both sexes, and was used to estimate growth of the ascending part of the growth trajectory of the species. Difference in growth rates between males and females across populations sampled were tested using an analysis of Homogeneity-of-slopes, with *L(1)* as the independent variable. The interaction term between the categorical predictor (sex) and the continuous predictor (*L(5)*) variables was used to assess if the relationship between initial size *L(1)* and adult size *L(5)* differed among the sexes. The analysis was performed using the General Regression Models module in STATISTICA. All populations sampled were included in the analysis.

2.2.7. Variation in the magnitude of sexual size dimorphism in *Ctenochaetus striatus* across the Indo-Pacific region

We examined the relationship between the magnitude of sexual size dimorphism and adult size of males and females using correlation analysis. The magnitude *M* of sexual size dimorphism was calculated as the difference in adult size between males and females as follows: $M = L(5)_{Male} - L(5)_{female}$. Adult size of both sexes was scaled to remove the confounding effect of body size on the magnitude of sexual size dimorphism (allometry, Fairbairn 1997) as follows: Mean scaled adult size of males (M) or females (F) at any given location $\mathrm{Z} = \dfrac{MeanL(5)_{location}}{MeanL(5)_{\sum locations}}$.

Analysis and calculations were performed on the bias-adjusted means of the bootstrapped estimates of *L(5)* for all populations sampled in both species, and correlation analysis estimated the relationship between *M* and scaled adult size of males Z_{male} and females Z_{female} separately. Pearson's correlation coefficient was used to indicate the proportion of the variance in *M* explained by male size and female size. The Correlation Matrix module in Basic Statistics and Tables in STATISTICA was used to perform the analysis.

2.3. Results

Analysis of the relationship between size, age and sex in nine populations of *Ctenochaetus striatus* from the Indian Ocean (2 populations), the west Pacific Ocean (4 populations) and the central Pacific Ocean (3 populations) revealed a clear pattern of sex-specific growth trajectories that was consistent across populations sampled in the Indo-Pacific region (Figure 3). At all locations, growth was asymptotic in both males and females, indicating that both sexes displayed the general form of growth of the species as described in Chapter 1 and a number of previous publications (Choat and Axe 1996, Choat and Robertson 2002). Both sexes experienced fast initial growth, which reduced simultaneously in males and females within the first 10 to 40% of their life span. When asymptotic size was reached, there was comparatively little or no change in size over most of males and females' reproductively active life. The re-parameterized equation of the Von Bertalanffy Growth Function (rVBGF) adequately described growth in both males and females across the species' range.

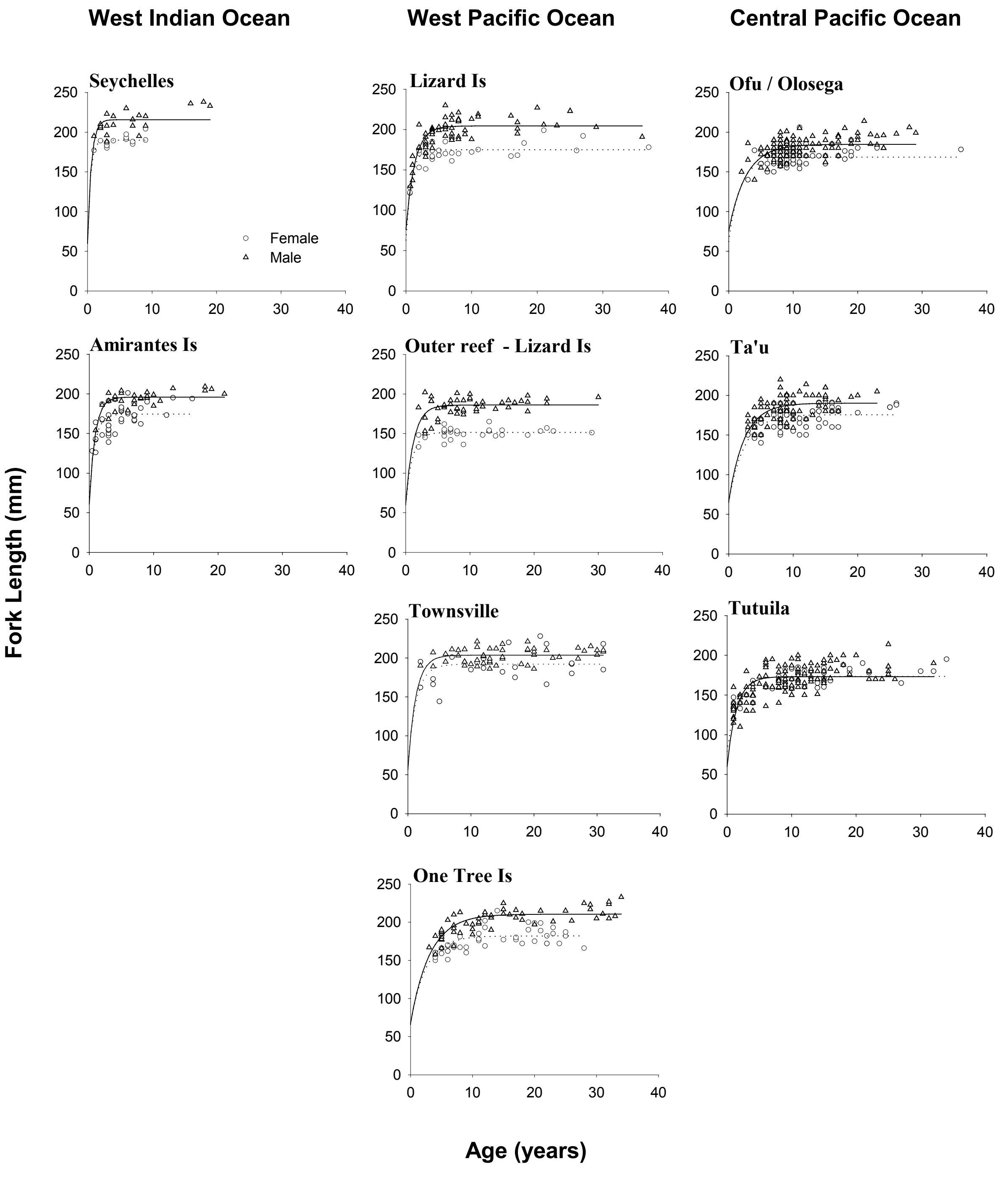


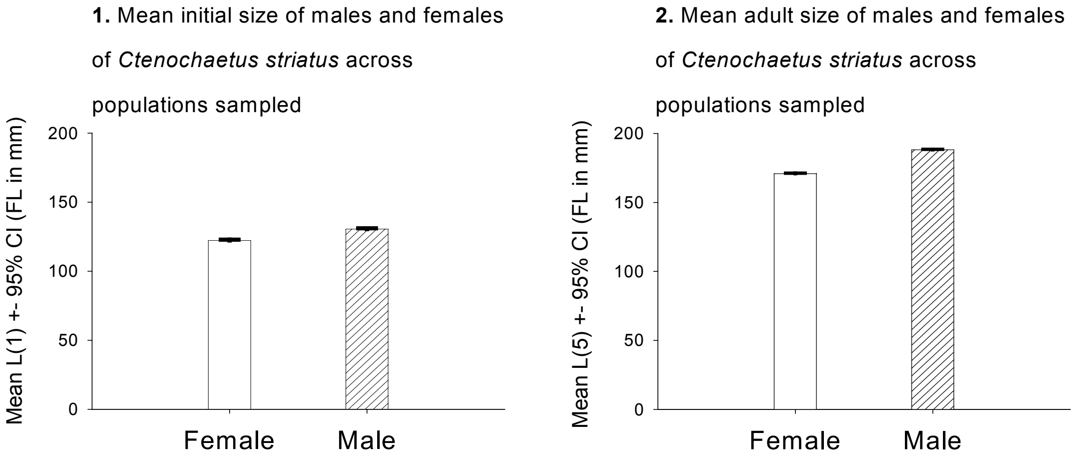
Figure 3. Sex-specific growth trajectories of *Ctenochaetus striatus* across the Indo-Pacific region. Re-parameterised VBGF was fitted through observed size-at-age data of males and females at each sampled location. On each graph, open circles and dotted lines represent female growth, and open triangles and continuous lines represent male growth. All nine populations sampled in the West Indian Ocean, West Pacific Ocean and Central Pacific Ocean (American Samoa) are presented.

Whilst the form of growth was consistent in males and females and across populations sampled, there was a substantial amount of variation in the relationship between size, age and sex. Firstly, differences in size could be observed among locations sampled across geographical scales, which have been examined in Chapter 1 of this thesis. Secondly, analysis of sex-specific growth revealed clear differences in asymptotic size achieved within each sampled population between the sexes (Figure 3). Males achieved a larger asymptotic size than females at all locations sampled, with the exception of Tutuila (American Samoa) where the relationship between size and age was similar in males and females. Analysis of variance on rVBGF model parameter *L(5)* confirmed there was a significant difference in adult size across locations and between males and females across all nine locations sampled (Table 1). Average adult size of males was larger than that of females indicating that the pattern of sexual size dimorphism in *C. striatus* is biased towards large size in males (Figure 4).

Dependent variable	Source of variation	*df*	*MS*	*F*	*p*
L(5)	Sex	1	1346263	22.939	***<0.01***
	Location	8	422019	7.191	***<0.01***
	Sex * Location	8	58688	7129.673	***<0.001***
	Residual	17982	8		
L(1)	Sex	1	305355	10.163	***<0.05***
	Location	8	1543868	51.386	***<0.001***
	Sex * Location	8	30045	1630.167	***<0.001***
	Residual	17982	18		

Table 1: Results of analysis of variance comparing adult size and initial size of males and females in *Ctenochaetus striatus* across populations sampled in the Indo-Pacific region. Analyses were performed on bootstrap estimates of rVBGF parameters *L(1)* and *L(5)*. Dependent variables were initial size *L(1)* and adult size *L(5)*, and categorical predictor variables examined were Sex (fixed factor) and Location (random factor). Significant differences in size are highlighted in bold.

