Barba, Jacquelyn (2010) ***Demography of parrotfish: age, size and reproductive variables.*** **Masters (Research) Thesis, James Cook University.**

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Demography of parrotfish: age, size and reproductive variables

Thesis submitted by

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Abstract

This thesis examined variation in demography and life history traits of scarine labrids across broad (across 27˚ latitude) and local (10-100's of kilometre) scales, as well as to what extent fishing had an influence. Eight parrotfish species were initially examined at a local level (GBR) to interpret differences in growth using an age-based approach. From this preliminary analysis parrotfish were then classified into two groups according to their growth pattern, indeterminate and asymptotic. This analysis revealed growth to be associated with other essential life history traits such as: growth, longevity and maturity. Next, a more detailed look was taken for five species on the GBR to examine variation at a local scale. For large parrotfish species, *Chlorurus microrhinos*, no differences in growth and life span were found between populations from mid and outer shelf reefs. However, for all small parrotfish species, populations from outer reefs had significantly reduced growth rates and shorter life spans. These results suggested that there will be short term changes in growth patterns depending on the habitat in which individuals will recruit into. Comparison of reproductive parameters, age and size at maturation and sex change, revealed earlier maturation and sexual transformation occurred in populations from outer shelf reefs. Timing of both maturation and sex change was not only driven by how long an individual lived or how big they are, but by reproductive behavior. Two species, *Chlorurus sordidus* and *Scarus psittacus* were then used to address in more detail other drivers on life history variation. First, the demography and life history of both species was compared at a broad (geographic) scale between Guam and the GBR. Broad scale variation is generally explained by the temperature size rule, however in both species growth, life span and reproductive parameters were reduced at Guam locations (higher latitudes) compared to GBR locations (lower latitudes). Second, the potential impacts of fishing on demographic characteristics of both species were examined. Populations of both *C. sordidus* and *S. psittacus* from fished areas represented reduced growth, shorter life spans, earlier maturation and earlier sex reversal. However, this variation was minimal when compared variation in similar traits occurring at a local scale.

Table of Contents

Chapter 5: Comparative analysis of maturation patterns of the protogynous parrotfish *Scarus psittacus*…………………………………………………….85

List of figures

List of tables

Chapter 1: General Introduction

1.1 Levels of variation of life history traits

The evolution of life history characteristics can be explained in terms of a Darwinian perspective, where organisms adapt according to their surrounding environment (Conover *et al* 2005, Jørgensen *et al* 2007). Life history variation occurs at many taxonomic levels in fishes. The first level of variation in life history traits is between different taxonomic groups (or families). For instance, Beverton and Holt (1959) showed the relationship between two parameters that describe growth trajectories in fish correlated with natural mortality rates was different between different orders. The next level of variation is inter-specific (between species in a group). Some species from the flatfish family are small and mature in months, while others are large and mature after several years (Roff 1992). Lastly, there is considerable intra-specific variation (within species) in life history features. For example, Gust *et al* (2002) demonstrated that populations of the parrotfish *C. sordidus* were smaller and matured earlier on outer shelf reefs compared to populations from mid shelf reefs.

The relationship between growth, longevity and reproduction is of particular importance when understanding life history evolution. Trade-offs between traits, in particular growth and reproduction, play a central role in the development and evolution of life history traits of reef fishes (Wootton 1998). Trade-offs generally imply costs in the energy investment of an individual. For instance, the rate of growth is dependent upon the investment of energy into growth or reproduction (Cook *et al*. 1999). As more energy is invested into reproduction, the rate of somatic growth slows down (Stearns & Crandall

1983, Roff 1992, Stearns 1992). Therefore, early maturation typically results in small sized individuals at a given age, reduced fecundity and increased vulnerability to predation. However, maturing earlier optimizes the likelihood of reproductive success.

Two possible mechanisms may be used to explain the adaptive responses of trade-offs in fishes. First is phenotypic plasticity, where changes in traits are caused by environmental conditions (Wootton 1998). Second is the genetic alteration of a life history characteristic, where the target is commonly a specific trait (Law 2000, Heino & Godø 2002). Distinguishing between the two mechanisms has proved to be challenging (Stearns & Koella 1986, Reznick & Bryga 1987, Stearns 1989, Rijnsdorp 1993, Olsen *et al*. 2004, Fenberg & Roy 2007, Ghalambor *et al*. 2007, Swain *et al*. 2007). However, the importance of knowing which adaptation occurs is essential because the chronology of the two mechanisms are very different, phenotypic plasticity takes place within a generation, while genetic adaptation occurs between generations.

Three main factors influence the life history patterns of marine fishes by directly affecting growth and survival rates of individuals: (1) genetic inheritance, (2) environmental influences and (3) anthropogenic changes. Genetic inheritance is very complex and will not be considered further. Environmental pressures can be classified as either abiotic influences, such as: temperature (Green & Fisher 2004), salinity (Swanson 1996) and turbidity (Fiksen & Folkvord 1999): or biotic influences, such as food availability (Clifton 1989, Clifton 1995, Green & McCormick 1999), predation and competition (Menge & Sutherland 1976). Anthropogenic changes are simply described as human induced changes. The single most widespread source of human disturbance is fishing; therefore, it is important to understand the consequences of fishing on reef fishes (Polunin & Roberts 1996).

1.2 How fishing might influence important life history traits

Responses to selection forces of fishing might be observed at both the population and individual level (Heino & Gødo 2002). At the population level, the obvious and easily detected changes occur in the abundance of the stock; the response of the stock is an overall decrease in abundance caused by fishing down the food web. However, the responses of selection forces at the individual level are not as obvious because such responses cannot be measured by observation alone.

Responses at the species level caused by fishing may not be easily detected; however, changes in life histories may influence population productivity and dynamics. Fisheries exploitation can be highly selective, since fishing gears typically target older and larger individuals, therefore, fishing may favor genotypes that mature at relatively younger ages, at smaller body sizes or that grow at slower rates (Pauly *et al*. 1998, Jennings *et al.* 1999, Stokes & Law 2000, Ernande *et al*. 2003, Law 2007, Hutchings & Fraser 2008). Fishing might also have profound influences on the longevity of individuals. Because exploitation generally targets specific age classes, the age structure of the population may be altered. Furthermore, a decline in the maximum lifespan of the individual may be observed. Changes in longevity and the age structure of the population will influence the size structure of the stock since age and size are correlated (Ricker 1981, Hutchings 1996, Ratner & Lande 2001).

Although heavy fishing pressure typically causes a shift towards smaller fish that mature earlier (Anderson & Brander 2009), fishing mortality may also impact growth rates of these smaller individuals (Discussion with Howard Choat). For large species, the targeting of both mature and immature stages generates a positive growth response and, given the link between maturation and size, faster growing fish mature earlier and spend less time as vulnerable juveniles.

1.3 Natural variation of life history traits of reef fishes

The central problem in understanding variation in life history traits caused by fishing is that variation also occurs naturally. Reef fishes display considerable demographic variation across their geographic ranges, where variation is most obvious in growth, size and age structures. Demographic variation occurs at a number of spatial scales ranging from 100's of metres to 100's of kilometres (Choat & Axe 1996, Meekan *et al*. 2001, Gust *et al*. 2002). Latitudinal gradients are useful for sampling large scale variation in vital traits (Hood et al. 1994, Meekan & Choat 1997, Choat & Robertson 2002, Robertson *et al*. 2005). However, a number of multi-scale analyses of reef fish life histories have reported differences in length, longevity, and age at maturity between habitats (Clark & Evans 1954, Jones 1986, Choat & Axe 1996), which provides insight into the demographic variation at small spatial scales.

Studies on surgeonfish across the Tropical West Atlantic showed considerable variation over a latitudinal gradient of 5500 km (Robertson *et al*. 2005). Size, growth and longevity all demonstrated a positive relationship with latitude, with the strongest effect observed on maximum life span. Moreover, the strong variation distinguished in growth was likely to correspond to genetically distinct populations (Rocha *et al.* 2002, Robertson *et al*. 2005).

Studies on parrotfish species from the Great Barrier Reef displayed significant differences in growth and maturation between mid and outer shelf locations (Gust *et al*. 2001, 2002, Gust 2004). Individuals on outer reefs were found to mature at much younger ages compared to those from mid shelf. A reduction in growth rate was also observed for individuals on the outer reefs. Differences in growth and maturation of the parrotfish, however, suggested that phenotypic plasticity, rather than genetic factors, were responsible (Dudgeon *et al*. 2000).

1.4 Thesis objectives

The primary aim of this thesis was to establish demographic characteristics, in particular growth rate, longevity, body size, timing of maturation and sex reversal of protogynous parrotfish species in the Indo Pacific. In addition, there is evidence that fishing pressure can influence demographic patterns. For these reasons, this thesis will look at demographic variation of parrotfish species not only at local and geographic scales, but also consider the potential impacts of fishing. These data should encourage future work on the relationship growth rate, maturity and longevity.

Chapter 2: Methodology. In this chapter I introduce the study species and describe in detail the two study locations, Guam and the Great Barrier Reef. I explain in detail the sampling techniques (age determination and gonad histology) used. Also described in this chapter is growth modeling, calculating maturity and sex change and other statistical analysis used.

Chapter 3: Habitat associated patterns of growth for eight species of parrotfish on the northern GBR. In this chapter I first investigate growth patterns for 8 species within the parrotfish family, which represent a wide range of terminal sizes and life spans. Five of these species (*Chlorurus microrhinos*, *Scarus frenatus*, *Scarus niger*, *Chlorurus sordidus* and *Scarus psittacus*) were then examined in greater detail to compare demographic traits at a local scale to establish the extent of short term and local change in growth, as well as other life history traits. These data inform the following two chapters.

Chapter 4: Natural and anthropogenic effects on the life history patterns of *Chlorurus sordidus* at different geographic scales. In this chapter, otoliths and gonads were used to establish the growth, longevity and maturation characteristics of the scarid, *Chlorurus sordidus,* between two demographically distinct locations, the Great Barrier Reef (hereafter GBR) and Guam with three objectives:

1) To compare populations of the same species with different habitat requirements.
2) To compare populations of the same species between two locations, Guam and the GBR, to identify any biogeographic effects.
3) To determine to what extent fishing effects influence life history variation.

Chapter 5: Comparative analysis of maturation patterns of the protogynous parrotfish *Scarus psittacus*. In this chapter, otoliths and gonads were used to establish growth, longevity and maturation characteristics of the scarid, *Scarus psittacus*, between two demographically distinct locations, the Great Barrier Reef (hereafter GBR) and Guam with three objectives:

1) To compare populations of the same species with different habitat requirements.
2) To compare populations of the same species between two locations, Guam and the GBR, to identify any biogeographic effects.
3) To determine to what extent fishing effects influence life history variation.

Chapter 6: Unifying Discussion. This thesis adds to our understanding of age and size based maturation patterns in coral reef fish by describing natural variation and fishing effects on essential demographic variables on several spatial scales. These data should promote future research to address questions on the relationship between growth rate, maturity and longevity.

Chapter 2: Methodology

This chapter provides background information regarding the study species and localities sampled and a detailed description of variables analysed. Age determination and histology techniques are also described.

Study species

Scarids were chosen for investigations of demographic variability for several reasons. First, parrotfish are often the most numerically dominant group in coral reef environments (Russ 1984, Choat & Bellwood 1991, Streelman *et al*. 2002). Parrotfish are a functionally important group, in terms of bioerosion (Bellwood & Choat 1990, Bellwood 1995), turnover rates on coral reefs, main producers of sand in reef environments and determinants of benthic community structure (Streelman *et al*. 2002). Scarid fish exhibit two distinct colour phases, known as initial phase (IP) and terminal phase (TP). In most species the initial phase is a dull, brown or grey colour, while the terminal phase is vividly green or blue with bight pink or yellow patches.

The sexual biology of parrotfish is very complex. Most parrotfish are protogynous, changing sex from female to male (Choat & Robertson 1975). Within these species, some individuals develop directly to males (primary males). Finally, a few species are gonochroistic, where some females do not change sex and the ones that do, change from female to male while still in the immature stage (Hamilton *et al*. 2008).

Parrotfish also have complex social and mating behaviours. Parrotfish are highly adaptable and can change their social strategies in response to factors such as population density and resource availability (Thresher 1984). Some populations live in territories consisting of a group of females with a single large male (Warner & Hoffman 1980, Clifton 1989, Bruggeman *et al.* 1994, Robertson *et al.* 2005). This type of harem appears to benefit feeding and reproduction. If the male is removed, then the largest female in the territory will reverse sex. Other parrotfish species hold territories with multiple male groups among twice as many females. Parrotfish display two mating strategies: pair spawning and group spawning (Choat & Robertson 1975, Warner & Robertson 1978, Warner & Hoffman 1980). Both foraging and social strategies will influence which mating strategy the population uses.

The eight parrotfish examined in this study fall within the range of 20 cm to 100 cm (all size ranges are reported as standard length SL) and are described as follows:

Cetoscarus bicolor or the Bicolour parrotfish (Rüppell 1802) has a maximum reported length on 900 mm (Choat & Robertson 1975). This species is reef associated in 1 m to 30 m waters throughout the Indo-Pacific with a climate range of 24°C – 28°C; 33°N – 24°S. In this species, juveniles are generally solitary, while adults form harems.

Chlorurus microrhinos, the Steephead parrotfish (Bleeker 1854), has a size range from 105 mm to 499 mm (Choat & Robertson 1975). The common length of males is typically 490 mm; while females are commonly reach 400 mm. The maximum reported age and length are 14 years and 700 mm (Choat & Robertson 1975). The Steephead parrotfish is reef associated in waters ranging from 1 m to 35 m deep and has a range of 30°N – 23°S.

The species complex comprises of *Chlorurus gibbus* in the Red Sea, *Chlorurus strongylocephalus* in the Indian Ocean and *Chlorurus microrhinos* in the west-central Pacific.

Scarus frenatus (Lacepède 1802) is known as the Bridled parrotfish. The size range of this parrotfish is 106 mm to 295 mm, with a maximum recorded length of 470 mm (SL: male, unsexed) and maximum reported age of 20 years (Choat & Robertson 1975). The Bridled parrotfish is reef associated in depths of 3 m to 20 m in the tropical range is 32˚N – 32˚S. The distribution is across the Indo-Pacific and is usually found on exposed reefs is shallow water. *Scarus frenatus* is generally a solitary species, but is often found in schools while feeding.

Scarus niger, the Dusky parrotfish (Forsskål 1775) has a size range of 112 mm to 278 mm, with the maximum reported length of 400 mm (Choat & Robertson 1975). This species is commonly found on reef associated environment with a depth range of 0 m to 15 m throughout the Indo-Pacific. The Dusky parrotfish’s tropical climatic range is 32˚N – 27˚S. Western Pacific *S. niger* populations are monochromatic, while the western Indian Ocean populations have a distinctive reddish initial phase.

Scarus rivulatus or the Surf parrotfish (Valenciennes 1840) is common in the Western Pacific, but also found in the Atlantic and Indian Oceans. This species is reef associated with a species range of 30°N – 32°S. The size range of the Surf parrotfish is from18 mm to 290 mm. The maximum recorded length is 400 mm (SL: male/unsexed) and the common length is 200 mm (SL: male/unsexed) (Choat & Robertson 1975).

Scarus schlegeli, Yellowband parrotfish (Bleeker 1861) has a known size range from 22 mm to 248 mm. Maximum recorded length is 400 mm for males and 300 mm for females (Choat & Robertson 1975). This species is typically found in reef associated environments between 1 m to 50 m depth throughout the Pacific Ocean, with a tropical range of 30°N – 28°S.

