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COMPARATIVE GROWTH DYNAMICS OF ACANTHURID FISHES

Thesis submitted by
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for the degree of Masters of Science in Marine Biology
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Abstract

Considerable variation exists in the demographic characteristics of coral reef fishes. Growth trajectories of size, growth and longevity of four species of the wide-spread coral reef family, Acanthuridae, were investigated. Growth data were obtained from growth increments in sagittal otoliths. Three species of these were studied in the tropical Atlantic, and one in the tropical South Pacific. The focus of the study is the variability of the demographic parameters at both large and small spatial scales. Large scales studies were conducted along both latitudinal and longitudinal gradients. Latitude has a direct influence on sea temperature, and this affects the growth and demography of teleosts. Longitudinal effects are not as well studied, and comparing the demographic characteristics of teleosts along a longitudinal gradient is the first of this type of study. Longitudinal comparisons of longevity and growth allow us to analyse the variability of life history characteristics of organisms at different localities across an ocean without having to consider the effects of sea temperature. In order to completely understand the mechanisms behind large scale variability in demography, a small regional scale study can aid in pinpointing possible factors that can discern these differences within a small region. A local scale study was conducted at Bermuda with study habitats 10's of kilometres apart.

Analysis of size at age data revealed that these acanthurids exhibit fast initial growth, until age 4, after which is substantially reduced generating a characteristic "square" growth curve. This indicates evidence that size and age of some reef fishes may be decoupled. All species at every study site follow similar growth patterns within the first four years of life. Acanthurids, including the species in this study, generally reach maximum size within the first 10% of their life span, irrespective of their maximum size and longevity. Nevertheless it must be noted that as most populations reach asymptotic size, there are exceptions for three species (*A. coeruleus, A. chirurgus* and *A. lineatus*) at two locations (Isla de Margarita and Marquesas). In these populations growth was reduced at older ages, but did not reach asymptote. Upwelling events and nutrient blooms may be responsible for these non-asymptotic growth trajectories, providing sufficient resources to allow growth to occur more prominently.

The species in this study exhibit a wide range of sizes, although maximum sizes and longevities were not correlated. This study found that populations of the longest lived acanthurids do not necessarily reach the largest body sizes contradicting previous age and body size correlation studies of acanthurids, and indeed ectotherms in general.

In the tropical Atlantic Ocean, the demography of *Acanthurus bahianus, A. coeruleus* and *A. chirurgus* was assessed at 12 locations on a large (56°) latitudinal scale. Mean sea temperature (MST) negatively correlated with longevity, absolute body size, and instantaneous growth (size-at-age at ages 1, 2.5 and 4) over a large latitudinal gradient. Decreasing growth with increasing temperature is a trend which is opposite to many previous demographic studies of ectotherms, and more specifically, teleosts. Populations of all Atlantic species in this study from cooler (i.e. lower MST) environments are longest lived, but not necessarily largest in size (i.e. Bermuda), while populations of all species in warmer waters consistently exhibited small size and short lifespan (i.e. Belize), indicating MST may not be the only factor driving these growth patterns. Mass island effects can also influence growth, as populations from the isolated oceanic islands have the longest lifespans and larger body sizes.

To assess the potential influences of other environmental and fishing impacts, a study was conducted along a longitudinal scale at constant sea temperature. The demography of *A. lineatus* was estimated at five localities spanning 75° longitude across the South Pacific Ocean. The variation in body size and instantaneous growth among sites was equivocal. A negative relationship was found between longevity and longitude from the west to east end of the Pacific Ocean, however within Oceania, the difference was not so great. This is in accordance with previous studies demonstrating exceptionally long life spans of coral reef fishes on the Great Barrier Reef.

Comparisons of the demographic patterns of *A. coeruleus* and *A. chirurgus* between the lagoonal and outer reefs of Bermuda allowed me to assess any variability in the life history characteristics on a small regional scale. Juveniles of *A. chirurgus* settled onto the lagoonal reefs and migrated to the outer reef as adults, while both juveniles and adults of *A. coeruleus* inhabited the outer reef. These differences in spatial distribution on a local scale may give us a better indication of the environmental effects on the general demographic patterns found at larger spatial scales.

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Chapter 1: General Introduction

Reef fishes are dominated by Perciformes and contain a very high diversity of species representing distinct evolutionary lineages. The co-occurrence of such a variety of vertebrates sharing broad common distributions provides an opportunity to analyse demographic variation both within and among species. This opportunity is enhanced by the fact that reef fishes are ectotherms and they are expected to be sensitive to variation in temperature. In addition, most species occur in shallow water and are susceptible to changes in the environment. Finally, the distribution of their major habitat, coral reefs, spanning substantial latitudinal and longitudinal gradients, provide a unique opportunity to use multi-scale sampling programs to analyse demographic variation.

Assessing the variability of the demographic characteristics, such as growth and longevity, is essential to understanding the population dynamics of a species. Mechanisms that influence population dynamics function at a number of spatial and temporal scales (Levin 1992), and can reveal demographic variation within and among species. Examining differences in demography over a range of spatial scales allows us to pinpoint where major changes occur and can help identify the causes of changes (Sale 1998). General life history theories such as Bergmann's rule, predict that fishes at higher latitudes (i.e. lower temperatures) attain a larger final body size but have slower growth (i.e. smaller size-at-age) (Gilligan 1991, Atkinson 1994, Belk and Houston 2002) because slower growth is usually accompanied by later maturation and greater longevity (Stearns and Koella, 1986). There are a number of mechanisms that can influence the demographic variability in reef fishes.

The demographic characteristics of an organism vary as a function of intrinsic (genetic) and extrinsic (food availability, temperature, predation etc.) effects. Biotic mechanisms such as food availability and quality (Forrester 1990, Jones and McCormick 2002, Ruttenberg et al. 2005), habitat (Munday 2001), population density (Victor 1986, Gust et al. 2001, 2002), predation (Werner et al. 1983, Holbrook and Schmitt 1988, Hixon and Webster 2002, Jones and McCormick 2002), competition (Jones 1987, Steele and Forrester 2002), genetic structure (Planes and Flauvelot 2002) and fishing pressure (Rijnsdorp and van Leeuwen 1992, Manickchand-Heileman and Phillip 2000, Halpern and Warner 2002) can influence demography. Although most studies of these effects are carried out at a very local scale, to develop a more comprehensive picture of demography and life history of reef fishes may be useful to also examine populations over a wider geographic scale. A combination of local geographical studies can provide a comprehensive picture of reef fish population biology. The analysis of reef fish demography over both broad and local spatial scales is the focus of this thesis.

On a broad latitudinal scale, sea surface temperatures differ considerably. Temperature has a pervasive effect on the size structure and growth rates of ectotherms (Ayers and Scriber 1994, Angilletta et al. 2004). Thus, a substantial section of this study will examine size patterns and growth rates of fish over latitudinal gradients that are associated with predictable trends in ambient temperature. Moreover, a strong, indirect correlation between temperature and reproductive output occurs over large (McIntyre and Hutchings 2003) and small (Ruttenberg et al. 2005) spatial scales. Fishes in warmer waters may be allocating more energy to reproductive activities reducing available energy for growth and maintenance, and possibly causing increased mortality (Ackerman 2004). Additionally, on a global scale, fish living in colder waters tend to live longer hence they have more reproductive cycles during their lifespan (Longhurst 2002). Temperature can also have a direct effect on body size and reproduction. Many temperate fishes grow and reproduce only when temperatures are warm (Conover 1990, 1992). While marine ectotherms are generally larger in colder environments (Pauly 1980, Atkinson 1994, Atkinson and Sibly 1997) some studies indicate that these trends can be ambiguous in fishes (Belk and Houston 2002, Williams et al. 2003, Ackerman

2004). The subject is controversial (Jones 1991) and a more comprehensive analysis of the relationship between growth size and water temperature would help resolve the mechanisms associated with differing demographic trends.

In addition to distributions along latitudinal gradients, reef fishes can occur along extensive longitudinal ranges. One of the most important attributes of coral reef fishes is that they are strongly affiliated with warm, shallow, tropical waters within 25^o of each side of the equator in habitats that are structurally complex and extend completely around the world, which can cause significant differences amongst life history traits. Assessing demographic variation over a longitudinal scale allows the examination of patterns in demographic parameters associated with reef structure, historical characteristics and fishing effects potentially without the overriding influence of variable water temperatures.

This study focuses on age-based demographic characteristics, specifically longevity, body size and growth, of coral reef fishes across spatial scales spanning thousands of kilometres. Four species of Acanthuridae (surgeonfishes), *Acanthurus bahianus* (ocean surgeonfish)*, A. chirurgus* (doctorfish), and *A. coeruleus* (blue tang), at 17 locations within the tropical Atlantic Ocean, and one species, *A. lineatus* (lined surgeonfish), in the tropical South Pacific Ocean, were used to test the demographic observations. Among the 80 species of surgeonfish, 73 occur in the Indo-Pacific, and five occur in the tropical Atlantic Ocean and Caribbean Sea. *Acanthurus* is one of four genera in the subfamily Acanthurinae, and is characterised by a single caudal spine that folds into a horizontal groove used for defence and to exert dominance over other reef fishes (Randall 2005). Most Acanthurids have thin-walled stomachs and graze on algae; some have a thick-walled gizzard-like stomach to use sand to break down detritus, although a few species have been observed feeding on zooplankton (Kuiter and Debelius 2001). Surgeonfishes have a long pelagic larval stage (~60-90 days), and this can lead to a wide distribution of a species extending across an entire ocean (Randall, 2005).

Differences in longevity and body size could be due to differences in growth between habitats of similar latitudes and with similar water temperatures (Robertson et al. 2005). Gust et al. (2002) found that variation in growth in a population was explained by differences in habitat. Populations from the outer reef of the Great Barrier Reef achieved smaller asymptotic sizes relatively quickly and had shorter lifespans than populations on the mid-shelf a few kilometres away. This study covers the age-based demographic characteristics of *Acanthurus chirurgus* and *A. coeruleus* on a local scale in Bermuda.

The main objective of this study is to compare longevity, body size and growth of four species of Acanthurids over both large and small spatial scales where water temperature, geography, environmental influences, historical characteristics or any combination of these factors may influence the variation in the demographic characteristics in a population. Evaluation of the populations of these species over different regional scales will provide information for future analysis of the causes of demographic variability within species. In particular, Chapter 2 will analyse the differences in demographic characteristics of *A. bahianus, A. chirurgus,* and *A. coeruleus* over a latitudinal gradient in the tropical Atlantic Ocean using sea surface temperature as a proxy for latitude. Chapter 3 will examine various environmental and ecological factors influencing variation in *A. lineatus* by analysing the demographic characteristics along a longitudinal gradient in the South Pacific Ocean. Chapter 4 will consider local scale variation at the habitat level in Bermuda for *A. chirurgus* and *A. coeruleus*. This is the first study to ascertain the critical demographic parameters of longevity, size and growth of *Acanthurus chirurgus* and *A. coeruleus*, and takes a unique approach of examining these parametres over a large spatial scale on a longitudinal gradient at sites that have similar sea temperatures.

Chapter 2: Comparisons of demographic characteristics among three species of surgeonfish in the tropical Atlantic Ocean and Caribbean Sea

2.1 Introduction

There is a surprising amount of variation in reef fish life history characteristics, and this diversity emerges at a variety of spatial scales (Russ 1984a, b, Choat and Axe 1996, Choat et al. 1996). In coral reef fish populations, knowledge of size-at-age, longevity and their variability in response to environmental conditions and ecological processes is important to understanding the natural mechanisms underlying abundance and population dynamics (Conover 1992, Rocha 2002). Large scale comparisons complement basic information on the known range of demographic variation and are important for providing a context for the results of more comprehensive studies at specific locations.

Life history characteristics of fishes can vary over large geographical ranges, especially over a latitudinal gradient (Conover 1990, Present and Conover 1992, Meekan and Choat 1997, Choat and Robertson 2002, Floater et al. 2004). Fishes at higher latitudes with lower sea temperatures grow more slowly but attain larger final body sizes due to longer lifespans compared to fishes at lower latitudes with higher sea temperatures

(Pauly 1994, 1998, Stearns and Koella 1996, Stergiou 2002). Most data are from temperate species, thus it is unknown whether such predictions pertain to coral reef fishes. A number of studies demonstrate alternative results (Hood et al. 1994, Kohda 1996, Mosse 2001, Ackerman 2004, Robertson et al. 2005) suggesting that patterns can be ambiguous in fishes. To further investigate general global patterns I examined large spatial gradients in demographic traits within tropical oceans using one group of fishes.

To increase our knowledge of fish biology from tropical areas that are increasingly exploited, we need to gain a better understanding of their life cycles (Munday and Jones 1998). I derived length-at-age information for *Acanthurus bahianus, A. coeruleus* and *A. chirurgus* by extracting, sectioning and analysing their sagittal otoliths. Otoliths are a valuable tool for understanding the demography of reef fishes more (Doherty and Fowler 1994, Ferreira and Russ 1994, Worthington et al. 1995, Choat and Axe 1996, Hart and Russ 1996). This demographic information derived from otoliths is essential to determine the growth rates and life spans of coral reef fishes, and to make comparisons between species and localities.

The purpose of this study was to document the longevity, size and instantaneous growth of coral reef fishes on a latitudinal scale in the tropical Atlantic Ocean, using three species (*Acanthurus bahianus*, *A. coeruleus* and *A. chirurgus*) from the family Acanthuridae. As temperature may be an underlying variable contributing to these variations over large latitudinal gradients in ectotherms (Sebens 1987), I use mean surface temperature (MST) to discern a possible asymptotic growth pattern among these surgeonfish. The three selected study species are closely related and have similar geographic distributions and life history patterns, prerequisites to comparing demographic rates (Choat and Robertson 2002). After a pattern can be established with similar species, we can then further explore species of various growth trajectories, but of ecological similarities.

2.2. Materials and methods

2.2.1. Study sites and field sampling

Samples were collected in the Atlantic Ocean and Caribbean Sea over a widely distributed and representative range of habitats used by the three species of surgeonfish. Juvenile and adult fish were sampled at 12 locations covering 56° of latitude and 5.5°C mean annual sea temperature (Figure 2.1). These sites were chosen so that the locations would have a broad range of latitudinal positions, temperatures, habitat characteristics and degree of isolation. Nine of these locations were spread over 23° of latitude in the North Atlantic: Barbados, Los Roques and Las Aves archipelagos, Isla de Margarita

(Venezuela), Punta de San Blas (Panamá), Carrie Bow Cay (Belize), Lee Stocking Island (Bahamas), Jamaica and Bermuda; and three locations spanned 15^{o} of latitude in the South Atlantic: Cabo Frio (Brazil), and two isolated oceanic islands, Ascension and St. Helena. *Acanthurus bahianus* was collected at all 12 sites, *A. coeruleus* was collected at Los Roques, Isla de Margarita, San Blas, Belize, Lee Stocking, Bermuda and Ascension, and *A. chirurgus* was collected at Los Roques, Isla de Margarita, San Blas, Belize and Bermuda (Table 2.2). All three species are found in the shaded areas in Figure 2.2 except *A. coeruleus* and *A. chirurgus* are not found at St. Helena (Rocha et al. 2002). Table 2.1 illustrates the positions in latitude, the dates of sampling and the mean sea surface temperatures (MST) at these sites. Sea surface temperature was acquired from Global Ocean Services System satellite data from 1982 to 2003: IGOSS nmc Reyn_Smith0Iv1 weekly SST from http://ingrid.ldgo.columbia.edu. Due to major upwelling and variable ocean currents, the temperature cycle, which influences seasonality of fish growth (Conover 1990), is not associated with latitude in the tropical Atlantic study locations (Choat and Robertson 2002). Mean sea temperature (MST) was used as a variable to discern the variation in demographic characteristics at each study site for all three species of Acanthurids.

For a full description of the habitat characteristics of 10 of the 12 study sites refer to Choat et al. (2003) and Robertson et al. (2005). At Jamaica, individuals were collected within Montego Bay, a well developed fringing reef on the northwest coast. It is ostensibly a marine reserve, but it is not regulated or protected. Fish are constantly caught from this area without being recorded (D.R. Robertson, pers. comm., Jones et al. 2004). Individuals sacrificed by spear were caught at 6-15 m depths, and those taken by trap were collected from deeper waters at 20 m depth (D.R. Robertson, pers. comm.). Isla de Margarita is located in a high upwelling area 38 km northeast off the mainland of Venezuela. Maintaining centuries of fishing traditions, it is one of the primary fishing areas in the vicinity (Buitrago et al. 2005). Most of the individuals were caught from inshore reefs (D. R. Robertson, pers. comm.).

In total 2168 individuals (1101 *A. bahianus* at 11 study sites, 651 *A. coeruleus* at 7 study sites and 416 *A. chirurgus* at 5 study sites) were collected using pole spears on SCUBA and snorkel or fish traps at 5-20 m depths at all localities. Both juveniles and adults were sacrificed. To collect a diverse range in sizes and ages, collectors swam indiscriminately in all directions and speared adults in the order in which they were discovered, not taking size in consideration. However, the largest and smallest individuals at each study site were targeted. Once captured, individuals were immediately placed in ice on the boat until the samples were delivered to the laboratory for processing on the same day of collection. For each individual, fork length (FL) was measured to the nearest millimetre (mm), and weight (total wet weight) was measured to the nearest gram (g). The sagittal pair of otoliths was removed surgically from the skull, and stored cleaned and dry in separate cells in culture plates.

2.2.2. Otolith preparation and age determination

I used the *A. bahianus* data set from Robertson et al. (2005) to derive length-at-age data, and extended the number of locations by adding *A. bahianus* samples from one site that is heavily fished (Jamaica) and another that is influenced by major upwelling events (Isla de Margarita). I derived length-at-age data for *A. bahianus, A. chirurgus* and *A. coeruleus* by aging their sagittal otoliths. Otoliths were prepared according to the protocol described in Choat and Axe (1996), Secor et al. (1991) and Robbins and Choat (2002). Robertson et al. (2005) validated the annual sagittal otolith increments of *A. bahianus* with tetracycline; however, annual increment deposition has not been validated for *A. coeruleus* and *A. chirurgus*. For the purpose of this study it will be assumed that otolith increment deposition in *A. coeruleus* and *A. chirurgus* follow a similar trend since they have identical otolith structures to *A. bahianus* and belong to the same genus.

One sagitta from each pair was weighed to the nearest 10^{-4} grams for adults and juveniles in order to formulate a pattern between age and sagittal weight. The otolith was embedded in thermoplastic glue (Crystalbond^{TM}) on a glass slide with the rostral side suspended over and the nucleus positioned just below the edge of the slide. The suspended piece was filed to the edge of the slide using wet 600 or 1200 grade SLS^{TM} diamond lap depending on the size of the otolith. The diamond lap was used in lieu of sandpaper which has been typically used in previous studies. The half-sectioned otolith was then mounted filed-face down on the glass slide to allow the distal side to be filed until rings could be differentiated from the nucleus and the outer border of the otolith. Otolith sections were then polished with 9µm and 3µm grade lapping paper and covered with Crystalbond^{TM} to improve the clarity of the rings. Sagittae were examined under a high power (400x) microscope, a dissecting microscope using transmitted light, or an imaging analysis microscope depending on the size of the otolith and the clarity of the increments (representing age). Age was estimated based on established techniques (Fowler 1990, Lou 1992, Choat and Axe 1996, Meekan et al. 2001, Choat and Robertson 2002, Choat et al. 2003, Mosse 2001, Laman Trip 2004). Three blind readings of the annual increments from each otolith were made at least three days apart to ensure independent counts. If the readings differed by more than 10% of each other, the second otolith was processed. If the second otolith was unavailable, the individual was not included in the analyses. If the increments were not sufficiently clear to interpret, the individual was not included in the analyses. The number of insufficient otolith reads was negligible. The final read was the average of all of the reads. To ensure the standardisation of the readers in each study, I read a number of the otoliths from Robertson et al. (2005).

For the smallest sagittae, daily ageing of acanthurids was performed following the techniques Lou and Moltschaniwskyj (1992). Sagittal otoliths were filed down by hand and polished with 3- and 12μm-grade lapping paper. Daily increments were counted both digitally and by eye at 400x magnification. Estimation of the daily increments was very time consuming which allowed only one attempt of age estimation for most of the samples.

2.2.3. Sagittal otolith growth

The relationship between sagittal weight and age was determined for *A. coeruleus* and *A. chirurgus* at all study sites and for *A. bahianus* at Jamaica and Isla de Margarita by fitting. See Robertson et al. (2005) for sagittal weight and age relationships for the other localities for *A. bahianus.*

2.2.4. Age-based growth modelling

Length-at-age data were fit to nine growth models to determine the best fit model indicated by sum of squares results, and estimates were derived to construct an average growth curve for every population from analysing their sagittal otoliths. For all populations except one (Isla de Margarita) growth trajectories were estimated by fitting the length-at-age data to an age-based model, the von Bertalanffy growth functions (VBGF),

$$L_t = L_\infty e^{(-k(t-t_o))}$$

where L_t = estimated length at age t

L_∞ = theoretical mean asymptotic fork length

k= rate at which the growth curve approaches the asymptotic length

t = age of fish in years

t_o = hypothetical age at zero length.

e= base of the natural logarithm

This model is based on the constant k, a curvature parameter (units of time^{-1}) that defines the time at which the asymptotic length theoretically can be reached. The k parameter is not a growth rate (Cerrato 1991, Choat and Robertson 2002). The VBGF parameter estimates can be sensitive to the range of ages and sizes used (Ferreira and Russ 1994, Craig 1999) especially if a broad representation of size and age in a species is not available. To obtain a more reliable estimate of initial growth, intercepts can be constrained to a particular size-at-settlement (L_o) or a specific t_o (Leis and Rennis 1983). Subsequently, in this study the parameter L_o was constrained to 27 mm for all populations of every species in this study because a sufficient number of juveniles were not able to be collected from some localities (see Robertson 1992). This size was chosen because it is the approximate size at which the juveniles recruit to the reef in the tropical Atlantic Ocean (Robertson 1992, Rocha et al. 2002).

Initial analysis of the observed size-at-age data indicated that the estimates for the entire lifespans of *A. chirurgus* and *A. coeruleus* at Isla de Margarita did not fit the VBGF model. The data were examined with nine growth models to determine the best fit which was indicated by the values of the sum of squares results.

Estimates of longevity and body size are regularly recorded as maximum ages (T_{max}) and maximum lengths (L_{max}) respectively for a specific population or at a specific location. Outliers in the age distribution may heavily influence, and over-accentuate T_{max} and L_{max} estimates if the sample sizes are small (Gust et al. 2002). In order to avoid this potential problem, longevity and body length estimates for every species at every locality were calculated on the basis of the oldest 20% of the individuals sampled. Gust et al.

(2002) found little difference in estimates between the oldest 10% and the oldest 20% of a population.

A one-way analysis of variance (ANOVA) was used on the 20% longevity estimates to determine any temperature effects on longevity and absolute body size. For the population at each sample site, 1000 combinations of best-fit parameter values were calculated, and confidence regions were generated around the original sample size. Mean T_{max} and mean L_{max} were calculated as the average age of 20% of the oldest and largest individuals respectively (Haddon 2001, Ackerman 2004). A linear regression was fit to these results to discern any trends along the latitudinal gradient.

Even though the standard VBGF is used extensively in fisheries research, and is used extensively to distinguish size-at-age (Roff 1984) and as a comparison model among species to describe fish growth (Roff 1980) it is often criticised for various reasons. For example, the extent of the model may not provide accurate extrapolations with the unknown data, therefore it may not be biologically applicable (Roff 1980, Francis 1988); the statistical comparison of the demographic properties is difficult among individuals (Cerrato 1991); individual variability may discriminate against parameter estimates (Wang and Ellis 1998, Welsford and Lyle 2005); and the absence of a denomination of units of length per unit of time, which is significant when dealing with growth (Jensen 1996, Ackerman 2004). Despite these criticisms, the VBGF, when used correctly, is an ideal model to compare growth trajectories of various populations of fishes. It must be acknowledged that all populations do not necessarily fit this model, and alternative models must not be dismissed. As such, a re-parameterised von Bertalanffy equation can be considered for appropriate use.