As a result of the asymptotic form of growth of males and females, sex-specific size distributions within each population sampled were determined early in the life history of both sexes. Males and females were both present across all age classes of all nine populations sampled, suggesting that differential size distributions were not associated with a sex-specific age structure, and that the mechanism driving larger adult size in males of the study species was growth-based. Analysis of variance of average size at age 1 between males and females *L(1)* across populations sampled revealed analogous trends as these found in the analysis of variation in adult size. Firstly, there were significant differences in initial size among populations sampled across the Indo-Pacific, and these were described in Chapter 1 of this thesis. Secondly, there was a significant difference in initial size between the sexes across locations (Table 1), and mean initial size of males was significantly larger than that of females (Figure 4). Together with the analysis of sex-specific adult sizes, these results reveal that males are larger than females at both adult size and initial size across populations sampled.


1. Mean initial size of males and females of *Ctenochaetus striatus* across populations sampled

2. Mean adult size of males and females of *Ctenochaetus striatus* across populations sampled

Figure 4. Mean initial body size and adult body size of *Ctenochaetus striatus* across populations sampled in the Indo-Pacific region. Means are bias-adjusted values of bootstrap rVBGF parameter estimates L(1) and L(5), and are presented with 95% confidence intervals. Graph 1 illustrates the difference in body size between the sexes at age 1, and graph illustrates the difference in body size between the sexes at age 5. On both graphs, open bars represent mean size of females, and closed bars represent mean size of males.

There was a significant relationship between size at age 1 and size at age 5 in both males and females across populations sampled, suggesting that in both sexes adult size is determined by initial size (Figure 5). Comparison between males and females of the slopes of the sex-specific relationships between initial size and adult size revealed significant differences in growth rates between the sexes (Table 2). This indicated that males increased in size at a faster rate than females, and suggested that males achieved a larger adult size by growing comparatively faster than females during the ascending part of the asymptotic growth trajectory.

Predictor variable	*df*	*MS*	*F*	*p*
Sex	1	4515	15.66	*<0.001*
L(5)	1	7603628	26364.25	*<0.001*
Sex * *L(5)*	1	23924	82.95	***<0.001***
Residual	1	288		

Table 2: Results of Homogeneity-of-slopes Model testing for significant differences in mean growth rate between males and females of *Ctenochaetus striatus* across the Indo-Pacific region. Sex-specific growth rates are estimated as the slope of the relationship between mean initial size and mean adult size of males and females across locations sampled. Variable tested is initial size, categorical predictor variable is sex, and continuous predictor variable is adult size. Analysis was performed on bootstrap estimates of rVBGF parameters *L(1)* and *L(5)*. Interaction term represents the effect of sex on the relationship between initial size and adult size, and is used here to test for the presence sex-specific growth rates. Significant result of interaction is highlighted in bold.

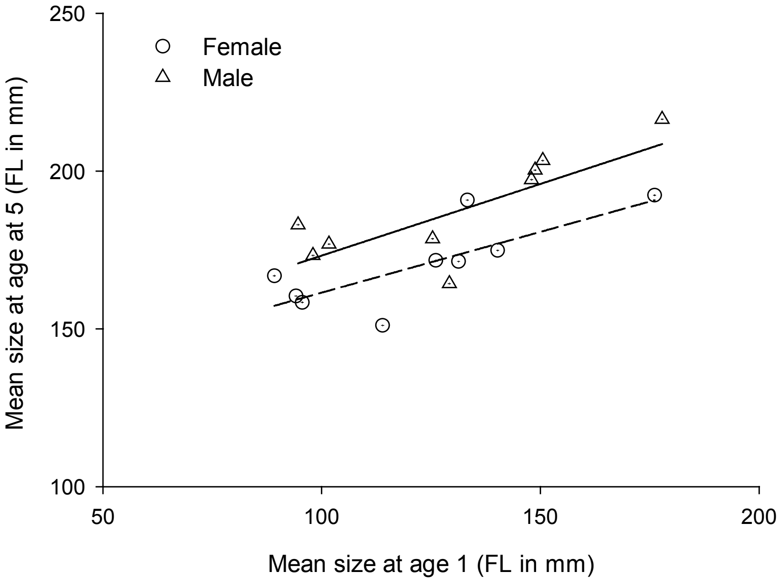
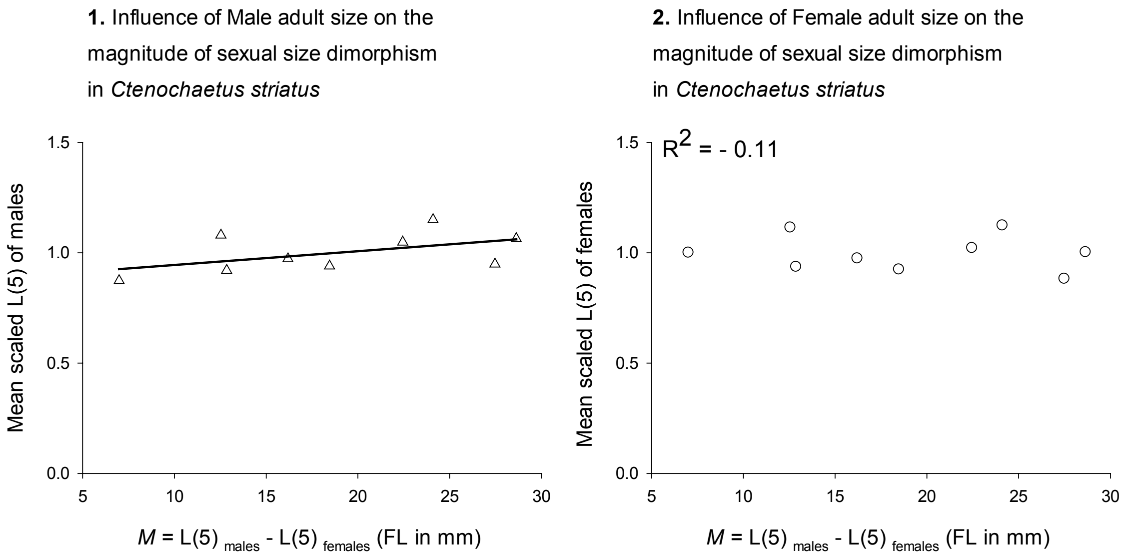


Figure 5. Relationship between initial size and adult size of males and females in *Ctenochaetus striatus* across the Indo-Pacific region, illustrating sex-specific growth rates in the case of male-biased sexual size dimorphism. Males are represented by open triangles and continuous regression line, and females by open circles and dashed regression line.

Although there was a consistent pattern of faster male growth within each of the nine populations sampled, the effect of sex on size differed significantly among locations (Table 1), suggesting that the difference in size between males and females varied among populations. Analysis of the relationship between the magnitude of sexual size dimorphism in *C. striatus* and scaled adult size of males and females revealed that the magnitude of the differential size distributions increased with male size (r^2 = 0.51) and did not vary with female size (r^2 = - 0.11) (Figure 6).


1. Influence of Male adult size on the magnitude of sexual size dimorphism in *Ctenochaetus striatus*

2. Influence of Female adult size on the magnitude of sexual size dimorphism in *Ctenochaetus striatus*

Figure 6. Regression plot showing the influence of male and female adult size on the magnitude of sexual size dimorphism in *Ctenochaetus striatus* across the Indo-Pacific region. Graph 1 illustrates the relationship between L(5) of males and the magnitude *M* of the difference in size between the sexes, and graph 2 illustrates this relationship with L(5) of females. For each graph, sex-specific mean sizes of rVBGF bootstrapped parameter L(5) are scaled to average size of each sex across locations sampled. R^2 values are Pearson's correlation coefficient.

2.4. Discussion

Major findings

Examination of the relationship between size, age and sex in *Ctenochaetus striatus* across the Indo-Pacific region shows a consistent pattern of sex-specific growth across the species' range. Males achieve a larger than females for any given age in all populations sampled, with the exception of Tutuila (American Samoa), where the study species has been heavily targeted in the past as part of the local artisanal fishery (Craig 2002), and growth rates of males are significantly higher than that of females. Furthermore, whilst the direction of sexual size dimorphism and the mechanism underlying larger size in males is consistent across broad geographical scales, the magnitude of the difference in size between the sexes varies among populations, and is positively correlated with adult body size of males. These results have a number of implications. 1) The mechanism underlying male-biased sexual size dimorphism in the study species is a mechanism of fast initial growth, suggesting that the patterns of early growth are critical in determining adult body size of males and females of a population, as well as the presence, direction, and magnitude of sex-specific size distributions. 2) The magnitude of sexual size dimorphism increases in populations where males are larger. And 3) Fishing may influence the presence of sexual size dimorphism through size-specific removal of large and fast growing individuals.

Mechanism underlying male-biased sexual size dimorphism in Ctenochaetus striatus

We found that males achieve a larger adult body size than females through a mechanism of fast initial growth. Two general scenarios have been proposed in the literature to explain the ontogeny of sex-specific growth rates (Badyaev 2002). A population may show a sex-biased genetic variance in growth, in which case there may be a relationship between fast growth and the ontogeny of male sexual identity. Alternatively, individuals of a population may experience sex-specific selection mechanisms during the period of growth. In this case, fast growth may be selected for in a number of individuals of a population during the early life history of the species, and species with polygynous mating systems may tend to generate fast growth in males (through mechanisms of sexual selection). Results of this study do not allow distinguishing between these hypotheses, however our results coincide with increasing evidence for a number of fish species that increased growth rates during the early life history of a species may be associated with male sexual ontogeny (Francis and Barlow 1993, Adams and Williams 2001, Munday et al 2004). This may suggest that primary determination of male sexual identity in *C. striatus* may be the result of a fast rate of growth, and would be influenced by the rate of growth of the surrounding members of a newly recruiting cohort. It will prove interesting to further investigate the mechanisms of sex determination in fish, in order to determine whether these results are consistent across species or the result of a species-specific mechanism.