Chlorurus sordidus (Forsskål 1775), the Bullethead parrotfish is commonly distributed in the Indo-Pacific. *C. sordidus* has a size range between 77 mm to 224 mm (Choat & Robertson 2002). The maximum reported age and length of this species is 9 years and 400 mm (SL: male/unsexed). This species inhabits both coral rich and open pavement areas of shallow reef flats, lagoon and seaward reefs, as well as drop-offs between the depth range of 0 m to 50 m and a latitudinal range of 30°N – 33°S, 30°E – 130°W, the behaviour of this species varies between each environment found. Juveniles and individuals in the initial phase form large groups that migrate great distances between feeding and sleeping grounds.

Scarus psittacus (Forsskål 1775), the Common or Palenose parrotfish, has a size range between 104 mm to 193 mm, with maximum length of 300 mm (SL: male) and maximum reported age is 5 years (Randall *et al*. 1990, Choat *et al*. 1996). *S. psittacus* reside in a reef associated environments with a depth range of 2 m to 25 m. The Common parrotfish has a tropical range of 32˚N – 32˚S, with a distribution concentrated in the Indo-Pacific.

Study location

Parrotfish were sampled at two locations, Guam and the Great Barrier Reef, which allowed for comparison of demographic variation at a broad (geographic) scale. The Great Barrier Reef (GBR) is the world’s largest reef system composed of over 2,500 individual reefs (Williams & Hatcher 1983) (Fig. 2.1a). The GBR is located in the Coral Sea off the coast of Queensland in north-east Australia and stretches over 2,000 km (Williams & Hatcher 1983). The GBR is composed of three distinct reef types: fringing, cresentic and planar. Fringing reefs are widely distributed throughout the system, but are most common towards the southern parts. Cresentic reefs are most common in the middle of the system and planar reefs are generally found in the northern and southern parts of the system. The species sampled from the GBR were collected from Lizard Island (14˚ 40′ S, 145˚ 28′ E), on the northern GBR where both fringing and cresentic reefs were found (Fig. 2.1b). At Lizard Island replicate reefs from both mid and outer shelf localities were sampled. Since the study species is not currently harvested on the GBR, differences in demographic variation are expected to reflect responses at the local (habitat) scale.

Guam, located in the tropical West Pacific (13^{o}28’N, 144 ^{o}45’E), is the southernmost island of the Mariana Archipelago and is both the largest and economically developed island in Micronesia (Fig. 2.2). The relatively limited reef development around Guam is reflected with a narrow diversity of marine habitats. Guam is surrounded by offshore banks, as well as fringing, patch, submerged and barrier reefs (NOAA 2009). Fishing is an important livelihood in Guam, not only by contributing to the needs of the original inhabitants and immigrant populations but by perpetuating their history and cultural identity.

There are currently ten marine protected areas (MPA) in Guam: five of the marine preserves are Territory MPAs and the other five are natural heritage Federal MPAs (NOAA 2009). While management practices are enforced in the five marine reserves, there is currently limited management and enforcement in the other areas. The two reserves, Achang Reef Flat and Tumon Bay, are both territory MPAs with a conservation goal of sustainable production (Fig. 2.3). Both Tumon Bay Reserve and Achang Reef Flat Reserve were established in 1997, however, these preserves were not fully enforced until 2001 (Porter *et al*. 2005). The size between each reserve varies; however, all extend from 10 m above the mean high tide mark to 600 feet depth contour. Limited inshore fishing is authorized in the Tumon Bay Reserve, including both hook and line and cast net fishing, for specific species. Limited offshore fishing is allowed within all marine reserves, whereas bottom fishing is only allowed in the Tumon Bay Reserve.

Study variables

The four main life history variables examined throughout this thesis are size, growth, longevity and age at maturity. As parrotfish are protogynous hermaphrodites, the timing of sexual transformation was also examined.

Size: Individual size is often a critical feature of marine fish populations (Peters 1983, Calder 1984). The size structure of a population may consist of multiple size classes, where ontogenetic processes impact each size class differently (Godin 1999). For instance, large-bodied, less abundant individuals are more vulnerable to perturbations, due to having a lower capacity to replace the numbers removed from the population by the disturbance (Reynolds *et al.* 2001). Body size also relates to other life history traits, such as: fecundity, somatic growth rate, age at maturity, longevity. For instance, larger sized individuals tend to be more fecund, slower growing, and mature later in adult life and reach a greater maximum age than smaller sized individuals, which is a result of lower predation (Reynolds *et al*. 2001, Hutchings 2002).

Growth: Growth is defined as a change in size of an individual, generally an increase, which is measured in units of length, weight or energy (Wootton 1998, Bone & Moore 2008). The relationship between weight and length given in an individual's growth rate provides a good indication of the condition of the fish. Growth in fishes is generally indeterminate and highly flexible, therefore fishes may respond to environmental changes with a change in growth rate (Wootton 1998). Marine fishes can represent either fast-growth or slow-growth (Cowan *et al*. 1996). Individuals with fast growth rates invest all of their initial energy towards growth to reach a larger adult size very quickly in life. In contrast, individuals having slow growth rates will invest their energy towards reproduction, and thus achievement of a large adult size occurs later in life. In terms of overall fitness; however, fast-growing individuals typically have lower survivorship than their slower-growing counterparts.

Longevity: By definition, longevity, or life expectancy in demography, generally refers to the length of life and/or lifespan (time between birth and death). Tropical marine fishes demonstrate two types of longevity patterns: long-lived individuals or short-lived individuals. Longevity is directly linked with growth and size, and thus long-lived species generally have slower growth rates with a large asymptotic size, whereas short-lived species display faster growth rates with a small asymptotic size (Hernaman & Munday

2005). Longevity is an important parameter in predicting population dynamics because of the linkage with reproductive output and life-time fecundity (Phillips 1964, Gunderson *et al*. 1980, Berkeley *et al*. 2004, Cailliet & Andrews 2008). For instance, long-lived reef fishes often are characterized by rapid growth to asymptotic size and sexual maturity, followed by a relatively long period of reproductive activity (Choat & Robertson 2002).

Age at maturity: Maturity is an important transition point for individuals and populations, as it signifies the moment at which an individual first enters the reproductive population (Sadovy 1996), as well as their potential to contribute to future generations (Sadovy 1996). Maturation is a highly labile feature in marine fishes, where some individuals have genotypes that represent early maturation and others allow for late maturation. Age at maturity directly influences survival until maturity, successive reproductive effort and growth, offspring survival, the duration of reproductive lifespan and expected lifetime fecundity of individuals (Roff 1992, Stearns 1992, Hutchings 2000). Furthermore, because growth typically slows after maturation, early maturing individuals result in a smaller size at age later in life; and, since fecundity is dependent on size, a trade off between current and future reproductive success is observed (Heino & Godø 2002).

Otolith preparation and age determination

Prior to cutting the sagittae otoliths, one sagitta was weighed to the nearest 0.1 mg using an electronic balance in order to formulate a pattern between age and sagittal growth. Otoliths were prepared according to the protocol described in Robbins and Choat (2002) (Fig. 2.4). This method grinds the otolith down on both sides until a cross-section with the centrum (the middle of the otolith) is exposed. Several steps are taken to expose the centrum. First the otolith is mounted on the edge of a slide with a mounting media. The media used for this experiment was thermoplastic glue (Crystalbond ^{TM}). The otolith was mounted on the slide in a way that ensured the centrum was half exposed. Once the otolith was secured to the slide, the otolith was then ground down to the edge of the slide using a diamond blade grinding apparatus. The slide was then placed on a hot plate in order to re-melt the bonding media to remove the otolith from the slide. Once the otolith was removed, the sectioned otolith was placed cut edge downwards on a new, labeled slide, and left to allow the media to harden. Next, by holding the slide horizontally (parallel to the grinding wheel) the otolith was ground down again. During this step, the otolith was checked several times for readability. If the otolith was left too thick it would not be possible to make an accurate reading. Similarly, if over-ground the otolith would be destroyed. Finally when ground sufficiently, the cross-sectioned otolith was placed back onto a hot plate to place more Crystalbond ^{TM} on the slide. This final step ensures that the otolith is protected and will also fill in any scratches left from grinding, which increases the optical quality of the otolith. Sagittae were then examined under a high power (400x) microscope and a dissecting microscope using transmitted light depending on the size of the otolith and the clarity of the increments (representing age). Age was estimated based on techniques from previous studies (Choat & Axe 1996, Choat & Robertson 2002, Choat *et al*. 2003). Age was established by taking three readings of the annual increments from each otolith. Readings were taken a few days apart to insure independent counts. Individuals of some species found to be less than one year old, by examination of annual increments, were reanalysed for daily ages to provide higher precision to size at age plots and represent a more accurate initial slope of growth curves.

Age-based growth modelling

Growth trajectories were estimated for all populations by fitting the length-at-age data to an age-based model. The age-based model used was the von Bertalaffy Growth Function (VBGF) (Cerrato 1990),

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

where L_t = the estimated length at age t

L_∞ = the theoretical mean asymptotic fork length

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

t = age of fish in years

$t_\circ$ = the hypothetical age at zero length

e = the base of the natural logarithm

This age-based model is based on the *k* parameter, which is a constant. The curvature parameter, k, measures the time at which the asymptotic length can theoretically be reached. The *k* parameter is not a growth rate (Cerrato 1991). The parameter estimates by the VBGF can be sensitive to the range of ages and sizes used especially if a broad representation of age and size for a species is not available (Ferreira & Russ 1994, Choat *et al*. 2003). In order to facilitate comparisons between the populations the intercepts of the growth curves generated by the model were constrained to approximate sizes at settlement. Subsequently, in this study the parameter L_o was constrained to 20 mm for all populations of scarids since a sufficient amount of juveniles was not collected. The parameter t_o was constrained to -1 for all populations of species at each location.

The second model used to fit size-at-age data was with (Francis 1988) re-parameterized von Bertalaffy Growth Function (rVBGF) (Moulton *et al*. 1992, Welsford & Lyle 2005, Trip *et al*. 2008). This version of the VBGF describes growth similar to the traditional VBGF and is based on three parameters, $L\tau$, $L\omega$ and $L\mu$. These parameters express expected average body size at three arbitrary ages τ, ω and μ. As a result, the biological significance of the parameters allows for a direct comparison of mean size-at-age data between populations. Ages τ and μ are randomly chosen within the range of the data set to represent the general form of growth, and ω is determined by the average age of τ and μ. The re-parameterized equation of the VBGF is:

$$Lt = L\tau + \frac{(L\mu - L\tau[\,1 - r\,(2^{t-\tau}/\mu - \tau)]}{1 - r^2}$$

where $r = \dfrac{L\mu - L\omega}{L\omega - L\tau}$, and L$t$ is the average size-at-age t to be predicted by the model, provided $L\tau < L\omega < L\mu$ and $(L\mu - L\omega) \neq (L\omega - L\tau)$, which are limitations that affect both the generalized and the re-parameterized VBGF models. The rVBGF parameters estimated for all parrotfish species were $L(1)$ and $L(3)$, generating estimates of mean body size-at-ages one and three years.

Gonad histology

Gonads were weighed to the nearest 0.001g and then cut into 4 mm sections with a razor blade. The sections were placed into tissue processing cassettes, labeled and left in 70% ethanol. The sectioned gonads where then processed overnight in a Shandon Hypercenter XP through the steps (where A= Ambient):

Steps	Reagent/ Concentration %	Temp (^{o} C)	Vac	Immersion Time	Drain Time
1	70% Alcohol	A	N	00:10:00	2:00
2	70% Alcohol	A	N	01:00:00	2:00
3	80% Alcohol	A	N	01:00:00	2:00
4	90% Alcohol	A	N	01:00:00	2:00
5	95% Alcohol	A	N	01:00:00	2:00
6	Absolute Alcohol	A	N	01:00:00	2:00
7	Absolute Alcohol	A	N	01:00:00	2:00
8	Absolute Alcohol	A	N	01:00:00	2:00
9	Xylene	A	N	01:00:00	2:00
10	Xylene	A	N	01:00:00	2:00
11	Paraffin	60	Y	02:00:00	2:00
12	Paraffin	60	Y	02:00:00	2:00

The sectioned gonads were then ready to be embedded. To embed the gonad section, metal trays were filled with wax. Then the gonads were placed into the trays using electron forceps and secured to the bottom of the metal trays. The waxed trays were then set onto an ice plate and left to harden. Once hardened, the excess wax was removed and gonads were cut on the Microtome until tissue was exposed. Gonads were placed on ice, ripe females were placed on ammonia and ice, before the tissue samples taken. Once cooled, three to four 5µ cuts of the section gonad tissue were taken using the Microtome, floated in a hot waterbath, and then recovered on appropriate labelled slides. The slides were placed into an oven for 30 minutes at 60^o C. The slides were then stained following the Mayer's Haemalm and Young's Esoin method:

Steps	Reagent/ Concentration %	Immersion Time
1	Xylene	2:00
2	Xylene	2:00
3	Absolute Alcohol	20 dips
4	Absolute Alcohol	20 dips
5	Absolute Alcohol	20 dips
6	70% Alcohol	20 dips
7	Water	20 dips
8	Mayer's Haemalum	8:00
9	Water	20 dips
10	Blue Solution	0:30
11	Water	20 dips
12	Eosin Stain	3:00
13	Water	20 dips
14	70% Alcohol	20 dips
15	Absolute Alcohol	20 dips
16	Absolute Alcohol	20 dips
17	Xylene	20 dips
18	Xylene	20 dips
19	Xylene	20 dips
20	Xylene	Sections kept here until mounted

Slide covers were the mounted to the stained gonad tissue using D.P.X. After all the slides were mounted, they were placed into an oven at 40^{o}C for 3 days.

Maturation modelling: assigning stages

To minimize bias, gonads were processed and staged in random order without knowledge of the size, age or colour patterns of the fish or the location from which the sample was collected. Initially, a subset of 40 gonad samples were sectioned in the anterior, medial and posterior regions to determine whether consistent differences in gonad development could result along the gonad length. Analysis of the subsampled gonad sections showed no variation in development status along the length of the gonads. Therefore, transverse sectioning of the medial section of each gonad lobe was considered to provide representative information of reproductive development stage and sexual identity of each gonad.

All histological sections were examined under a high power microscope. Each gonad was classified according to its sex and state of development, without knowledge of fish identity, size or age. Assignment of a development class depended upon the predominant stage of gametogenesis observed in the gonad. Stages of oocyte development were classified by the latest non-atretic stage present in the gonad tissue with minor modifications with regards to scarid gonads: stage I—chromatin nuclear stage, stage II—peri-nucleolar stage, stage III—yolk vesicle formation (cortical aveoli stage), stage IV—vitellogenic (yolk) stage, stage V—hydrated stage (classification from West 1990) and stage VI—spent oocyte (post ovulatory follicle). For this study, spent females were estimated with regards to the percentage of post ovulatory follicles. The classification of the individual was "spent" if 50% or more of the gonad tissue contained post ovulatory follicles. Spermatogenesis occurred in small crypts and all cells were generally at the same stage. The development and appearance of spermatocytes, spermatids and mature sperm followed very closely with the description of Lou (1992). Gonads were then classified as one of the following: (i) "immature female", when stages I and II of oogenesis was observed, (ii) "mature female", when stages III to V of oogenesis was observed, (iii) "primary male", when gonads were readily identified as large, (iv) "secondary male", when gonads were identified as quite small, lots of mature sperm present and sperm duct was located at the top of the gonad, and (v) "transitional" when degenerating female oocyte stages could be seen within the developing testicular tissue. Criteria used in the diagnosis of gonad sexual identity, development stage and oocyte/spermatocyte stage are summarized in Table 2.1 (also see Appendix Fig. 14 & 15).

Table 2.1 The classification of gametogenesis of *C. sordidus* used in the diagnosis of sexual development.