Size at a certain age can be a proxy of growth that can be used to analyse growth rates among species from various localities. In this study a technique described by Cerrato (1991) was used which extends the use of the von Bertalanffy growth model to estimate and compare instantaneous growth rates at specific ages. This model is based on re-parameterised von Bertalanffy estimates proposed by Francis (1988), and it has been used extensively in other studies (Moulton et al. 1992, Hoedt 2002, Ewing 2003, Ackerman 2004, Laman Trip 2004, Welsford and Lyle 2005). This version is more biologically applicable and has more statistically comparable parameters than the standard version. However the standard growth model is completely suitable if used properly (Schnute 1981, Essington et al. 2001), and both versions are used in this study for their appropriate means. This re-parameterized VBGF equation (rVBGF) is:

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

where $L_{(\tau)}$ = estimate body size at age τ

$L_{(\omega)}$ = estimate of body size at age ω

$L_{(\mu)}$ = estimate of body size at age τ

and $r = \frac{L\mu - L\omega}{L\omega - L\tau}$, and *L(t)* is average size at age *t*, assuming that $L_{(\tau)} < L_{(\omega)} < L_{(\mu)}$ and $(L\mu - L\omega) \neq (L\omega - L\tau)$. This model was used to estimate average body size at specific ages to determine instantaneous growth at various localities differing in sea surface temperatures. Ages τ and μ are chosen haphazardly within the data range of the appropriate growth form, and ω is calculated by the average of τ and μ. For the purpose of this study, size-at-age data during dramatic growth of the early life history stages was obtained. Where τ was chosen to represent mean size-at-age in the initial growth trajectory and μ was chosen to represent mean size-at-age immediately before the asymptotic growth trajectory plateaued. Consequently, age τ was chosen to be 1 year old to represent the initial size *L(1)*, and age μ was chosen to be 4 years old to represent body size at the approximate end of the dramatic growth trajectory *L(4)*. Therefore, age ω was calculated to be 2.5 years old with the parameter of *L(2.5)*.

2.2.5. Randomization

In a few data sets in this study there was only one body size value for a certain age within a site. As this imbalancing might cause problems with the robustness of Analysis of Variance (ANOVA), a randomization test was used in place of parametric ANOVA to test for statistical significance (Manly 1997). ANOVA was used to test if the differences of the reparameterized von Bertalanffy parameters of size at age (*L(1), L(2.5), L(4)*) were significantly different among sites for all three species at the various locations throughout the tropical Atlantic (Cassell 2002). One of the assumptions of ANOVA is a consistency of the amount of variation within a group (Manly 1997), but this does not occur in the original data set. The randomization test was carried out by reshuffling the data 1000 times and recalculating the Analysis of Variance. The observed p-value was compared with the distribution of randomized p-values, and if it occupied the lower 5% of the distribution, then it was deemed statistically significant.

2.3 Results

2.3.1 Sagittal growth

Sectioned sagittal otoliths from all localities and all three species of Acanthurids displayed opaque and translucent bands. In all populations, regressions produced significant and strong power relationships, further evidence that sagittal otoliths continue to grow throughout an individual's lifetime (Figures 2.2, 2.3, 2.4, see Robertson et al. 2005 for the remaining *A. bahianus* sagittal weights).

2.3.2 Geographic variation in demography

Acanthurus bahianus, A. coeruleus and *A. chirurgus* demonstrated the highly characterized growth pattern of asymptotic growth for most populations (Figures 2.5, 2.6, 2.7). The growth curves had the same asymptotic shape where there is very rapid growth in the early stages of the lifespan, and asymptotic body length was reached at the same age for all species and at all localities. All populations of the three species approached terminal size at around age 4, and most of their growth occurred within the first 10% of their lifespan, and approximately 85% of their somatic size was attained within the first year (Figure 2.8). However, there was high variability in longevity and mean maximum size for every species and study site. For *A. bahianus,* and the mean maximum age ranged from 5 years in Jamaica to 26 years in Bermuda with a maximum longevity of 32 years in Bermuda. For *A. coeruleus*, the mean maximum age varied from 8 years in Belize to 37 years in Bermuda with a maximum longevity of 43 years in Bermuda. For *A. chirurgus*, the mean maximum age fluctuated from 7 years in Belize to 16 years in Bermuda with a maximum longevity of 29 years in Bermuda.

Body size was extremely variable among the species and populations (see Table 2.3). Body size ranged from smallest at Jamaica (mean max $L = 153$ mm) to largest at St. Helena (mean max $L = 236$ mm) for *A. bahianus*, smallest at Belize (mean max $L = 174$ mm) to largest (mean max $L = 258$ mm) at Isla de Margarita for *A. coeruleus*, and smallest at Los Roques (mean max $L = 220$ mm) to largest (mean max $L = 281$ mm) at Isla de Margarita.

2.3.3. Growth trajectories at Isla de Margarita

Acanthurus coeruleus and *A. chirurgus* at Isla de Margarita did not exhibit the traditional asymptotic growth trajectory that all other Acanthurids portray (Figure 2.9). Length-at-age estimates from these populations were fit to nine growth models (see Table 2.4) to ensure a best fit model. It was determined that the non-asymptotic Power^2 model

$$L = (at^k)^2$$

fit the data best as indicated by the sum of squares results, where a and k are constants. Consequently during the rapid growth period up to age 4, the both the Power^2 and VBGF models fit best with sum of squares results differing by 0.002% and 0.006% for *A. coeruleus* and *A. chirurgus*, respectively. The VBGF model fit at these ages allows the data to fit the parameters of the rVBGF. To determine size-at-age, data were fit to these populations at Isla de Margarita similar to the other populations accordingly.

2.3.4. Longevity and body size

Temperature was used as an underlying variable to examine patterns in the demographic characteristics. Temperature increased among the localities, the mean maximum age decreased for *A. bahianus*, *A. coeruleus* and *A. coeruleus* (Figure 2.10) and mean maximum size decreased only for *A. bahianus* (Figure 2.11). The negative relationship between body size and temperature is not significant for *A. coeruleus* (p=0.70) and *A. chirurgus* (p=0.42). Consequently the body size of *A. bahianus* had the strongest relationship with temperature among the three species.

2.3.5. Temperature versus size-at-age growth

Size at a particular age is a direct proxy of growth that can be used to analyse growth rates among and within populations. The re-parameterised von Bertalanffy growth parameters, *L(1), L(2.5)* and *L(4)*, were used to assess the relationship between instantaneous growth and temperature. As temperature increased, size-at-age decreased with all of the rVBGF parameters for *A. bahianus* (p=<0.0001) (Figure 2.12a). For *A. chirurgus* and *A. coeruleus* there was a negative relationship between the size-at-age parameters of *L(2.5)* and *L(4)* and temperature, but the results were not statistically significant for parameter *L(1)*. (Figure 2.12b,c). There were significantly larger differences (p<0.001 for all ANOVA tests for all three species) between the growth trajectories of year 1 and year 2.5 than between the growth trajectories of year 2.5 and year 4 for every species within the study sites.

2.4 Discussion

2.4.1 Growth trajectories

Throughout the tropical Atlantic Ocean the size- and age-based estimates of *Acanthurus bahianus, A. coeruleus* and *A. chirurgus* populations further confirmed the common latitudinal gradient observations in two of the demographic characteristics that were analysed in this study, where at lower latitudes (warmer sea temperatures) coral reef fish display smaller mean maximum sizes and shorter lifespans than at higher latitudes (cooler sea temperatures) (see Appendix A and B). Plots of size-at-age were counterintuitive to the life history observations which indicate fishes in warmer waters grow faster than fishes in cooler waters. The size-at-age trajectories of all three surgeonfish fluctuated among locations, including locations geographically near each other with similar sea surface temperatures. These similar sea surfaces among localities imply that the size-at-age trajectories may be influenced by factors other than sea temperature.

All populations of all three species of Acanthurids exhibited asymptotic patterns of growth except *A. coeruleus* and *A. chirurgus* at Isla de Margarita. There is consistent criticism regarding the VBGF model as having the best fit for these populations. The data in this study illustrate the VBGF models exhibit an adequate fit despite the unusual configuration of determinant growth reaching asymptote at age 4. There are growth models that fit the data more accurately (JH Choat, pers. comm.), but there may be a lack in statistical meaning to the models. For now simple parametric stats (mean maximum age and size) are used to compare populations until a more suitable model can be developed. There are exceptions to this asymptotic growth pattern as exhibited in Isla de Margarita.

The population in Isla de Margarita had the traditional growth models exhibited in surgeonfish, yet they still exhibit fast initial growth and growth slows with increasing age but their growth trajectory does not asymptote. I suggest this growth curve to be caused by major upwelling events in this area influencing continued growth in the older individuals (D. R. Robertson, pers. comm.). Pauly (1997, 1998) has argued that the asymptotic growth pattern of all fish are described by the von Bertalanffy equations, and are based on the limitation by the organisms' capacity to support the energy demanded. However, Blier et al. (1997) tested this theory and found no evidence that growth rate was limited by the ability of exchange of oxygen from the environment. Thus, it should not be assumed that all species of fish fit the von Bertalanffy growth model. Errors in estimation of growth trajectories of fish can lead to incorrect presumptions about basic life history mechanisms (Jackson and Choat 1992), as well as a profound misunderstanding of the impact that fishing has on a population.

Rapid initial growth rates were found at all localities; with all species at all study sites reaching their respective asymptotic size at approximately age 4 (with the exception of *A. coeruleus* and *A. chirurgus* at Isla de Margarita), regardless of final age or final size. Beyond age five the asymptotic growth pattern indicates that size and age are decoupled, and no matter how long they live beyond this point, they do not grow any larger. Clearly this leads to the potential of inaccurate aging based only on body size because the sagittal otoliths continue to grow throughout the entire life of an individual despite cessation of somatic growth, and size-at-age data from the otoliths can accurately be derived.

2.4.2 Sagittal growth

Sagittal growth of all three acanthurid species varied with no apparent pattern among the populations. Sagittal weight and age were correlated for all three species, indicating that the sagittal otoliths of an individual continue to grow throughout its lifetime (Campana and Nielson 1985) even though its body size ceases to increase at an early age. Although reef fish otoliths are frequently difficult to read at lower latitudes (Caldow and Wellington 2003), in this study sagittal otoliths from lower latitudes (warm water) were no more difficult to age than higher latitudes (colder water).

2.4.3 Geographic variation in longevity

At one time, coral reef fishes were generally presumed to be short-lived, attain small adult size with high rates of mortality compared to temperate fishes (Sale 1980). Leaman and Beamish (1984) define longevity in fishes to be between 15 and 50 years, and extreme longevity to be over 50 years. Approaching 50 years in age, all three species indicate that acanthurids can be extremely long lived in the tropical Atlantic Ocean, even to the standards of fishes from temperate waters (see Appendix D). This study demonstrated a pattern where longevity decreases with increasing MST following the general life history observations (Conover 1990, 1992). Consequently, these tropical acanthurids are longer lived than might be expected, suggesting that sea temperature and latitude are not the only factors that are influencing life history patterns, and that the life history characteristics and patterns are species-specific (see Appendix A and D).

The longest lived individuals of all three species are those located at the isolated oceanic islands of St. Helena, Ascension and Bermuda regardless of sea surface temperature indicating a possible isolated oceanic island effect on longevity (see Schultz and Cowen 1994). This may be a mechanism to buffer populations as an attempt to safeguard against recruitment failures (Meekan et al. 2001) at isolated locations where settlement may be limited. When adult populations are isolated at such an extent, the chance of the planktonic larvae to return is small. This may encourage a strong selection for greater lifespans in order to maximise reproductive output (Hutchings 1997). Schultz and Cowen (1994) found evidence where populations in Bermuda are replenished from larvae that are spawned locally and kept in the proximity of the Bermuda Islands, and are not supplied with recruits advected from distant localities by ocean currents. Even though the strong negative relationship between longevity and temperature for all three species seems to suggest an isolated island effect as a factor that describes this confined pattern, the isolated island sites are at the extreme ends of the species' geographic ranges, leaving this test relatively weak. An ideal test would involve isolated islands in both warm and cool water temperatures in the mid- geographic ranges of the fishes.

2.4.4. Geographic variation in body size

As latitude increases, body size of ectotherms generally increases (Conover 1990, Cowen 1990, Atkinson 1994). Body size followed the predicted latitudinal pattern for all three species of surgeonfish in this study. As with longevity, the populations with the largest body sizes were those at the isolated oceanic islands at the most northern and the most southern extent of all of the fishes' geographical ranges (Bermuda, Ascension, St. Helena, Cabo Frio) suggesting a possible isolated island effect. Consequently these study sites encompass the colder sea temperatures within the geographical range of the surgeonfish.

Countergradient variation in growth, where temperature gradients are inversely related to body size and lifespan in genetically-controlled growth capacity of fish, may depict a function which allows individuals to adapt to a shorter growing season caused by low sea temperatures at high latitudes (Conover 1990, Conover and Shultz 1995, Schultz et al. 1998). Results in the present study are consistent with the concept that species with large latitudinal ranges do tend to have inverse temperature/growth gradients. A number of studies conducted on various species within the tropical Atlantic Ocean and Caribbean Sea (Luckhurst et al. 2000, Choat et al. 2003, Ferreira et al. 2004), as well as in the Indo Pacific (Craig et al. 1999, Meekan et al. 2001, Choat and Robertson 2002) have revealed a trend of growth inversely related to sea temperature. However, these patterns are not necessarily based on genetics but may be the result of variable environmental factors influencing the growth (Rocha et al. 2002, Bergenius et al. 2005). Factors such as habitat variance (see Ackerman 2004) resulting in variable exposure to predation (see Holbrook and Schmitt 2003), food availability (see Atkinson and Sibly 1997) and physical elements, such as wave action, exposed to the study site (see Crossman et al. 2001, Fulton and Bellwood 2004), in addition to sea surface temperature, can influence the patterns of the growth trajectories in fishes. These factors have yet to be examined in the species of surgeonfish presented in this study, but it is likely that the growth patterns are not determined by temperature alone (see also Bergenius et al. 2005).

Available data suggest that a positive linear relationship between size and longevity is not exclusively applicable to coral reef fishes (Choat and Robertson 2002, Hernaman and Munday 2005). Surgeonfish are small in body size, but are long lived, and the idea of big fish live longer does not pertain to this study. Species with similar lifespans can greatly differ in maximum body size (Choat and Robertson 2002). At Bermuda, the most northern site where Atlantic acanthurids are found as well as one of the colder locations, all three species are longest lived, but not largest in size. *A. coeruleus* in Bermuda displays one of the smaller populations for body size, but is the longest lived relative to the other populations where it can live to be more than 40 years old.

2.4.5. Geographic variation in growth

Growth rates in ectotherms can be variable over latitudinal gradients. For ectotherms, it is known that adult body size and longevity are greater in individuals exposed to colder environments during development. It is likely that temperature may be the reason for this gradient pattern since it has been found that increases in the breeding temperature of fish increases the initial growth but stumps the final size (Atkinson 1994). Consequently, there is speculation that the geographic trend of the demography of temperate fishes could differ from tropical fishes (Meekan et al. 2001, Sponaugle et al. 2006). On similar spatial scales, in temperate waters there can be much larger temperature variability than in tropical waters due to lack of seasonal fluctuations in water temperature in tropical waters, and temperate fishes adapt to these fluctuations different than tropical fishes across a large geographical scale. However, in this study, for all parameters ($L(1)$, $L(2.5)$, $L(4)$) of *A. bahianus* and parameters $L(2.5)$ and $L(4)$) of *A. chirurgus* and *A. coeruleus* there was a negative relationship between size-at-age and temperature paralleling a trend described by Yamahira and Conover (2002) using a temperate species. They found that the Atlantic silverside, *Menidia menidia,* exhibited greater growth at high latitudes due to cold temperature adaptation driven by selection for larger size at higher latitudes. Larger individuals had a higher probability of survival over high latitude winters, for which higher growth rates were selected.

While a negative relationship was seen in *A. bahianus* populations, it is not consistent with the *A. chirurgus* and *A. coeruleus* populations from settlement to age 1 (parameter *L(1)*). Size-at-age values among the various water temperatures was not significantly different at age 1 for *A. coeruleus* and *A. chirurgus*, suggesting that growth from settlement to age 1 did not differ among the sites. In these two species most of the variation in growth occurred between age 1 and 4. However these results should be treated with caution, since the number of study sites was relatively small for the latter two species. When sample sizes are small, errors in analysis are likely to occur and obscure any potential trends on a large geographic scale. However, mortality rates and environmental and oceanic processes can significantly influence growth (Bergenius et al. 2002). High mortality rates can influence a population of fishes to grow faster and attain smaller adult body sizes (Searcy and Sponaugle 2001), while a number of environmental variables can influence the variation in larval growth (Bergenius et al. 2005). These factors were not tested in this study, but much additional work should be done to increase our knowledge in the variability of growth in tropical fishes.

The growth trajectories of all three tropical Atlantic acanthurids demonstrate the characteristics of indeterminate growth where initial growth rate seems to have little effect on maximum size or age. Consequently, at least 85% of the final body size was attained in the first year of life for all three species of acanthurids at all localities.

After comparing the Analysis of Variance (ANOVA) test results between the observed data and the randomly distributed data, the p-values for both tests were very similar (Table 2.5). This suggests that despite the non-normal distribution of the observed data, the ANOVA results are accurate. A randomization test demonstrates whether or not a particular pattern in the data is likely to have occurred by chance. This only adheres to the data that is being considered. If the collectors were able to decipher the age among the individual fish in the field, we would have more samples for each temperature group, and a randomization test would not be required.

A more in-depth examination of the life history traits of these tropical Atlantic acanthurids is needed to completely understand these patterns, including the influence of reproduction, predation and population density. Some NW Atlantic reef fishes exhibit stronger seasonally temporal reproduction patterns at increasing latitudes (Robertson 1991b). It has been found that many fish species at low latitudes (i.e. minimal seasonal fluctuations) reproduce year round, since they generally do have short life spans (Robertson el al. 2005). Since many coral reef fishes are continuously reproducing their energy is transferred to reproduction instead of growth they typically have smaller absolute body sizes (Ruttenberg et al. 2005) at early life history stages. The reproductive cycles of fishes from higher latitudes (i.e. relatively large seasonal fluctuations) are likely to be affected by unpredictable and harsh environmental seasonal conditions where it is difficult to reproduce on a regular basis. Fishes from these regions may have longer lifespans because mortality due to reproduction is a result of shorter reproductive seasons (Mangel 2001). Environmental factors such as wave exposure (Fulton and Bellwood 2004) and habitat variation need to be examined. The variation of the habitat at a local scale and the effects it may impose on the demographic characteristics of Acanthurids populations will be addressed in Chapter 4.

Study site	**Latitude**	**MST (^oC)**	**Collection dates**
St Helena	15.9^{o}S	22.6	June-July 1997
Bermuda	32.2^{o}N	22.9	October 2001, July 2002
Cabo Frio	22.9^{o}S	24.3	October 1997
Ascension	8.0^{o}S	26.0	March-June1997
Margarita	11.0^{o}N	26.0	April 2005
Lee Stocking	23.8^{o}N	26.9	November 1998 and 1999
Las Aves	12.0^{o}N	27.1	August 2002
Los Roques	11.8^{o}N	27.1	July 2000, August 2002
Barbados	13.2^{o}N	27.6	July 2000
San Blas	9.5^{o}N	28.0	1995-1999
Jamaica	18.2^{o}N	28.0	April 2005
Belize	16.8^{o}N	28.1	September 2002

Table 2.1: Study sites arranged in order of mean sea surface temperatures (MST), with the latitude and collection dates.

Study site	***A. bahianus***	***A. coeruleus***	***A. chirurgus***
St Helena	x		
Bermuda	x	x	x
Cabo Frio	x		
Ascension	x	x	
Margarita	x	x	x
Lee Stocking	x	x	
Las Aves	x		
Los Roques	x	x	x
Barbados	x		
San Blas	x	x	x
Jamaica	x		
Belize	x	x	x

Table 2.2. The locations in the tropical Atlantic Ocean where every species of Acanthurid was sampled.

A. chirurgus **L_o=27mm**

Study site	n	t_o (yrs)	k	L_∞ (mm)	Size range FL (mm)	MMA (yrs)	Max. age (yrs)	Mean size at age FL(mm) at:			r^2 (VBGF)
								1 yr	2.5 yr	4 yr.	
Belize	47	-0.1244	1.10	210	103-163	9	12	177	203	208	0.76
Bermuda	116	-0.1464	0.82	240	26-285	16	29	162	215	232	0.80
Los Roques	43	-0.1275	1.10	206	86-243	10	14	165	198	204	0.88
Margarita	113	-	-	-	86-330	6	16	196	241	250	0.88
San Blas	97	-0.1649	0.73	239	66-276	8	13	158	210	227	0.89

A. coeruleus **L_o=27mm**

Study site	n	t_o (yrs)	k	L_∞ (mm)	Size range FL (mm)	MMA (yrs)	Max. age (yrs)	Mean size at age FL(mm) at:			r^2 (VBGF)
								1 yr	2.5 yr	4 yr.	
Ascension	112	-0.0917	0.42	244	89-304	29	37	118	177	208	0.71
Belize	92	-0.1502	1.03	188	38-242	10	15	139	176	185	0.86
Bermuda	105	-0.1420	1.01	203	32-250	38	43	149	190	200	0.83
Lee Stocking	77	-0.1494	0.88	219	113-256	20	27	155	201	213	0.68
Los Roques	81	-0.1122	0.39	199	106-285	17	20	111	155	174	0.78
Margarita	74	-	-	-	97-335	8	20	180	210	215	-
San Blas	110	-0.2511	0.49	231	38-261	12	16	120	176	204	0.91

Table 2.3: Demographic data on the populations of *Acanthurus chirurgus, A. coeruleus* and *A. bahianus* at the respected study sites. Size at age zero (L_o) in the growth trajectories were constrained to 27 mm for each species. Size at age is derived from the reparameterized von Bertalanffy growth function (rVBGF). MMA refers to mean maximum age and is represented in years. Values for t_o, k and L_∞ do not pertain to Margarita for *A. coeruleus* and *A. chirurgus* since the growth trajectories do not fit the VBGF model.

A. bahianus **L_o=27mm**

Study site	n	t_o (yrs)	k	L_∞ (mm)	Size range FL (mm)	MMA (yrs)	Max. age (yrs)	Mean size at age FL(mm) at: 1 yr	2.5 yr	4 yr.	r^2 (VBGF)
Ascension	109	-0.1070	1.23	219	94-263	15	19	175	211	218	0.79
Barbados	94	-0.2028	0.94	156	33-132	10	15	116	145	153	0.68
Belize	58	-0.1868	0.86	182	40-151	7	10	125	166	177	0.52
Bermuda	81	-0.2252	0.63	204	19-179	26	32	121	170	190	0.72
Cabo Frio	93	-0.1022	1.28	221	98-180	11	21	180	214	219	0.66
Jamaica	59	-0.1153	1.71	151	40-136	5	8	134	150	151	0.91
Las Aves	108	-0.1395	1.22	172	60-138	8	12	139	166	171	0.66
Lee Stocking	124	-0.1504	1.06	183	36-145	8	13	139	173	181	0.87
Los Roques	86	-0.1604	1.12	164	40-134	8	12	130	157	162	0.69
Margarita	135	-0.1053	1.33	207	57-275	12	18	173	201	205	0.82
San Blas	175	-0.1004	1.64	178	25-156	6	10	157	176	177	0.70
St Helena	102	-0.0808	1.58	225	108-174	23	31	196	221	224	0.73

Table 2.3 cont.

	VBGF	Gompertz	Richards	Linear	Logistic	Exponential	Power	Power^2	Quadratic
A. coeruleus ALL	82368.41	91957.71	91957.87	496338.38	94384.55	198719.36	1578990.30	27437.18	1073916.55
A. coeruleus Age 0-4	10252.14	12472.85	12472.91	126002.19	13687.35	83483.93	282404.86	8566.49	192999.98
A. chirurgus ALL	78552.91	120613.30	120614.60	166232.11	146375.11	371579.43	2946168.02	44225.04	2238697.06
A. chirurgus Age 0-4	43476.42	59836.41	59837.11	248622.55	75428.53	246969.26	790938.22	31182.53	450406.81

Table 2.4: Sum of squares results for nine growth models fitted to *A. coeruleus* and *A. chirurgus* at Isla de Margarita. Power^2 growth model fits the growth trajectories best for both species for the entire lifespan. Power^2 and VBGF form the growth trajectories best for both species in their early life history stages. VBGF was used in this study in order to properly be fit with rVBGF, and tested similarly to the other populations.