Asymptotic growth and male-biased sexual size dimorphism: implications for a trade-off between growth and reproduction

Analysis of sex-specific growth in *Ctenochaetus striatus* revealed highly asymptotic growth trajectories in both males and females within all sampled populations. Furthermore, results showed that both sexes reach asymptotic size at a similar age, and that, within the limited proportion of the life span devoted to somatic growth, males achieve a larger adult size than females. It has been demonstrated for a number of closely related species that both sexes are reproductively active by the time adult size has been reached (Hart and Russ 1996, Fishelson et al 1987, Lamantrip and Choat unpubl. data). This contradicts general life history theory, which predicts that determinate growth may be the result of a trade-off between somatic and reproductive growth, whereby resources are exclusively allocated to growth during the ascending part of the trajectory, and to reproduction when asymptotic size is reached (Lester et al 2004). This may suggest for *C. striatus* the presence of substantial selective pressures during the early life history of the species to both achieve adult size and start reproducing early in life. In turn, this suggests that the early life history of the study species is critical for both the somatic and sexual development of the species.

Variation in the magnitude of the difference in size between the sexes in Ctenochaetus striatus

We found a positive relationship between the magnitude of male-biased sexual size dimorphism and adult size of males in the study species across populations sampled.

In contrast, the magnitude of sex-specific size distributions did not vary with female size. It has been shown in a number of animal taxa that variation in the degree to which males are larger than females is associated with the degree of polygyny in the mating system of a given population (Blondel et al 2002, Lindenfors et al 2002, 2003). This suggests that males may adjust growth rate in function of the degree of competition existing within a given population, and that the evolution of large male size in the study species may be the result of sexual selection acting during the early growth of males. However, juvenile individuals of the study species often live in separate habitats than those of adults, hence it appears unlikely that juvenile males would experience selection for adjusting the rate of growth according to the degree of sexual selection present in the population where they settle. Alternatively, it has been demonstrated that the magnitude of the differences in adult body size between the sexes may be the result of the intrinsic difference in growth rates between the males and females of a population. In this case, variation in the degree to which males are larger than females may be the result of an allometric relationship between sexual size dimorphism and adult size of males, rather than an effect of variation in the selective environments across populations of the study species (Fairbairn 1997). Estimates of variation in the abundance and sex ratios of males and females of the study species would be necessary to distinguish between these hypotheses. However, in the case where variation in the magnitude of sexual size dimorphism in *C. striatus* is generated by fast growth in males, these results suggest that the magnitude of the differences in size existing between males and females within a population may be influenced by the absolute adult size and growth rate of a population at a given location. In chapter 1, results suggested that growth in the study species is largely influenced by local environmental conditions. In combination with the results of the present study, this implies that: 1) Adult size of both sexes will vary in accordance across geographical scales, and that: 2) In the case where local habitat conditions favour larger adult sizes, this will result in an increase of the amplitude of the difference in adult size between the sexes. These results indicate that the conditions experienced by a newly recruiting cohort will be critical in determining absolute adult size as well as the magnitude of the differences in size between the sexes, and that there is no difference in the response of male and female growth rates to local environmental conditions, as opposed to the patterns found for many insect taxa (Nylin and Gotthard 1998). The presence of an allometric relationship between sexual size dimorphism and body size may constitute a hypothesis explaining variation in the magnitude of sexual size dimorphism observed for a number of Acanthurid species (Robertson 1985).

Sexual size dimorphism may be reduced through size-selective fishing

In this study, we found a consistent pattern of larger male size across the populations sampled in the Indo-Pacific region but in Tutuila in the Central South Pacific Ocean, where there was no difference in adult size between the sexes. This population was the only location sampled where the study species has been heavily spear fished in the local artisanal fishery (Craig 2002). We hypothesize that the absence of sexual size dimorphism in Tutuila may be the result of the removal of the larger and faster growing males of the population through size-selective fishing, and that removal of the larger individuals may be a result of behavioral patterns associated with larger size in males whereby these individuals were more readily targeted. These results may suggest an effect of fishing on the presence and magnitude of sexual size dimorphism by reducing growth of male populations, and suggests that fishing of sexual dimorphic species may affect growth of male and female populations differently (as seen in

Adams et al, 2000). This may affect the population's mating system and subsequently its reproductive success (Rowe and Hutchings 2003, Hutchings 2004). It will prove interesting to further our understanding of the sex-specific effects of fishing on growth of males and females, and most importantly to determine whether size-selective removal of large individuals affects female-biased sexually dimorphic species in a similar way. In the case where fishing would similarly affect growth in females, we could expect substantial impacts on the future reproductive success of these populations (Palumbi 2004).

Conclusion

Our results suggest that male-biased sexual size dimorphism in *Ctenochaetus striatus* is associated with a mechanism of fast initial growth in males, and that variation in the magnitude of sex-specific size distributions in the study species is associated with an allometric relationship between sexual size dimorphism and body size of males. These results suggest that males may have a comparatively higher intrinsic potential for flexibility in growth than females. In the context of evolutionary mechanisms underlying male-biased sexual size dimorphism in the study species, this may indicate the presence of selective pressures maintaining both an optimum adult body size in females and the capacity for plasticity in growth in males, which coincides with the predictions of the Size-advantage Model. However these conditions do not appear to be associated with the evolution of sex change in the study species, and this may indicate the presence of substantial physiological constraints or adaptive advantages for early sexual maturation in both males and females, which may be associated with life history trade-offs between somatic growth, survival and lifetime reproductive success (Charnov 1986). Furthermore, in the case where sex reversal occurs at 72% of the life span of a given species, the asymptotic form of growth of the study species may have constrained the evolution of sex change, as females would then change sex into reproductively active males before sexual maturation is reached (Allsop and West 2003a, 2003b). It will prove interesting to examine the mechanisms underlying variation in size in species with female-biased sexual size dimorphism to determine whether fast initial growth is associated with a sex-specific trade-off in somatic and reproductive growth correlated with sex-specific costs in reproduction, or with an asymptotic form of growth, in which case a mechanism of fast growth may be the result of trade-offs between survival and the fitness of males and females.

Chapter 3: Demographic analysis of female-biased sexual size dimorphism: the mechanisms and evolution of large body size in females in a widely distributed coral reef fish family

Synopsis

In this study we examined the demographic and evolutionary mechanisms underlying female-biased sexual size dimorphism in coral reef fish. Size-at-age estimates were collected for over 1000 individuals of *Acanthurus nigricans* and *Acanthurus leucosternon*, where females are larger than males, and *Ctenochaetus striatus*, in which males are larger than females, from 6 localities across the Indo-Pacific region. Our results identified a mechanism of fast initial growth underlying large female size in *A. nigricans* and *A. leucosternon* suggesting a positive correlation between the costs of reproductive and somatic growth in the study species. Magnitude of female-biased sexual size dimorphism increased with female size, which provided evidence for an allometric relationship between growth and sexual size dimorphism, and suggested that differences in adult body size between the sexes are greater in populations where local environmental conditions favour large size of males and females. Finally, our results indicate that variation in the direction of sexual size dimorphism among acanthurid species is the result of variation in the size of males, suggesting that the evolutionary mechanisms underlying female-biased sexual size dimorphism in the study species are the result of selection on adult body size of males.

3.1. Introduction

Female-biased sexual size dimorphism is a common feature of many animal taxa. Large reproductively active females are primarily found in invertebrate and poikilothermic vertebrate species, including many species of fish (Fairbairn 1997, Parker 1992). The evolution of female-biased sexual size dimorphism has been largely documented, and the adaptive advantage of large female size is often explained by the positive correlation between female body size and the amount, or quality, of the reproductive output ("Fecundity-advantage Model", Darwin 1874, Shine 1988). While the high costs of reproduction in females has largely been used to explain the scarcity of female-biased sexual size dimorphism in species with determinate growth, there is increasing evidence that large female size occurs in a number of coral reef fish species, where the relationship between size and age is effectively decoupled. These include several Lutjanid (Grimes 1987, Newman et al 1996, 2000) and Acanthurid species (Robertson 1985, Choat and Robertson 2002).

Several alternative hypotheses have been put forward to explain the evolution of female-biased sexual size dimorphism. It has been hypothesized that large size in females may be the result of inter-sexual competition resulting in niche differentiation between the sexes (Shine 1989, Pearson et al 2002). Alternatively, it has been suggested that large size in females may be the result of sexual selection for small size in males. Small male size may allow increased mobility and activity in males when males' mating success depends upon encounter rates with females (scramble competition) ("Guiselin-Reiss Hypothesis", Neems et al 1990, Blanckenhorn et al 1995, Preziosi and Fairbairn 1997, Moya-Larano 2002, Yasuda and Dixon 2002). In this case, evolution of female-biased sexual size dimorphism would be the result of selection for small size in males, rather than that of a selection for large size in females, as proposed by the Fecundity-advantage Model. Here we test this hypothesis by exploring the demographic and evolutionary mechanisms underlying large size in females in a widely distributed coral reef fish family, Acanthuridae. In contrast to most coral reef fish groups, acanthurid fishes (surgeonfish) appear to be particularly labile with respect to sexual size dimorphism. In eleven species examined, six were found to be macroandrous (large male size), three macrogynous (large female size), and four in which no sexual dimorphism (isomorphism) was detected (Robertson 1985). Asymptotic growth has been demonstrated for a number of acanthurid species in previous publications (Choat and Axe 1996, Choat and Robertson 2002).