Developmental Stage	Oocyte Stage/ Spermatocyte Stage	Oocyte stage description	Other Criteria
1- Immature Female (IM)	Stage I, II and III oocytes	***Pre-vitellogenic oocytes*** • Oogonia, **oo** • Chromatin nucleolus, **cns** • Early perinucleolus, **eps** • Late perinucleolus, **lps**	• No brown bodies • Thin gonad wall • Compact, lamellae well packed
2-Resting Female (RE)	Stage I, II and III	***Pre-vitellogenic oocytes*** (as above)	• Brown bodies common but not always present • Thick gonad wall • Lamellae not compact, often vaculated
3-Ripe or Developed Mature Female (RI)	Stage I, II, III and IV oocytes	***Vitellogenic oocyte:*** • Yolk vesicles, **yy** • Migratory nucleus stage, **mns**	• May have atretic oocytes, post-ovulatory follicles or bb from previous spawning
4- Running Ripe or Hydrated Female (RR)	Stage V oocytes	***Hydrated oocytes,* hy**	Post-ovulatory follicles and atretic oocytes may be present
5- Spent Female (SP)	Ovulatory follicles present: Very early (pof1) Early (pof2) Mid (pof3) Post (pof4)	The gonad consisted of 50% or post ovulatory follicles. In some samples, the ovary was distended, with many empty follicles and degenerated stage III and IV oocytes.	
1- Primary Male (PM)	Spermatids, Primary and Secondary Spermatocytes	Large testes with centrally located sperm ducts. No signs of female gonia.	
2- Secondary Male (SM)	Spermatid, Spermatocytes	Lobate in appearance, central lumen and peripheral sperm ducts	
3- Transitional (TRN)	Spermatids and Oocytes	Functional females having sperm crypts and/or functional males having atretic eggs or immature oocytes	

Age- and size-at-maturity and sex change

Age- and size-at-maturity were estimated by calculating the age and size at which 50% of females were mature (proportion of mature females relative to the total number of females within each age or size class). Information used for this calculation was age (in years), size (fork length, FL) and maturity (immature or mature). Since the relationship between maturity (dependent variable) and age or size (independent variable) is non-linear, a logistic function was used (following Moore *et al*. 2007, Williams *et al*. 2008). The logistic function used for calculating age- and size-at-maturity was:

$$P_a = \left[1 + e^{[-\ln(19)(a - a_{50}) / (a_{95} - a_{50})]} \right]^{-1}$$

Where P_a is the proportion of mature females in age or size class a, a_{50} is the age or size at which 50% of the females are mature, and a_{95} is the age or size at which 95% of females are mature. Parameters evaluated for this study were age-at-50% maturity (T_{50}) and size-at-50% maturity (L_{50}). Age classes were based on one year increments and size classes were based on 50mm increments. The logistic function was also used for secondary males to evaluate age- and size- at sex change. For each parameter value of a_{50}, 95% confidence intervals were estimated using a bootstrapping procedure, where the data were randomly re-sampled 1000 times with replication (Moore *et al*. 2007).

Statistical analysis

One way Analysis of Variance (ANOVA) was used to determine locality differences in mean age and size of both female and male for all species. The model tested the effects of location (a fixed effect), using mean age/size as replicates in this broad scale analysis. Prior to the ANOVA calculations, the assumption of homogeneity of variances was examined using box plots of residuals and log10 (X+1) transformations were used to remove heterogeneity of variances as required.

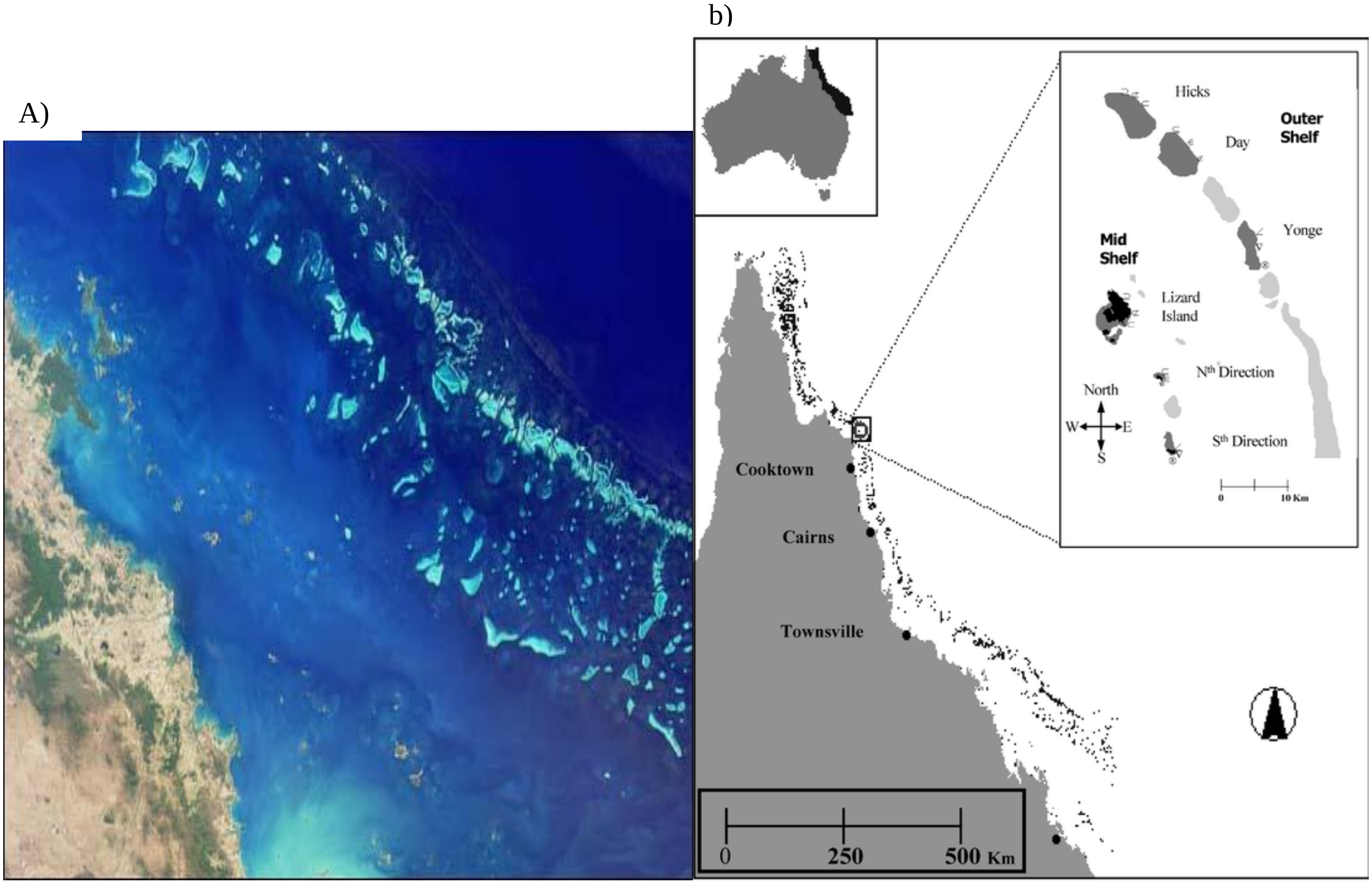

Fig. 2.1: (a) Satellite image of the Northern Great Barrier Reef, illustrating positions of mid and outer shelf reefs, where mid shelf reefs are located closer to the coast line, are composed of numerous small reef patches and have lower numbers of large schooling predators. Outer shelf reefs, on the other hand, form continuous reef fronts exposed to open ocean influences and have large numbers of schooling predators (Credit: NASA www.solcomhouse.com). (b) Location of Lizard Island on the GBR with insert showing mid and outer shelf reefs sampled (Credit: Gust 2004).

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Fig. 2.2: Illustrates the study location of Guam, located in western Pacific. Guam habitats are mainly fringing reefs around a large island. The reefs vary due to levels of exposure and location. All reefs are readily accessible to the local population (Credit: http://www.defenseindustrydaily.com/us-military-gearing-up-on-guam-03011/).

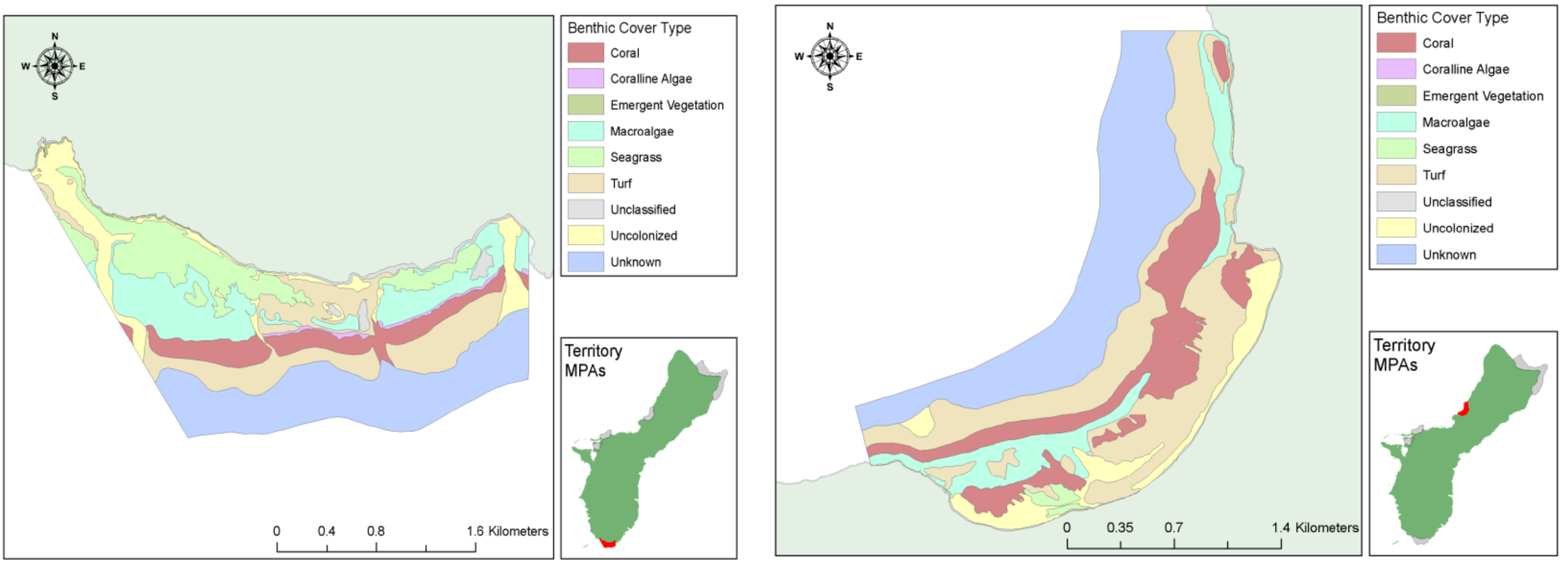


Fig. 2.3: Map of Achang Reef Flat Reserve in Guam, located at the southern tip of Guam (left) and the map on the right represents the Tumon Bay Reserve in Guam (Credit: NOAA 2009).

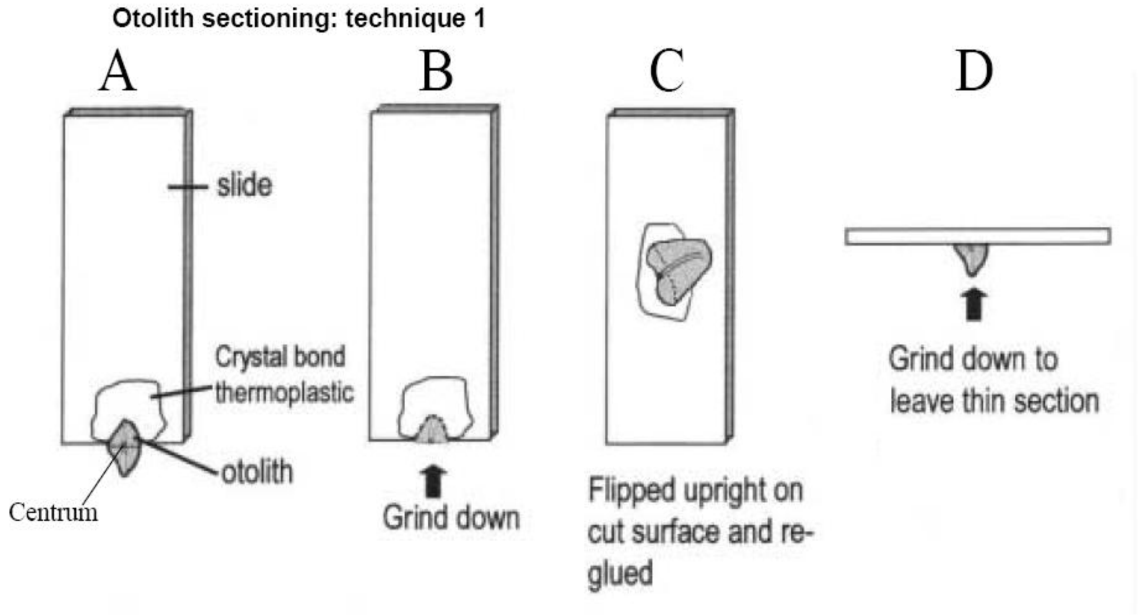


Fig. 2.4: Illustration of the process used for grinding the sagittal otoliths (Credit: Robbins and Choat 2002).

Chapter 3: Habitat associated patterns of growth for eight species of parrotfish on the northern GBR

3.1 Introduction

In reef fish, both the rate and pattern of growth vary over their distributional ranges and appear to be influenced by scale-dependent processes (Brandt *et al*. 1992). This includes both broad (geographic scale) and local (habitat scale) distribution. Ideally, the analysis of growth in reef fishes should include multiple sampling across appropriate spatial scales in order to describe this variation and to identify the relevant processes. Failure to do this can result in confounding of broad scale patterns which reflect the influence of larger scale environmental gradients such as temperature, predation and food availability with local patterns, which reflect the influence of adjacent habitats (Pauly 1980, Anderson 1985, Charnov 1993, Wilson & Meekan 2002, Gust *et* al. 2002, Munch & Conover 2003, Ackerman *et al*. 2004, Ruttenberg *et al*. 2005, Kingsolver & Huey 2008, Trip *et al*. 2008).

In this study I investigated rates and patterns of growth in an abundant group of reef fishes, the scarine labrids, in habitat scale distribution. As growth patterns are strongly linked to other life history parameters (Beverton & Holt 1959, Stearns & Koella 1986, Charnov & Berrigan 1991, Conover & Munch 2002) these comparisons will also include estimates of reproductive performance, including age and size at maturity and sex reversal, in this predominately protogynous group. Moreover the populations in this study were not subject to anthropogenic disturbances which enabled the investigation of local variation without the complication of direct human disturbance.

The analysis of growth has many forms, however, two patterns are consistently observed. The comparison of growth in fishes is commonly between indeterminate growth, where growth is continuous throughout an individual's life, and a determinate growth pattern, where individuals have rapid initial growth and then abruptly reduce somatic growth (Fig. 3.1) (but see Choat & Robertson 2002). Individuals with asymptotic growth are generally longer lived and come to maturity faster; however, they often have a smaller adult body size compared to individuals with indeterminate growth. Such patterns of growth appear to be a phylogenetically determined, fixed by evolutionary differences between families of perciform fishes (Beverton & Holt 1959).