Species	DF	SS	MS	F Value	Pr>F	Random P
A. bahianus $L_{(1)}$						
Model	11	89033.98	8094.00	39.78	**<.0001**	**<.0001**
Error	143	29093.22	203.45			
A. bahianus L(2.5)						
Model	11	60781.62	5525.60	13.42	**<.0001**	**<.0001**
Error	177	72862.08	411.65			
A. bahianus L(4)						
Model	11	38740.66	3521.88	9.78	**<.0001**	**<.0001**
Error	100	36023.62	360.24			
A. coeruleus L(1)						
Model	6	452.74	90.55	0.39	0.852	0.843
Error	21	4912.89	233.95			
A. coeruleus L(2.5)						
Model	6	23613.82	3935.64	12	**<.0001**	**<.0001**
Error	78	25584.98	328.01			
A. coeruleus L(4)						
Model	6	18022.37	3003.73	9.71	**<.0001**	**<.0001**
Error	70	21646.91	309.24			
A. chirurgus L(1)						
Model	4	5493.87	1373.47	2.2	0.0888	0.108
Error	35	21820.53	623.44			
A. chirurgus L(2.5)						
Model	4	21629.73	5407.43	13.65	**<.0001**	**<.0001**
Error	53	20994.84	396.13			
A. chirurgus L(4)						
Model	4	21146.35	5286.59	16.42	**<.0001**	**<.0001**
Error	60	19320.67	322.01			

Table 2.5: A randomization test was used in place of parametric ANOVA to test for statistical significance associated with the parameters of rVBGF, *L(1), L(2.5)* and *L(4)* of *A. bahianus, A. coeruleus* and *A. chirurgus*. The observed p-value was compared with the distribution of randomized p-values, and if it occupied the lower 5% of the distribution, then it was deemed statistically significant. The bold values indicate significant results.

Figure 2.1: Map of the study sites at which *Acanthurus bahianus, A. chirurgus and A. coeruleus* were collected throughout the tropical Atlantic Ocean. All three species are found in the shaded areas except *A. chirurgus* and *A. coeruleus* are not found at St. Helena.

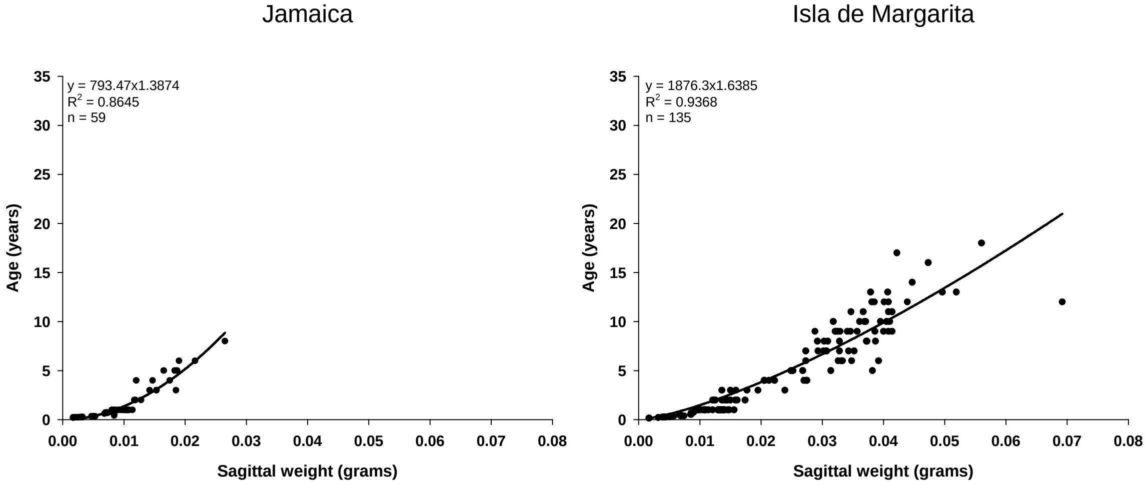

Figure 2.2: Otolith growth trajectories of *Acanthurus bahianus*: power functions of sagittal weight and age at Jamaica and Isla de Margarita. Correlations for the other populations are found in Robertson et al. (2005). There was a positive correlation between age and sagittal weight at all study sites indicating the continuous growth of otoliths throughout an individual's lifetime.

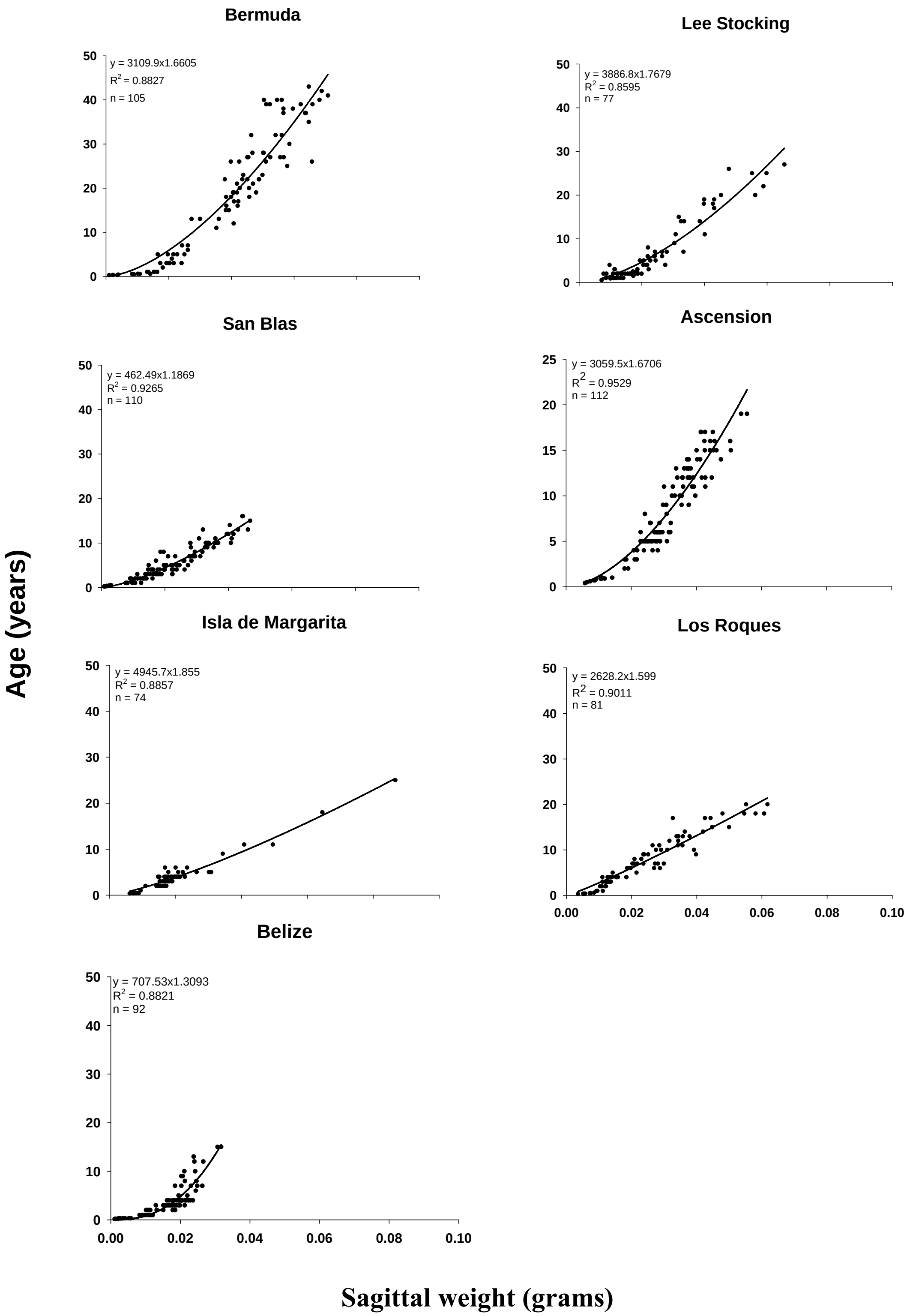

Figure 2.3: Otolith growth trajectories of *Acanthurus coeruleus*: power functions of sagittal weight and age at seven sites. There was a positive correlation between age and sagittal weight at all study sites.

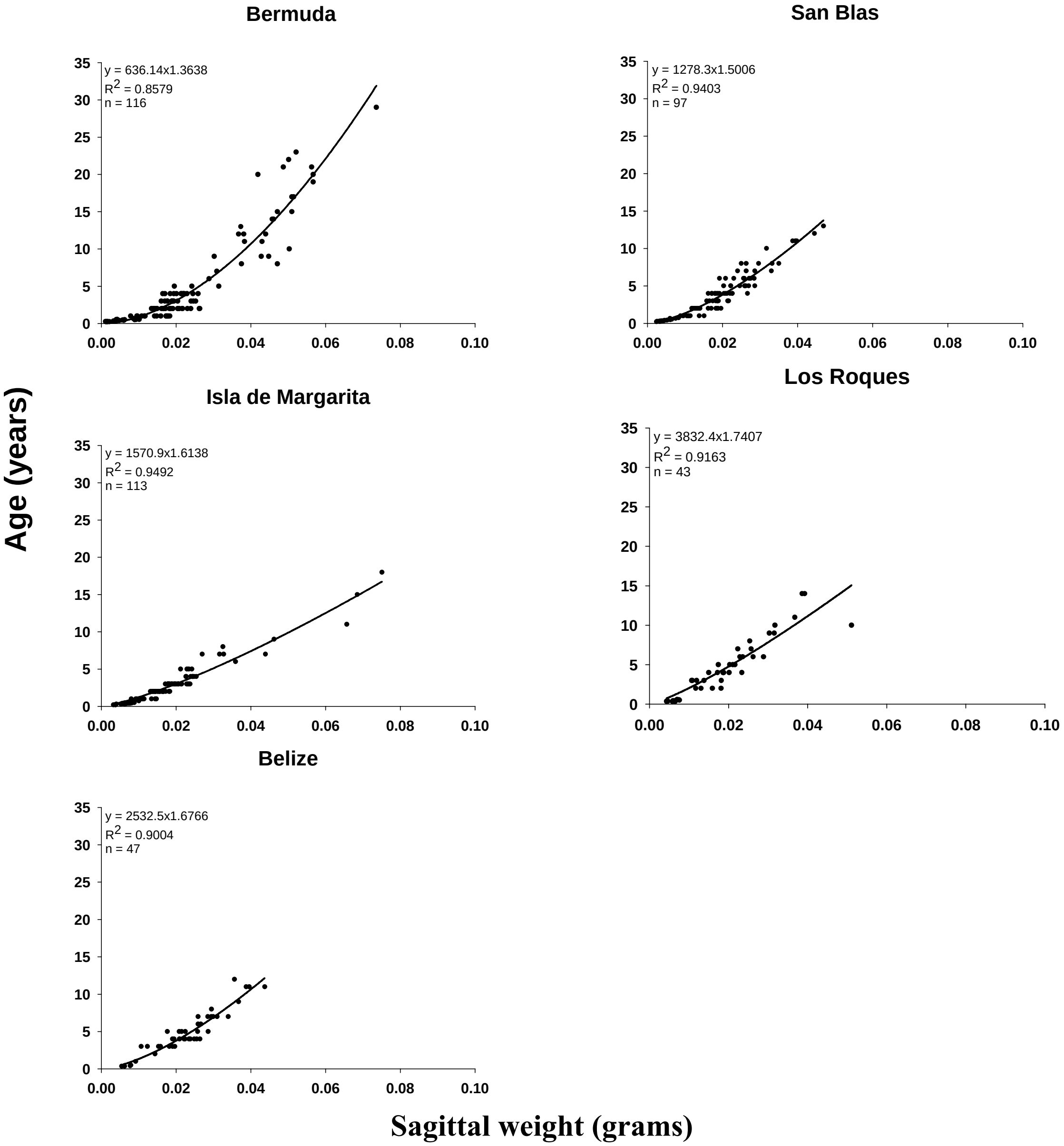

Figure 2.4: *Acanthurus chirurgus*: Using least squares linear regression, the relationship between sagittal weight and age was calculated for *A. chirurgus* at all five localities. There was a positive correlation between age and sagittal weight at all study sites.

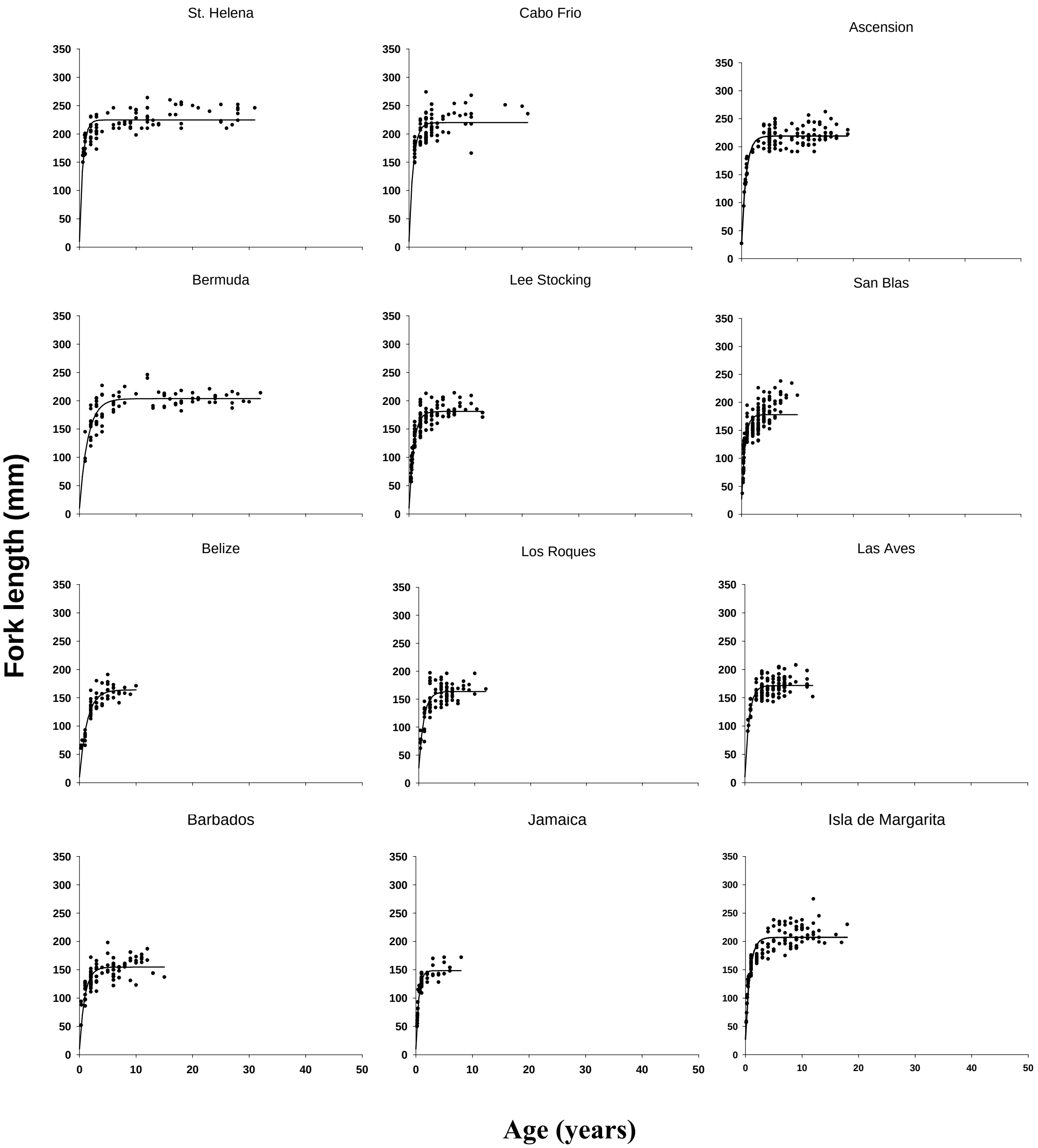

Figure 2.5: *Acanthurus bahianus*: Von Bertalanffy growth curves at 12 study sites. All of the graphs were constructed from the data from Robertson et al. (2005) except Jamaica and Isla de Margarita.

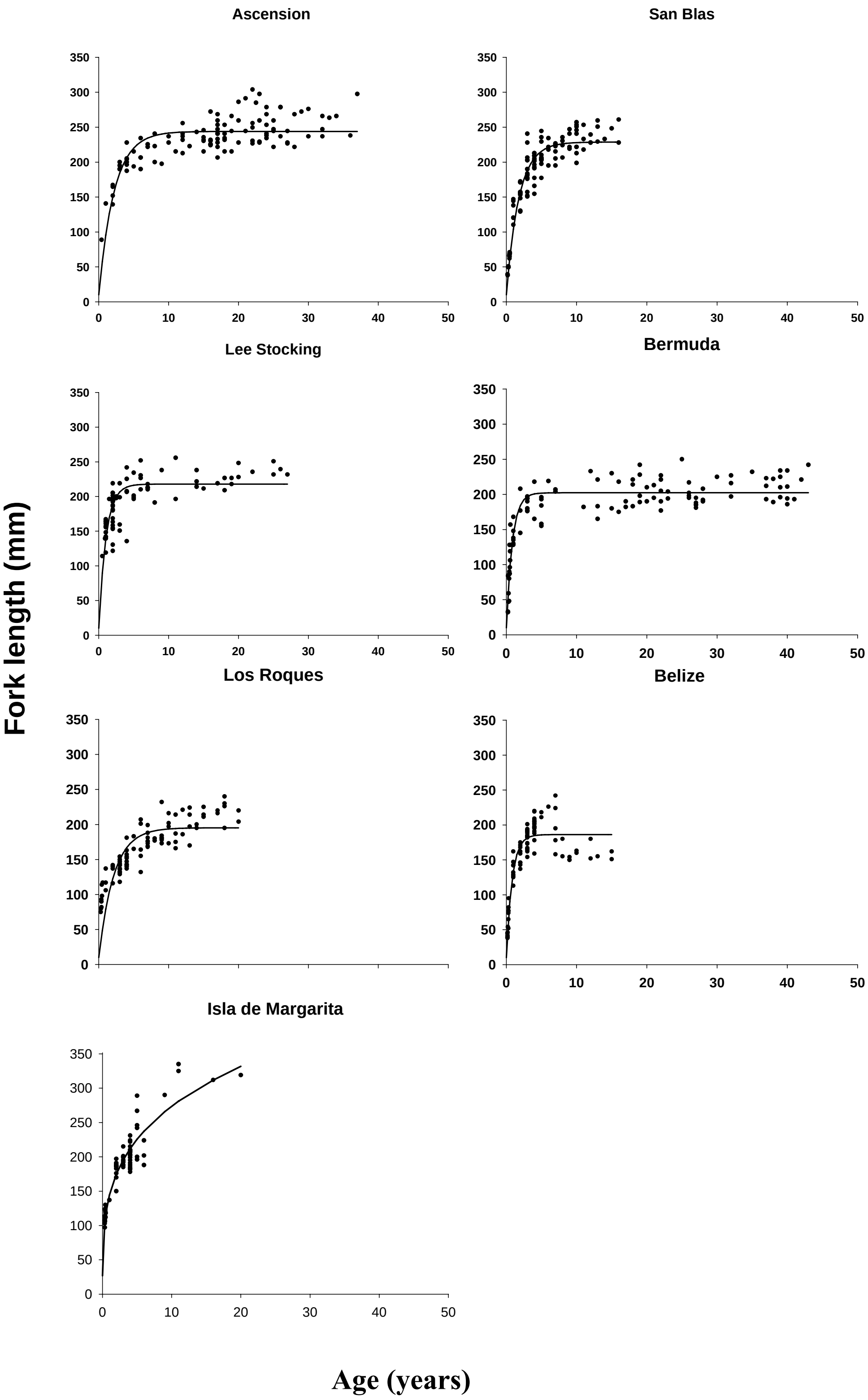

Figure 2.6: *Acanthurus coeruleus*: Growth trajectories at 7 study sites. All populations fit the VBGF except Isla de Margarita which fits the Power^2 model best.

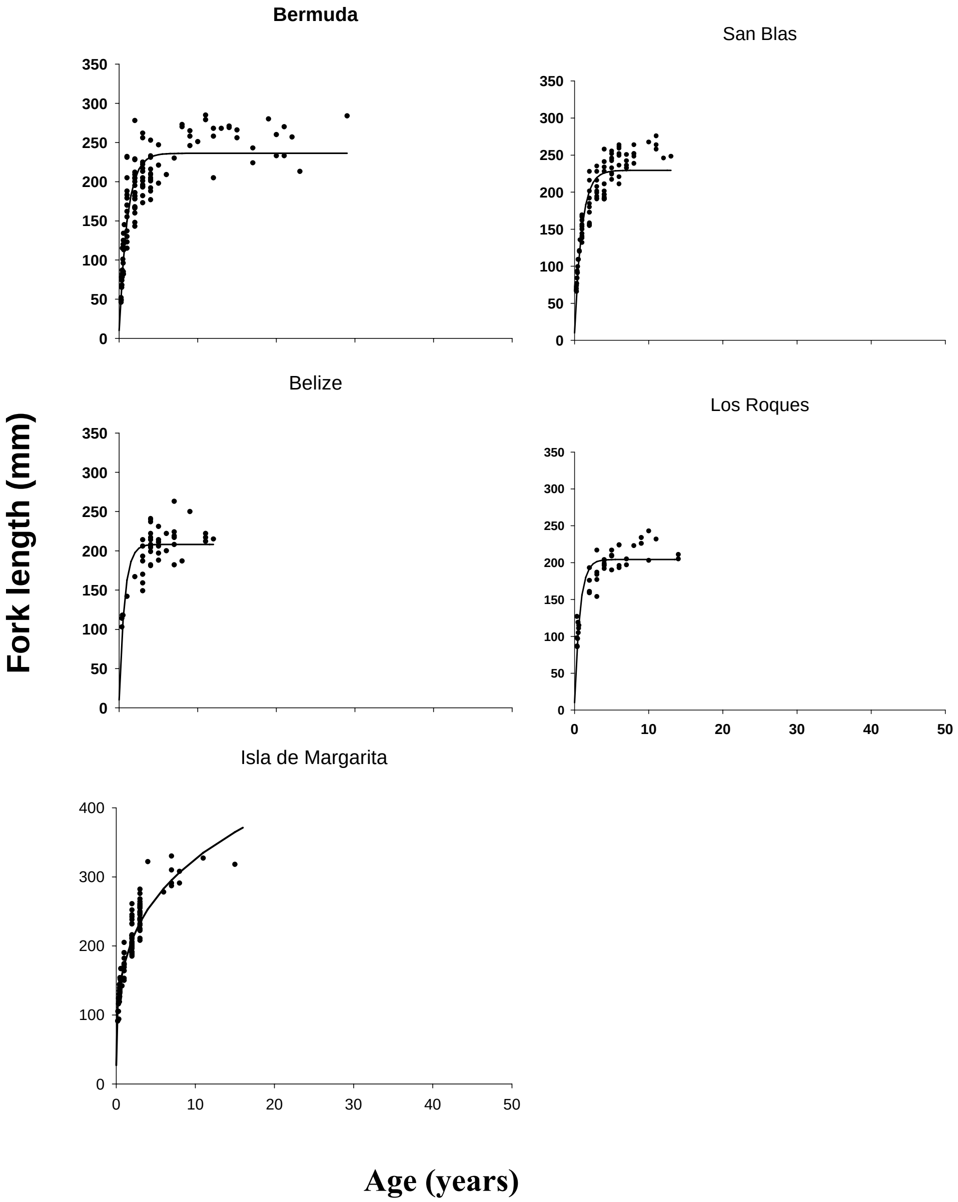

Figure 2.7: *Acanthurus chirurgus*: Growth trajectories at 5 study sites. All populations fit the VBGF except Isla de Margarita which fits the Power^2 model best.