Determinate growth implies that the potential for growth, and hence the potential for variation in adult size, is restricted to the early post-settlement life history of a species. There are a number of hypotheses that may explain variation in size between the sexes in these species. These include variation in the rate of growth, or in the proportion of the life span allocated to growth. In the case of a trade-off between somatic and reproductive growth, and assuming that the costs of reproduction in females exceeds that of males, females may achieve a large adult size through an increase of the proportion of the life span allocated to growth. This hypothesis assumes a negative correlation between the costs of somatic and reproductive growth, which is often found in conditions of limited resource availability. Alternatively, females may achieve a larger size than males through a mechanism of faster initial growth. This hypothesis assumes a positive correlation between the costs of somatic and reproductive growth in females, and suggests the presence of inter-sexual variation in resource acquisition, as opposed to variation in the strategy of energy allocation between the sexes ("Van Noordwijk and De Jong Model", Van Noordwijk and De Jong 1986, Glazier 1999, Reznick et al 2000).

The general aim of this study is to examine the demographic and evolutionary mechanisms underlying female-biased sexual size dimorphism. We used 3 model-species within the acanthurid group including *Ctenochaetus striatus*, in which males are larger than females, and *Acanthurus nigricans* and *A. leucosternon*, in which females are larger than males (Robertson 1985). The mechanism underlying male-biased sexual size dimorphism has been examined for *C. striatus* in the previous chapter. We first examine the relationship between size, age and sex in *A. nigricans* and *A. leucosternon* across a number of populations over the Indo-Pacific region, in order to distinguish between the hypotheses of sex-specific variation in the duration of growth and sex-specific variation in the rate of growth as potential mechanisms underlying large size in females in these species. In the case of a mechanism of fast initial growth, we expect an increase in the slope of the relationship between initial size and adult size in females. Alternatively, in the case of an increase in the duration of growth, we expect to find no relationship between the rate of initial growth and adult body size achieved. Secondly, we explore the relationship between adult size of males and females, and variation in the magnitude of sexual size dimorphism across female-biased sexually dimorphic populations. In the case of an allometric relationship with body size, we expect to find a positive correlation between the magnitude of sexual size dimorphism and female size (Fairbairn 1997). Finally, we examine the evolutionary mechanism underlying variation in the direction of sexual size dimorphism across acanthurid species. If large female size is associated with the Fecundity-advantage Model, we expect that female size will be large in species with female-biased sexual size dimorphism and comparatively small in species with male-biased sex-specific size distributions. Alternatively, in the case where large female size is the result of adaptive mechanisms selecting for small size in males, we expect to find variation in the size of males across species with contrasting directions of sexual size dimorphism. Examination of the mechanisms underlying large size in females will allow better understanding of the evolution of sexual size dimorphism, and the trade-offs associated with the growth of females.

3.2. Material and methods

3.2.1. Study species

Ctenochaetus striatus is commonly known as the stripped bristletooth surgeonfish (Lieske and Myers 1994). It is an abundant coral reef fish species across the Indo-Pacific region (Randall et al 1990). Spawning has been observed in *C. striatus* within polygynous mating units as well as in spawning aggregations of several thousands of individuals, and male-biased sexual size dimorphism has been described for this species (Robertson 1983).

Acanthurus nigricans (Linnaeus 1758) (also identified as *A. glaucopareius* Cuvier) is found throughout the tropical Pacific Ocean, from Cocos Keeling Islands in the northeastern Indian Ocean to the west coast of Panama and the Galapagos Islands in the eastern Pacific region, and from Japan to south of the Great Barrier Reef on the east coast of Australia (Randall 1987, Randall et al 1990). In the Indian Ocean, *A. nigricans* is replaced by *Acanthurus leucosternon* (Randall 1987). The distribution of *A. leucosternon* (Benett) ranges across the Indian Ocean from the east coast of Africa to Christmas Island southwest of Indonesia (Lieske and Myers 1994). Spawning of *A. nigricans* and *A. leucosternon* has been observed in pairs, and both species display female-biased sexual size dimorphism (Robertson et al 1979, Robertson 1983).

3.2.2. Data collection and sampling locations

A total of 1456 individuals were speared on scuba and snorkel across the Indo-Pacific Ocean in the three study species: *Acanthurus nigricans*, *Acanthurus leucosternon* and *Ctenochaetus striatus*, spanning 135° of longitude and 9° of latitude. 556 individuals of *A. nigricans* were collected in the Western Pacific region from the exposed reef fronts of the outer shelf of Lizard Island (145.27°E, 14.4°S) on the northern Great Barrier Reef (GBR) (Australia) to American Samoa in the Central South Pacific (170°W, 14.2°S) on the fringing coral reefs of Ofu / Olosega Islands, Ta'u Island and Tutuila Island. 46 individuals of *A. leucosternon* were sampled in the western Indian Ocean in the Seychelles (55°E, 5°S) and the Amirantes Islands group (53.1°E, 6°S). 854 individuals of *C. striatus* we sampled in the Seychelles and Amirantes Islands in the western Indian Ocean, on the exposed reef fronts of Lizard Island in the western Pacific region, and in American Samoa from Ofu / Olosega, Ta'u and Tutuila Islands in the Central Pacific Ocean. Sampling locations are summarised in Figure 1.

On collection, individuals were immediately placed in an ice slurry in the boat, until return to the laboratory for processing on the same day. For each individual, Fork Length (FL) was measured to the nearest millimetre, the sagittal pair of otoliths was removed through sectioning of the skull, otoliths were cleaned and stored dry in trays, and gonads were dissected. At all locations, sex was determined from macroscopic aspect of the gonads (Fishelson et al 1986, 1987, Fouda et al 1988).

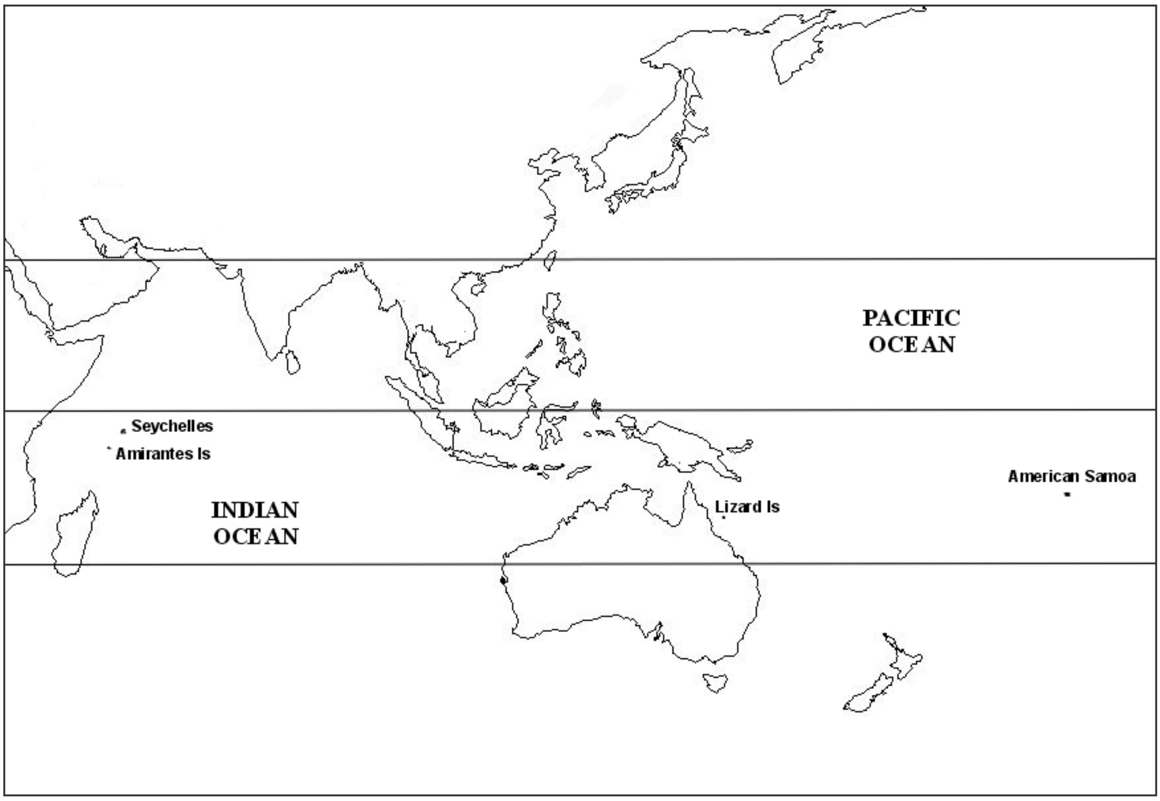


Figure 1: Map illustrating the sampling locations of the sister species *Acanthurus nigricans* in the Pacific Ocean, and *Acanthurus leucosternon* in the western Indian Ocean. Three islands were sampled in American Samoa: Ofu / Olosega, Ta'u and Tutuila. At Lizard Island we sampled in the outer shelf reefs northeast of the island.

3.2.3. Otolith preparation and determination of age

All age estimates were based on sectioned sagittal otoliths (Choat and Axe 1996, Hart and Russ 1996). The annual pattern of increment formation has been validated for a number of acanthurid species including *Ctenochaetus striatus* (Choat and Axe 1996). It is assumed here that a similar periodicity in the pattern of increment formation occurs in *Acanthurus nigricans* and *A. leucosternon*.

Preparation of sagittal otoliths and estimation of age are described in Chapter 1, section 1.2.2.

3.2.4. Modelling of somatic growth and estimation of initial growth

Growth was modelled separately for males and females of each sample using the re-parameterised equation of the Von Bertalanffy Growth Function (rVBGF) (Francis 1988). The rVBGF equation is described in Chapter 1, section 1.2.3. The model parameters $L(\tau)$, $L(\omega)$ and $L(\mu)$ are based on average body size at three arbitrary ages τ, ω and μ (with $\omega = \frac{\mu + \tau}{2}$). Age τ was chosen at 1-year-old, and age μ at 5-years-old. Age ω was calculated to be 3-years-old. Consequently, the parameters used for this study were *L(1), L(3)* and *L(5)*. However, for the purpose of this study we focused on two of the three parameters including *L(1)* as a measure of initial size and *L(5)* as an estimate of adult size. As the parameters generate expected mean size at age, *L(1)* was also considered as an estimate of the average amount of growth undergone during the first year of life of the fish.