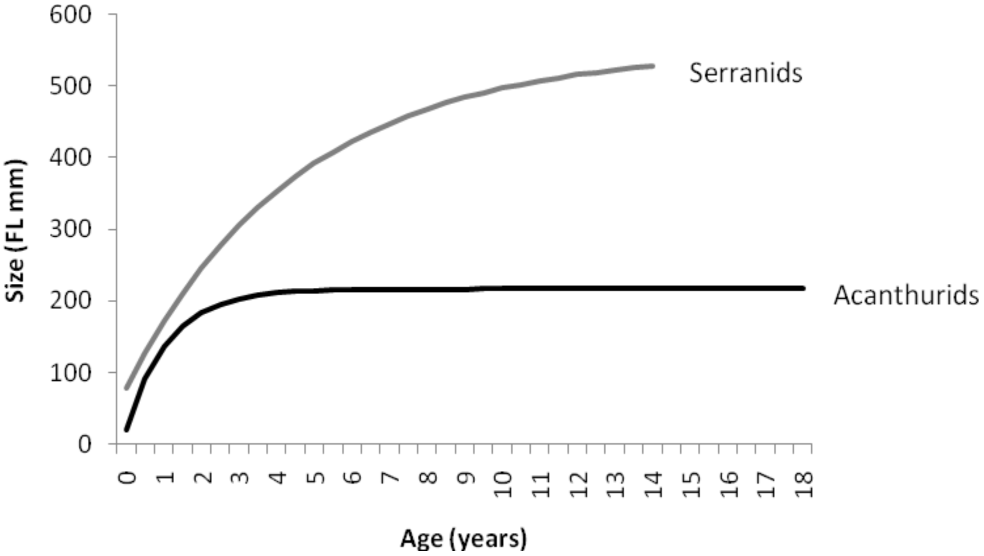


Fig. 3.1: Comparison of indeterminate (Serranids) and asympotic (Acanthurids) growth patterns.

Chapter 3: Habitat associated patterns of growth for eight species of parrotfish on the northern GBR

Growth is an important life history characteristic that often covaries with traits such as longevity, size, maturity and the expression of sex change (Stearns & Crandall 1983, Charnov & Berrigan 1991, Conover & Munch 2002, Gust *et al*. 2002, Gust 2004, Fenberg & Roy 2007). Growth demands allocation of resources, as such, it limits allocation to other important life history traits such as longevity. For example, indeterminate growing serranids have the capacity to grow fast, but the result is a trade off between growth and longevity, having a larger size at the expense of a shorter life span. Trade offs also occur between growth and reproductive parameters. For example, individuals with an asymptotic growth pattern generally display gonochorism, meaning separate sexes, while individuals with an indeterminate growth pattern display protogynous hermaphrodism, meaning the individual will undergo sex reversal from female to male. For serranids and parrotfish, which are protogynous, males are typically larger in size compared to females compared to similar sizes of both male and females for gonochoristic acanthurids.

While growth patterns may differ between groups of fish, it is also of interest to note where similar growth patterns within groups. Growth trajectories of eight parrotfish species (Fig. 3.2) identify the presence of either intermediate or asymptotic growth patterns (see Fig. 3.3). Depending on the growth pattern of the species, other traits, fir instance life span, maturity and percent of primary males are influenced.

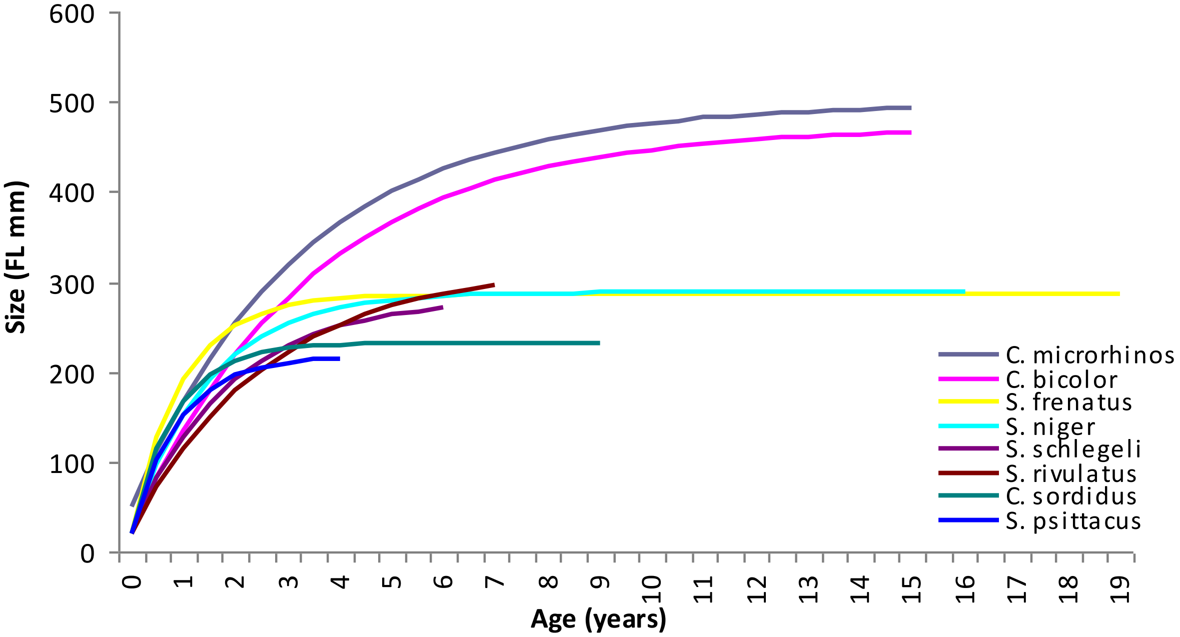


Fig. 3.2: Comparison of varing growth patterns of eight parrotfish species from the northern GBR.

I examined eight scarine labrid species that have sufficient age, size and reproductive data to allow for the comparison of deomgraphic traits at a local scale. The specific questions asked; are the patterns of growth within a species subject to short term and local change? And furthermore, how does growth relate to other life history traits of parrotfish?

Spatial variability in growth and maturation was studied for eight common parrotfish species: *Chlorurus microrhinos*, *Cetoscarus bicolor*, *Scarus frenatus*, *Scarus niger*, *Chlorurus sordidus*, *Scarus schlegeli*, *Scarus rivulatus* and *Scarus psittacus*. Parrotfish are characteristic of coral reefs, where they are often dominant in terms of number and biomass. These species represent a range of sizes (20- 100 cm) and are widely distributed across the continental shelf of the GBR (Russ 1984) and could be easily identified using the criteria of Randall *et al* (1997). All representative species are highly abundant in many Indo-Pacific localities and often are captured for food (Choat & Randall 1986, Randall *et al*. 1997); however, none of the species are currently targeted by fishermen on the GBR.

3.2 Methods

Study area

Research was conducted between two habitats (mid- and outer-shelf reefs) near Lizard Island on the northern GBR (refer to Chapter 2, Fig 2.1). Collection of the scarid species (57 *C.* bicolor, 125 *C. microrhinos*, 619 *C. sordidus*, 606 *S. frenatus*, 95 *S. niger*, 305 *S. schlegeli*, 306 *S. rivulatus* and 60 *S. psittacus*) was conducted from 1990 to 1997 (by Howard Choat, Nick Gust and Dong Chun Lou) by the use of hand spears and 1.5 x 30 m drive nets with 50 mm mesh. It is important to note that *C. bicolor* is a species characteristic of outer-shelf reefs, and thus no individuals represent mid-shelf reefs. Similarly both *S. schlegeli* and *S. rivulatus* are predominantly found in lagoons or on back areas of mid-shelf reefs, and therefore neither of these species are represented from outer-shelf habitats. Collected fish were stored on ice and processed on the day of capture. Fork and standard lengths were measured for each individual to the nearest millimetre. Whole body weights were also recorded to the nearest gram. Sagittal otoliths were removed, cleaned (to remove any residual material), washed in ethanol and stored to dry prior to aging. Gonad tissue was dissected from the individuals, weighed to the nearest gram and placed in FAAC, a formalin-based fixative (4% formaldehyde, 5%

glacial acetic acid, 1.3% calcium chloride dehydrate) then transported to the lab to undergo histological examination.

Age determination

Putative annual increments of sagittal otoliths were used to estimate age. Each ototlith was examined and read at least twice for verification of incremental bands representing annuli. Ageing process followed the techniques described in Choat *et al* (1996). See Chapter 2 for further details of otolith ageing.

Analysis

A principle component analysis (PCA) was performed for this study to investigate the variation in life history traits across parrotfish species, as well as between mid and outer shelf reefs. Seven information categories were identified: (i) asymptotic size (L_{inf}), (ii) percent life span an individual will reach at 50% growth, (iii) size (L_{max}), (iv) longevity (mean T_{max}), (v) age at maturity (T_{mat}), (vi) age at sex change ($T_{sex\ change}$) and (vii) primary males (as a percentage of the population). Variables were checked for the presence of skewed distributions across species and habitat using pair-wise correlation plots (Draftsman plots), but no transformations of the life history variables were required.

Modelling of growth

Growth for all eight parrotfish species was estimated by examination of the relationship between fork length (FL) and age. Size-at-age data were fitted by using both the von Bertalanffy Growth Function (VBGF) and Francis's (1988) re-parameterized equation of the von Bertalanffy Growth Function (rVBGF). The rVBGF parameters estimated for all parrotfish species were *L*(1) and *L*(3), generating estimates of mean body size-at-ages one and five years. For further details of growth modelling refer to Chapter 2.

Age- and size-at-maturity

Sexual identity was assessed from gonads (Chapter 2). Age- and size-at-maturity were estimated by calculation of the age and size at which 50% of females were mature (proportion of mature females relative to the total number of females within each age or size class) (Williams *et al*. 2008). The logistic function used for estimating age- and size-at-maturity is described in Chapter 2. 95% confidence intervals (CI) were also estimated for each parameter value of age-at-maturity (*T50*) and size-at-maturity (*L50*) using a bootstrapping procedure (Moore *et al*. 2007), also described in Chapter 2.

Age- and size-at sex change

A logistic regression approach was used to estimate age and size at which 50% of sex changing females undergo sex reversal (Williams *et al*. 2008). The logistic function used for calculating age- and size-at-maturity was:

$$P_a = \left[1 + e^{[-\ln(19)(a - a_{50}) / (a_{95} - a_{50})]} \right]^{-x}$$

Where P_a is the proportion of sex changing females in age or size class a, x is the observed frequency of males within each age or size class, a_{50} is the age or size at which 50% of sex changing females have changed sex, and a_{95} is the age or size at which 95% of sex changing females have changed sex. Parameters evaluated for this study were age-at-50% sex change T_{50}, age-at-95% sex change T_{95}, size-at-50% sex change L_{50}, and size-at-95% sex change L_{95}. Age classes were based on one year increments and size classes were based on 50mm increments. For each of the above parameters, 95% confidence intervals (CI) were estimated using a bootstrapping procedure, where the data was randomly re-sampled 1000 times with replication (Moore *et al*. 2007).

3.3 Results

Principle Component Analysis (PCA)

The initial PCA analysis partitioned the eight species into three groups (Fig. 3.3). The first group consists of *C. microrhinos* and *C. bicolor*, which clearly separate out by size. The next two groups: *S. niger*, *S. frenatus* and *C. sordidus* versus *S. psittacus, S. schlegeli* and *S. rivulatus* are all relatively similar in size but separate out along axes driven by the form of growth rate, life span and reproductive dynamics, where the group with *S. frentaus* are characteristic of asymptotic growth, late maturation, longer lived and larger sized compared the other group of species (Fig. 3.3). The PCA indicated that both PC1 and PC2, which together captured 85.9% of the variation in life histories, contributed to explaining the patterns of variation in life histories across parrotfish species. The primary contributor to explaining the variation between species was PC1 (64.0%; Table 3.1).

Comparison of information categories also revealed differences between the above three groups (Fig 3.4, but also see Appendix Fig. 1). The group of parrotfish consisting of *S. psittacus*, *S. schlegeli* and *S. rivulatus* demonstrated a larger percentage of primary males in the population compared to the other groups, with *S. frenatus* and *C. sordidus* populations representing the lowest percentage of primary males (Fig. 3.4). Similarly, differences in the percent life span populations reach at 50% growth rate (L_{inf}) revealed that species with asymptotic growth (*S. frenatus*, *S. niger* and *C. sordidus*) achieve half their growth much faster compared to species with indeterminate growth (*C. microrhinos*, *C. bicolor*, *S. psittacus*, *S. rivulatus* and *S. schlegeli*) (Fig. 3.4).

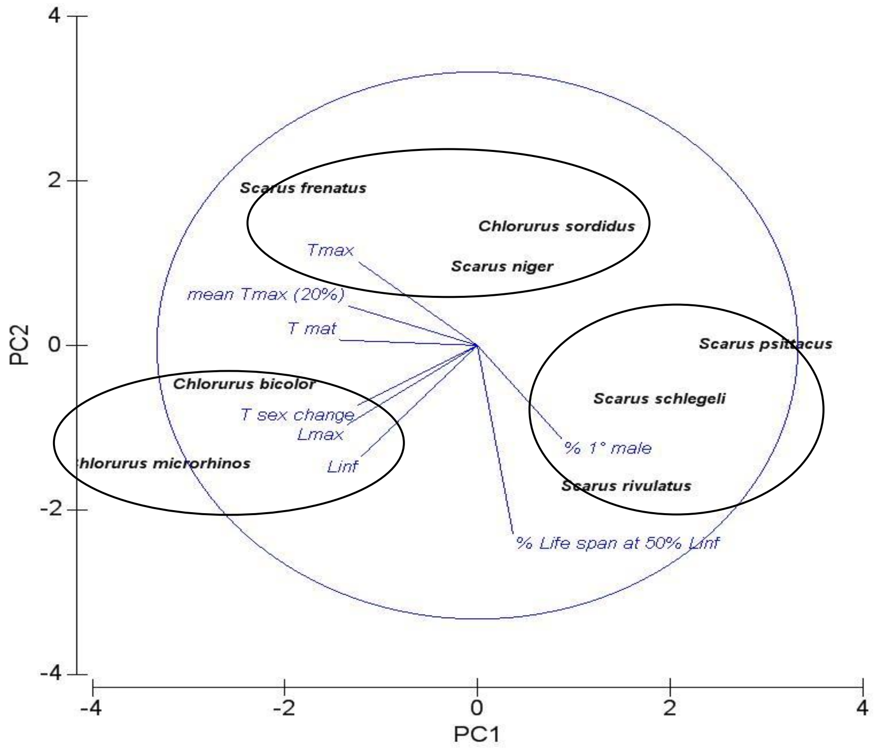


Fig. 3.3: Ordination of life history parameters of populations of *Chlorurus microrhinos*, *Cetoscarus bicolor*, *Scarus frenatus*, *Scarus niger*, *Chlorurus sordidus*, *Scarus schlegeli*, *Scarus rivulatus* and *Scarus psittacus* showing the direction (eigenvectors) and contribution (relative length of eigenvectors) of the life history variables. Tmax: maximum age; mean Tmax: 20% longevity; Tmat: age at maturity; Tsex change: age at sex change; Lmax: maximum length; Linf: growth curve; % life span at 50% Linf; % 1º males in the population. The results of the PCA seperated the species into three groups, with *C. microrhinos* and *C. bicolor* seperating out by size, the other species partition out according to growth, life span and reproductive dynamics.