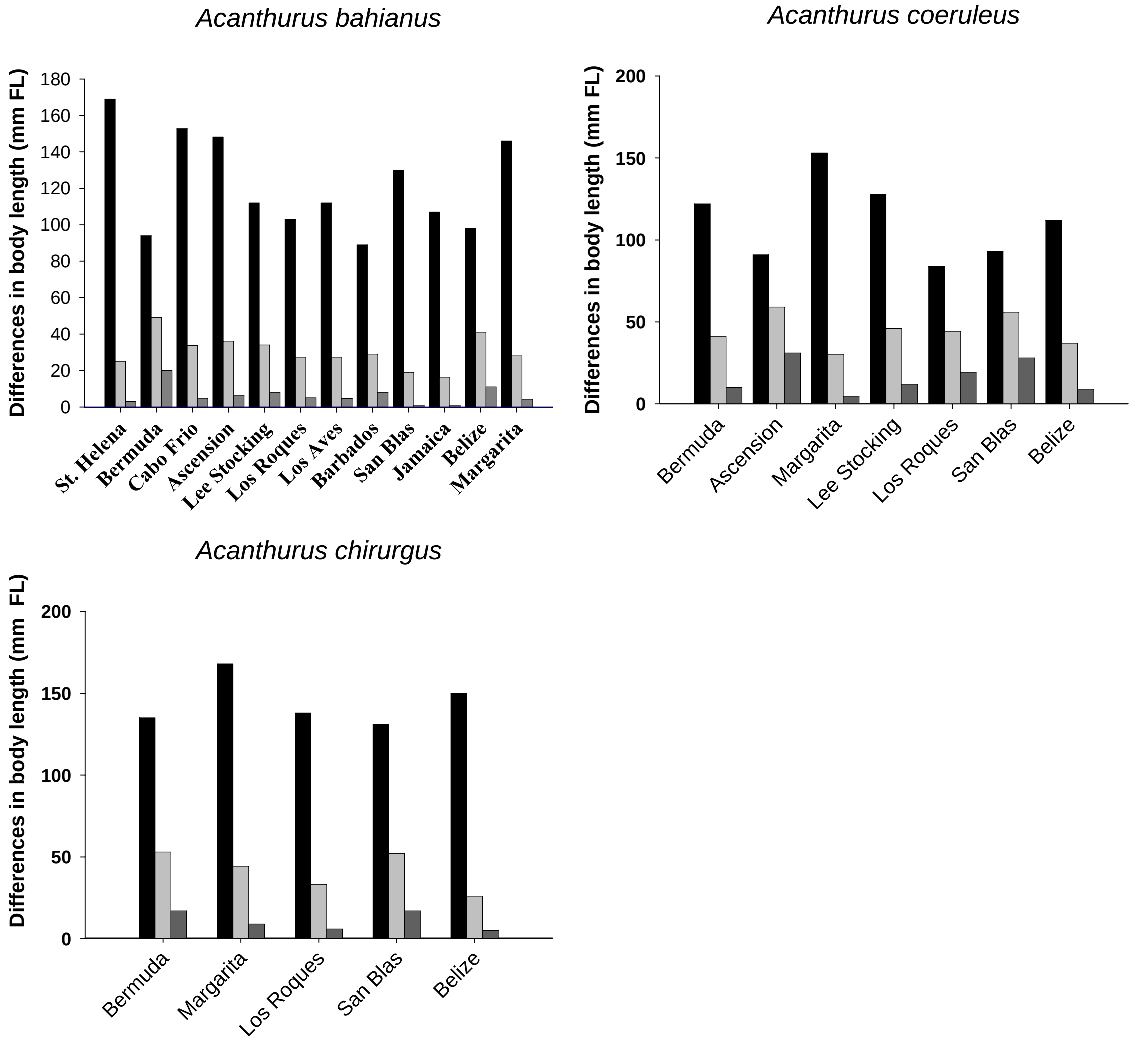

Figure 2.8: Differences in body length in the early life history stages of all of the populations of three species of *Acanthurus*. The black bars represent growth from settlement to age 1 year, the light grey bars represent growth from ages 1 to 2.5 years, and the dark grey bars represent growth from ages 2.5 to 4 years.

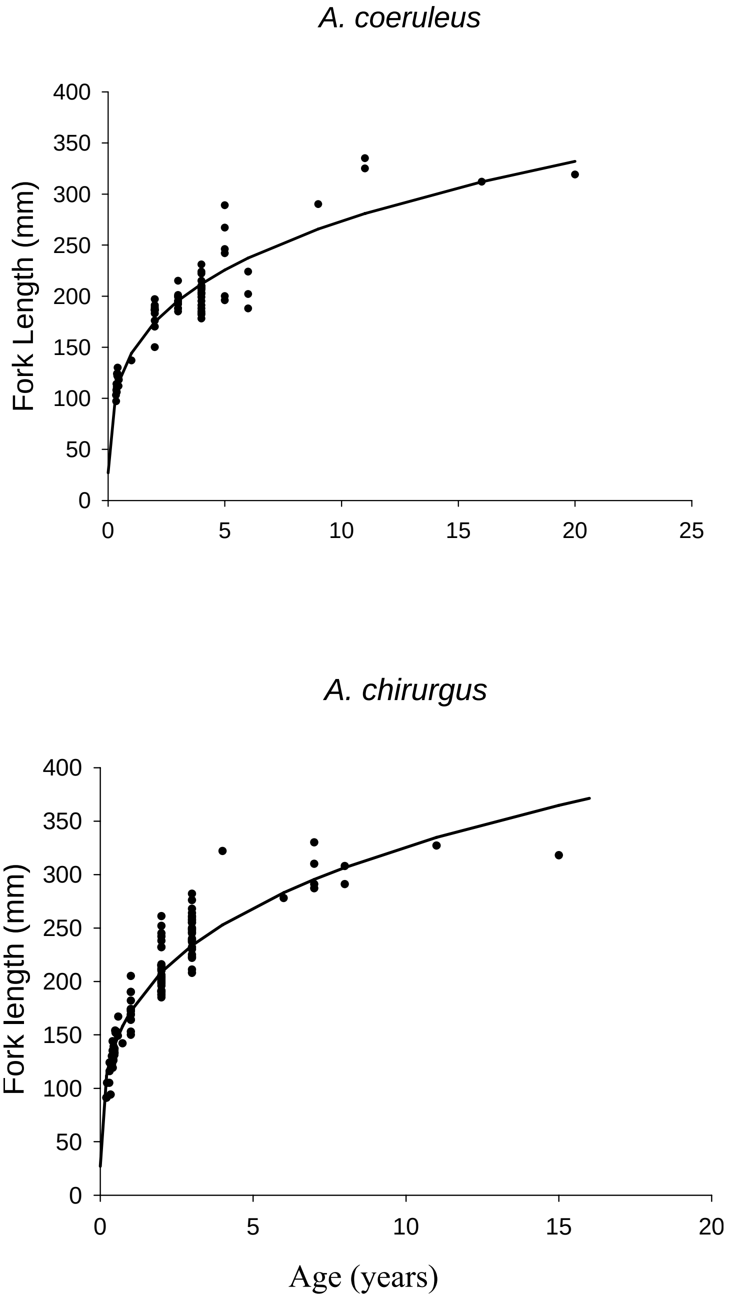

Figure 2.9: Power^2 growth models of *Acanthurus coeruleus* (SS=27437, r^2=0.88) and *A. chirurgus* (SS=44225, r^2=0.86) at Isla de Margarita. These two species do not demonstrate an asymptotic growth curve that is generally characteristic of Acanthurids around the world.

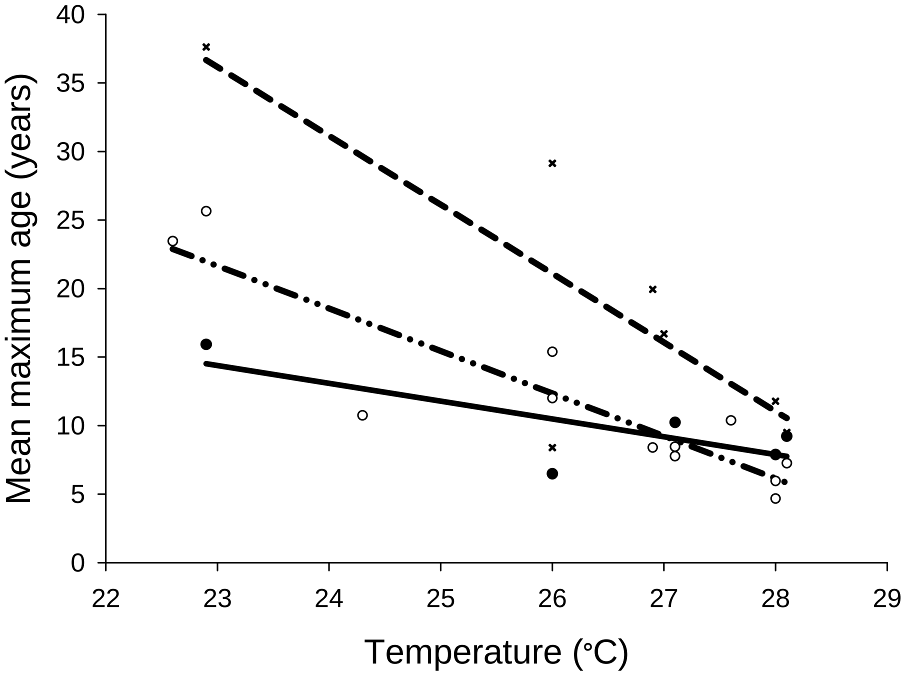

Figure 2.10: A linear regression of 20% maximum longevity vs. mean sea surface temperatures. The dashed line and exes represent (---, x) *A. coeruleus* (y = -5.0041x + 151.26, r^2=0.66; p=0.0283); 7 sites, the dash-dot line and open circles (—··—, °) represent *A. bahianus* (y = -3.1016x + 92.983, r^2=0.82.; p=0.0004); 11 sites, and the solid line and solid circles (——, •) represent *A. chirurgus* (y = -1.3117x + 44.701, r^2=0.66; p=0.0408); 5 sites.

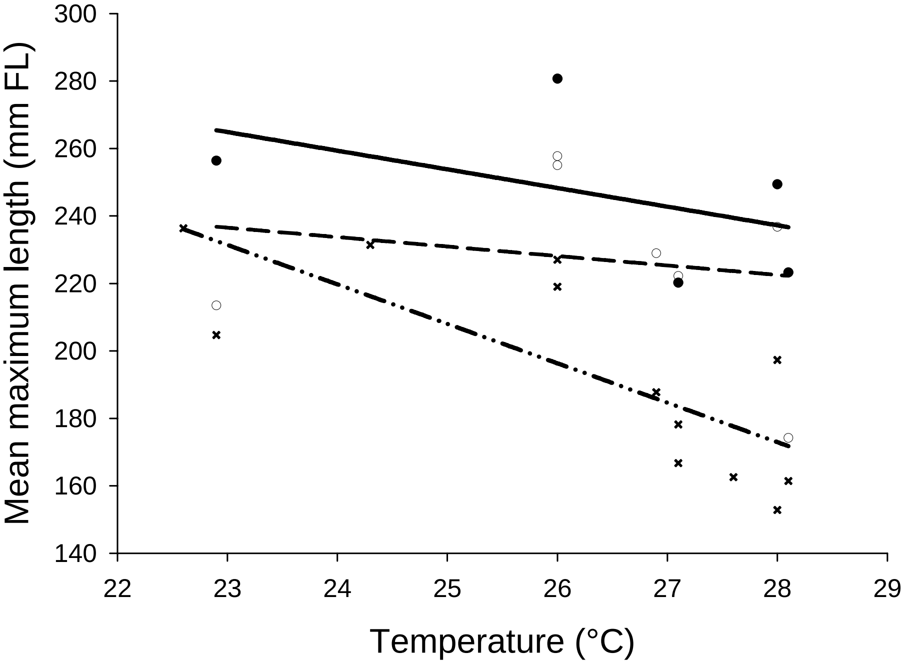

Figure 2.11: Linear regressions of 20% maximum body size vs. mean sea surface temperatures. The solid line and solid circles (——, •) represent *A. chirurgus* (y = -5.531x + 392.1, r^2=0.22; p=0.4206); 5 sites, the dashed line and exes (---,°) represent *A. coeruleus* (y = -2.8026x + 300.96, r^2=0.03; p=0.7079); 7 sites, the dash-dot line and open circles (—··—, x) represent *A. bahianus* (y = -10.764x + 477.68, r^2=0.58; p=0.0061); 12 sites. There is an indication of a negative trend in *A. chirurgus* and *A. coeruleus* even though the trend is not statistically significant.

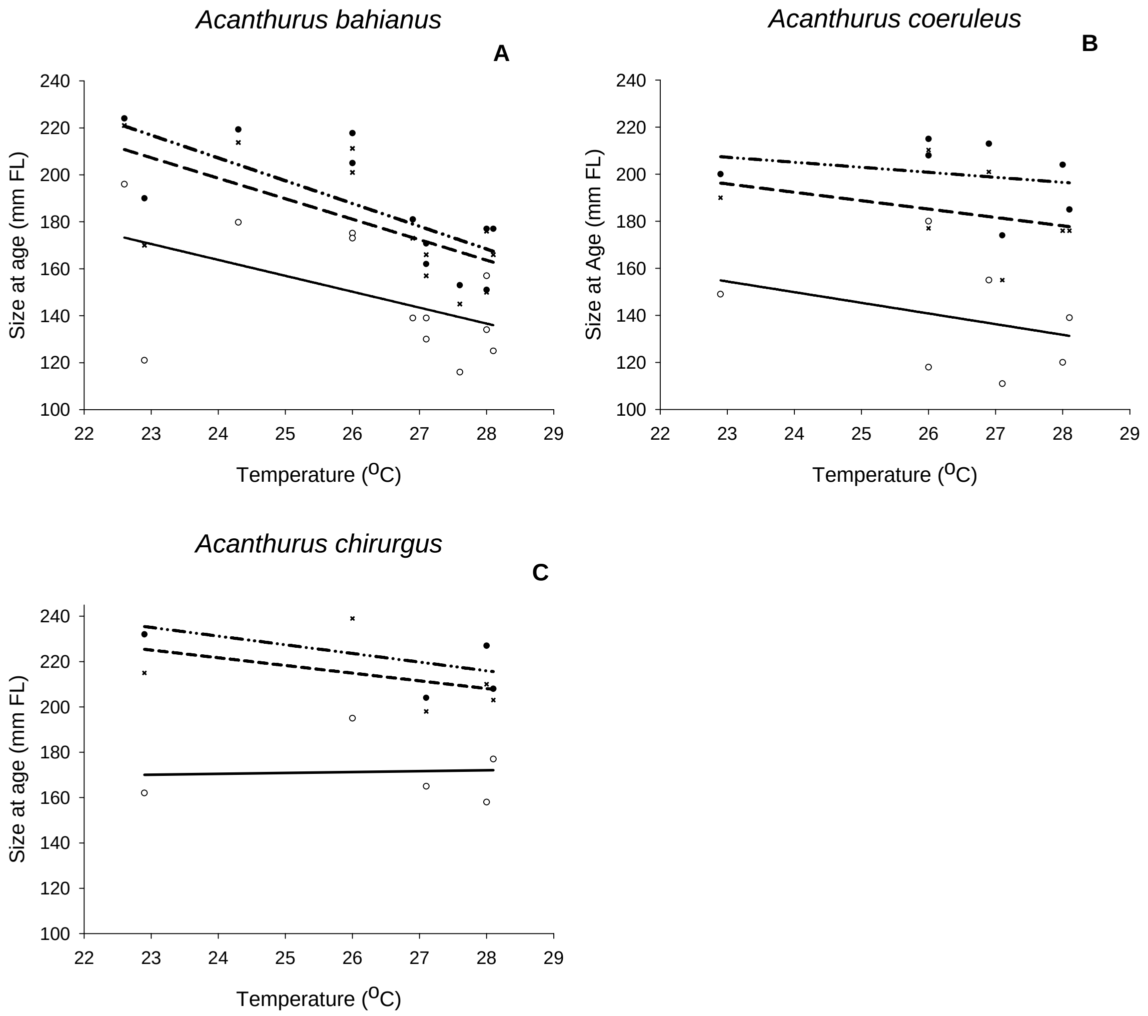

Figure 2.12: Instantaneous growth rates measured as size-at-age for populations of all three species of surgeonfish at three different ages vs. mean sea surface temperature. The solid line and open circles (——,°) represent size at age 1 year, the dashed line and exes (---, x) represent size at age 2.5 and the dash-dot line and solid circles (—··—, •) represent size at age 4. (A) *Acanthurus bahianus*: age 1 $y = -6.8112x + 327.37$, $r^2=0.25$, $p=<0.0001$; age 2.5 $y = -8.7492x + 408.58$, $r^2=0.45$, $p=<0.0001$; age 4 $y = -9.6897x + 439.65$, $r^2=0.54$, $p=<0.0001$. (B) *Acanthurus coeruleus*: age 1 $y = -4.5308x + 258.6$, $r^2=0.11$, $p=0.8520$; age 2.5 $y = -3.5636x + 277.79$, $r^2=0.12$, $p=<0.0001$; age 4 $y = -2.1324x + 256.21$, $r^2=0.06$, $p=<0.0001$. (C) *Acanthurus chirurgus*: age 1 $y = 0.3848x + 161.23$, $r^2=0.003$, $p=0.0888$; age 2.5 $y = 587.73x^{-0.3109}$, $r^2=0.13$, $p=<0.0001$; age 4 $y = 978.74x^{-0.4518}$, $r^2=0.22$, $p=<0.0001$.

Chapter 3: Demographic characteristics of Acanthurus lineatus on a longitudinal gradient across the tropical South Pacific Ocean

3.1 Introduction

As a compliment to the latitudinal gradient studies, I investigated the pattern of demographic variation of acanthurids on a longitudinal scale across the South Pacific Ocean. Much research has been conducted on teleosts on the latitudinal gradients (Present and Conover 1992, Conover et al. 1997, Gust et al. 2002, Choat et al. 2003, Ackerman 2004, Ferreira et al. 2004, Floeter et al. 2004, Robertson et al. 2005), but this is the first time demographic characteristics have been compared over a longitudinal scale. Considering the potential influences of reef history and environmental and fishing impacts on reef fish demography along a longitudinal scale is a unique approach in that sea temperature may not vary significantly among locations, and therefore can be eliminated from consideration as a cause of variability of the demographic rates.

Demographic information is needed due to the increasing importance of surgeonfish in artisanal reef fish catches, specifically in American Samoa (Craig et al. 1997), and in the aquarium trade (Kuiter and Debelius 2001). There is speculation that fishing can influence the demographic patterns of fishes (Halpern and Warner 2002).

This may be likely in American Samoa because of the large human population and extensive subsistence and artisanal fishing that occurs in this region (Craig et al. 1997).

The purpose of this study was to document the longevity, body size and instantaneous growth of coral reef fishes along a longitudinal scale from the west to central Pacific Ocean using the lined surgeonfish, *Acanthurus lineatus*, to test these observations. Many species exhibit variable life history properties across their geographic ranges in order to adapt to variable environmental conditions (Brown 1995). Life history tradeoffs can be analysed due to the tendency of organisms in different environments to differentially allocate energy to maintenance and growth, and accurate estimates of these demographic characteristics may benefit management (Ruttenberg et al. 2005). This study analyses the age-based demographic characteristics of populations of *A. lineatus* retrieved through reading growth increments in sagittal otoliths to obtain accurate estimates of age and growth at five localities spread along a longitudinal gradient across the tropical South Pacific. Specifically, this study compared maximum longevities, absolute mean body sizes and the estimation of growth parameters of *A. lineatus* populations at Lizard Island, the Outer Great Barrier Reef (GBR), American Samoa, Moorea Island and the Marquesas Islands.

3.2 Materials and methods

3.2.1 Study species

The lined surgeonfish, *Acanthurus lineatus,* was used to estimate absolute growth, size-at-age and longevity based on sagittal annuli. This species is widespread throughout the Indo Pacific, and belongs to the Acanthuridae, the most abundant and species-rich family of coral reef fishes (Hart and Russ 1996). These herbivores which feed on red and green turfing and filamentous algae (Choat et al. 2004) are found in the shallow coastal waters to the outer reef flats in exposed reefs subject to surge (Craig 1996). Adults are usually found in schools, while solitary juveniles are found on shallow, sheltered, rubble habitats. *A. lineatus* is territorial, can be very aggressive, has a venomous caudal spine and they spawn year-round at all sites, but generally during the austral summer (Randall 2005). Lined surgeonfish are strongly site-attached (Craig 1996), but can occasionally be found to move to other reefs (Craig et al. 1997).

3.2.2 Study sites and field sampling

Samples of *Acanthurus lineatus* were collected at five sites spanning 75^{o} longitude across the South Pacific Ocean (Figure 3.1). These locations, Lizard Island, Outer Great Barrier Reef (GBR), American Samoa, Moorea and Marquesas, have a broad range of positions in longitude, similar water temperatures and variable habitat and historical characteristics (Table 3.1).

At Lizard Island samples were collected from reefs surrounding the island. Lizard Island is a granite island located in the mid-shelf region of the Great Barrier Reef (GBR). Lizard Island is a resort island, where human impact affects the reef environment minimally. Samples at Outer GBR were collected on reef fronts and passes of the outer barrier reefs (Hicks, Day and No-Name Reefs) 15 to 25 km northeast of Lizard Island where there are no human inhabitants. American Samoa is a steep volcanic island with 55 km of fringing coral reef. Samples were collected on coral reefs in shallow waters and reef flats which consisted of live coral cover of only 3.5% caused by *Acanthaster* invasions and hurricanes allowing elevated algal turf cover on the reefs (Craig et al. 1997). Moorea, located in French Polynesia, is surrounded by a narrow coral zone of 2 km maximum width (Galzin and Pointier 1985), and samples were collected directly on the outer areas of the barrier reef on the north side of the island. This island is inhabited by approximately 10,000 people. The Marquesas Islands are of volcanic origin and sheer ridges immerse steeply into the sea, and there is no fringing reef (pers. obs., Signorini et al. 1999, Martinez and Maamaatuaiahutapu 2004). Samples were collected on the one coral reef lagoon in Anaho Bay on the north side of Nuku Hiva, and on the steep rocky reefs around Ua Huka, Hiva Oa, Tahuata and Nuku Hiva where approximately 500 people live on that area of the island.

A total of 399 individuals was collected using pole spears on SCUBA and snorkel in depths of 2-15 m at all study sites. The depth of collections varied consistently among the locations, and as there were no extreme thermoclines at any of the sites, sea surface temperature was used as a proxy to represent the overall sea temperatures among the study sites. Both adults and juveniles were caught at all locations except Lizard Island and Outer GBR where the minimum age was one. Some samples were taken from artisanal fishery markets in American Samoa. Collectors followed the collection, body size and weight measurement and otolith extraction and storage protocols detailed in chapter 2.

3.2.3 Sagittal preparation and growth and age determination

I derived length-at-age data for *A. lineatus* from all locations except American Samoa by aging sagittal otoliths. Data for American Samoa were obtained from Craig et al. (1997) and to the appropriate growth model. Choat and Axe (1996) previously validated the annual sagittal otolith increments of *A. lineatus* with oxytetracycline.

Sagittal otoliths were processed according to the methods described in Chapter 2. Power functions of age and sagittal otoliths weight were compared to assess any correlations.

3.2.4 Age based growth modelling

All populations were tested on 10 growth models to determine the best fit model indicated by sum of squares values. At all study sites, except Marquesas, age-based growth data were chosen to fit the von Bertalanffy growth function (VBGF):

$$L_t = L_\infty e^{(-k(t-t_o))}$$

where L_t is the estimated length at age t, L_∞ is the theoretical mean asymptotic fork length, k is the rate at which the growth curve approaches the asymptotic length, t is the age of the fish in years, t_o is the hypothetical age at zero length and e is the base of the natural logarithm. This model is based on the constant, K, a curvature parameter that measures the time at which the asymptotic length can theoretically be reached (unit of time^{-1}). Initial observation of the size-at-age data in the Marquesas indicated that it did not conform to the traditional asymptotic growth trajectory of acanthurids, thus length-at-age data from the Marquesas were fit to the non-asymptotic Power^2 model:

$$L = (at^k)^2$$

where a and k are constants, and t is age in years.

Since samples of juveniles were not available at Lizard Island and the Greater GBR sites, and to get a more reliable estimate of initial growth, intercepts were constrained to approximate size at recruitment to the reef (L_o) for all localities (Leis and Rennis 1983, Robertson 1992). L_o = 25 mm was chosen because it is the approximate size at which the juveniles settle on the reef crest in the Indo Pacific (Robertson 1983, Choat and Robertson 2002).

Each data set of longevity and body length estimates for *A. lineatus* was bootstrapped 1000 times to calculate mean maximum age (mean T_{max}) and size (mean L_{max}) as the average measurement of 20% of the oldest and largest individuals respectively. The data sets were sampled 1000 times with replication, preserving sample size *N* and the population age structure (Haddon 2001, Ackerman 2004). A linear regression was fit to the 20% longevity (mean maximum age) and body size (mean maximum size) data to ascertain any patterns across the ocean from the west to central Pacific. These sites were proportionally scaled (in nautical miles) from west to east by calculating the rumb lines between all of the sites.

As described in detail in Chapter 2, the re-parameterized VBGF equation (rVBGF) was applied to growth data at all localities:

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

where $L_{(\tau)}$ = estimate body size at age τ

$L_{(\omega)}$ = estimate of body size at age ω

$L_{(\mu)}$ = estimate of body size at age τ

and $r = \frac{L\mu - L\omega}{L\omega - L\tau}$, and $L(t)$ is average size at age t, assuming that $L_{(\tau)} < L_{(\omega)} < L_{(\mu)}$ and $(L\mu - L\omega) \neq (L\omega - L\tau)$. This model was used to estimate body size at specific ages to determine instantaneous growth at various localities which can be used as a proxy to examine growth rates among species at all localities. In this study τ=1, ω=2.5 and μ=4 which are the ages at which growth is most evident. A randomization test was used in place of parametric Analysis of Variance (ANOVA) to test for statistical significance of growth at all three parameters, *L(1), L(2.5)*and *L(4),* among all sites on a longitudinal gradient across the Pacific.