Parameters were estimated for males and females by minimising the negative Log of the Likelihood given a probability density function with a Poisson distribution (Kimura 1980, Haddon 2001), and sex-specific growth trajectories were plotted through observed size-at-age estimates of both sexes at all locations sampled.

Confidence regions were generated around the rVBGF parameters *L(1)*, *L(3)* and *L(5)* for males and females of all sampled populations using a bootstrapping technique, as described in Chapter 1, section 1.2.4. Briefly, for each sampled location sex-specific size-at-age estimates were re-sampled 1000 times with replication, maintaining sample size *N* and population age structure (Haddon 2001). This generated for males and females of each population 1000 combinations of best-fit parameter values thereby producing confidence regions around the original parameters *L(1)*, *L(3)* and *L(5)*.

3.2.5. Mechanisms underlying female-biased sexual size dimorphism in *Acanthurus nigricans* and *Acanthurus leucosternon* across the Indo-Pacific region

3.2.5.1. Direction of sexual size dimorphism

As most previous studies of SSD in the study species have been largely size-based, we first determined sex-specific growth trajectories, and compared size-at-age between sexes. We performed an analysis of variance (ANOVA) on the bootstrapped estimates of *L(5)* for males and females of the two species so as to test for significant differences in adult size between the sexes at all location sampled. In order to maintain a balanced design, a subset of two locations for *A. nigricans* was included in the analysis. Choice of the locations did not affect the result of the analysis therefore the two locations were chosen from distinct geographical locations: Lizard Island in the west Pacific and Ta'u in American Samoa. The analysis included three predictor variables: species, location and sex. Location was nested within species, and was treated as a random factor. Sex and species were treated as fixed factors. The General Linear Models module in STATISTICA 6.2 (StatSoft, Inc., Tulsa, Okla.) was used for the analyses.

Mean adult size of males and females across populations sampled was plotted with 95% confidence intervals, separately for *A. nigricans* and *A. leucosternon*, to illustrate the direction of sexual size dimorphism in the study species across the Indo-Pacific region. Means of parameter values were bias-corrected for the difference between the original parameter value and the mean of the bootstrapped estimates of the parameter (Bias-adjusted mean = original value − bias) (Haddon 2001). Confidence intervals were calculated as: $CI = 1.96 * SE$ of the bootstrapped estimates (Haddon 2001).

3.2.5.2. Mechanism underlying large female size in *Acanthurus nigricans* and *Acanthurus leucosternon* across the Indo-Pacific region

In order to investigate the mechanism underlying larger female size in the two study species, we compared initial body size and growth rate between males and females within each species.

We performed an analysis of variance (ANOVA) on the bootstrapped estimates of *L(1)* for males and females of the two species so as to test for significant differences in initial size between the sexes at all location sampled. In order to maintain a balanced design, a subset of two locations for *A. nigricans* was included in the analysis. Choice of the locations is detailed in the above section 3.2.5.1. The analysis included three predictor variables: species, location and sex. Location was nested within species, and was treated as a random factor. Sex and species were treated as fixed factors. The General Linear Models module in STATISTICA was used for the analyses. Bias-adjusted mean initial size of males and females across all sampled populations was plotted with 95% confidence intervals to illustrate the direction of the differences.

Sex-specific growth rates were estimated from the slope of the relationship between initial size and adult size independently for males and females across all populations sampled. *A. nigricans* and *A. leucosternon* are sister species, with *A. nigricans* distributed across the Pacific and *A. leucosternon* across the Indian Ocean, and both show female-biased sexual size dimorphism (as tested above). Therefore, analysis of male and female growth rates was performed across both species, and focused on the difference in growth between the sexes. Analysis was performed on bootstrap estimates of rVBGF model *L(1)* as a measure of initial size, and *L(5)* as measure of adult size. Linear relationship between the parameters represented the average amount of growth achieved between age 1 and age 5 for both sexes, and was used to estimate growth of the ascending part of the growth trajectory of the species. Difference in growth rates between males and females across populations sampled were tested using an analysis of Homogeneity-of-slopes. Variable tested was adult size *L(5)*, categorical predictor variable was sex, and continuous predictor variable was initial size *L(1)*. Interaction term between the categorical predictor (sex) and the continuous predictor (*L(1)*) variables was used to test the effect of sex on the relationship between initial size and adult size. The analysis was performed using the General Regression Models module in STATISTICA. All populations sampled were included in the analysis.

3.2.5.3. Variation in the magnitude of sexual size dimorphism in *Acanthurus nigricans* and *A. leucosternon* across the Indo-Pacific

We examined the relationship between the magnitude of sexual size dimorphism and adult size of males and females using correlation analysis. The magnitude *M* of sexual size dimorphism was calculated as the difference in adult size between males and females as follows: $M = L(5)_{Male} - L(5)_{female}$. Adult size of both sexes was scaled to remove the confounding effect of body size on the magnitude of sexual size dimorphism (allometry, Fairbairn 1997, Smith 1999) as follows: Mean scaled adult size of males or females at any given location $\mathrm{Z} = \dfrac{MeanL(5)_{location}}{MeanL(5)_{\sum locations}}$.

Analysis and calculations were performed on the bias-adjusted means of the bootstrapped estimates of *L(5)* for all populations sampled in both species, and correlation analysis estimated the relationship between *M* and scaled adult size of males Z_{male} and females Z_{female} separately. Pearson's correlation coefficient was used to indicate the proportion of the variance in *M* explained by male size and female size. The Correlation Matrix module in Basic Statistics and Tables in STATISTICA was used to perform the analysis.

3.2.6. Influence of male and female size on the direction of sexual size dimorphism in Acanthurid species

In order to examine the effect of male and female size on the direction of sexual size dimorphism in acanthurid species, we used analysis of variance (ANOVA) to test for differences in male and female size between species with male-biased sexual size dimorphism and species with female-biased sexual size dimorphism (SSD). We used *Ctenochaetus striatus* as a model species for male-biased SSD and *Acanthurus nigricans* and *A. leucosternon* as model species for female-biased SSD. Dependent variable tested was the mean adult size of males and females at each location sampled across the Indo-Pacific region. Locations included were those where both model-species had been sampled so as to cover the distributional range of the study species: Seychelles and Amirantes Islands group (*A. leucosternon* and *C. striatus*) in the Indian Ocean, outer reefs of Lizard Island (*A. nigricans* and *C. striatus*) in the West Pacific region, and Ofu / Olosega Islands, Ta'u Island and Tutuila Island (*A. nigricans* and *C. striatus*) in American Samoa, Central South Pacific Ocean. Predictor variables were Sex (male and female), and Direction of SSD (female-biased and male-biased). Mean adult body size at each location was considered as a replicate value within each group of sex and direction of sexual size dimorphism, thus there were six replicate values within each group, and on which analysis of variance was then calculated. The interaction term between Sex and Direction of SSD was used to examine a potential difference in the effect of sex on adult size between large female and large male species. We used Tuckey's Test for pair-wise comparison of group means to determine the nature of the significant effect of the interaction between Sex and Direction of SSD on mean adult body size of the model species, as determined by ANOVA (see results). Levene's Test was used to examine assumption of homogeneity of variance, and data did not require transformation (Levene's Test, $p>0.05$). The General Linear Models module in STATISTICA was used for the analyses. We then plotted bias-adjusted means of males and females in species with female-biased SSD and species with male-biased SSD with 95% confidence intervals calculated as described in section 3.2.5.1 to illustrate the patterns found in ANOVA.

3.3. Results

Analysis of the relationship between size, age and sex of four populations of *Acanthurus nigricans* across the Pacific region and two populations of *Acanthurus leucosternon* in the Indian Ocean (2 populations), revealed a clear pattern of sex-specific growth trajectories (Figure 2), with the exception of *A. nigricans* in Tutuila and Ofu where the observed sex-specific growth trajectories may be attributed to the presence of unusually large males in these populations. Nonetheless, males and females of each sampled population were present across all age classes, and females consistently achieved a larger asymptotic size than males. This suggested that in both species examined females were larger than males at any given age of their respective life spans. At all locations, growth was asymptotic in both males and females, which coincide with the general form of growth found for of the acanthurid species as described in previous publication (Choat and Axe 1996, Choat and Robertson 2002, chapters 1 and 2 - present thesis). Both sexes experienced fast initial growth, which reduced simultaneously in males and females within the first 10 to 40% of their life span. When asymptotic size was reached, there was comparatively little or no change in size over most of males and females' reproductively active life.