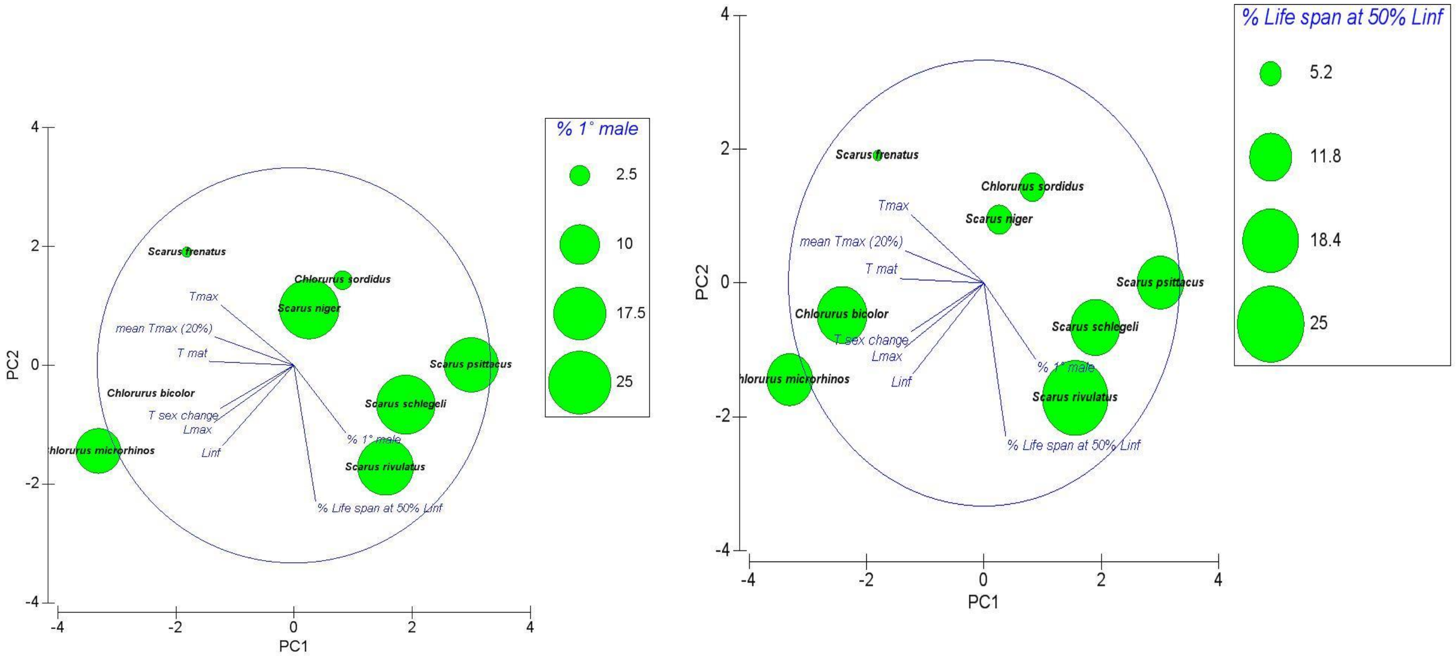


Fig. 3.4: PCA ordination of life history parameters of eight parrotfish species from the GBR, showing eigenvectors of life history variables and the shape of gradients for percent primary male (left panel) and percent life span at 50% *Linf* (right panel). Bubble size represents gradients from lowest to highest values of primary males and percentage of lifespan when individual reaches 50% growth.

Table 3.1: Results of Principle Component Analysis (PCA) of life history variables of several parrotfish species on the Great Barrier Reef: (A) Eigenvalues of variables included in the ordination, and (B) PC scores of species sampled.

A.

Variable	PC1	PC2
	(64.00%)	(21.90%)
Linf	-0.363	-0.407
% life span at 50% Linf	0.111	-0.688
L max	-0.405	-0.289
Mean T max	-0.403	0.145
T mat	-0.43	0.02
T sex change	-0.372	-0.218
% primary male	0.263	-0.34

B.

Species	Score 1	Score 2
Chlorurus microrhinos	-3.31	-1.44
Cetoscarus bicolor	-2.42	-0.475
Scarus frenatus	-1.81	1.91
Chlorurus sordidus	0.826	1.43
Scarus niger	0.259	0.947
Scarus psittacus	3	1.17E-03
Scarus schlegeli	1.89	-0.662
Scarus rivulatus	1.89	-1.71

Growth

Size-at-age data plotted for each species revealed variable patterns of growth. Growth was partitioned into two groups: indeterminate and asymptotic (determinate). *C. microrhinos*, *C. bicolor*, *S. psittacus*¸ *S. schlegeli* and *S. rivulatus* showed continuous growth over the age classes sampled. This group also contained both the largest and smallest species examined. *C. sordidus*, *S. frenatus* and *S. niger* showed determinate growth with an asymptotic size established relatively early in life. The eight species exhibited a range of asymptotic lengths (Table 3.2). *C. microrhinos* and *C. bicolor* were the largest species (over 45 cm), while *C. sordidus* and *S. psittacus* were the smallest species (under 23 cm). Although growth varied considerably between individuals, clear variation in growth was evident between habitats (Table 3.2, Fig. 3.5). *S. frenatus*, *S. niger*, *C. sordidus* and *S. psittacus* showed smaller asymptotic sizes on outer shelf reefs. Furthermore, *S. frenatus*, *S. niger* and *C. sordidus* populations from outer shelf reefs had reduced maximum life spans compared to populations on mid shelf reefs. Both *S. psittacus* populations displayed similar life spans. For *C. microrhinos*, both mid and outer shelf reef populations had similar growth patterns and life spans.

Variation in length-at-age one was observed not only between species but also between habitats (Table 3.3: mid-shelf, Table 3.4: outer-shelf). *C. bicolor* represented the largest length-at-age one of 266.8 mm on outer shelf habitats, while *S. niger* populations on outer shelf reefs reached the smallest length-at-age one [121.4 mm]. *C. microrhinos*, *S. niger* and *S. psittacus* populations from mid shelf habitats reached a larger size by their first year compared to populations from outer shelf habitats (Fig. 3.6). While only a small difference in size by age one was seen for *C. sordidus* populations between habitats. However, *S. frenatus* populations on outer-shelf reefs demonstrated a larger length-at-age one (190.7 mm) compared to mid shelf reef populations (162.5 mm) (Fig. 3.6).

Differences in length-at-age three were also observed (Table 3.3: mid-shelf, Table 3.4: outer-shelf). *C. bicolor* populations from outer shelf reefs reached the largest size of 384.7 mm, while the smallest size by age three was demonstrated by *C. sordidus* on outer shelf reefs [184.9 mm]. For *S. frenatus, S. niger* and *C. sordidus* length-at-age three was noticeably reduced on outer-shelf reefs compared to mid shelf reefs (Fig. 3.8). *C. microrhinos* and *S. psittacus* illustrated similar lengths by age three from both habitats, though *S. psittacus* populations from outer shelf reefs were slightly larger (Fig. 3.8).

Table 3.2: von Bertalanffy growth function (vBGF) parameters for eight parrotfish species at both mid- and outer-shelf reef habitats. L_∞ represents the mean theoretical asymptotic length and *k* describes the rate at which the individual will reach the asymptotic length.

Species	**Location (Habitat)**	**L∞ (FL mm)**	***k***
C. microrhinos	mid shelf	497.5	0.30
	outer shelf	549.9	0.22
C. bicolor	mid shelf	—	—
	outer shelf	471.5	0.29
S. niger	mid shelf	288.4	0.68
	outer shelf	214.9	0.93
S. frenatus	mid shelf	285.4	1.03
	outer shelf	230.8	1.76
C. sordidus	mid shelf	231.3	1.19
	outer shelf	162.5	2.61
S. psittacus	mid shelf	217.8	1.09
	outer shelf	157.2	1.80
S. schlegeli	mid shelf	281.4	0.53
	outer shelf	—	—
S. rivulatus	mid shelf	317.1	0.38
	outer shelf	—	—

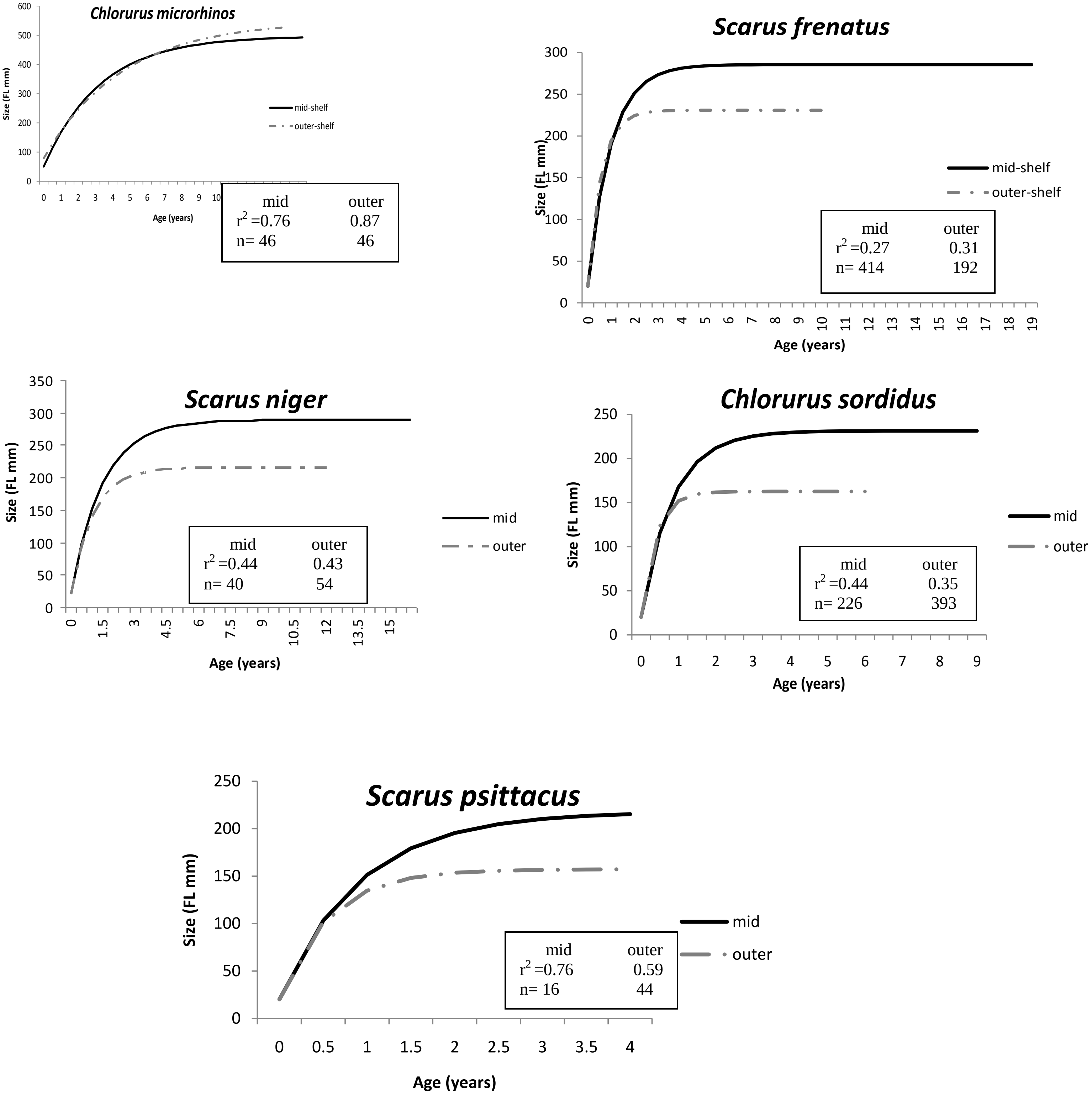


Fig. 3.5: Comparison of growth across representative parrotfish species between two habitats, mid and outer shelf reefs, GBR.

Table 3.3: Re-parameterized von Bertalanffy growth parameters for length-at-age 1 and length-at-age 3 for representative parrotfish species on mid shelf reefs with confidence intervals.

Species	**L_1 (FL mm)**	**CI +**	**CI -**	**L_3 (FL mm)**	**CI +**	**CI -**
C. microrhinos	204.6	10.23	2.32	354.2	5.88	1.45
S. frenatus	162.5	9.09	1.11	258.8	5.29	1.62
S. niger	143.5	7.45	3.59	241.1	5.29	2.22
S. schlegeli	139.0	8.47	6.95	225.8	5.57	3.42
S. rivulatus	125.7	12.57	3.33	226.3	5.36	3.87
C. sordidus	167.7	5.04	4.37	220.3	5.53	4.54
S. psittacus	148.1	8.32	7.41	192.6	9.29	4.33

Table 3.4: Re-parameterized von Bertalanffy growth parameters for length-at-age 1 and length-at-age 3 for representative parrotfish species on outer shelf reefs with confidence intervals.

Species	**L_1 (FL mm)**	**CI +**	**CI -**	**L_3 (FL mm)**	**CI +**	**CI -**
C. microrhinos	183.6	9.18	4.59	348.1	4.64	1.61
C. bicolor	266.8	18.01	13.34	384.7	13.13	5.17
S. frenatus	190.7	4.77	2.13	221.4	5.54	1.27
S. niger	121.4	9.26	5.73	192.4	5.38	3.86
C. sordidus	162.1	3.63	8.10	184.9	7.29	1.26
S. psittacus	132.9	6.78	5.01	193.5	9.68	4.12

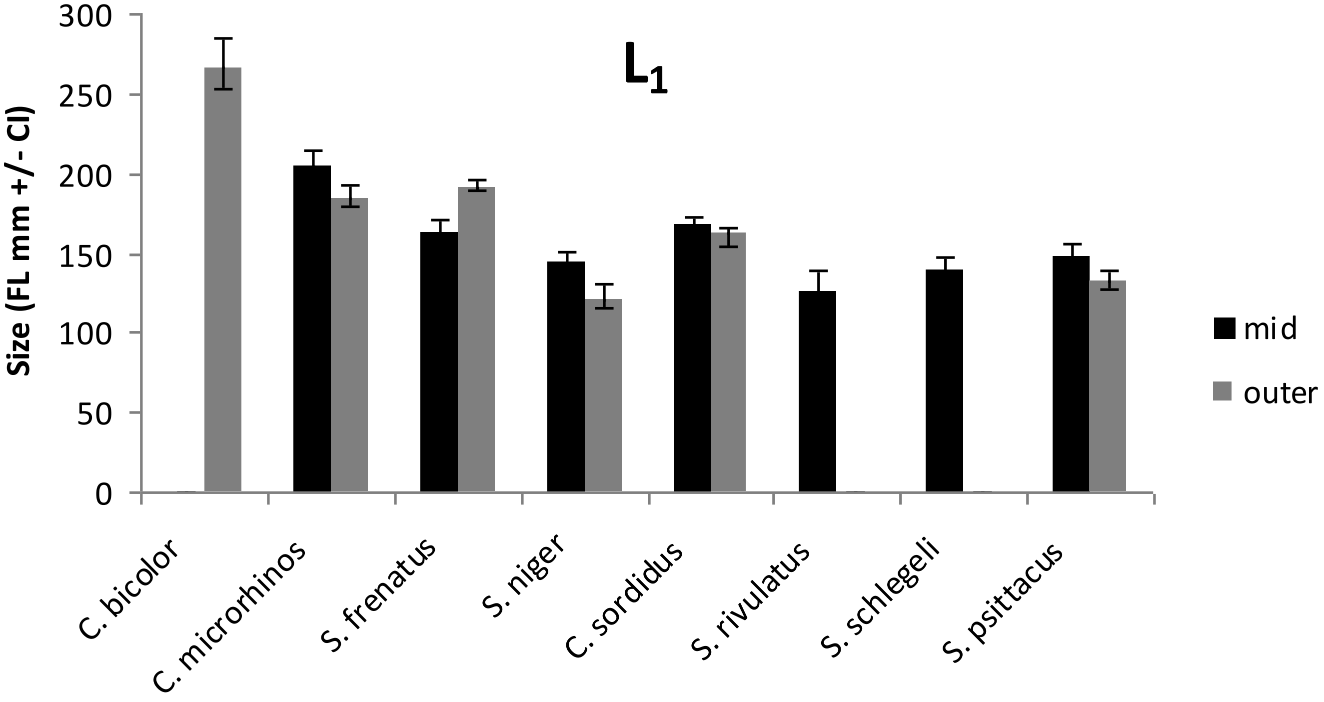


Fig. 3.6: Re-parameterized growth parameter (rVBGF) comparing length-at-age one (L_1) for parrotfish species between mid and outer shelf reefs on the GBR.