3.3 Results

3.3.1 Sagittal preparation and growth and age determination

The transverse section of the sagittal otoliths displayed well defined orderly increments with alternating opaque and translucid bands (Figure 3.2). In all five populations regressions produced significant and strong power relationships, indicating that sagittal otoliths continue to grow throughout an individual's lifetime (Figure 3.3), and that sagittae are useful tools for assessing size at age growth trajectories.

3.3.2 Geographic variation in demography

Size-at-age data of *A. lineatus* was fit to 10 different growth models to discern the best fit model to the data. A VBGF or a Power^2 growth model was fit to *Acanthurus lineatus* depending on the initial observations of the size-at-age plots from each site. *A. lineatus* demonstrated the 'characteristic' pattern of asymptotic growth in four out of the five South Pacific populations. In the Marquesas, sums of squares indicated that a Power^2 growth model (SS = 25359) fit length-at-age data better than a VBGF model (SS = 28765). *Acanthurus. lineatus* from the Marquesas Islands exhibited a more round-shaped growth trajectory, and reached the largest body sizes compared to the other South Pacific populations which exhibited "square-shaped" growth trajectories (Figure 3.4). Similar to its counterparts in the tropical Atlantic the lined surgeonfish approached terminal size at around age 4, with most of the growth occurring within the first 10% of its lifespan.

During the rapid growth period up to age 4 in the Marquesas population, the VBGF model (SS = 15449) fit better than the Power^2 growth model (SS = 16260), allowing the estimation of the rVBGF parameters. The size-at-age data were fit to the population in the Marquesas to determine size-at-age growth similar to the other populations.

The mean longevity estimates for the oldest 20% of individuals sampled and mean maximum size of *A. lineatus* varied throughout the tropical Pacific Ocean. The population with the shortest lifespan was at American Samoa with the mean maximum age of 11 years, while the population at Lizard Island lived longest, reaching the mean maximum age of 32 years. Populations at Moorea and Lizard Islands attained maximum ages of 43 and 42 years, respectively (Table 3.2). There was a strong suggestion of longevity exhibiting a negative pattern across the Pacific Ocean from the western to the central tropical Pacific, but the there was not a significant trend (Figure 3.5). There was no apparent cross oceanic pattern in mean maximum body size (Figure 3.6).

An analysis of variance (ANOVA), using the Randomization test (Cassell 2002) which is described in detail in Chapter 2, indicated that the body lengths of *A. lineatus* associated with the parameters of rVBGF, *L(1), L(2.5)* and *L(4)*, displayed no significant spatial gradient pattern across the tropical Pacific Ocean (Table 3.3). There were no apparent significant differences in body sizes at all of the tested ages (Figure 3.7), and there was a larger difference between the *L(1)* and *L(2.5)* parameters compared to *L(2.5)* and *L(4)* parameters within each site illustrated in the bar graph in figure 3.8.

3.4 Discussion

3.4.1 Growth trajectories

The demographic characteristics for populations of *Acanthurus lineatus* varied across the tropical South Pacific Ocean from west to east with no apparent pattern indicating locality specific variation rather than a general environmental trend among these study sites. Four out of the five populations exhibit the traditional ‘squared’ growth curve, illustrating fast initial growth and abrupt reduced growth at age four which is ‘characteristic’ of the general population of acanthurids (Choat and Axe 1996, Hart and Russ 1996, Gust et al. 2002, Laman Trip 2004, Robertson et al. 2005). Although each curve has the same asymptotic shape, there is large variability in longevity and absolute size. Terminal size is attained at year four, and most of the growth of A. *lineatus* occurs within the first 10% of their lifespan regardless of location. Populations in the Marquesas illustrated a round curve similar to *A. coeruleus* and *A. chirurgus* at Isla de Margarita where the population still exhibits fast growth in the early life history stages, growth was reduced at older ages, and the growth curve did not asymptote.

The Marquesas Islands are the farthest group of islands from any continent in the world (Wagner and Lorence, 1997). Unlike the other sites in this study, the Marquesas Islands are located in an oligotrophic ocean area, but are associated with abundant phytoplankton production causing predictable phytoplankton blooms (Signorini et al. 1999). Phytoplankton blooms occur when micronutrients and macronutrients mix together to the surface of the ocean where there is enough light to instigate a photosynthetic process. The initiation of these blooms is due to island mass effect brings nutrients into the photic zone (Signorini et al. 1999) and is explained by the interaction of the geostrophic current within the group of the Marquesas islands, as well as other surface currents (Martinez and Maamaatuaiahutapu 2004). Since *A. lineatus* has a thin-walled stomach which is associated with feeding on filamentous algae by which it accesses by acid lysis, (Choat et al. 2002), the mass island effect may be an essential contributor to the productivity in the area influencing the growth in the older individuals allowing them to feed more quality of food.

3.4.2 Sagittal growth

Similar to other taxa of surgeonfish (Choat and Axe 1996, Hart and Russ 1996, Laman Trip 2004, Robertson et al. 2005) the sagittal growth of *A. lineatus* positively correlated with age. Sagittal weight and age correlations indicated that the sagittae of an individual continue to grow throughout its lifetime despite cessation of somatic growth (Campana and Nielson 1985) at a relatively early age. Increments in the sagittal otoliths of acanthurids from the Indo Pacific are more prominent than the increments of acanthurids in the tropical Atlantic (pers. obs., JH Choat, pers. comm.).

3.4.3 Longevity, size-at-age and terminal growth

There were no discernable patterns in longevity, body size or size-at-age across the tropical South Pacific Ocean. This indicates that any variability in these characteristics among the sites may be specific to each locality. Differences in historical characteristics, environmental factors, predation pressures, phylogenetic characteristics, or population dynamics of a specific location may contribute to the variability among the sites. *Acanthurus lineatus* reached largest sizes in the Marquesas and American Samoa. While the predictable nutrient blooms in the Marquesas may be an influential factor for growth, an increased food supply of enhanced algal turfs caused by hurricane damage to the reefs may contribute to the large growth in American Samoa.

Phylogenetic differences and a strong genetic population structure can account for the differences in body size across the Pacific. *Acanthurus lineatus* live bipartite lives with larvae being transported through pelagic waters, and adults live sedentary lives associated with the reef (Robertson 1983). Pelagic larvae of *A. lineatus* are known to have the opportunity to expand a population over large distances, and consequently, as adults, dispersal is very limited since individuals generally are rarely found far from the reef in which they settled (Leis 1991). When determinate populations are separated for enough time, different mutations develop in each population caused by genetic drift or natural selection. The differences dissipate when individuals from a population mix their genetic material with the local population (Bernardi et al. 2001). *Acanthurus lineatus* have a long pelagic larval stage (Randall 2005) which allows dispersal capabilities on a large scale which may result in high gene flow and variabilities in body sizes among the study sites.

Longevity was variable at sites with similar temperatures, suggesting a number of mechanisms that could be driving these patterns. Interactions between growth, reproduction, lifespan and the predictability of recruitment can be affecting these variabilities. Interestingly, there was a negative relationship between longevity and longitude from the west to central Pacific Ocean (although, not significant) with populations on the Great Barrier Reef (GBR) living notably longer than the populations in the central region of the Pacific. This finding is consistent with previous observations that coral reef fishes are longer-lived in the tropical western Pacific, more specifically the GBR, than in any other tropical locality in the Indo Pacific (Choat and Robertson 2002). Greater lifespans in the GBR compared to other localities in the Indo Pacific have been recorded for *Ctenochaetus striatus* (Laman Trip 2004), *Epinephelus polyphekadion* and *Cephalopholis genus* (Pears 2005) suggesting that greater longevities in the GBR may be a general phenomenon among coral reef fishes. Because greater longevity is a mechanism by which multiple spawners adapt to undesirable and unpredictable conditions allowing long term populations to persist (Warner and Chesson 1985, Longhurst 2002), this pattern suggests lower recruitment levels and less predictability of environmental conditions and resources on the GBR than at the other localities in the central Pacific. Further studies on recruitment rates in regional areas within the Pacific are required to test this hypothesis.

There was no discernable pattern in body size and growth at study sites across the tropical Pacific Ocean. With this information and the findings in Chapter 2 is evidence that temperature may be playing a major role, yet not the only role, in the variabilities of these demographic characteristics on large spatial scales. Variance in productivity, food availability and quality, habitat structure, density-dependent growth and mortality, levels of predation and competition, fishing pressure and wave action are all potential factors that can contribute to differences in the demographic characteristics of a species. The need to examine longevity, body size and growth at a smaller scale where water temperature and geographical and historical characteristics are similar, but habitat conditions are variable will be addressed in the next chapter.

Site	Latitude	Longitude	MST	Reference
Lizard Island	14° 40' S	145° 27' E	28°C	www.reeffutures.org/topics/bleach/presentAIMS.cfm
Outer GBR	14° 39' S	145° 37' E	28°C	www.reeffutures.org/topics/bleach/presentAIMS.cfm
American Samoa	13° 35' S	172° 20' W	29°C	Craig et al. 1997
Moorea	17° 30' S	149° 50' W	28°C	MCR LTER
Marquesas	08° 49' S	140° 12' W	28°C	Martinez and Maamaatuaiahutapu 2004

Table 3.1: Five study sites in the tropical South Pacific Ocean. MCR LTER = Moorea Coral Reef Long Term Ecological Research.

L_o=25mm

Study site	n	t_o (yrs)	k	L_∞ (mm)	Size range FL (mm)	MMA (yrs)	Max. age (yrs)	MMS FL (mm)	Mean size at age FL(mm) at:			r^2 (VBGF)
									1 yr	2.5 yr	4 yr.	
Lizard Island	49	-0.0906	1.33	221	175-244	32	42	229	169	214	220	0.91
Outer GBR	41	-0.2643	0.44	201	113-228	21	25	217	89	145	173	0.83
American Samoa	94	-0.1241	1.14	190	59-229	11	18	245	137	181	189	0.75
Moorea	122	-0.1481	0.88	205	41-235	13	43	212	130	185	200	0.95
Marquesas	93	-	-	-	100-263	14	19	247	142	208	227	-

Table 3.2: Demographic data on the populations of *Acanthurus lineatus* at the respected study sites. Size at age zero (L_o) in the growth trajectories were constrained to 25 mm for each species. Size at age is derived from the reparameterized von Bertalanffy growth function (rVBGF). MMA refers to mean maximum age and is represented in years. MMS refers to the mean maximum size and is represented in FL millimetres. MMA and MMS values are taken from the average ages and sizes of the top 20% of a population. Values for t_o, k and L_∞ do not pertain to Marquesas since the growth trajectories do not fit the VBGF model.

Species	DF	SS	MS	F Value	Pr>F	Random P
A. lineatus L(1)						
Model	1	71.90238	71.90238	0.07	0.8138	0.8540
Error	3	3267.4757	1089.1586			
A. lineatus L(2.5)						
Model	1	327.46285	327.36285	0.37	0.5865	0.6030
Error	3	2663.7738	887.92459			
A. lineatus L(4)						
Model	1	297.25853	297.25853	0.53	0.5181	0.4450
Error	3	1672.4408	557.48016			

Table 3.3: Results of analysis of variance (ANOVA) using the Randomization test indicated that the body lengths of *A. lineatus* associated with the parameters of rVBGF, *L(1), L(2.5)* and *L(4)*, displayed no significant spatial gradient pattern across the tropical Pacific Ocean. The observed p-value was compared with the distribution of randomized p-values, and if it occupied the lower 5% of the distribution, then it was deemed statistically significant.

Figure 3.1: Study sites spanning 75° longitude or 8500 km across the South Pacific Ocean.

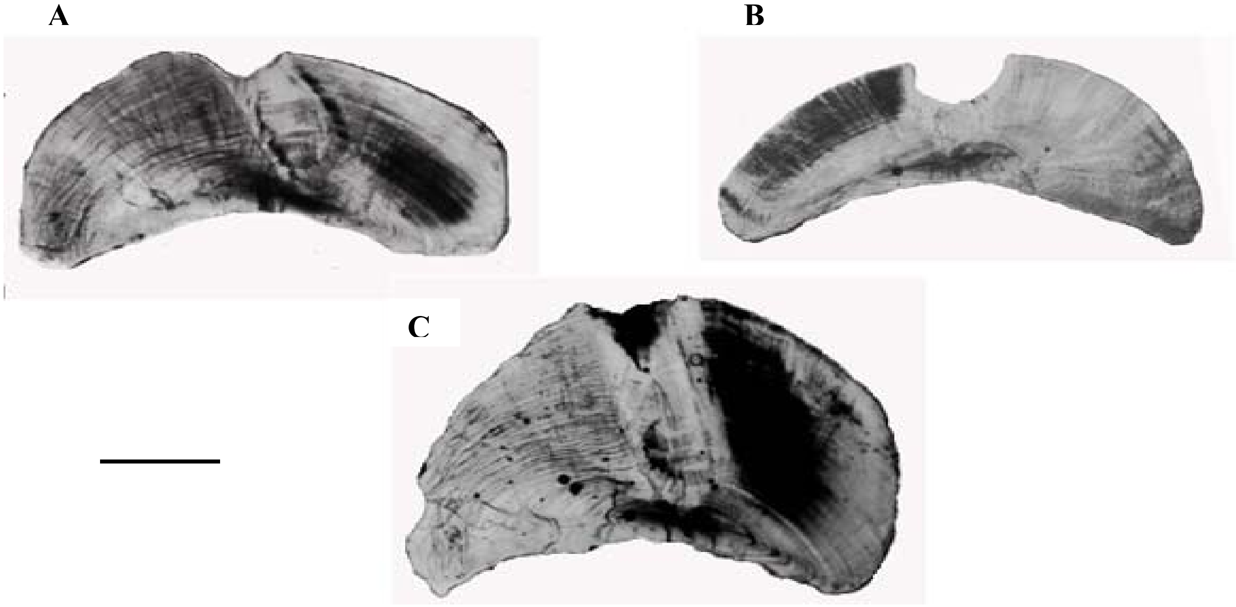

Figure 3.2: Cross sections of sagittal otoliths of *Acanthurus lineatus* from A) Marquesas, 19 years B) Moorea, 18 years and C) Moorea, 43 years, the oldest *A. lineatus* in this study. Line measures 1 mm.

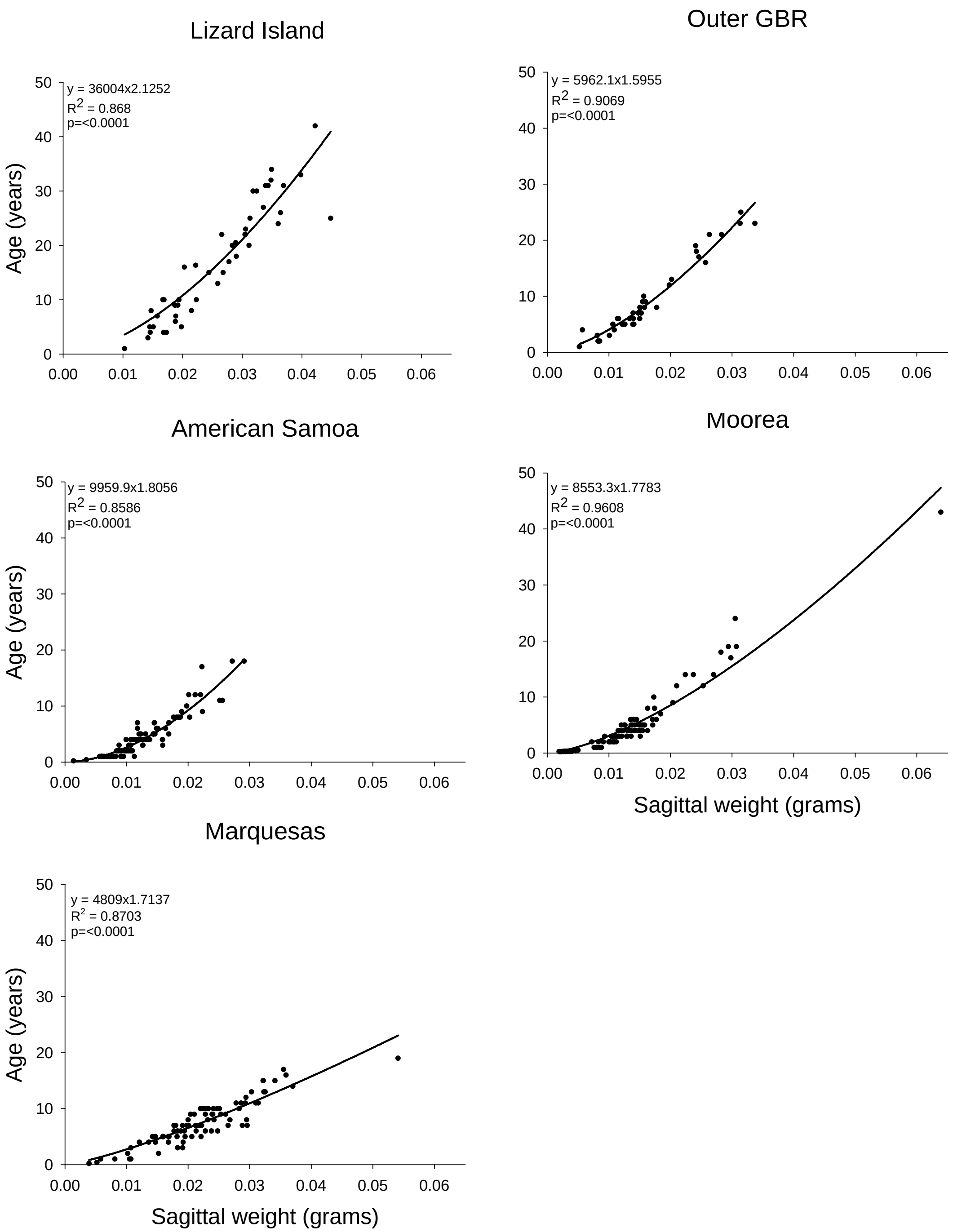

Figure 3.3: *Acanthurus lineatus* otolith growth trajectories. Power functions of sagittal weight and age at locations in the tropical South Pacific Ocean. There was a positive correlation between age and sagittal weight at all study sites indicating the continuous growth of otoliths throughout an individual's lifetime.

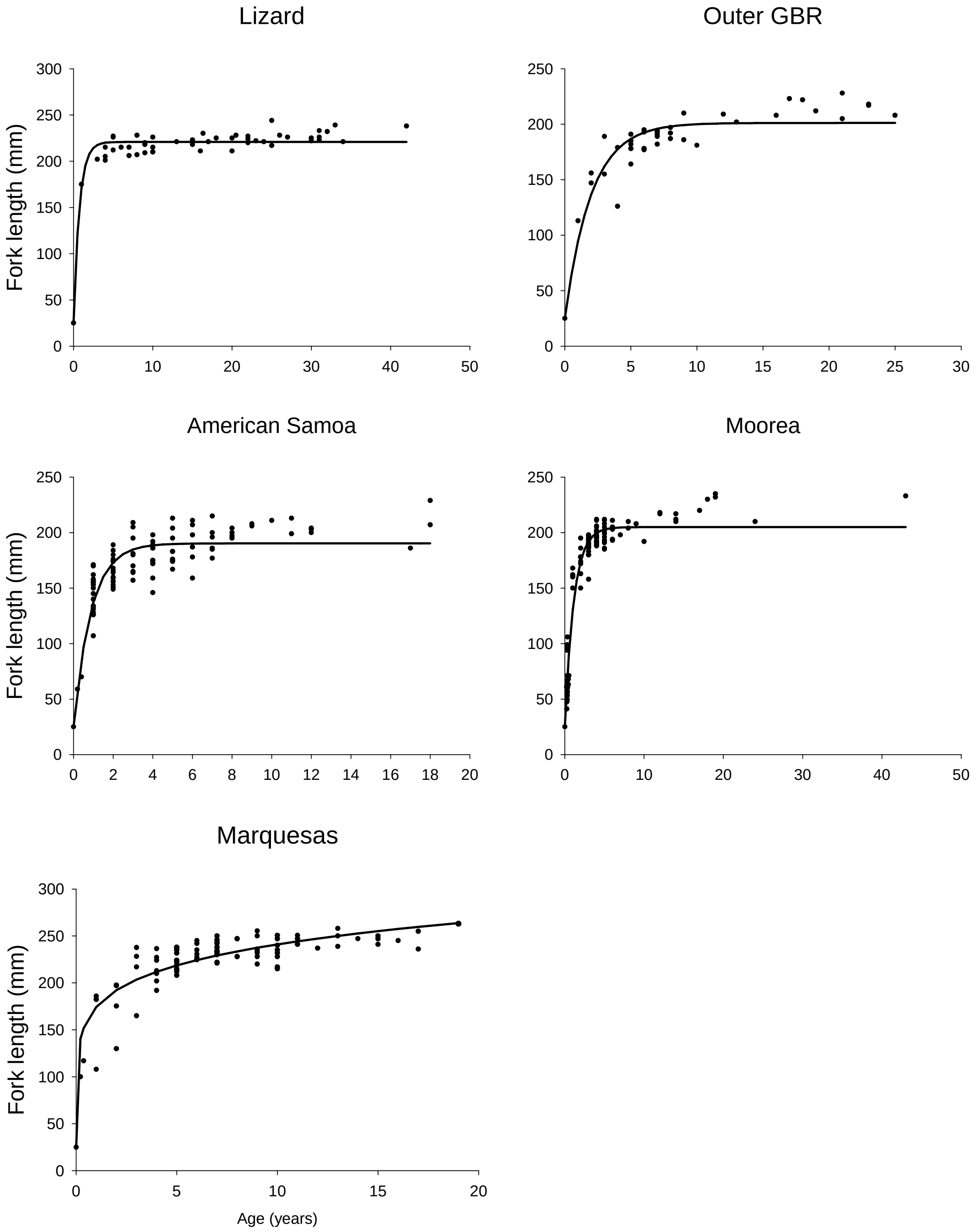

Figure 3.4: *Acanthurus lineatus*: Growth models from all populations in the tropical South Pacific Ocean. Von Bertalanffy growth function (VBGF) models fit four of the five populations best, but the size at age data from Marquesas fit the Power^2 model best indicated by sum of squares results.

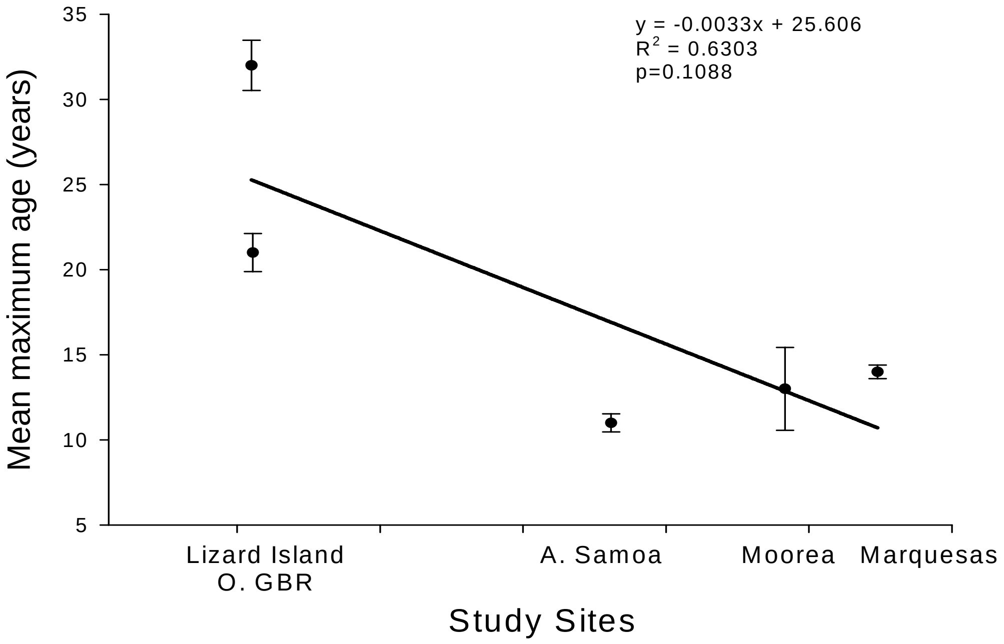

Figure 3.5: A linear regression of mean of 20% maximum longevity of *Acanthurus lineatus* from west to east across the South Pacific Ocean on a proportional, spatial scale. There is no apparent spatial gradient in longevity across the Pacific Ocean.