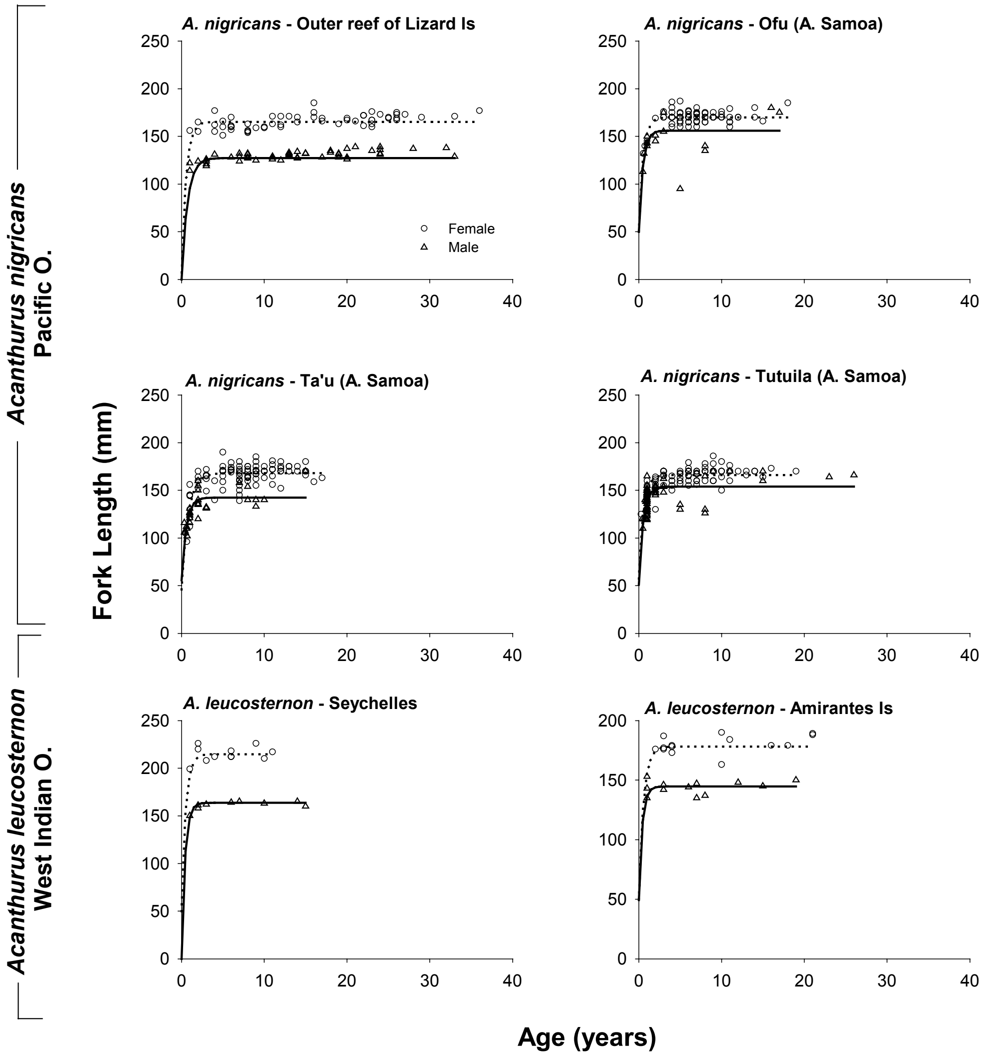


Figure 2. Sex-specific growth trajectories of sister species *Acanthurus nigricans* and *Acanthurus leucosternon* across the Indo-Pacific region. Re-parameterised VBGF was fitted through size-at-age of males and females at each sampled location. Open circles and dotted lines represent female growth, and open triangles and continuous lines represent males growth trajectories.
A. nigricans was sampled on the outer reefs of Lizard Island in the West Pacific region, and in Ofu, Ta'u and Tutuila in American Samoa - Central South Pacific. *A. leucosternon* was sampled in the Seychelles and Amirantes Islands in the Western Indian Ocean.

Analysis of variance on rVBGF model parameter *L(5)* confirmed there was a significant difference in adult size between males and females in both species examined and within all locations sampled (Table 1). Average adult size of females was larger than that of males indicating that the pattern of sexual size dimorphism in *A. nigricans* and *A. leucosternon* is biased towards large size in females (Figure 3). Similar results were found in the analysis of variance of rVBGF model parameter L(1), suggesting a significant difference in initial size between the sexes of both species and at all locations sampled (Table 1). Initial size of females was consistently larger than that of males, indicating that females had undergone a comparatively higher amount of growth during the first year of life (Figure 3). Examination of sex-specific growth rates revealed a significant difference between the sexes in the relationship between initial size and adult size, suggesting that females increase in size at a higher rate than males (Table 2, Figure 4). These results indicated that females grew faster than males during the first of life as well as between age 1 and age 5.

Dependent variable	Source of variation	*df*	*MS*	*F*	*p*
L(5)	Species	1	1321273	3.5	*> 0.05*
	Location (Species)	2	375739	0.6	*> 0.05*
	Sex (Species * Location)	4	630038	123744.1	***< 0.001***
	Residual	7992	5		
L(1)	Species	1	2786126	6.35	*> 0.05*
	Location (Species)	2	438748	0.73	*> 0.05*
	Sex (Species * Location)	4	597966	78839.54	***< 0.001***
	Residual	7992	8		

Table 1: Results of nested analysis of variance comparing adult size and initial size of males and females of *Acanthurus nigricans* and *A. leucosternon* across the Indo-Pacific region. Analysis was performed on bootstrap estimates of rVBGF parameters *L(1)* and *L(5)*. Variables tested were initial size *L(1)* and adult size *L(5)*, and categorical predictor variables were Species (*A. nigricans* and *A. leucosternon*), Location nested within species (Lizard Island and Ta'u for *A. nigricans*, and Seychelles and Amirantes Islands for *A. leucosternon*), and Sex (male and female). Significant results are highlighted in bold.

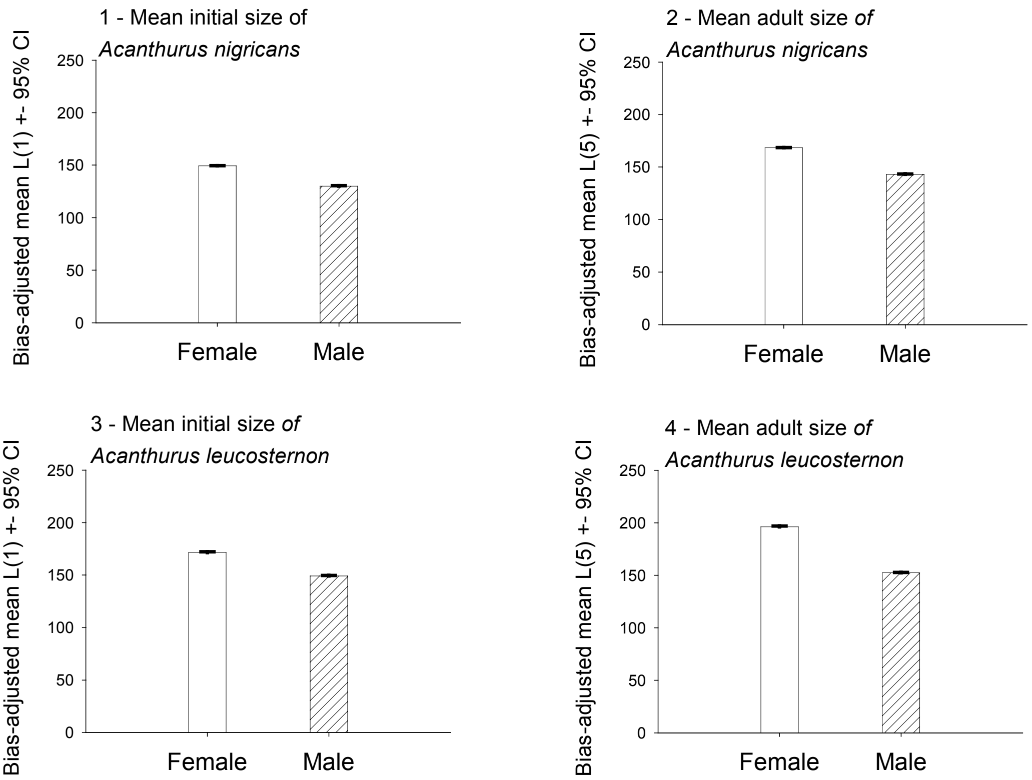


Figure 3. Mean initial size and adult body size of *Acanthurus nigricans* (graphs 1 & 2) and *A. leucosternon* (graphs 3 & 4) across populations sampled in the Indo-Pacific region. Means are bias-adjusted average values of bootstrap estimates of rVBGF parameters *L(1)* and *L(5),* and are presented with 95% Confidence Intervals. Open bars represent mean size of females, and closed bars represent mean size of males.

Predictor variable	*df*	*MS*	*F*	*p*
Sex	1	536	22.39	*< 0.001*
L(1)	1	1826236	76240.81	*< 0.001*
Sex * *L(5)*	1	11346	473.66	***< 0.001***
Residual	7996	24		

Table 2: Results of Homogeneity-of-slopes Model testing for significant differences in mean growth rate between males and females of the sister species *Acanthurus nigricans* and *A. leucosternon* across the Indo-Pacific region. Sex-specific growth rates are estimated as the slope of the relationship between mean initial size and mean adult size of males and females across species and locations. Variable tested is adult size, categorical predictor variable is sex, and continuous predictor variable is initial size. Analysis was performed on bootstrap estimates of rVBGF parameters *L(1)* and *L(5)*. Interaction term represents the effect of sex on the relationship between initial size and adult size, and is used here to test for the presence sex-specific growth rates. Significant result of interaction is highlighted in bold.

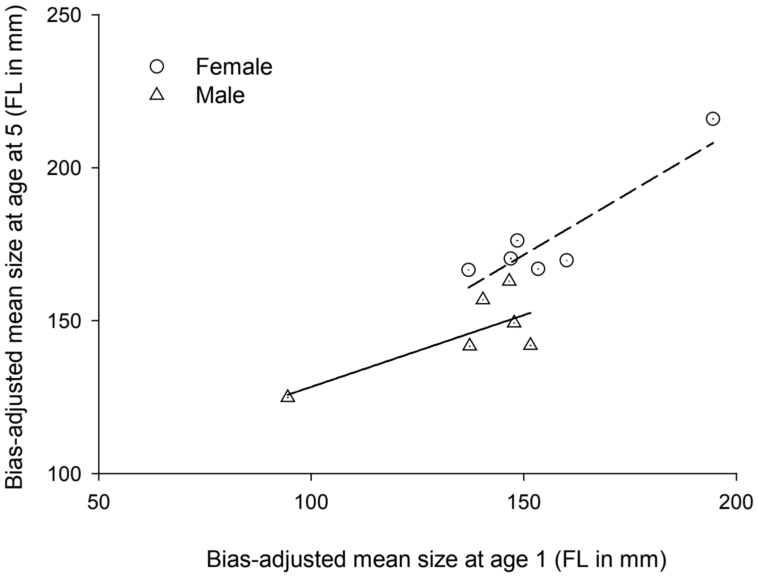


Figure 4. Relationship between mean initial size and adult size of males and females in *Acanthurus nigricans* and *A. leucosternon* across populations sampled in the Indo-Pacific O., illustrating sex-specific growth rates in species with female-biased sexual size dimorphism. Males are represented by open triangles and continuous regression line, and females by open circles and dashed regression line.