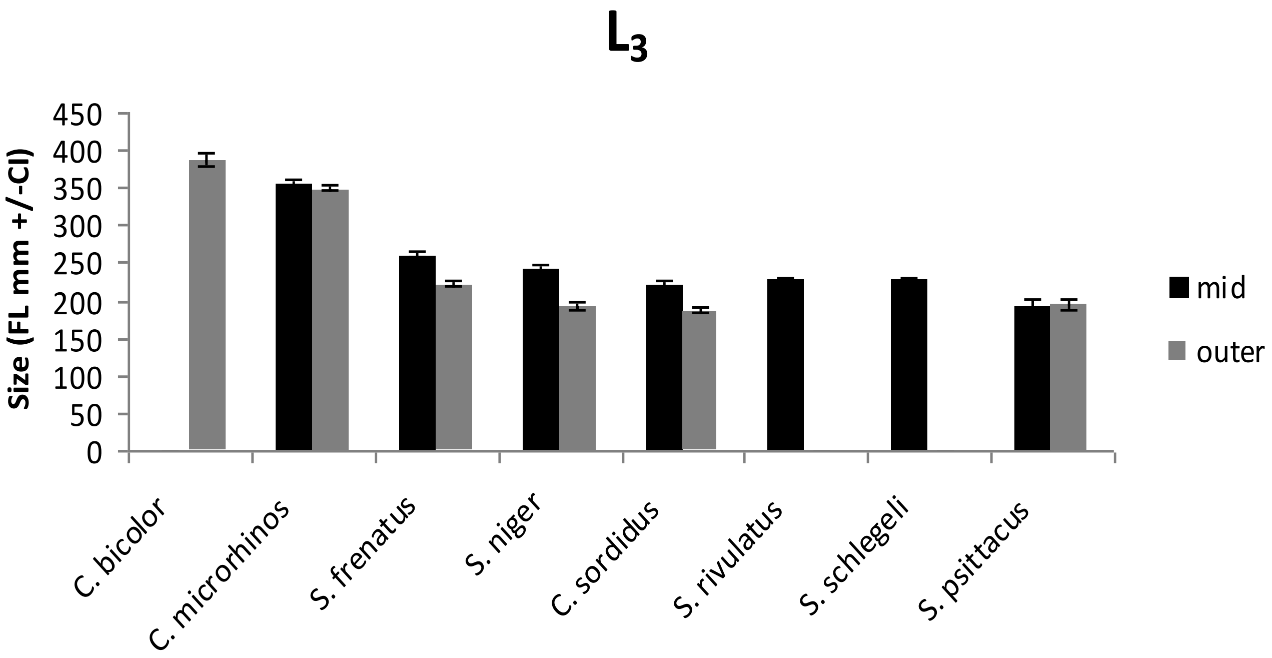


Fig. 3.7: Re-parameterized growth parameter (rVBGF) comparing length-at-age three (L_3) for parrotfish species between mid and outer shelf reefs on the GBR.

Age- and Size- at maturity

Age and size at maturity were calculated for parrotfish species from mid- and outer-shelf reefs (Table 3.5, 3.6 respectively). Variation in age at maturity occurred both between species and within each species (between habitats) (Fig. 3.8). The two larger species, *C. bicolor* and *C. microrhinos,* reached maturity at older ages compared to the other parrotfish species. *C. microrhinos*, *S. frenatus* and *C. sordidus* all matured at an older age on mid shelf reefs compared to outer shelf reef populations. *S. niger* demonstrated similar age at maturity for both populations, while *S. psittacus* populations on outer shelf reefs matured at a much older age compared to mid shelf populations. Difference in size at maturity occurred between each species examined (Table 3.5, Table 3.6). Larger parrotfish species, *C. microrhinos* and *C. bicolor*, matured when they reached a size of 345 mm while smaller parrotfish species, *S. psittacus* and *C. sordidus,* reached maturity at a size of 130 mm. Only small differences were observed in size at maturity between habitats (Fig. 3.9). All species showed a reduced size at maturity on outer-shelf reefs compared to mid shelf reefs.

Table 3.5: Results of female maturity of representative parrotfish species from mid shelf reef habitats on the GBR, with age- and size-at-50% maturity with confidence intervals (CI).

Female maturity						
Species	**Age at 50% Maturity (years)**	CI +	CI -	**Size at 50% Maturity (FL mm)**	CI +	CI -
C. microrhinos	6.0	0.36	0.30	378.4	37.84	18.92
S. frenatus	4.9	0.26	0.35	220.9	23.13	8.32
S. niger	1.9	0.09	0.16	166.3	18.39	11.38
S. schlegeli	1.6	0.26	0.08	214.2	10.71	16.30
S. rivulatus	1.5	0.17	0.16	185.5	18.55	9.28
C. sordidus	2.8	0.08	0.30	154.7	15.47	7.68
S. psittacus	0.9	0.06	0.12	129.5	6.47	12.71

Table 3.6: Results of female maturity of representative parrotfish species from outer shelf reef habitats on the GBR, with age- and size-at-50% maturity with confidence intervals (CI).

Female maturity						
Species	**Age at 50% Maturity (years)**	CI +	CI -	**Size at 50% Maturity (FL mm)**	CI +	CI -
C. microrhinos	4.6	0.59	0.25	365.4	36.86	11.50
C. bicolor	5.0	0.25	0.50	345.1	0	0
S. frenatus	2.9	0.15	0.22	189.2	18.92	11.41
S. niger	1.9	0.19	0.18	150.4	15.04	15.04
C. sordidus	0.8	0.08	0.08	140.3	3.58	14.03
S. psittacus	1.4	2.89E-15	-2.89E-15	121.5	0.05	0

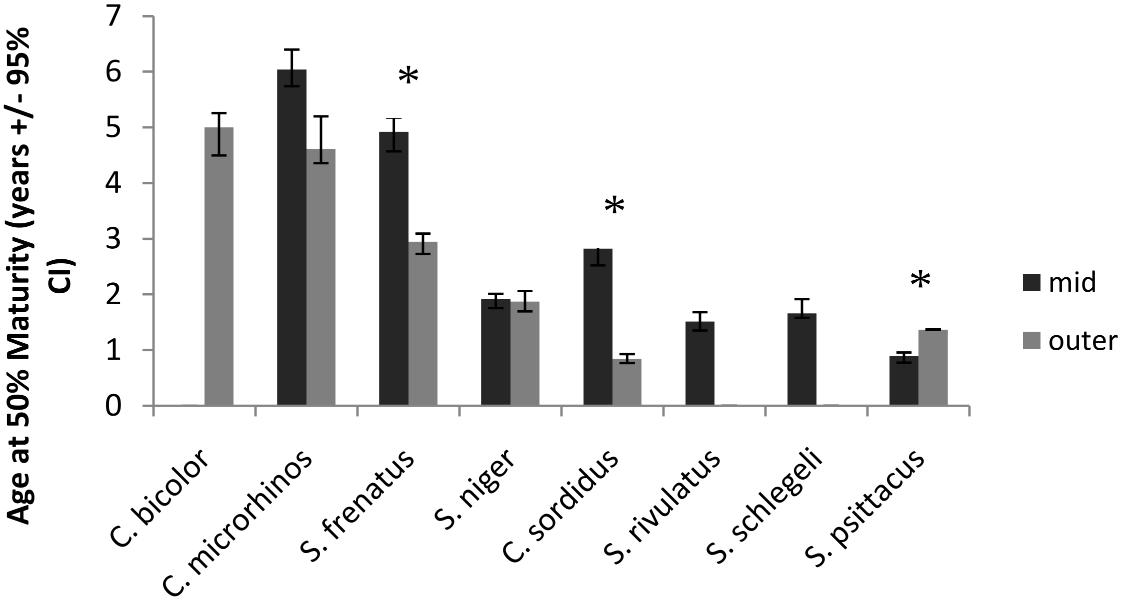


Fig. 3.8: Comparison of age at 50% maturity for parrotfish species between mid and outer shelf reefs on the GBR. (* represent considerable difference between mid and outer populations)

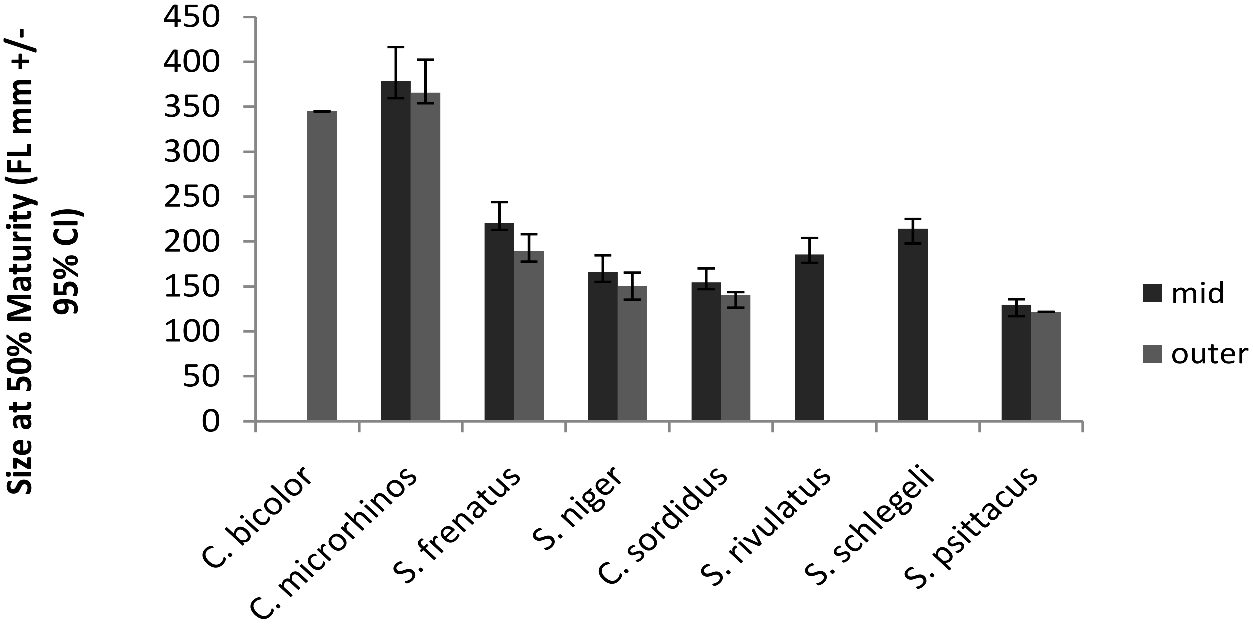


Fig. 3.9: Evaluates size at 50% maturity of representative parrotfish populations between mid and outer shelf reefs on the GBR.

Age- and Size- at sex change

Age and size at sex change of secondary males was estimated for a range of parrotfish species on both mid and outer shelf reefs (Table 3.7, 3.8 respectively). Variation in age at sex change occurred both between species and within each species (between habitats) (Fig. 3.10). *C. microrhinos*, *S. frenatus* and *C. sordidus* all changed sex at much older ages on mid reefs compared to outer reef populations. Age at sex change was similar for *S. niger* populations, where populations on mid shelf reefs changed sex at 2.9 years and 2.9 years on outer shelf reefs. *S. psittacus*, on the other hand, showed a reduced age at sex change on mid shelf reefs [2 yrs] compared to males from outer shelf reefs [2.9 yrs].

Size at sex change varied both between and within species (Fig. 3.11). *C. microrhinos* and *C. bicolor* change sex when they reach much larger sizes compared to *S. psittacus* and *C. sordidus*. *C. microrhinos* changed sex at 424.9 mm on mid-shelf reefs, but only 310.3 mm on outer shelf reefs. *S. niger* and *C. sordidus* also displayed significant differences in size at sex change between habitats, with individuals on mid shelf reef changing sex at a much larger size compared to those on outer shelf reefs. For *S. frenatus* and *S. psittacus*, individuals on mid shelf reefs changed sex at a slightly larger size compared to individuals on outer shelf reefs.

Table 3.7: Results of secondary male parrotfish populations from mid shelf reef habitats on the GBR, with age- and size-at-50% sex change with confidence intervals (CI).

Secondary males: timing of sex change						
Species	**Age at 50% sex change (years)**	CI +	CI -	**Size at 50% sex change (FL mm)**	CI +	CI -
C. microrhinos	5.9	0.59	0.39	424.9	27.80	21.24
S. frenatus	4.0	0.42	0.23	243.4	13.89	2.34
S. niger	2.9	0.23	0.28	280.2	14.01	28.02
S. schlegeli	3.1	0.09	0.00	244.6	14.26	1.93
S. rivulatus	3.3	0.33	0.05	247.3	18.30	12.37
C. sordidus	2.9	0.29	0.17	226.7	12.47	7.39
S. psittacus	2	0.2	0.18	179.6	35.93	6.87

Table 3.8: Results of secondary male parrotfish populations from outer shelf reef habitats on the GBR, with age- and size-at-50% sex change with confidence intervals (CI).

Secondary males: timing of sex change						
Species	**Age at 50% sex change (years)**	CI +	CI -	**Size at 50% sex change (FL mm)**	CI +	CI -
C. microrhinos	3.9	0.39	0.23	310.3	18.29	49.20
C. bicolor	3.5	0.26	0.44	371.7	18.58	37.17
S. frenatus	2.2	0.67	0.299	215.3	23.11	10.76
S. niger	2.9	0.59	0.15	201.5	18.54	3.04
C. sordidus	1.9	0.06	0.09	165.4	4.68	11.89
S. psittacus	2.9	0.26	0.3	162.0	10.67	13.23

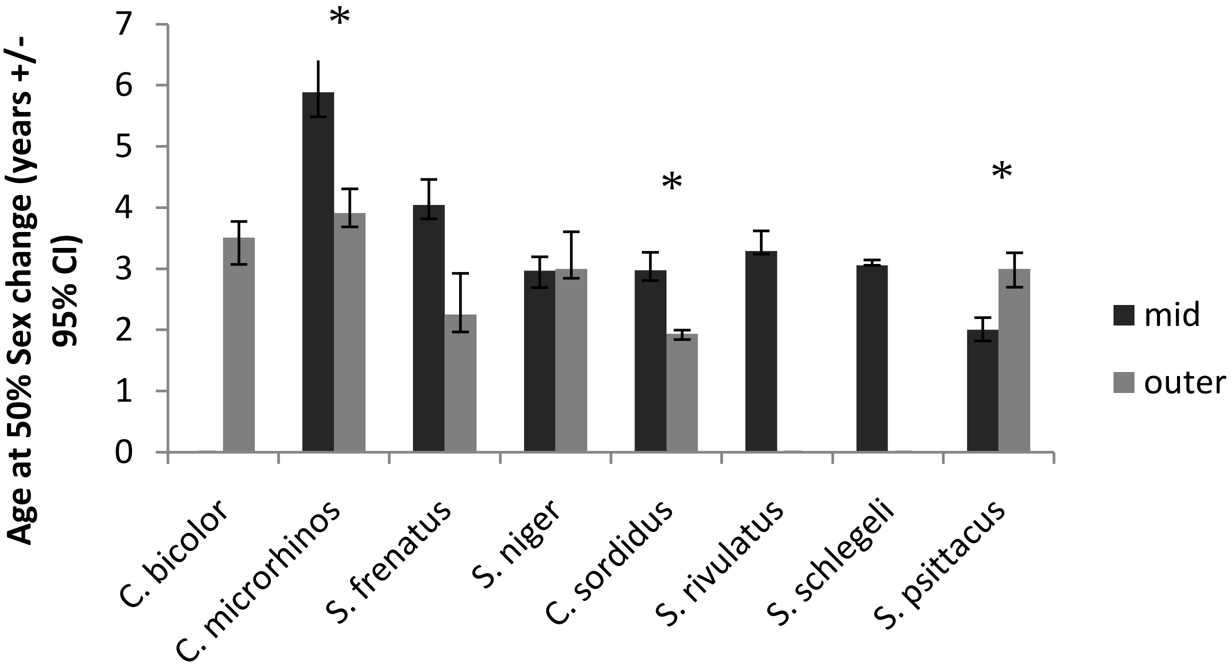


Fig. 3.10: Compares age-at-50% sex change of eight parrotfish species from both mid and outer shelf reefs on the GBR. (* represent considerable difference between mid and outer populations)