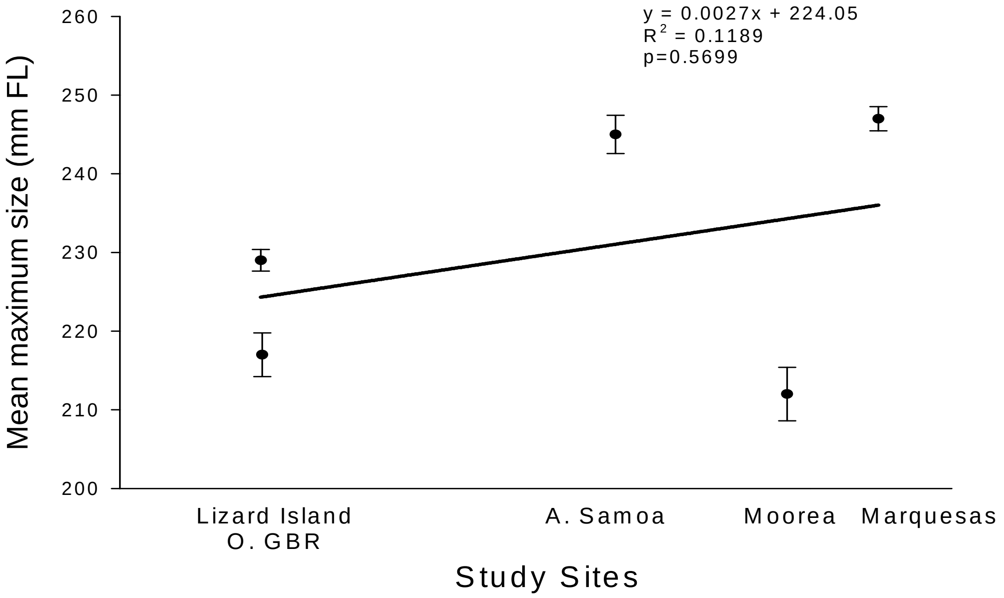

Figure 3.6: A linear regression of mean of 20% of maximum body size of *Acanthurus lineatus* from west to east across the South Pacific Ocean on proportional, spatial scale. There is no apparent spatial gradient in body size across the Pacific Ocean

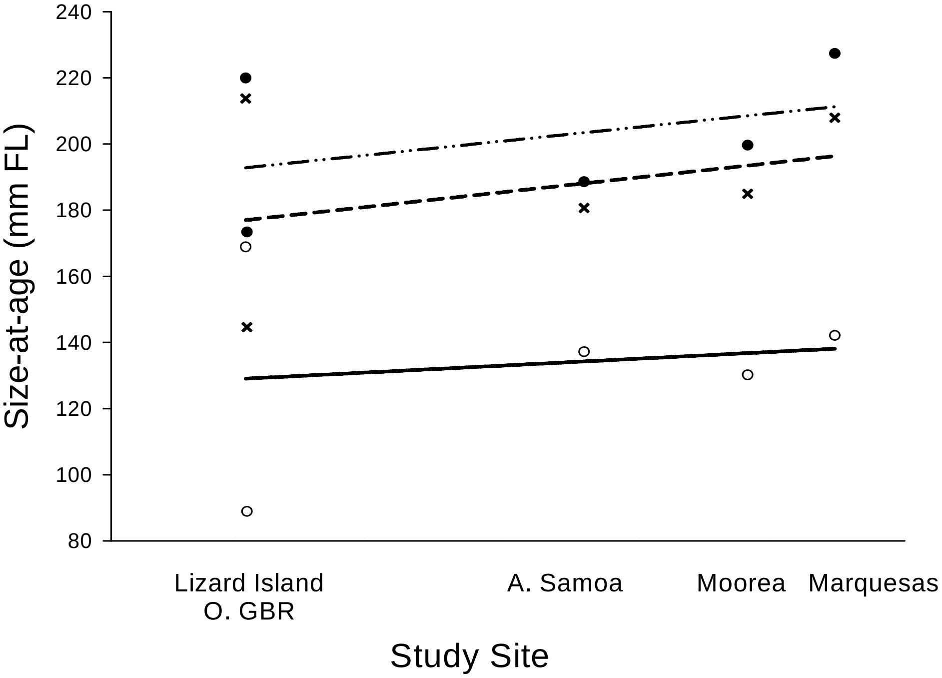

Figure 3.7: Instantaneous growth rates of *Acanthurus lineatus* at different ages vs. location from west to central tropical South Pacific. The solid line and open circles (—, o) represent size at age 1 year, the dashed line and exes (---, x) represent size at age 2.5 and the dash-dot line and solid circles (—··—, •) represent size at age 4. Age 1: y = 0.0021x + 128.84, r^2=0.0215, p=0.8138; age 2.5: y = y = 0.0044x + 176.54, r^2=0.1095, p=0.5865; age 4 y = 0.0042x + 192.39, r^2= 0.1509, p=0.5181. There is no apparent trend in initial growth across the Pacific Ocean.

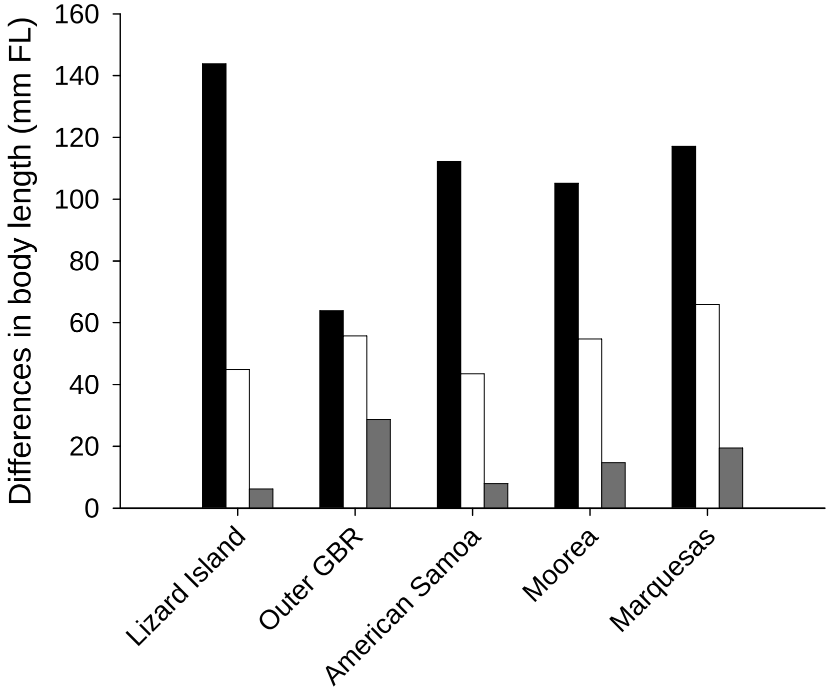

Figure 3.8: Differences in body length of *Acanthurus lineatus* between settlement and age 1 (black bar), ages 1 and 2.5 (white bar) and ages 2.5 and 4 (grey bar). As this species gets older, growth decreases.

Chapter 4: Age-based demographic comparisons on a local spatial scale in Bermuda

4.1 Introduction

There is a whole range of spatial scales over which ecological environments function. To fully understand patterns over large spatial scales many data sets on a variety of different species should be collected on many different scales (Fowler and Doherty 1992, Caselle and Warner 1996, Chessen 1998, Munday 2002). Many individual reef fish, including territorial acanthurids, spend most of their lives in an area covering of tens of meters (Sale 1998). Thus it is useful to examine within-reef variation in the demography of fish populations. Certain species of coral reef fishes are found in particular zones and habitats. Species that inhabit specific types of habitat are more likely to be affiliated with their preferred habitats if they are available than are the species that utilise a broad habitat (Munday 2002). The two species involved in this study, *Acanthurus coeruleus* and *A. chirurgus*, are relatively site attached (Chapman and Kramer 2000), and rarely observed far from the reef.

This chapter describes the variation in the longevity, growth and size of two tropical Atlantic coral reef fishes, the doctorfish *Acanthurus coeruleus,* and the blue tang *A. chirurgus,* and examines whether these demographic characteristics differ between two habitats, inside the lagoon and outside the reef, on coral reefs in Bermuda. Many studies, including the present one, have shown evidence of reliable estimates of age in coral reef fishes of the Caribbean by using growth segments in sagittal otoliths (Manooch 1987, Sadovy et al. 1992, Sponaugle and Cowen 1997, Manickchand-Heilman and Phillip 2000, Choat et al. 2003, Kingsford and Hughes 2005, Robertson et al. 2005). Robertson and colleagues (2005) have conducted an extensive study on the demography of *A. bahianus* in western tropical Atlantic, and growth and age-based studies of various Acanthurids from the Indo Pacific have been conducted (Choat and Axe 1996, Hart and Russ 1996, Craig et al. 1997, Gust et al. 2002, Choat and Robertson 2002, Laman Trip 2004). Although it is important to understand the population dynamics of this as an economically and ecologically important genus in the Caribbean, there are no age- and size-based studies available for *A. coeruleus* and *A. chirurgus*.

This is the first study to explore the demographic parameters of age, growth and longevity of *A. coeruleus* and *A. chirurgus*, and one of few studies of these characteristics of acanthurids in the tropical Atlantic (although see Robertson et al. 2005). This study builds upon previous studies of the life history of the family Acanthuridae that used cross-sections of sagittal otoliths (Choat and Axe 1996, Hart and Russ 1996, Bergenius et al. 2002, Laman Trip 2004, Robertson et al. 2005). The purpose of this study was to measure these demographic characteristics on a local scale to assess any trends in these demographic parameters associated with habitat structure.

4.2 Methods and Materials

4.2.1 Study species

Acanthurus chirurgus and *A. coeruleus* are two common obligate reef fishes on tropical Atlantic reefs. *Acanthurus chirurgus* has been observed in West Africa and in the Western Atlantic from Massachusetts south to Bermuda, West Indies, Gulf of Mexico, Panamá and as far south as Brazil (Myers 1999, Rocha et al. 2002). *Acanthurus coeruleus* is found in shallow waters from New York (although they are very rarely observed that far north) to Brazil including Gulf of Mexico and Bahamas (Myers 1999, Rocha et al. 2002). These two species are relatively similar in body size, behaviour, and habitat and foraging preferences (Kuiter and Debelius 2001). As herbivores, they feed on fleshy turf algae and filamentous algae (Robertson 1991a). They aid in controlling the growth of algae on coral reefs (Lawson et al. 1999), and even graze on other animals, such as sea turtles, where algae accumulate on their shells (Sazima et al. 2004). While grazing, *A. chirurgus* consumes inorganic sediment and detritus to aid in digestion by abrading the algal material in their thick-walled gizzard-like stomachs, while, as browsers, *A. coeruleus* has a more selective diet, and feeds only on algae (Robertson 1991a, Randall 1996).

Acanthurus coeruleus and *A. chirurgus* play an important role in the coral reef ecosystem. While these surgeonfish are not generally caught for commercial fisheries, they are important to subsistence (Robertson 1988, Semmens et al. 2005) and artisanal fisheries (Garrison et al. 2004). Excessive subsistence fishing can reduce the local populations of acanthurids which can have detrimental effects on a coral reef. Jamaica experienced a heavy loss of coral cover following the mass mortality of the sea urchin, *Diadema antillarum*, in 1983, and the intense fishing of herbivorous fishes contributed to this destruction (Liddell and Ohlhorst 1986) due to the overgrowth of algae on the corals (Hughes 1994).

4.2.2 Study sites and field sampling

Samples of *Acanthurus chirurgus* and *A. coeruleus* were collected from the northern and southern sides of the island of Bermuda (32°18'N) in October 2001 and July 2002. Bermuda is a 150 km^2 coralline island located on the southern side of a 200 km^2 shallow reef platform in the western Atlantic. The inner reef consists of many patchy reefs with scattered corals and gorgonians covered in algae in depths of 2-10 m. The outer reef consists of enormous dense hard coral around the edges of the Bermuda platform on a slope with depths from 7-25 m (Robertson et al. 2005).

A total of 116 samples of *A. chirurgus* (86 from inner reef; 30 from outer reef) and 105 samples of *A. coeruleus* (11 from inner reef; 94 from outer reef) were collected using pole spears on SCUBA and snorkel at 5-25 m depths. Both juveniles and adults were sacrificed. To collect a diverse range in sizes and ages, collectors swam indiscriminately in all directions and speared adults in the order in which they were discovered, not taking size in consideration. However, the largest and smallest individuals at each study site were targeted. Once captured, individuals were immediately placed in ice on the boat until the samples were delivered to the laboratory for processing on the same day of collection. For each individual, standard length (SL) was measured to the nearest millimetre (mm), and weight (total wet weight) was contrived to the nearest gram (g). The sagittal pair of otoliths was removed surgically from the skull, and stored cleaned and dry in separate cells in culture plates.

4.2.3 Otolith preparation and age determination

Sagittal otoliths continue to grow throughout the entire life of an individual even though somatic growth of the individual ceases, so I can accurately derive size-at-age data from *A. chirurgus* and *A. coeruleus* otoliths. Sagittal otoliths were processed according to the methods described in Chapter 2. Power functions of age and sagittal otoliths weight were compared to assess any correlations.

4.2.4 Age based growth modelling

Plots of size-at-age data of *A. coeruleus* and *A. chirurgus* were compared between areas inside the lagoon and outside the reef crest. Lifetime growth trajectories were estimated by fitting these data to an age-based model, the von Bertalanffy growth functions (VBGF) which is explained in detail in Chapter 2.

4.3 Results

4.3.1 Sagittal growth

Power functions of age verses sagittal weight were calculated for *A. chirurgus* and *A. coeruleus* in the lagoon and outer reef (Figure 4.3). Sagittal growth of both species did not differ significantly between the two habitats. There was a significant positive correlation ($p<0.0001$ in all instances) between sagittal weight and number of increments (expressed as age) in both inner and outer reefs for *A. chirurgus* (Figure 4.3a): inside lagoon: $y = 178.74x^{1.0983}$, $r^2=0.80$; outside reef: $y = 10160x^{2.1382}$, $r^2=0.81$. Similar to *A. chirurgus,* in both habitat zones the sagittal weight was positively correlated with age for

A. coeruleus (Figure 4.3b): inside lagoon: $y = 80.715x^{0.9357}$, $r^2=0.83$; outside reef: $4714.8x^{1.7795}$, $r^2=0.88$.

4.3.2 Growth trajectories

Both species of acanthurids demonstrated very fast initial growth in the early stages of their lifespan, and at approximately age four years the asymptotic length is reached in both species which was examined in Chapter 2. The ages and body lengths of each species were bootstrapped to obtain the mean of the oldest 20% of fish sampled for each species (defined as longevity or mean maximum age). Maximum age (T_{max}) estimates can overestimate the age of a species due to outliers and small sample sizes. I, therefore, used more conservative longevity estimates based on the oldest 20% of individuals sampled for each species. Considering this, the longevity of *A. coeruleus* was 38 years ($T_{max} = 43$) while *A. chirurgus* only attained an estimated 16 years of age ($T_{max} = 29$). *A. coeruleus* reached a somatic size of 202 mm while *A. chirurgus* reached 240 mm. Although *A. coeruleus* can live twice as long as *A. chirurgus*, this species did not reach the body sizes of *A. chirurgus* (Table 4.1).

The otoliths of both *A. chirurgus* and *A. coeruleus* revealed relatively clearly defined increments (Figure 4.1), total counts of bands were able to be made in all of the species analysed. Increments in the sagittal otoliths from acanthurids in Atlantic tropical waters are generally not as prominent as increments in acanthurids from the Indo Pacific (pers. obs., J. H. Choat pers. comm.). However, only one individual from the *A. coeruleus* sample set was not used in the analysis because the otolith sections were not clear, and was considered unreliable.

4.3.3 Age-based demographics on a local scale

A. chirurgus. Individuals reached maximum sizes on inner and outer reefs. Consequently fish from the outer reef reached a larger mean maximum body size of 253 mm (derived from 20% or the largest individuals in a population) than fish from inside the lagoon (MMS = 220 mm) (Table 4.1, Figure 4.2a). Individuals ranged in ages 2-29 years on the outer reef, while fish only reached 10 years of age on the inner reef regardless of size. However only two individuals reached such high ages, and the mean maximum age of 20% of the oldest individuals was estimated to be 5 years old which is a more accurate representation of the population. No individuals were found Juveniles and fish smaller than 205 mm FL were found only inside the lagoon.

A. coeruleus. The demographics of *A. coeruleus* differ substantially from *A. chirurgus* when making a comparison at a local spatial scale. Juveniles were caught both inside and outside the reef crest (Figure 4.2b). Subsequently individuals only reached 4 years of age inside the lagoon, while ages up to 43 years were attained outside the reef. The asymptotic length of individuals inside the reef was slightly larger compared to the outer reef, however these results were derived from a small sample size (n = 11) and should be interpreted cautiously, although *A. coeruleus* are rarely found inside the reef which is the explanation for the small sample size.

4.4 Discussion

4.4.1 Sagittal growth

Otoliths continue to grow despite achieving asymptotic size early in their lifespans, due to the positive linear relationship between the number of otolith increments (age) and otolith weight. Sagittal growth of both *A. chirurgus* and *A. coeruleus* did not vary significantly between the inner and outer reefs. Sagittae from the inner reef were found to be larger at age compared to the outer reef for both species, but these results should be taken with caution. If not for the influence of the two oldest individuals on the *A. chirurgus* inner reef plot (Figure 4.3A), the sagittal growth would be very similar to the outer reef. For *A. coeruleus* sagittal growth, there is not a big enough sample size on the inner reef to discern any differences from the out reef (Figure 4.3B).

4.4.2 Age-based demographics on a local scale

A. chirurgus. Younger individuals were found on the inside of the lagoon while older individuals inhabited the outer reefs. Pelagic juveniles of *A. chirurgus* settle in sheltered lagoonal habitats (Adams and Eversole 2002, Bergenius et al. 2005), prefers the lagoon patch-reef as a nursery, and return to the outer reef permanently (Adams and Eversole 2002). This explains the longevity attained on the outer reef, the absence of juveniles on the outer reef and the reduced density of adults in the lagoonal habitat and the smaller terminal size reached on the inner reef. This trend may be related to their diet, as *A. chirurgus* are grazers, an abundant amount of these nutrient resources are available on the outer reef. These demographic characteristics are comparable to *A. bahianus*, a morphologically and ecologically similar species, in studies conducted in Bermuda (Robertson et al. 2005), Barbados (Mahon and Mahon 1994), St. Croix (Risk 1998) and Panamá (Robertson 1991a).

A. coeruleus. An explanation of the demography of *A. coeruleus* is more complex than that of *A. chirurgus* at a local scale in Bermuda. Individuals of all sizes and ages were found on the outer reef, while only a small number of juveniles occur on the inner lagoonal habitats. *A. coeruleus* prefer to settle onto hard reef substrata, and they were rarely observed off of the reef (Robertson 1991a, Lawson et al. 1999), which coincides with the substantial use of the reef crest observed in this study. I speculate that the fish in the lagoonal habitats are not surviving in the patchy, sandy lagoonal environment because of the unsuitable habitat with insufficient habitat complexity and shallow water which can create natural barriers to the movement and possibly increased exposure to predation inside the lagoon (Chapman and Kramer 2000). *A. coeruleus* prefers complex habitats full of high biogenic structure (Robertson 1991a, Lawson et al. 1995, Semmens et al. 2005). The few that are on the inner reef probably do not last to older ages due to the insufficient availability of the specific resources and habitat complexity provided in the patchy habitat which forces individuals to cover a larger territory between patches of reef, and is therefore exposed more frequently to predation; or they simply move to the outer reefs to the more suitable and complexly structured habitat (Chapman and Kramer 2000). Another explanation for the demographic patterns of *A. coeruleus* can be related directly to diet and feeding mode. *A. coeruleus* have a more selective diet and contain less sediment in their diet, and they may have a preference of feeding in regions where algal cover is less prominent, but contain less sediment. This study is consistent with Robertson (1991a), Lawson et al. (1999) and Bell and Kramer (2000) all of whom reported that *A. coeruleus* occurs primarily on the outer reef.

4.4.3 Demographic patterns of reef fishes at local spatial scales

There are numerous studies indicating variations in demographic patterns of reef fishes at local spatial scales: Choat and Bellwood (1985) ascertained differences in abundance and species composition in herbivorous fishes at two adjacent study sites; Caselle and Warner (1996) investigated the variability in the recruitment of reef fishes at adjacent reefs at St. Croix in the Virgin Islands; Gust (2004) found that in protogynous reef fish age- and size-at-maturity and sex reversal, overall growth, mortality and population densities differed at two reefs just 20 km apart; Ruttenberg et al. (2005) described the robust demographic variability (resembling that of a latitudinal gradient at large spatial scales) of a damselfish at four nearby locations that exhibit dissimilar environmental conditions in the Galapagos Islands. Variation in demographic characteristics between geographic areas can be driven by both genetic and environmental influences (Sebens 1987). However since coral reef populations tend to be genetically open populations (Sale 1991), and acanthurids have an extensive pelagic larval stage (Robertson 1992) genetic selection at such a small scale is unlikely (Warner 1991). Small scale variation in demography is common for reef fishes and the variation of *A. chirurgus* and *A. coeruleus* at Bermuda encompass just as much diversity as any other reef fish. *A. chirurgus* and *A. coeruleus* do seem to fit the typical metapopulation model for coral reef fishes, where the adults are restricted to one coral reef, and the only means of dispersal among reefs is by pelagic larval dispersal.

Study site	n	t_0 (yrs)	k	L_∞ (mm)	Size range FL (mm)	MMA (yrs)	Max age (yrs)	MMS (mm FL)	r^2 (VBGF)
A. chirurgus									
Inner reef	86	-0.1182	1.12	218	46-278	5	10	220	0.78
Outer reef	30	-0.149	0.75	254	201-285	23	29	253	0.76
Total	116	-0.1464	0.82	240	26-285	16	29	256	0.8
A. coeruleus									
Inner reef	11	-0.1136	1.17	216	48-218	4	4	197	0.9
Outer reef	94	-0.1181	1.21	203	32-250	38	43	214	0.78
Total	105	-0.142	1.01	203	32-250	38	43	213	0.83

Table 4.1: *Acanthurus chirurgus and A. coeruleus.* Demographic data on the populations in the inner and outer reefs of Bermuda. In the VBGF growth trajectories size at age zero (Lo) was constrained to 27 mm. MMA refers to mean maximum age and MMS refers to mean maximum size. These estimates were derived from 20% of the oldest and largest individuals in a population respectively.

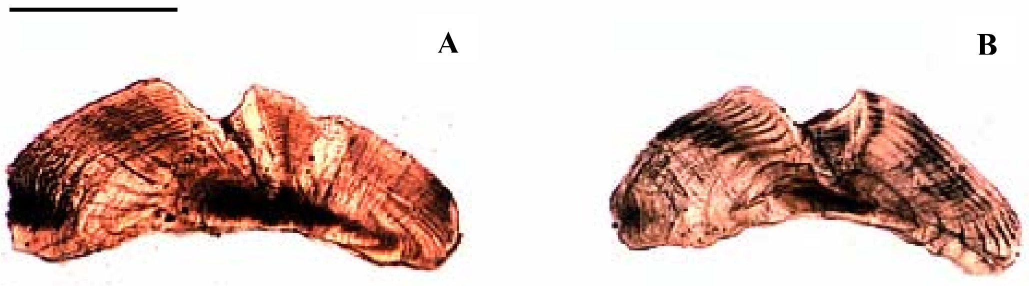

Figure 4.1: Cross sectioned sagittae of (A) *A. coeruleus* (16 years) and (B) *A. chirurgus* (10 years) from Bermuda. These images illustrate the clear and consistent increments that are formed from each species. Line measures 1.5 mm.