Analysis of the relationship between the magnitude *M* of sexual size dimorphism in *A. nigricans* and *A. leucosternon* and scaled adult size of males Z_{males} and females $Z_{females}$ revealed that the magnitude of the differential size distributions increased with female size (r^2 = 0.74) and did not vary with male size (r^2 = -0.03) (Figure 5).

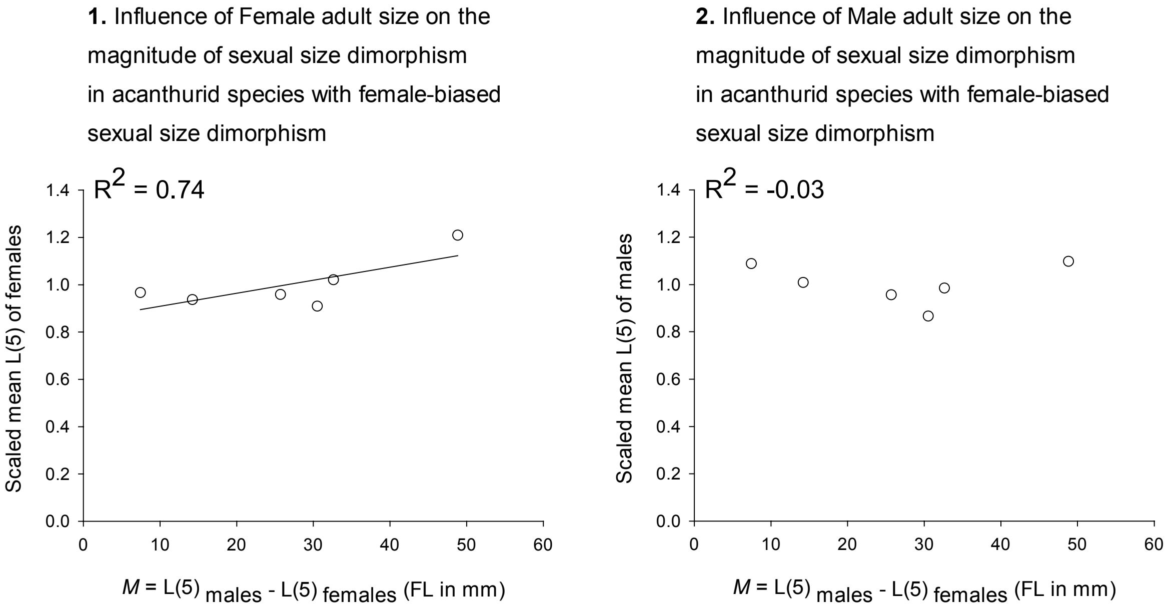


Figure 5. Regression plot showing the influence of male and female adult size on the magnitude of sexual size dimorphism in species with female-biased sexual size dimorphism. Graph 1 illustrates the relationship between L(5) of females and the magnitude *M* of the difference in size between the sexes, and graph 2 illustrates this relationship with L(5) of males. For each graph, sex-specific mean sizes of rVBGF bootstrapped parameter L(5) are scaled to average size of each sex across locations sampled.

Analysis of variance of mean adult body size of males and females of *C. striatus*, *A. nigricans* and *A. leucosternon*, which display opposite patterns of sexual size dimorphism, revealed a significant effect of sex on the direction of sexual size dimorphism across acanthurid species (Table 3). Pair-wise comparisons between the groups further revealed that the significant result of the interaction was the result of significant a difference in mean adult body size of males between species with female-biased and species with male-biased sexual size dimorphism (Table 4). In contrast, there was no difference in mean adult body size of females between species with opposite patterns of sexual size dimorphism. Therefore, results suggested that the direction of sexual size dimorphism was the result of variation in the mean adult body size of males (Figure 6). Furthermore, there was no significant difference in mean adult body size between species examined across locations sampled in the Indo-

Pacific region, and between sexes across the model species, which suggested that the significant result of the interaction term would not be hindered by the allometric relationship between the amplitude of sexual size dimorphism and body size.

Source of variation	*df*	*MS*	*F*	*p*
Sex	1	155.1	0.556	*> 0.05*
Direction of SSD	1	1047.1	3.753	*> 0.05*
Sex * Direction of SSD	1	2766.0	9.915	***< 0.01***
Residual error	20	279.0		

Table 3: Analysis of variance of mean adult size of males and females on the direction of sexual size dimorphism (abbreviated as SSD; may be female-biased or male-biased) in three Acanthurid species across the Indo-Pacific region: *Ctenochaetus striatus* where males grow larger than females, and *Acanthurus nigricans* and *A. leucosternon* where females grow larger than males. Dependent variable is mean value of bootstrap estimates of rVBGF parameter size-at-age 5 *L(5)* at each location sampled (6 locations included), and predictor variables are sex and the direction of sexual size dimorphism of the species (2 levels: female-biased and male-biased). Null hypothesis tested is that male or female size does not influence the direction of sexual size dimorphism. Significant result is highlighted in bold.

Sex	*Direction of SSD*	*Group*	*A*	*B*	*C*	*D*	*Results*
Female	Female-biased	A		>0.05	>0.05	>0.05	
Female	Male-biased	B			>0.05	>0.05	
Male	Female-biased	C				***<0.01***	C ≠ D
Male	Male-biased	D					

Table 4: Pair-wise comparison of group means using Tuckey's Test. Direction of sexual size dimorphism (SSD; female-biased or male-biased) was significantly affected by sex (Male, Female) in ANOVA (table 3). Here we examine the nature of this difference, in order to identify the groups that differed significantly. Group A represents female adult size of species with female-biased SSD, group B represents female adult size in species with male-biased SSD, group C represents male adult size in species with female-biased SSD, and group D represents male adult size in species with male-biased SSD. Significant differences are highlighted in bold.

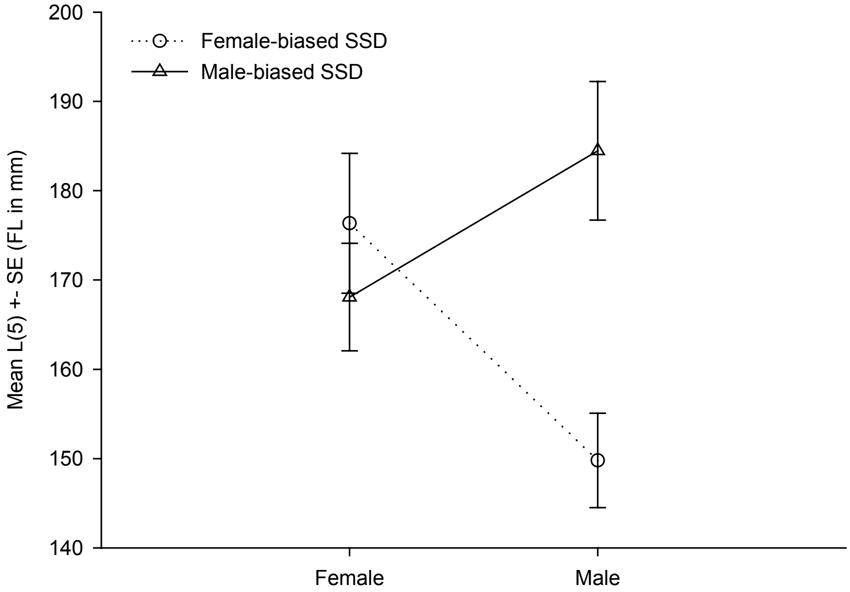


Figure 6. Variation in mean adult size of males and females in species with opposite patterns of sexual dimorphism within the coral reef fish family Acanthuridae. Species examined are *Ctenochaetus striatus*, *Acanthurus nigricans* and *Acanthurus leucosternon*. Mean adult size is based on bias-adjusted mean of bootstrap estimates of rVBGF parameter L(5), and is plotted with estimates of standard error.
Open circles and dotted line illustrate species in which females grow larger than males, and open triangles and continuous line illustrate species in which males grow larger than females.

3.4. Discussion

Major findings

Examination of the relationship between size, age and sex in *Acanthurus nigricans* and *Acanthurus leucosternon* across the Indo-Pacific region shows a consistent pattern of sex-specific growth in all populations sampled. Females of *A. nigricans* and *A. leucosternon* are larger than males for any given age, and females grow faster than males during the early life history of both study species. Whilst the direction of sexual size dimorphism and the mechanism underlying larger size in females of both study species is consistent across geographical scales, the magnitude of the difference in size between the sexes varies among populations, and is positively correlated with body size of females. In contrast, the direction of sexual size dimorphism across species with opposite patterns of sexual size dimorphism (female-biased and male-biased) is the result of variation in adult body size of males. There results suggest that: 1) The demographic mechanism underlying female-biased sexual size dimorphism is a mechanism of fast initial growth, which implies that early life history plays a critical role in the mechanism underlying female-biased size distributions in the study species, 2) There is a positive correlation between reproductive and somatic growth in the study species, which contradicts the general life theory of the presence of high costs in somatic growth associated with reproductive growth of females, 3) There is an allometric relationship between the magnitude of sexual size dimorphism and female growth rate in species with female-biased sexual size dimorphism, and that: 4) The evolutionary mechanisms underlying sexual size dimorphism in acanthurid species is the result of variation in the size of males.