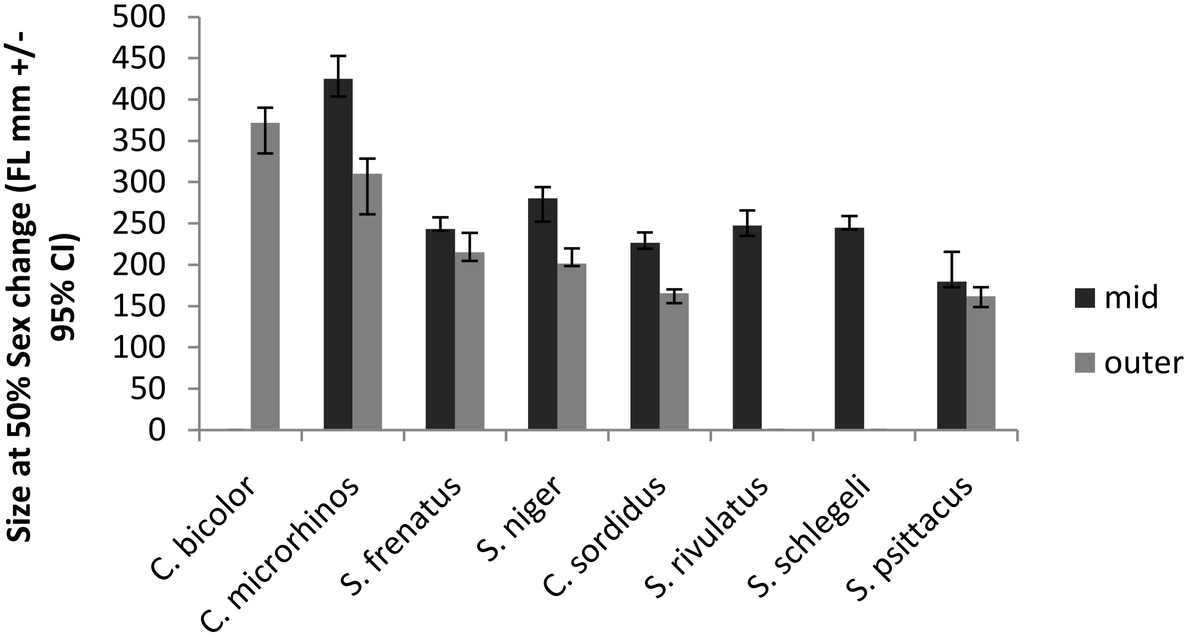


Fig. 3.11: Compares size-at-50% sex change of representative parrotfish species between two habitats on the GBR.

3.4 Discussion

Differences in growth patterns occur between phylogenetic groups that are associated with a long distinct evolutionary history. Differences in growth pattern within a single group, the parrotfish, showed that similar differences in growth can occur within a single evolutionary grouping the scarine labrids. While there are differences in growth between species of the parrotfish, this study uncovered differences in growth also occur within a species and revealed that evolutionary history was not the only determinant of growth patterns; habitat may also exert a strong effect.

Growth is commonly associated with lifespan, age at maturity and sex change (Roff 1984, Stearns & Koella 1986). Therefore, growth pattern and its potential consequences are important in understanding life history variation. This is particularly important for parrotfish because of their reproductive biology, age at maturity and sex reversal, as well as having primary and secondary males. The comparison between parrotfish species in this study revealed two growth patterns, indeterminate (*Chlorurus microrhinos*, *Chlorurus bicolor*, *Scarus psittacus*, *Scarus rivulatus* and *Scarus schlegeli*) and asymptotic growth (*Scarus frenatus*, *Scarus niger* and *Chlorurus sordidus*). Primary males were more abundant in species which displayed indeterminate growth, while few if any where observed in species with asymptotic growth. Moreover, species with asymptotic growth reached 50% maximum size faster than species with indeterminate growth when comparing the lifespan of populations.

Habitat was a significant correlate of the growth patterns for several parrotfish species, suggesting that growth reflects the habitat in which individuals will recruit into. For large individuals, in particular *C. microrhinos*, there were no differences in growth between mid or outer shelf reef. However, all small species demonstrated considerable differences in the growth between shelf positions, where populations from outer shelf reefs displayed a significantly reduced growth rate compared to populations from mid shelf reefs. A similar pattern of reduced growth on outer reefs have been reported by Gust et al. (2002)

and suggests that increased mortality (natural predation) on outer shelf reefs is the cause. Although differences in temperature, food availability and reproductive output were not examined in this study, they also have the potential to influence the observed patterns of parrotfish life history.

Impacts of habitat on the growth patterns of parrotfish species also correlated on both timing of maturation and sexual transformation. Reduced growth on outer shelf reefs by *Scarus frenatus* and *Chlorurus sordidus* was also associated with earlier maturation and sex change. Although *Chlorurus microrhinos* showed similar growth trajectories from mid and outer shelf reef populations, outer shelf populations changed sex from female to male about two years earlier compared to mid shelf populations. When comparing abundance information (dicussion with Howard Choat) of species studied, all revealed higher densities on outer reefs, which suggests that there are more benefits of being male on outer shelf reef environments compared to mid shelf reefs.

In conclusion, this study provided evidence of habitat influences on growth and other life history traits at a species level. Although this chapter only shows variation at a local scale, other variables, in particular broad scale and fishing pressure may also provide important information. Therefore, two species, *Chlorurus sordidus* and *Scarus psittacus*, were used to address in more detail other drivers on life history variation.

Chapter 4: Natural and anthropogenic effects on the life history patterns of *Chlorurus sordidus* at different geographic scales

4.1 Introduction

Reef fishes are widespread and occupy a wide range of habitats over their latitudinal and longitudinal range. Both habitat and geographic location are associated with different life history patterns, which usually co-vary (Roff 1992, Stearns 1992). Fishing, which changes the mortality schedule for many fishes, may also influence life history traits (Heino 1998). For example, fishing mortality generally removes larger, older individuals from the population, resulting in a shift in body size and age structure to smaller, younger individuals (Ricker 1981, Sinclair *et al*. 2002, Harvey *et al*. 2006, Walsh *et al*. 2006). Fishing may also alter growth and reduce age at maturity (Stokes *et al*. 1993, Heino & Godø 2002, Sinclair *et al*. 2002, Swain *et al.* 2007), however the effects of exploitation on these critical traits are poorly understood (Buxton 1993). Therefore, to understand the impacts of human disturbance on life histories of fishes, it is important to assess the impact of natural variation as well as those attributed to fishing. This can be done by comparing essential life histories across a set of geographically distinct locations exposed to fishing (Jennings & Polunin 1996, Choat *et al*. 2003, Hawkins & Roberts 2003, Dulvy *et al*. 2004, Williamson *et al.* 2004).

Important life history characteristics of a species are growth, life span, maturity, sexual composition and size structure. However, life histories of many reef fishes are poorly known and reliable data on growth and maturity are scarce (Choat *et al*. 1996, Sadovy

1996, Jennings *et al*. 1999). This study examined growth, longevity, age/size structure, maturation and sexual composition in populations of Indo Pacific. Differences in mortality schedules are likely to influence these essential traits across localities, where the source and magnitude will vary according to the environment.

Body size, growth and longevity can all be expected to vary at geographic, latitudinal and habitat scales (Choat & Robertson 2002), primarily because of differences in temperature, food availability and mortality. Across the Great Barrier Reef (hereafter GBR), higher levels of mortality on outer shelf reefs contribute to a prevelance of smaller sized individuals (Gust *et al*. 2001). This reduced body size caused significant changes in the growth curves and lead to an overall reduced asymptotic size (Gust *et al*. 2002). Outer shelf parrotfish also die earlier compared to individuals from mid shelf reefs (Gust *et al*. 2002). Differences in mortality may in turn, effect age schedules of growth and reproduction (Roff 1992, Stearns 1992, Heino 1998).

Reproductive parameters, especially age and size at maturity, may be strongly determined by environmental conditions (Heino & Kaitala 1999) and resource availability (Siems & Sikes 1998). However, reliable data on maturation for many Indo Pacific reef fishes is scarce (Robertson & Warner 1978, Choat *et al*. 1996, Sadovy 1996, Jennings *et al*. 1999). Timing of maturation is a highly variable trait, which presumably maximizes an individual’s reproductive success. Thus, differences in mortality may greatly influence reproductive fitness. Reduced adult survival should promote earlier maturation and increased reproductive effort in fishes (Reznick *et al*. 1990, Kozlowski 1992). Maturation is tightly correlated with growth and trade-offs are commonly observed between the two. For example, energy allocation towards reproduction will decrease growth rate and future fecundity (Reznick 1983), but also cause maturation to occur at smaller sizes as well as younger ages.

Sex change is a common and important reproductive parameter for reef fishes (Sadovy & Liu 2008). Like all life history traits, sex change may vary within and across populations (Munday *et al*. 2006), which allows individuals to optimize reproductive output in variable environmental conditions (Angilletta 2009). Most parrotfish species are sequential hermaphrodites (sex change) and exhibit protogynous (female-to-male) sex reversal (Choat & Robertson 1975). Identification of sexual ontogeny of scarids has proven to be complex. This is primarily because the presence of two male development pathways (Choat & Robertson 1975). Some males may develop directly from juvenile gonads (primary males), while other males are a result of sex reversal of functional females (secondary males) (Shapiro & Rasotto 1993, Munday *et al*. 2006). Male development depends on the social system of the assemblage, which can be strongly influenced by local density. Differences in mortality rates are predicted to influence the timing of sex reversal (Sadovy & Shapiro 1987, Clifton & Rogers 2008). Increased mortality is likely to shift sex reversal to younger ages and smaller sizes (Gust 2004, Clifton & Rogers 2009). This may be further complicated by the presence of fishing (Hawkins & Roberts 2004).

The use of otoliths and gonads are valuable tools for understanding the variations in life histories of reef fishes (Ferreira & Russ 1994, Choat & Axe 1996, Hart & Russ 1996, Sadovy & Shapiro 1987, Pears *et al*. 2006). Information derived from otoliths and gonads is essential to determine growth rates, life spans and reproductive parameters of reef fishes, and allow the comparisons between species/populations and localities. For this study, otoliths and gonads were used to estimate growth, survivorship and maturation of the scarid, *Chlorurus sordidus,* between two demographically distinct locations, the Great Barrier Reef (hereafter GBR) and Guam in order to analyze three objectives:

1) To compare populations of the same species with different habitat requirements.
2) To compare populations of the same species between two locations, Guam and the GBR, to identify any biogeographic effects.
3) To determine to what extent fishing effects influence species life history variation.

Chlorurus sordidus (Forsskål, 1775), the Bullethead parrotfish is dichromatic, with different discontinuous phases (males and females display different color phases): initial and terminal. Individuals in the initial phase (“drab” phase) are characterized as having a dark brown body with red around the mouth. Larger individuals generally represent the terminal phase (“gaudy” phase) and are characterized by a blue-green body with pinkish scale edges and a bright yellow area on the body. *Chlorurus sordidus* grows up to 40 cm in length (FL) and is commonly distributed on reefs of the Indo-Pacific (Jennings *et al*. 1995, Gust *et al*. 2002). This fish is not currently harvested on the GBR, however they are important targets of reef fisheries in Asia and other parts of the Pacific (Jennings *et al*. 1995, Russ & Alcala 1998).

4.2 Methods

Study Area

A total of 291 individuals of *C. sordidus* were collected from Guam, located in the tropical Western Pacific (13°28’N, 144 °45’E) (Fig. 4.1), with 102 individuals taken from marine reserves (51 from Tumon Bay Reserve and 51 from Achang Reserve) and 189 individuals represented samples from fished areas. Fish were collected in Guam from September 2007 to October 2008. It was made sure that the samples taken represented the size structure at each site. This usually entailed extra effort at the fished sites, as larger fish were harder to spear. However, despite the heavy fishing pressure this is an abundant fish, so while the larger fish were somewhat more difficult it was possible to sample them. A total of 507 individuals of *C. sorididus* were sampled from reefs on the northern GBR (14º4’S, 145º3’E) from both mid and outer shelf reef positions. Fish were collected from Lizard Island between December 1996 to February 1997 (expansion of Gust 2001) (see Fig. 2.1b). It is important to note that while samples were taken almost a decade apart and that the time variation could have the potential to confound the comparison, continued monitoring of the GBR has proved little to no change in the environment between the times the samples were collected. This allowed me to focus entirely on spatial variation.

Fish were collected by hand spearing from each location. Each individual’s fork length (FL), standard length (SL), total weight (TW), and gutted weight (GW) were measured and recorded to the nearest millimeter and gram, respectively. Sagittal otoliths were removed, cleaned, washed in ethanol, and stored to dry before ageing. Whole gonads were removed and placed in FAAC, a formalin-based fixative (4% formaldehyde, 5% glacial acetic acid, 1.3% calcium chloride dehydrate) before histological investigation of reproductive status. Gonads were also measured to the nearest millimeter.

Gonadosomatic indices (GSI) were calculated for each individual as the female's percent gonad contribution to total body weight (Beverton 1992):

$$\text{GSI}= \frac{\text{Female ovary weight}}{\text{Total body weight}} \times 100$$

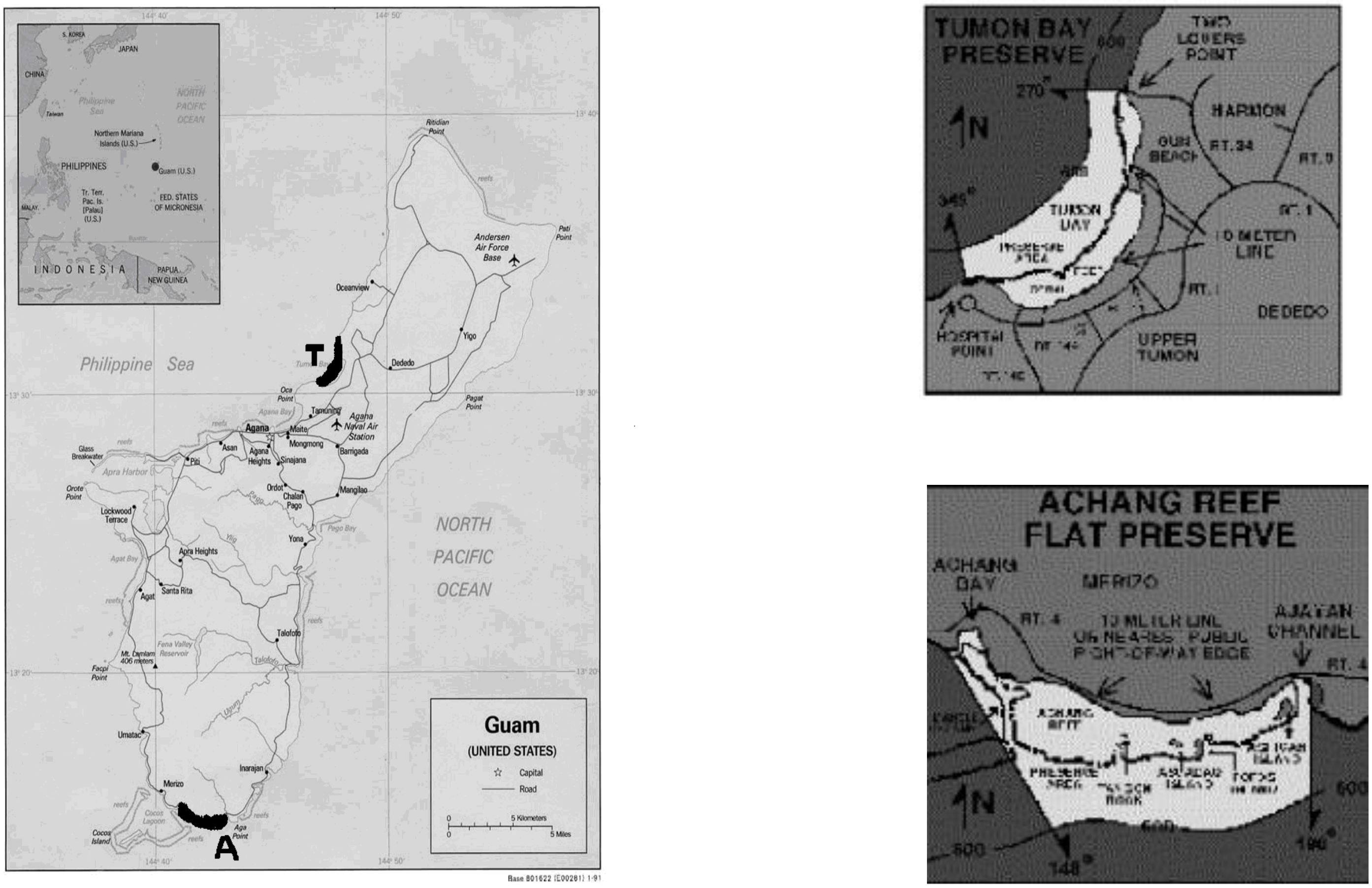


Fig. 4.1: Map showing sampling locations of *Clorurus sordidus* in Guam (where T represents Tumon Bay Reserve and A represents Achang Reserve), with detailed maps of sampling sites at two marine preserves, Tumon Bay and Achang, repsectively.