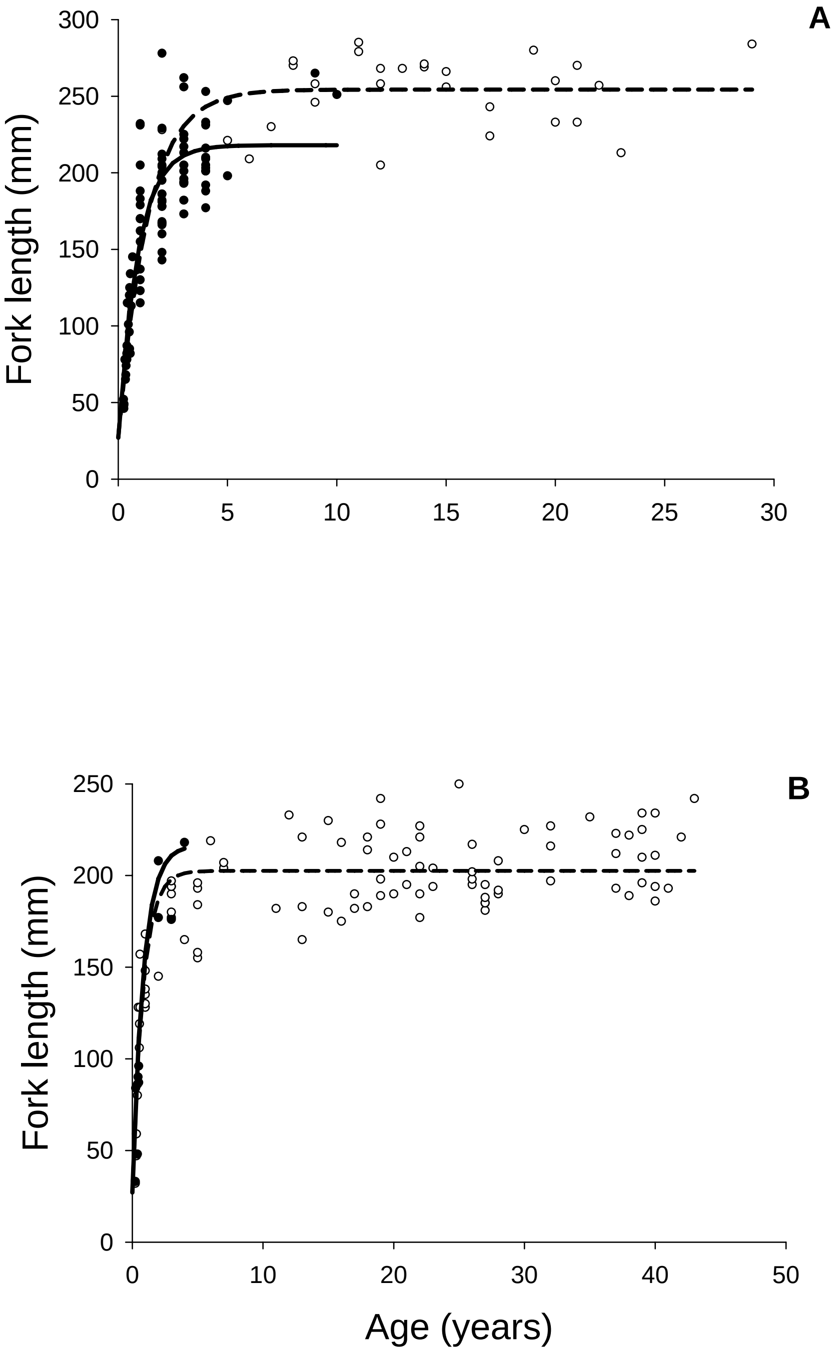

Figure 4.2: Von Bertalanffy growth trajectories of (A) *Acanthurus chirurgus* (n=86 on the inner reef and n=30 on the outer reef) and (B) *A. coeruleus* (n=11 on the inner reef and n=94 on the outer reef) in two habitats at Bermuda. Open circles and broken line (◦, ---) indicate samples taken from outside the reef and solid circles and line (•,—) indicate samples taken from inside the lagoon.

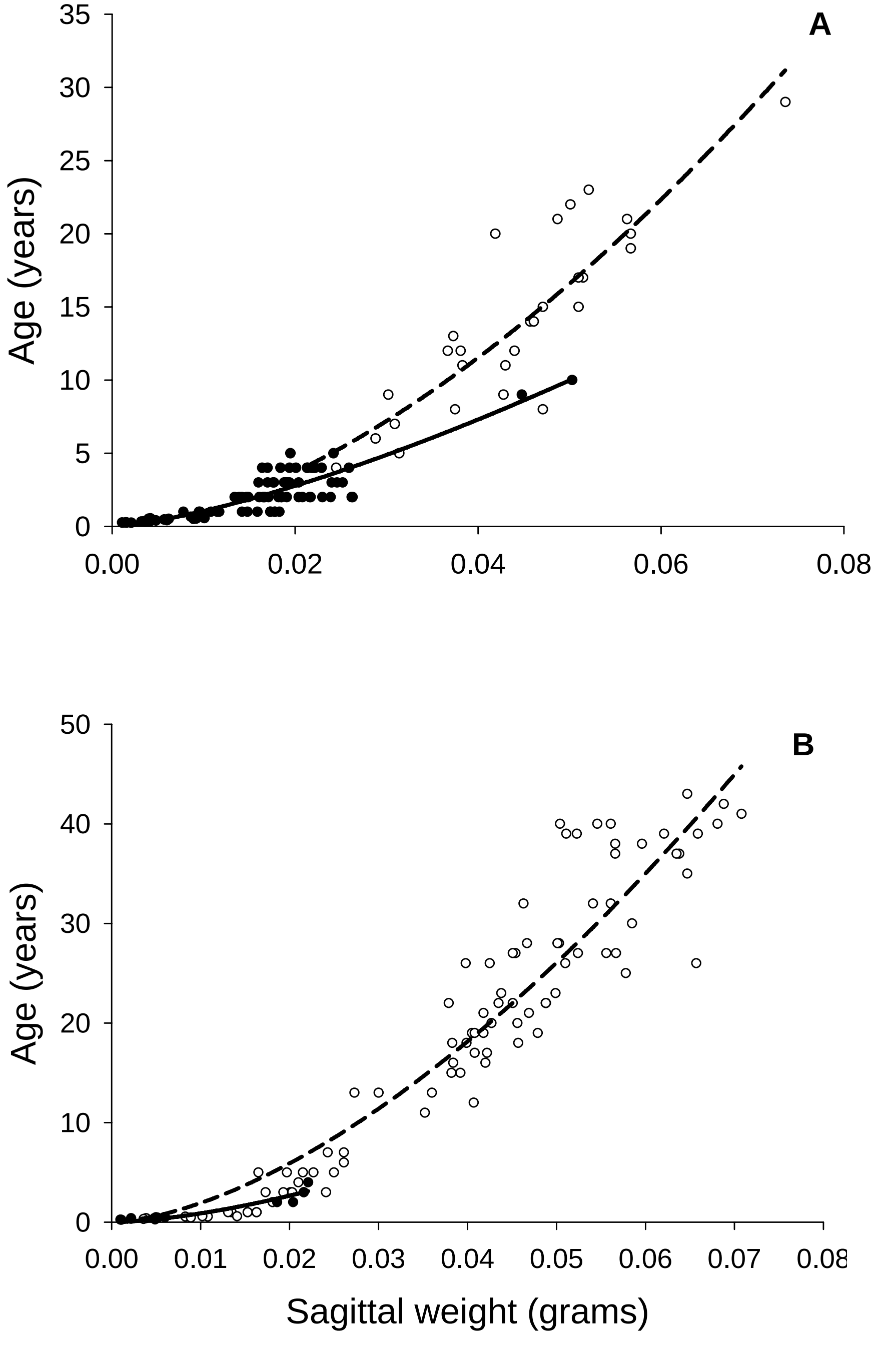

Figure 4.3: Sagittal growth trajectories of (A) *Acanthurus chirurgus* and (B) *A. coeruleus* in Bermuda. Open circles and broken line (◦, ---) indicate samples taken from outside the reef, and solid circles and line (•,—) indicate samples taken from inside the lagoon. *A. chirurgus*: outer reef: $y=10160x^{2.1382}$, $r^2=0.81$, $p=<0.0001$; inner reef: $y=178.74x^{1.0983}$, $r^2=0.80$, $p=<0.0001$. *A. coeruleus*: outer reef: $y=4714.8x^{1.7795}$, $r^2=0.88$, $p=<0.0001$; inner reef: $y=80.715x^{0.9357}$, $r^2=0.83$, $p=<0.0001$.

Chapter 5: General Discussion

5.1 Discussion

All four species of acanthurids examined in this study generally demonstrated asymptotic “square” growth patterns with the asymptote achieved early in life at the majority of locations from both the tropical Atlantic and South Pacific Oceans. This pattern appears to be representative of all members of *Acanthurus* although localities subject to high productivity may be an exception. While the forms of growth patterns are similar among most species there is substantial variation in initial growth rates, sizes and life spans both within and among species. Geographic variation by location especially along latitudinal gradients proved to be the best predictor of demographic variability. Similar latitudinal variation and demographic features have been found in other acanthurid studies (Robertson et al. 2005, Laman Trip 2004).

Latitudinal gradients were found in longevity, body size and growth of the three species in the tropical Atlantic. Generally, as mean sea surface temperature increased these parameters decreased over a large spatial gradient. The trend associated with growth is counterintuitive to many previous demographic studies that usually show that as temperature increases growth increases. These studies indicate that fishes at low latitudes and high temperatures display faster growth, small body size and short lifespans (Pauly 1980, Atkinson and Sibly 1997) compared to their cooler water counterparts. It is likely that all three species of surgeonfish exhibit countergradient variation in growth where a function within individuals allows them to adapt to cooler environmental conditions with temperatures differing by as much as 4.5°C resulting in the negative relationship between growth and temperature (i.e. latitude).

In the tropical South Pacific there were no cross-oceanic patterns in longevity, body size or size-at-age growth. The absence of a longitudinal pattern may indicate that temperature may have a fundamental influence on these demographic characteristics since there were negative correlations between these two parameters and temperature in the tropical Atlantic Ocean. However, it must be noted at localities across an ocean, reef history and biogeography also have important effects that are not directly related to such a simple factor such as temperature. The western Pacific and more specifically the Great Barrier Reef support populations with longer mean maximum lifespans. Localised oceanographic conditions such as conditions seen in the Marquesas have very strong effects, and this is further confirmed by the results found in Isla de Margarita.

Geographic location involving differences in temperature does have a persuasive effect, but there are some interesting exceptions involving localised productivity and upwelling, and coastal effects versus isolated island effects. A few groups of acanthurids in the Marquesas and Isla de Margarita abandoned the traditional asymptotic growth model that is generally seen in acanthurids. Acanthurids at these locations still exhibited fast initial growth followed by slowing growth with increasing age but their growth trajectory demonstrated a more "round" growth pattern opposed to the traditional asymptotic "square" growth patterns with the asymptote achieved early in life. For *Acanthurus lineatus* in the Marquesas this growth curve is speculated to be caused by nutrient and phytoplankton blooms caused by an island mass effect that are carried through the area by surface currents, influencing the growth in the older individuals allowing them to feed more quality of food. For *A. coeruleus* and *A. chirurgus* in Isla de Margarita I suggest this growth curve is caused by major upwelling events in this area influencing continued growth in the older individuals. A possible isolated island effect on longevity was observed in the Atlantic where the longest living populations for all three species were those located at the isolated oceanic islands of regardless of sea surface temperature. This may be a mechanism to buffer populations as an attempt to safeguard against recruitment failures (Meekan et al. 2001) in the locations where it may be difficult for the recruits to reach the isolated oceanic islands (Swearer et al. 1999) causing recruitment to be unpredictable.

In these large scale comparisons care must be taken to standardise for habitat since local habitat-associated variation is strong, as seen with the two species in Bermuda in Chapter 4. Each group of *A. coeruleus* and *A. chirurgus* in Bermuda may exhibit different demographic patterns between areas just 10's of kilometres apart. Only young individuals of *A. chirurgus* are found inside the lagoon making the area a crucial part of the early life history stage, and only older individuals are found outside the reef indicating that the older individuals return to the outer reef for the duration of their lives. The lagoon is not a suitable habitat for *A. coeruleus* at any age, and the majority of the population was observed on the outer reef.

There are a number of studies that do not support the general life history observations where coral reef fishes have smaller average maximum size and shorter average lifespans compared to their temperate counterparts. Just as tropical fish cannot be generalised as being short lived and small in size, not all long-lived marine fishes live in deep water. The yelloweye rockfish, *Sebastes ruberrimus* (Love et al. 2002), and the Atlantic halibut, *Hippoglossus hippoglossus*, (Jákupsstovu and Haug 1988) are long-lived

(T_{max} = 118 yrs and 50 yrs respectively) and are not deep-sea dwellers. Additionally there are some short-lived fish that live in the deep sea (*Serranus cabrilla;* T_{max} = 6) (Tserpesa and Tsimenides 2001). A fast growing and small sized (max size = 120 mm) tropical damselfish, *Stegatus altus*, has been aged to more than 15 years, and a small sized anemonefish, *Amphiprion clarkii*, can reach 13 years (Kohda 1996). While the temperate sea bass, *Centropristis striata*, can grow to a considerable size (330 mm) it only reaches a maximum age of seven years (Hood et al 1994). The tropical common snook, *Centropomus undecimalis*, can reach over 1 m in length, and attain ages of up to 21 years (Taylor et al. 2000), and the humphead wrasse, *Cheilinus undulates*, can reach sizes that can surpass 2 m and live up to 32 years (Sadovy et al. 2003). These characteristics are not necessarily intrinsic to the environment, but they are intrinsic to the fish (see Appendix A-D). The results of age based analysis are highly complex and it reflects the structure of the reef environment, the varied assemblages of coral reef species and the interactions among the reef fishes.

Pauly's (1994, 1998) generalisations of the life history of coral reef fishes are too broad. He has previously defined coral reef fishes by means of their growth and mortality rates. However, there are a couple of factors that should be considered. Firstly, the database Pauly used contained very little information on age structure of coral reef fishes. Secondly, the analyses on which these studies are based used length as the primary metric for assessing population dynamics. However, in many groups of reef fishes such as acanthurids, lutjanids and scarids, size and age may not be related in any practical way (Hilborne and Walters 1992, Choat and Robertson 2002), where by size and age can be decoupled. With out accumulating a substantial data base on life history characteristics, it is difficult to generalise how populations respond to environmental change or exploitation because of the decoupling of size and age and the variability in growth rates between and among fish species (Choat and Robertson 2002). In addition many species of fish display complex life history patterns which can only be evaluated by combinations of size and age data. I have presented in this study the fundamental variables of the demographic characteristics of coral reef fishes. Growth and longevity are only one part of this study, and further research can expand on this study to find how reproduction is effected by key environmental factors.

5.2 Future directions

Many people have looked at the mechanisms that are driving the demographic patterns of longevity, body size and growth of tropical reef fish at local scales (Mugvillanueva et al. 1994, Gust 2004, Ackerman 2004, Robertson et al. 2005, Ruttenberg et al. 2005), but few researchers have considered these parameters on multiscales which have been addressed in this study. It must be acknowledged that the possibility of many tropical coral reef species may be long lived and display growth patterns that do not accommodate general life history observations. In the tropical South Pacific the longevity of *A. lineatus* was variable at sites of similar temperatures. So what is driving this variation? We must examine the growth, reproduction and lifespan tradeoffs and the predictability of recruitment that are affecting these differences at both large and small spatial scales in order to get a more detailed description of the life history patterns of surgeonfish. More specifically we need to document the pattern and magnitude of reproduction at each locality.

Further investigation on the oceanic influences should be conducted. Finding the reasons behind *A. bahianus*, an ecologically similar species to *A. coeruleus* and *A. chirurgus*, having a different growth curve than the other two species in the upwelling area of Isla de Margarita needs to be explored. This can be tested by examining the phylogenetic differences among the three species to ascertain the degree of difference in genetic structure, if any. Rocha et al. (2002) has initiated this study, but more detailed genetic analyses should be done. We can also test to see if the demographic parameters of other species of surgeonfishes are affected by the nutrient blooms in the Marquesas, or if it is specific to *A. lineatus*. We can then examine the effect the blooms may have on other groups of tropical fishes.

Commercial fishing does not seem to have an immediate and obvious demographic effect in this study, but fish populations may be affected because of intense artisanal and subsistence fisheries. Heavy fishing can reduce the longevity of a population if fishermen can actually target older individuals, but it is not possible to identify fishing effects on longevity in species in which size and age are decoupled. It could be argued that fishing pressure might be impacting the demographic parameters of surgeonfishes from Jamaica, San Blas or Lee Stocking in the Caribbean, or from American Samoa in the Pacific Ocean (Craig et al. 1997, Robertson et al. 2005). This argument can be resolved by comparing the size and age structure of populations of similar densities from fished and unfished sites with similar environmental characteristics in the same area. It is predicted that if a population from a fished site demonstrates different age and growth structures than a population at an unfished site of similar habitat characteristics then it can be assumed that fishing is affecting the demography of the population at the fished site; but it may not be the only factor involved in the demographic variability.

Recent studies have found that these trends and demographic characteristics are consistent across a number of groups of fish including serranids (Pears et al. 2006), lutjanids (Newman et al. 2000a, b) and labrids (Ackerman 2004). Further studies need to focus on the range of species and the ultimate mechanisms that are influencing these patterns in order to confirm or challenge the general life history observations.

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Family	Species	T_{max} (yrs)	L_{max} (TL mm)	Latitudinal range	Environment	Reference
Acanthuridae	*Acanthurus auranticavus*	30	235	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Acanthurus bahianus*	32	228	low latitude	tropical	Robertson et al 2005
Acanthuridae	*Acanthurus blochii*	35	276	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Acanthurus chirurgus*	30	268	low latitude	tropical	S. Mutz present study
Acanthuridae	*Acanthurus coeruleus*	43	276	low latitude	tropical	S. Mutz present study
Acanthuridae	*Acanthurus dussumieri*	28	308	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Acanthurus leucosternon*	21	175	low latitude	tropical	Laman Trip 2004
Acanthuridae	*Acanthurus lineatus*	46	380	low latitude	tropical	Choat and Axe 1996
Acanthuridae	*Acanthurus mata*	23	383	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Acanthurus nigricans*	34	143	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Acanthurus nigrofuscus*	25	210	low latitude	tropical	Hart and Russ 1996
Acanthuridae	*Acanthurus olivaceus*	33	210	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Acanthurus pyroferus*	28	143	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Acanthurus xanthopterus*	34	426	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Ctenochaetus striatus*	38	200	low latitude	tropical	Laman Trip 2004
Acanthuridae	*Naso annulatus*	23	626	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Naso brachycentron*	31	434	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Naso brevirostris*	25	304	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Naso hexacanthus*	44	527	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Naso lituratus*	39	211	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Naso tuberosus*	25	459	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Naso unicornis*	14	700	low latitude	tropical	Rathacharen et al 1999
Acanthuridae	*Naso vlamingii*	45	379	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Zebrasoma scopas*	33	133	low latitude	tropical	Choat and Robertson 2002
Acanthuridae	*Zebrasoma veliferum*	27	208	low latitude	tropical	Choat and Robertson 2002
Acipenseridae	*Acipenser oxyrinchus*	42	2510	high latitude	temperate	Stevenson and Secor 1999
Ammodytidae	*Ammodytes hexapterus*	6	236	high latitude	temperate	Robards et al 2002
Anoplopomatidae	*Anoplopoma fimbria*	114	1020	high latitude	deep	Cailliet et al 2001
Apogonidae	*Apogon lineatus*	5	110	low latitude	tropical	Kume et al 2003
Apogonidae	*Apogon erythrinus*	0.329	53	low latitude	tropical	Longenecker and Langston 2005
Artedidraconidae	*Dolloidraco longedorsalis*	19	132	high latitude	deep	Morales-Nin and Moranta 2000
Atherinidae	*Atherina presbyter*	1.5	106	medium latitude	temperate	Moreno and Morales-Nin 2003
Berycidae	*Centroberyx affinis*	44	321	high latitude	temperate	Morison and Rowling 2001

Appendix A: Life history data from 230 species of teleosts found all over the world from various geographic regions and environmental habitats. Shallow reef fishes defined as fishes living in habitats from short to 200m as defined by Randall 2005.

Family	Species	T_{max} (yrs)	L_{max} (TL mm)	Latitudinal range	Environment	Reference
Berycidae	*Beryx splendens*	23	516	medium latitude	temperate	Adachi et al 2000
Blenniidae	*Salarias patzneri*	1	51	low latitude	tropical	Wilson 2004
Bothidae	*Arnoglossus thori*	11	182	medium latitude	temperate	Deniel 1990
Bramidae	*Brama brama*	12	705	high latitude	deep	Lobo and Erzini 2003
Carangidae	*Seriola dumerili*	15	1660	low latitude	tropical	Kozul et al 2001
Carangidae	*Trachurus mediterraneus*	12	372	medium latitude	temperate	Karlou-Riga 2000
Carangidae	*Trachurus trachurus*	12	303	medium latitude	temperate	Karlou-Riga and Sinis 1997
Centrolophidae	*Seriolella brama*	22	702	high latitude	temperate	Horn 2001
Centrolophidae	*Seriolella caerulea*	21	534	high latitude	temperate	Horn 2001
Centropomidae	*Centropomus undecimalis*	21	1110	low latitude	tropical	Taylor et al 2000
Chaetodontidae	*Chaetodon baronessa*	12	108	low latitude	tropical	Berumen et al 2005
Chaetodontidae	*Chaetodon citrinellus*	8	90	low latitude	tropical	Berumen et al 2005
Chaetodontidae	*Chaetodon lunulatus*	12	104	low latitude	tropical	Berumen et al 2005
Chaetodontidae	*Chaetodon trifascialis*	12	102	low latitude	tropical	Berumen et al 2005
Channichthyidae	*Chionodraco myersi*	17	430	high latitude	deep	Morales-Nin and Moranta 2000
Cheilodactylidae	*Nemadactylus macropterus*	41	417	high latitude	temperate	Jordan 2001
Cottidae	*Scorpaenichthys marmoratus*	14	720	medium latitude	temperate	O'Connell 1953
Gadidae	*Gadus morhua*	13	1000	high latitude	deep	Morris and Green 2002
Gempylidae	*Rexea solandri*	17	908	high latitude	deep	Horn 1999
Gempylidae	*Thyrsites atun*	12	890	high latitude	temperate	Horn 2002
Gerreidae	*Gerres acinaces*	7	250	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Glaucosomatidae	*Glaucosoma buergeri*	26	513	low latitude	tropical	Newman 2002
Gobiidae	*Amblygobius bynoensis*	1	117	low latitude	tropical	Hernaman and Munday 2005
Gobiidae	*Amblygobius phalaena*	1	114	low latitude	tropical	Hernaman and Munday 2005
Gobiidae	*Asterropteryx semipunctatus*	1	77	low latitude	tropical	Hernaman and Munday 2005
Gobiidae	*Eviota epiphanes*	0.137	15	low latitude	temperate	Longenecker 2001
Gobiidae	*Istigobius goldmanni*	1	60	low latitude	tropical	Hernaman and Munday 2005
Gobiidae	*Valenciennea muralis*	1	106	low latitude	tropical	Hernaman and Munday 2005
Haemulidae	*Diagramma pictum*	13	553	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Kyphosidae	*Labracoglossa argentiventris*	8	191	high latitude	temperate	Watari and Yonezawa 2005
Kyphosidae	*Scorpis lineolatus*	54	370	high latitude	temperate	Stewart and Hughes 2005
Labridae	*Cheilinus undulatus*	32	2500	low latitude	tropical	Sadovy et al 2003
Labridae	*Lachnolaimus maximus*	15	896	medium latitude	temperate	K. Ranatunga unpublished data
Labridae	*Notolabrus fucicola*	20	388	high latitude	temperate	Ewing et al 2003
Labridae	*Semicossyphus pulcher*	15	550	high latitude	temperate	Cowen 1990
Labridae	*Thalassoma lunare*	8	160	medium latitude	tropical	Ackerman 2004

Appendix A cont.