Mechanisms underlying female-biased sexual size dimorphism in Acanthurus nigricans and Acanthurus leucosternon: implications for the costs of reproduction

We found that female-biased sexual size dimorphism in the study species is the result of comparatively faster initial growth in females. A corollary of this is that females may grow faster than males regardless of the reproductive costs associated with the sexual ontogeny and maturation of females. This result contradicts the general life history trade-off generally expected between somatic and reproductive growth of females, and suggests that there is a positive correlation between somatic growth and the costs associated with reproduction. Similar correlations have been demonstrated for a number of taxa to explain variation in life history traits among individuals within a given population, and have often been associated with variation in resource acquisition and allocation of energy (Van Noordwijk and De Jong 1986, Stearns 1992, Glazier 1999, Reznick et al 2000). It has been proposed that this relationship occurs when variation in resource acquisition among individuals is greater than variation in the strategy for energy allocation, which would suggest the presence of sex-specific differences in resource acquisition in the study species. Differences in the use of feeding microhabitats have been suggested between males and females of *A. leucosternon*, however these differences were relatively small, indicating that there is an overall high similarity in resource acquisition between the sexes (Robertson 1985). An alternative explanation may lie in the phylogeny of the species, and particularly in form of growth of the study species, which may have constrained evolution through phenotypic correlations (Stearns 1992). In the case where a decoupled relationship between size and age is associated with selection for fast growth and early sexual maturation, the form of growth may constrain the relationship between somatic and reproductive growth. It will prove interesting to compare the correlation between the form of growth, sex-specific resource acquisition, energy allocation and the costs of reproduction in species with asymptotic and continuous growth trajectories.

Variation in the magnitude of female-biased sexual size dimorphism in Acanthurus nigricans and Acanthurus leucosternon across the Indo-Pacific region

Analysis of the patterns of variation in the magnitude of sexual size dimorphism in *A. nigricans* and *A. leucosternon* revealed a positive relationship between the magnitude of the differences in size between the sexes and adult body size of females. In contrast, there was no correlation with adult body size of males in both study species. This suggests the presence of an allometric relationship between female body size and sexual size dimorphism in the study species (Fairbairn 1997). In this case, variation in the magnitude of the differences in size between the sexes may be a consequence of fast initial growth in females, which suggests that these patterns may not be the result of variation in the selective environments among populations of the study species across the Indo-Pacific region. These results may contribute to explain similar patterns of variation in the magnitude of sexual size dimorphism found in a number of acanthurid species in previous publications (Robertson 1985). Examination of the relationship between variation in the magnitude of sexual size dimorphism and adult size of males and females in a number of other species will be necessary to determine whether the results found in this study are species-specific or whether this is a general mechanism underlying sexual size dimorphism in coral reef fish species.

Evolutionary mechanisms underlying the direction of sexual size dimorphism: comparison of Acanthurus nigricans, A. leucosternon and Ctenochaetus striatus

Our results revealed that variation in the direction of sexual size dimorphism among acanthurid species is associated with variation in the size of males. In contrast, female size remains constant across species with contrasting patterns of sexual size dimorphism. These results have two major implications. First, this suggests that the evolution of sexual size dimorphism in Acanthuridae may be the result of selection acting on the size of males, which coincides with predictions of the Guiselin-Reiss Hypothesis, and contradicts those of the Fecundity-advantage Model. Secondly, these results suggest the presence of strong adaptive advantages selecting for an optimum adult body size in females.

These results support the hypothesis that the evolution of sexual size dimorphism is associated with evolution of adult body size in males, which appears to be associated with a greater potential for flexibility in the growth of males as compared to that of females. In the case of *Ctenochaetus striatus* where males are larger than females, intra-sexual competition selects for an increase in the size of males, which is often associated with higher mating success in polygynous mating systems (one male dominates over several females). The presence of polygynous mating systems in *C. striatus* coincides with the presence of male-biased sexual size dimorphism in this species. In the example of female-biased sexually dimorphic species, small size in males may increase reproductive success when pair spawning is associated with scramble competition for females, in which case small size in males increases encounter rates and pairing with females. High mobility in males has been observed in one of the study species, *A. leucosternon*, which does not appear to display sex-specific patterns in resource acquisition (Robertson et al 1979, Robertson 1985). These results may suggest that female-biased sexual size dimorphism in the Indo-Pacific sister species *A. nigricans* and *A. leucosternon* may be the result of an adaptive advantage for increased mobility and agility in males, which may be an equivalent hypothesis to the "Gravity Hypothesis" as proposed by Moya-Larano et al (2002). It will prove interesting to examine sex-specific behavioural mechanisms associated with pair spawning in female-biased sexually dimorphic coral reef fish species.

Conclusion

Our results suggest that the mechanism underlying female-biased sexual size dimorphism is a mechanism of fast initial growth in females, and that this mechanism generates an allometric relationship between the magnitude of sexual size dimorphism and body size across populations of a given species. Furthermore, examination of the relationship between the direction of sex-specific size distributions and body size of males and females suggests that the evolution of sexual size dimorphism is the result of variation in the size of males. These results have substantial consequences for our understanding of the life histories of fast growing species, and suggest that variation in the growth of males and females may be associated with a positive correlation between the costs of somatic and reproductive growth. Furthermore, our results coincide with current emerging evidence in the literature that evolution of sexual size dimorphism is associated with evolution of the size of males, as opposed to Darwin's theory of sexual selection for increased reproductive output and large size in females. It will prove interesting to compare these results in species with a continuous form of growth, in order to determine whether the results found in this study are associated with an asymptotic form of growth.

General Conclusions

General summary - key findings

This thesis demonstrates the importance of early life history in determining a species' demography and associated life history traits for species where the form of growth is highly asymptotic. Firstly, results presented here suggest that, in the case where all the potential for growth is restricted to the early years of an individual's life history, the conditions encountered by an individual in the environment where it settles will be critical in determining its initial rate of growth and resulting adult body size. And, whilst there is no predictable pattern in growth across ocean basins on a broad longitudinal scale, there is a predictable pattern in longevity, which differs between ocean basins (Chapter 1). Secondly, the effect of local environmental conditions affects both sexes in a similar fashion, and there is no sex-specific response to local habitat. However, in the case of sex-specific size distributions within a given population of fish, there is an increase in the magnitude of the difference in size between the sexes in conditions that favour fast growth and result in large absolute adult size. This is consistent for species with male-biased (Chapter 2) and female-biased (Chapter 3) sexual size dimorphism. Thirdly, the mechanism of fast initial growth underlying variation in adult size is consistent regardless of an individual's sexual ontogeny, suggesting that the underlying trade-offs in life history traits of species where the relationship between size and age is decoupled is associated with optimisation of juvenile survival and lifetime reproductive success, more than the relationship between somatic and reproductive growth (Chapters 2 & 3). Fourthly, the evolution of sexual size dimorphism in acanthurid species is associated with variation in the size of males relative to adult size in females, which remains constant, with males growing to a large adult size in male-biased sexually dimorphic species, and growing to a small size in female-biased species (Chapters 2 & 3).

General scope of this study & future directions

This study has revealed that asymptotic growth is associated with a high intrinsic potential for variation in growth among as well as within populations. This is a critical aspect of this study, and shows that, whilst a decoupled relationship between size and age may restrict the timeframe of an individual's opportunity for variation in growth, it does not reduce its capacity for plasticity in growth. In this case, all somatic growth is compressed to the initial 10 to 15% of the life span of fast growing species, and conditions encountered by an individual during the first years of life will determine adult body size for the remaining 85 to 90% of the life span.

The mechanism of fast initial growth underlying variation in growth is consistent across species, geographical scales and among the sexes. A corollary of this is that the same mechanism is responsible for variation in size among and within populations when growth is asymptotic. I hypothesise that an asymptotic form of growth does not limit the potential for flexibility in growth but restrains the nature of the mechanism that may be associated with variation in adult body size in these species. In this case, we may interpret the presence of fast growth associated with large adult body size in high latitude environments as a by-product of the selection for increased body size in colder water conditions, as opposed to a compensatory mechanism for a reduction in the length of the growing season. A high potential for plasticity in growth may be an adaptive advantage in species with asymptotic growth, particularly for species with a long pelagic larval phase where a juvenile's habitat may differ substantially from that of its parents.

The extended life spans and high initial growth rates found in the study species are characteristic of many Acanthurid fish. This contradicts the general predictions of a positive correlation between growth rate and mortality described for many species of fish, whereby individuals with relatively fast growth experience reduced life spans (Charnov 1993). However in fish, this positive correlation has primarily been described for species with indeterminate growth, suggesting that this life history invariant may not apply to species with asymptotic growth, and that the cost of increased growth does not necessarily lie in that of longevity. Rather, the life span of an individual appears to be predicted by the ocean basin where it comes from, which may be the result of broad geographical distributions and varying recruitment patterns, suggesting a genetic component in the determination of an individual's longevity. Ultimately, this implies that distinct evolutionary mechanisms may underlie key aspects of a species' demography such as growth and longevity.

Another aspect of fast growth lies in that reproductive and somatic growth are largely synchronous. This result contradicts the general life history theory explaining determinate growth, whereby a determinate form of growth is expected when there is a mutually exclusive relationship between the functions of growth and reproduction. This suggests the presence of overriding selective mechanisms for fast growth and early sexual maturation. This may be an expression of high juvenile mortality rates and low reproductive success of adults. Furthermore, this may explain the presence of a greater flexibility in the growth of males, as reproductive success of males and females often depends on that of males in any given mating system.

A critical point of future investigation will lie in the relationship between asymptotic growth and sex reversal. While most hermaphroditic species have indeterminate forms of growth, whereby the relationship between size and age is continuous, there are few examples of sex change in fast growing species. While the absence of a labile sexual ontogeny in such species may be the result of physiological constraints associated with fast early growth, it will prove interesting to examine the relationship between the schedule of growth and the evolution of sex reversal, and compare the mechanisms associated with variation in size across species with contrasting forms of growth. Furthermore, future investigation will need to address the genetic structure of the study species across its range, the relationship between recruitment levels and the patterns of longevity found across the Indo-Pacific region, as well as the effect of the form of growth and species' phylogeny on the mechanisms of plasticity in growth in coral reef fishes.

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