Family	**Species**	**T_{max} (yrs)**	**L_{max} (TL mm)**	**Latitudinal range**	**Environment**	**Reference**
Lethrinidae	*Lethrinus harak*	15	500	low latitude	tropical	Rathacharen et al 1999
Lethrinidae	*Lethrinus mahsena*	27	610	low latitude	tropical	Rathacharen et al 1999
Lethrinidae	*Lethrinus nebulosus*	27	785	low latitude	tropical	Rathacharen et al 1999
Lophiidae	*Lophius budegassa*	21	935	high latitude	deep	Landaa et el 2001
Lophiidae	*Lophius piscatorius*	24	1635	high latitude	deep	Landaa et el 2001
Lutjanidae	*Lutjanus adetii*	24	250	low latitude	tropical	Choat and Robertson 2002
Lutjanidae	*Lutjanus analis*	29	880	medium latitude	temperate	Burton 2002
Lutjanidae	*Lutjanus apodus*	26	492	medium latitude	tropical	K. Ranatunga unpublished data
Lutjanidae	*Lutjanus campechanus*	53	1039	medium latitude	temperate	Wilson and Nieland 2001
Lutjanidae	*Lutjanus carponotatus*	20	313	low latitude	tropical	Newman et al 2000b
Lutjanidae	*Lutjanus erythropterus*	32	603	low latitude	tropical	Newman et al 2000a
Lutjanidae	*Lutjanus fulviflammus*	24	276	low latitude	tropical	Shimose and Tachihara 2005
Lutjanidae	*Lutjanus fulvus*	9	288	low latitude	tropical	K. Ranatunga unpublished data
Lutjanidae	*Lutjanus griseus*	28	760	medium latitude	temperate	Burton 2001, K. Ranatunga unpublished data
Lutjanidae	*Lutjanus guttatus*	10	664	low latitude	tropical	Andrade-Rodriguez 2003
Lutjanidae	*Lutjanus jocu*	25	820	medium latitude	tropical	de Magalhães Rezende and Ferreira 2004
Lutjanidae	*Lutjanus malabaricus*	20	705	low latitude	tropical	Newman et al 2000a
Lutjanidae	*Lutjanus quinquelineatus*	31	190	low latitude	tropical	Choat and Robertson 2002
Lutjanidae	*Lutjanus sebae*	34	630	low latitude	tropical	Newman and Dunk 2002
Lutjanidae	*Lutjanus vitta*	12	245	low latitude	tropical	Newman et al 2000b
Lutjanidae	*Ocyurus chrysurus*	17	607	low latitude	tropical	Garcia et al 2003, Manooch and Drennon 1987
Lutjanidae	*Pristipomoides multidens*	30	805	low latitude	tropical	Newman and Dunk 2003
Lutjanidae	*Rhomboplites aurorubens*	13	5180	medium latitude	temperate	Hood and Johnson 1999
Macrouridae	*Coryphaenoides acrolepis*	73	372	high latitude	deep	Andrews et al 1999
Macrouridae	*Coryphaenoides rupestris*	45	324	high latitude	deep	Garren et al 2003
Megalopidae	*Megalops atlanticus*	55	2050	medium latitude	temperate	Andrews et al 2001
Merlucciidae	*Merluccius merluccius*	20	900	high latitude	deep	Pineiro and Sainza, 2003
Mugilidae	*Mugil cephalus*	9	900	medium latitude	temperate	Rathacharen et al 1999
Nototheniidae	*Trematomus eulepidotus*	18	250	high latitude	deep	Morales-Nin and Moranta 2000
Paralichthyidae	*Paralichthys californicus*	30	1180	medium latitude	temperate	Pattison and McAllister 1990
Pinguipedidae	*Parapercis colias*	18	500	high latitude	temperate	Carbines 2004
Platycephalidae	*Platycephalus indicus*	16	552	medium latitude	temperate	Masuda et al 2000
Pleuronectidae	*Colistium guntheri*	21	410	high latitude	temperate	Stevens et al 2005
Pleuronectidae	*Colistium nudipinnis*	16	571	high latitude	temperate	Stevens et al 2005
Pleuronectidae	*Hippoglossus hippoglossus*	50	2000	high latitude	temperate	Jákupsstovu and Haug 1988

Appendix A cont.

Family	Species	T_{max} (yrs)	L_{max} (TL mm)	Latitudinal range	Environment	Reference
Pleuronectidae	*Lepidopsetta bilineata*	22	520	high latitude	temperate	Stark and Somerton 2002
Pleuronectidae	*Lepidopsetta polyxystra*	18	430	high latitude	temperate	Stark and Somerton 2002
Pleuronectidae	*Limanda ferruginea*	25	556	high latitude	temperate	Dwyer et al 2003
Pleuronectidae	*Limanda limanda*	8	418	high latitude	temperate	Deniel 1990
Pleuronectidae	*Pleuronectes platessa*	17	617	high latitude	temperate	Deniel 1990
Polyprionidae	*Polyprion oxygeneios*	60	120	high latitude	temperate	Francis et al 1999
Pomacentridae	*Acanthochromis polyachanthus*	11	104	low latitude	tropical	Kingsford and Hughes 2005
Pomacentridae	*Parma microlepis*	37	183	high latitude	temperate	Tzioumis and Kingsford 1999
Pomacentridae	*Stegastes fuscus*	15	110	low latitude	tropical	Schwamborn and Ferreira 2002
Pomacentridae	*Stegastes partitus*	7	70	low latitude	tropical	Caldow and Wellington 2003
Pomacentridae	*Stegastes planifrons*	19	97	low latitude	tropical	Caldow and Wellington 2003
Scaridae	*Bolbometopon muricatum*	33	694	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Cetoscarus bicolor*	21	421	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Chlorurus sordidus*	40	200	low latitude	tropical	Gust 2004
Scaridae	*Hipposcarus longiceps*	12	350	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Scarus altipinnis*	13	377	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Scarus chameleon*	6	231	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Scarus frenatus*	20	470	low latitude	tropical	Munday et al 2004
Scaridae	*Scarus iserti*	8	117	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Scarus niger*	23	238	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Scarus psittacus*	5	175	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Scarus rivulatus*	8	309	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Scarus schlegeli*	8	239	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Sparisoma atomarium*	3	101	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Sparisoma aurofrenatum*	7	178	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Sparisoma chrysopterum*	5	258	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Sparisoma rubripinne*	7	238	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Sparisoma strigatum*	10	252	low latitude	tropical	Choat and Robertson 2002
Scaridae	*Sparisoma viride*	9	357	low latitude	tropical	Choat and Robertson 2002
Sciaenidae	*Cynoscion albus*	18	122	low latitude	tropical	Mugvillanueva et al 1994
Scombridae	*Scomber scombrus*	18	430	high latitude	temperate	Villamor et al 2004
Scombridae	*Scomberomorus commerson*	16	130	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Scombridae	*Scomberomorus munroi*	7	768	low latitude	tropical	Begg and Sellin 1998
Scombridae	*Scomberomorus queenslandicus*	10	628	low latitude	tropical	Begg and Sellin 1998
Scophthalmidae	*Psetta maxima*	23	736	high latitude	temperate	Deniel 1990

Appendix A cont.

Family	Species	T_{max} (yrs)	L_{max} (TL mm)	Latitudinal range	Environment	Reference
Sebastidae	*Helicolenus dactylopterus*	30	360	high latitude	deep	Massutí et al 2000
Sebastidae	*Sebastes aleutianus*	205	970	high latitude	deep	Love et al 2002
Sebastidae	*Sebastes alutus*	100	530	high latitude	deep	Love et al 2002
Sebastidae	*Sebastes atrovirens*	25	425	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes auriculatus*	45	560	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes aurora*	75	410	high latitude	deep	Love et al 2002
Sebastidae	*Sebastes babcocki*	106	655	high latitude	deep	Love et al 2002
Sebastidae	*Sebastes borealis*	157	1200	high latitude	deep	Love et al 2002
Sebastidae	*Sebastes brevispinis*	82	730	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes caurinus*	50	660	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes chlorostictus*	33	472	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes chrysomelas*	30	390	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes ciliatus*	67	460	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes constellatus*	50	580	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes crameri*	105	580	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes dalli*	25	520	medium latitude	temperate	Love 1981
Sebastidae	*Sebastes diploproa*	86	460	high latitude	deep	Love et al 2002
Sebastidae	*Sebastes elongatus*	54	430	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes emphaeus*	22	183	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes ensifer*	43	250	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes entomelas*	60	590	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes flavidus*	64	660	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes goodei*	35	590	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes helvomaculatus*	87	410	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes hopkinsi*	19	290	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes jordani*	32	350	medium latitude	deep	Love et al 2002
Sebastidae	*Sebastes levis*	55	940	high latitude	deep	Love et al 2002
Sebastidae	*Sebastes maliger*	95	610	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes melanops*	28	720	high latitude	temperate	Bobko and Berkeley 2004, Love et al 2002
Sebastidae	*Sebastes melanostomus*	87	610	high latitude	deep	Love et al 2002
Sebastidae	*Sebastes miniatus*	60	760	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes mystinus*	44	530	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes ovalis*	37	560	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes polyspinis*	57	480	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes proriger*	55	510	high latitude	deep	Love et al 2002

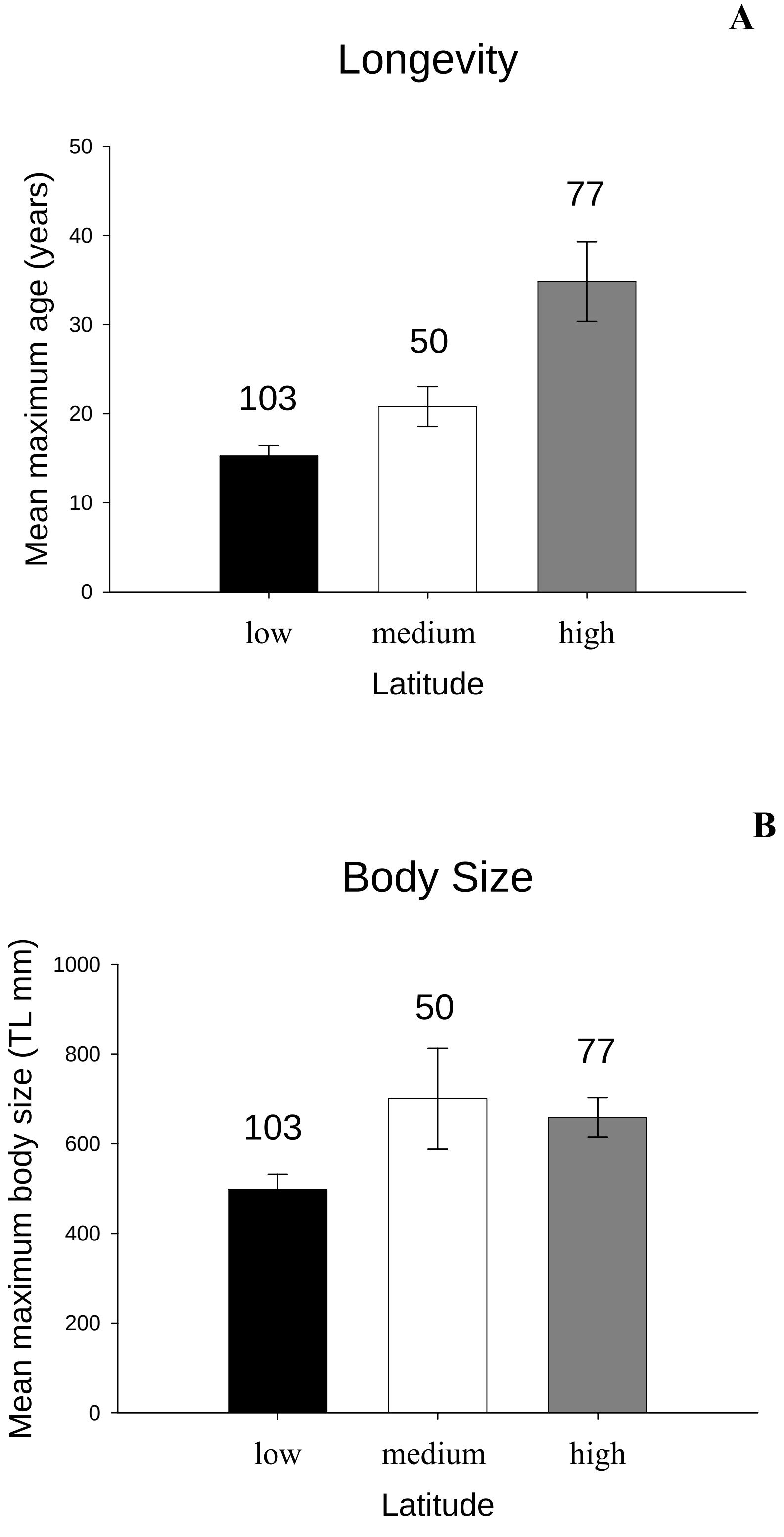
Appendix A cont.

Family	Species	T_{max} (yrs)	L_{max} (TL mm)	Latitudinal range	Environment	Reference
Sebastidae	*Sebastes rastrelliger*	23	560	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes rosaceus*	14	360	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes rosenblatti*	50	480	medium latitude	deep	Love et al 2002
Sebastidae	*Sebastes ruberrimus*	118	910	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes rufus*	85	552	high latitude	deep	Love et al 2002
Sebastidae	*Sebastes saxicola*	38	410	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes semicinctus*	15	250	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes serranoides*	30	610	high latitude	temperate	Love et al 2002
Sebastidae	*Sebastes serriceps*	23	410	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes umbrosus*	31	285	medium latitude	temperate	Love et al 2002
Sebastidae	*Sebastes zacentrus*	58	450	high latitude	deep	Love et al 2002
Sebastidae	*Sebastolobus alascanus*	100	800	high latitude	deep	Love et al 2002
Sebastidae	*Sebastolobus altivelis*	45	390	high latitude	deep	Love et al 2002
Serranidae	*Centropristis striata*	7	330	high latitude	temperate	Hood et al 1994
Serranidae	*Cephalopholis cruentatus*	8	242	medium latitude	tropical	K. Ranatunga unpublished data
Serranidae	*Epinephelus coiodes*	12	100	medium latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Serranidae	*Epinephelus damaelii*	55	1180	medium latitude	temperate	M. Francis unpublished data
Serranidae	*Epinephelus fasciatus*	14	400	low latitude	tropical	Rathacharen et al 1999, Randall et al 1997
Serranidae	*Epinephelus flavolimbatus*	35	985	medium latitude	temperate	Manickchand-Heileman et al 1999
Serranidae	*Epinephelus fuscoguttatus*	42	900	low latitude	tropical	Pears et al. 2006
Serranidae	*Epinephelus itajara*	37	250	medium latitude	temperate	Heemstra and Randall, 1993
Serranidae	*Epinephelus labriformis*	13	345	low latitude	tropical	K. Ranatunga unpublished data
Serranidae	*Epinephelus merra*	7	250	low latitude	tropical	Pothin et al 2004
Serranidae	*Epinephelus morio*	29	1026	medium latitude	temperate	Lombardi-Carlson et al 2002
Serranidae	*Epinephelus multinotatus*	27	550	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Serranidae	*Epinephelus niveatus*	29	800	medium latitude	temperate	Wyanski et al 1999
Serranidae	*Epinephelus polyphekadion*	31	590	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Serranidae	*Epinephelus tukula*	26	110	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Serranidae	*Mycteroperca interstitialis*	41	854	medium latitude	temperate	Manickchand-Heileman et al 1999
Serranidae	*Paralabrax clathratus*	33	720	high latitude	temperate	Love et al 1996
Serranidae	*Plectropomus laevis*	20	100	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Serranidae	*Plectropomus leopardus*	15	510	low latitude	tropical	Choat and Robertson 2002
Serranidae	*Plectropomus maculatus*	14	760	low latitude	tropical	Ferreira and Russ 1992
Serranidae	*Serranus cabrilla*	6	223	high latitude	deep	Tserpesa and Tsimenides 2001
Serranidae	*Variola louti*	15	500	low latitude	tropical	R. Pears unpublished data

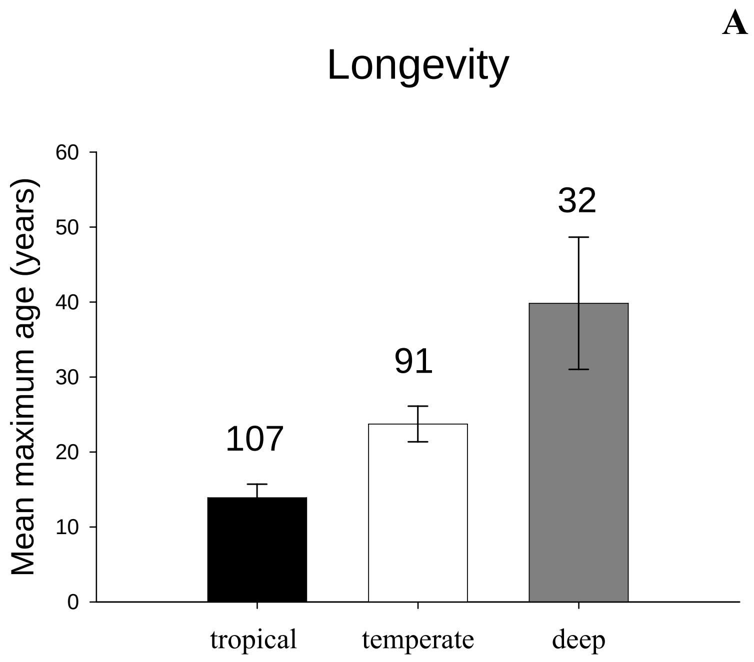
Appendix A cont.

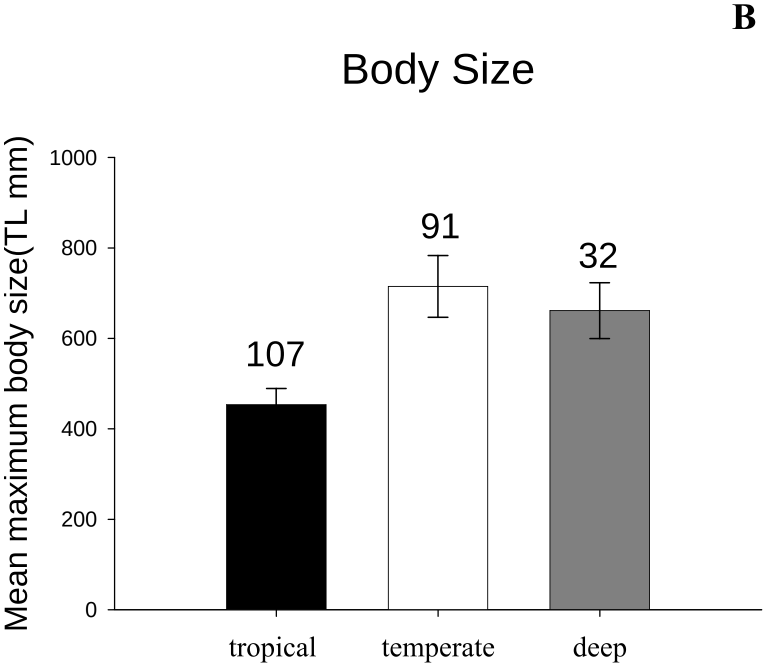
Family	Species	T_{max} (yrs)	L_{max} (TL mm)	Latitudinal range	Environment	Reference
Siganidae	*Siganus sutor*	4	470	low latitude	tropical	Rathacharen et al 1999
Siganidae	*Siganus canaliculatus*	8	300	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Soleidae	*Buglossidiurn luteum*	14	117	medium latitude	temperate	Deniel 1990
Soleidae	*Microchirus variegatus*	14	207	medium latitude	temperate	Deniel 1990
Soleidae	*Solea impar*	12	291	medium latitude	temperate	Deniel 1990
Soleidae	*Solea lascaris*	15	287	medium latitude	temperate	Deniel 1990
Soleidae	*Solea vulgaris*	26	482	medium latitude	temperate	Deniel 1990
Sparidae	*Acanthopagrus bifasciatus*	21	300	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Sparidae	*Argyrops spinifer*	9	500	low latitude	tropical	E.Grandcourt Env Res & Wldlf Dev Agcy UAE
Sparidae	*Argyrozona argyrozona*	30	651	medium latitude	temperate	Brouwer 2005
Sparidae	*Diplodus cervinus*	17	594	medium latitude	temperate	Pajuelo et al 2003
Sparidae	*Lithognathus mormyrus*	10	372	medium latitude	temperate	Lorenzo et al 2002
Sparidae	*Pagrus pagrus*	17	460	low latitude	tropical	Hood and Johnson 2000
Sparidae	*Rhabdosargus sarba*	16	720	low latitude	tropical	Radebe et al 2002
Trachichthyidae	*Hoplostethus atlanticus*	164	398	high latitude	deep	Green et al 2002
Trichiuridae	*Aphanopus carbo*	12	1300	high latitude	deep	Morales-Nin et al. 2002
Trichiuridae	*Trichiurus lepturus*	15	2000	medium latitude	temperate	Kwok and Ni 2000
Trichiuridae	*Trichiurus nanhaiensis*	12	2000	medium latitude	temperate	Kwok and Ni 2000
Triglidae	*Aspitrigla cuculus*	21	417	high latitude	deep	Baron 1985b from Colloca et al 2003
Tripterygiidae	*Enneapterygius atriceps*	0.321	31	low latitude	tropical	Longenecker and Langston 2005

Appendix A cont.

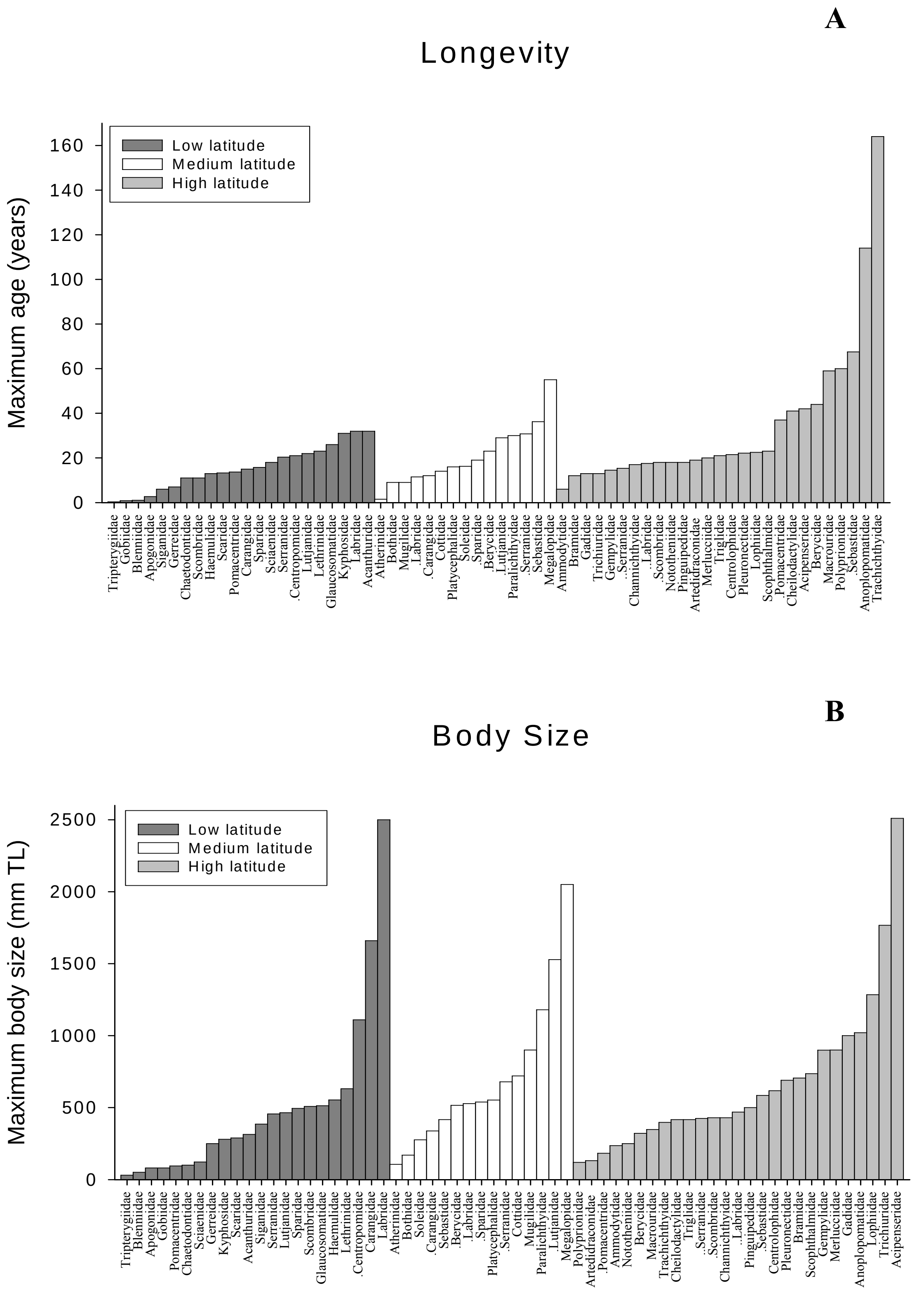


Appendix B: General life history observations on a global scale sorted by latitude range. Graphs were constructed from the data in Appendix A. Teleosts at higher latitudes (cooler waters) live longer and attain larger absolute sizes than teleosts at lower latitudes (warmer waters). The numbers above the bars are sample sizes.





Appendix C: General life history observations on a global scale sorted by environment. Graphs were constructed from the data in Appendix A. A) Mean maximum age and B) mean maximum body length of all species found in three different environmental habitats. Deep sea teleosts are longer lived than temperate and tropical species, and deep sea and temperate teleosts attain larger sizes than their tropical counterparts. The numbers above the bars are sample sizes.



Appendix D: General life history observations on a global scale sorted by family. Graphs were constructed from the data in Appendix A. A) Mean maximum age of each Family and B) mean maximum body size of each Family. Families are sorted by latitude ranges: dark grey bars = low; white bars = medium; light grey bars = high latitudes.