Age determination

Annual ageing was achieved using sagittal ototliths. Each ototlith was examined and read at least twice for verification of incremental bands representing annuli. Putative anual increments were used to estimate age. Ageing process followed the techniques described in Choat *et al* (1996). See Chapter 2 for further details of otolith ageing.

Modelling of growth

Growth of *C. sordidus* was estimated for all populations sampled by examination of the relationship between size (Fork Length, FL) and age. Size-at-age data were fitted by using both the von Bertalanffy Growth Function (VBGF) and Francis's (1988) re-parameterized equation of the von Bertalanffy Growth Function (rVBGF). The rVBGF parameters estimated for *C. sordidus* were $L(1)$ and $L(5)$, generating estimates of mean body size-at-ages one and five years. For further details of growth modeling refer to Chapter 2.

Estimates of longevity and adult body size

Mean maximum age T_{max} (longevity) and mean maximum body size L_{max} (adult body size) were calculated for each *C. sordidus* population of the 20% oldest and largest individuals. One way Analysis of Variance (ANOVA) were then used to determine locality differences in mean age and size of both female and male *C. sordidus*. The model tested the effects of location (a fixed effect), using mean age/size as replicates in this broad scale analysis. Prior to the ANOVA calculations, the assumption of homogeneity of variances was examined using box plots of residuals and log10 (X+1) transformations were used to remove heterogeneity of variances as required.

Age- and size-at maturity

Gonad histology was performed for *C. sordidus*. Following the histological processing described in Chapter 2. Sexual identity was assessed based on the criteria developed in Chapter 2. Age- and size-at-maturity were estimated by calculating the age and size at which 50% of females were mature (proportion of mature females relative to the total number of females within each age or size class) (Williams *et al*. 2008). The logistic function used for estimating age- and size-at-maturity is described in Chapter 2. 95% confidence intervals (CI) were also estimated for each parameter value of age-at-maturity (*T50*) and size-at-maturity (*L50*) using a bootstrapping procedure (Moore *et al*. 2007), also described in Chapter 2.

Age- and size-at sex change

A logistic regression approach was used to estimate age and size at which 50% of sex changing females undergo sex reversal (Williams *et al*. 2008). The logistic function used for calculating age- and size-at-maturity was:

$$P_a = \left[1 + e^{[-\ln(19)(a - a_{50}) / (a_{95} - a_{50})]} \right]^{-x}$$

Where P_a is the proportion of sex changing females in age or size class a, x is the observed frequency of males within each age or size class, a_{50} is the age or size at which

50% of sex changing females have changed sex, and a_{95} is the age or size at which 95% of sex changing females have changed sex. Parameters evaluated for this study were age-at-50% sex change T_{50}, age-at-95% sex change T_{95}, size-at-50% sex change L_{50}, and size-at-95% sex change L_{95}. Age classes were based on one year increments and size classes were based on 50mm increments. For each of the above parameters, 95% confidence intervals (CI) were estimated using a bootstrapping procedure, where the data was randomly re-sampled 1000 times with replication (Moore *et al*. 2007).

Analysis

A Principle Component Analysis (PCA) was performed in this study to explore the variation in life history traits across locations, Guam and the GBR, sampled. Variables were categorized according to the type of information provided. Six information categories were identified: (i) longevity (mean T_{max}), (ii) growth rate (Linf), (iii) primary males (as a percentage of the population), (iv) age at maturity (T_{mat}), (v) age at sex change ($T_{sex\ change}$) and the (vi) percentage of life span as individual reached at 50% L_{inf}. Variables were checked for the presence of skewed distributions across locations using pair-wise correlation plots (Draftsman plots), but no transformations of the life history variables were required.

4.3 Results

Variation in life history traits

PCA ordination of populations sample between Guam and the GBR confirmed the presence of differences in life history (growth rate, longevity, age at maturity and sex change, primary males and percentage of life span at 50% growth) across locations within

Chlorurus sordidus (Fig. 4.2, but see Appendix Fig. 2). Locations showed some spread, with all three Guam localities separating from the two GBR sites. PC1 and PC2 together captured 95.3% of the variation in life histories of *C. sordidus*. However, PC1 was the primary contributor to explaining the variation across locations (60.4%; Table 4.1)

Table 4.1: Results of Principle Component Analysis of life history variables of *Chlorurus sordidus* between Guam and the GBR: (A) Eigenvalues of variables included in the ordination, and (B) PC scores of locations sampled.

A.

Chlorurus sordidus		
Variable	PC1 (60.40%)	PC2 (34.90%)
Linf	-0.431	-0.374
% life span at 50% Linf	-0.031	-0.684
Mean T max	-0.476	-0.289
T mat	-0.501	0.057
T sex change	-0.46	0.262
% primary male	0.351	-0.486

B.

Chlorurus sordidus		
Location	Score 1	Score 2
Fished, Guam	0.451	-0.46
Tumon Bay Reserve, Guam	-0.431	-0.418
Achang Reserve, Guam	0.493	-1.94
Mid shelf, GBR	-2.88	1.08
Outer shelf, GBR	2.36	1.74

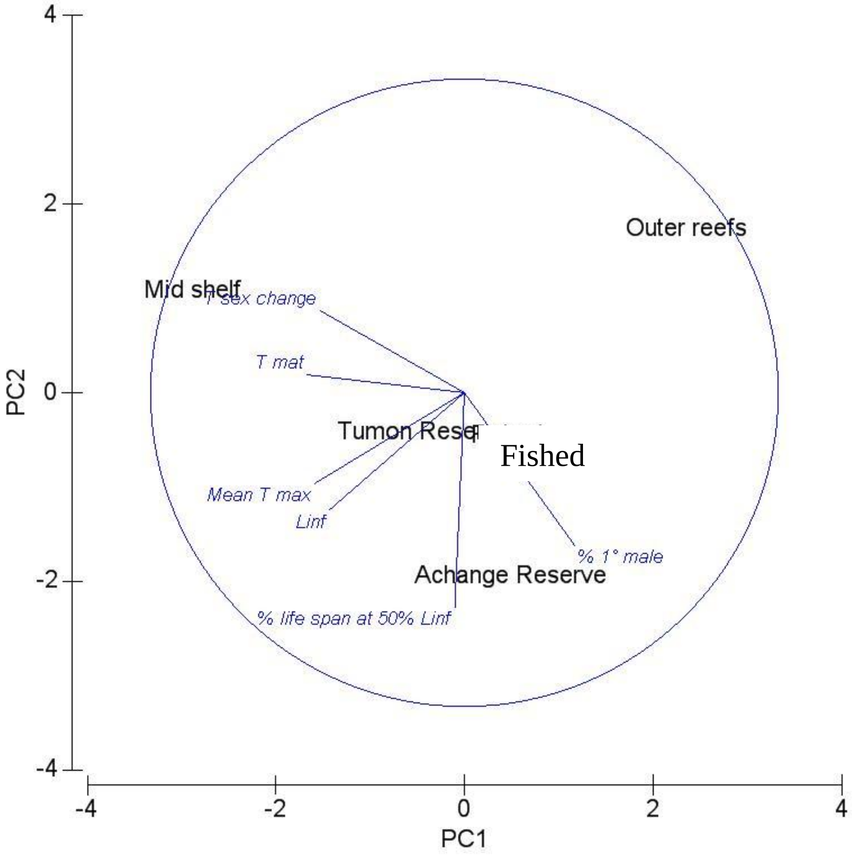


Fig. 4.2: Ordination of life history parameters of populations of *Chlorurus sordidus* from mid and outer reefs (GBR) and fished and reserve areas (Guam) showing the direction (eigenvectors) and contribution (relative length of eigenvectors) of the life history variables. Tmax: maximum age; mean Tmax: 20% longevity; Tmat: age at maturity; Tsex change: age at sex change; Lmax: maximum length; Linf: growth curve; % life span at 50% Linf; % of primary males in the population.

Comparisons of longevity, body size and growth

Mean age and length of *C. sordidus* populations sampled from the GBR and Guam varied for both males and females (Table 4.2, see Appendix for figures). Outer shelf reefs represented the lowest mean aged females (1.8 years), while Achang reserve had the highest mean aged females (3.5 years). Mean ages for males varied between a minimum of 3.2 years on outer shelf reefs from the GBR to 4.5 years on mid shelf reefs from the GBR. Mean body size also showed variation for both males and females across locations. For both males and females, outer reefs represented the smallest mean sizes of 189. 2 and 156.2 mm respectively, while mid shelf reefs on the GBR had the largest mean sizes of 243.9 and 197.4 mm respectively. Results from the one-way ANOVA revealed that both mean age and length for males and females were significantly different between each location sampled (Table 4.3).

Table 4.2: Mean ages (in years) for female and male *C. sordidus* from locations in Guam and the GBR.

Habitat	**Mean age females (years)**	**Mean age males (years)**	**Mean length females (FL mm)**	**Mean length males (FL mm)**
Achang Reserve	3.5	3.5	180.5	218.4
Tumon Bay Reserve	3.2	3.7	190	227.4
Fished Areas	3.1	3.8	182.7	222.3
Mid shelf, GBR	3.1	4.5	197.4	243.9
Outer shelf, GBR	1.9	3.3	156.2	189.2

Table 4.3: One-way ANOVA results comparing mean age and mean length of male and female *C. sordidus* populations from Guam and the GBR. (* P<0.05: **P<0.01: ***P<0.0001)

Sex	Dependent variable	Source of variation	DF	MS	F	p
Male	Size (FL mm)	Location	4	31426	71.03	0.0000***
		Residual	284	442		
Female		Location	4	24035	58.98	0.0000***
		Residual	371	407		
Male	Age (years)	Location	4	14.406	6.187	0.00008***
		Residual	284	2.329		
Female		Location	4	36.583	13.4248	0.0000***
		Residual	371	2.725		

The maximum recorded age for *C. sordidus* from each location was 9 years. The mean longevity for the oldest female *C. sordidus* individuals sampled varied between 4.2 years from outer shelf reefs (GBR) and 7.2 years on mid shelf reefs (GBR) (Table 4.4). For males, mean maximum longevity on the mid-shelf reefs (GBR) was 7.8, which was around one and a half years older than males from Achang and Tumon Bay reserve. The smallest calculated mean maximum length for female individuals was from outer shelf reefs, while the largest calculated lengths were from mid-shelf reefs (Table 4.4). Mean maximum length for male individuals also varied with the minimum mean max length of 220.6 mm (outer-shelf reefs) to 285 mm from mid shelf reefs. Results from the one-way ANOVA revealed that both mean maximum age and length for males and females were significantly different between each location sampled (Table 4.5).

Table 4.4: Comparison of calculated longevity for female and male *C. sordidus* from Guam and the GBR.

Habitat	**Mean max age females (years)**	**Mean max age males (years)**	**Mean max length females (FL mm)**	**Mean max length males (FL mm)**
Achang Reserve	6.7	6	196.3	244
Tumon Bay Reserve	6.7	6	216.3	253.7
Fished Areas	6.5	6.4	220	253.8
Mid shelf, GBR	7.2	7.8	230.9	285
Outer shelf, GBR	4.2	6.4	172.8	220.6

Table 4.5: One-way ANOVA results comparing mean maximum age and mean maximum length of oldest male and female *C. sordidus* individuals from populations in Guam and the GBR. (* P<0.05: **P<0.01: ***P<0.0001)

Sex	**Dependent variable**	**Source of variation**	**DF**	**MS**	**F**	**p**
Male	Maximum Length (FL mm)	Location	4	3936	106.97	0.000000***
		Residual	23	37		
Female		Location	4	5109	57.05	0.000000***
		Residual	32	90		
Male	Maximum Longevity (years)	Location	4	2.4851	4.425	0.008**
		Residual	23	0.5616		
Female		Location	4	13.930	11.3563	0.000008***
		Residual	32	1.227		

Chlorurus sordidus demonstrated asymptotic growth at each sampled site (refer to Appendix Fig. 3). When comparing the growth parameters of *C. sordidus,* individuals from the outer shelf population on the GBR displayed the lowest $L\infty$ of 189.6 mm, therefore they achieve a smaller asymptotic size compared to other populations (Table 4.6). Outer shelf reefs also demonstrated the highest k value of 1.47, which indicated they converge on their asymptotic size more rapidly compared to other populations (Table 4.6). Although it is important to note this does not necessarily mean they grow more rapidly. Female and male *C. sordidus* demonstrated similar initial growth, while males reached a larger asymptotic size at each sampled site (Fig. 4.3). Furthermore, non-overlapping confidence interval plots confirmed growth of females and males to be significantly different between mid shelf, outer shelf and Guam locations (Fig. 4.4); although for both females and males similar patterns in growth was observed for reserve and fished areas in Guam.

Length-at-age data from rVBGF varied across each location (Fig. 4.5). Analysis from re-parameterized von Bertalanffy growth function (rVBGF) revealed length at age 1 (L_1) was the lowest at Achang Reserve (137.9 mm, 17.39 +CI, 13.82- CI), compared to GBR mid shelf reefs with the highest L_1 of 165.9 mm (+5.65, - 8.32) (Table 4.7). GBR mid shelf reefs also had the highest L_5 calculated at 230.9 mm (+10.40, -4.9), while GBR outer shelf reefs displayed the lowest length-at-age 5 (Table 4.7).

Table 4.6: von Bertalanffy growth parameters for *C. sordidus* from locations in Guam and the GBR.

Location	**Growth function (L_∞)**	**Growth function (k)**
Achang Reserve	219.1	0.9
Tumon Reserve	223.2	0.94
Fished Areas	217.2	0.89
Midshelf-GBR	229.5	1.14
Outershelf-GBR	189.6	1.47

Table 4.7: Re-parameterized von Bertalanffy growth parameters for *C. sordidus* with Confidence Intervals.

Location	**L_1 (FL mm)**	CI +	CI -	**L_5 (FL mm)**	CI +	CI -
GBR mid shelf	165.9	5.65	8.32	230.9	10.40	4.90
GBR outer shelf	156.8	4.04	7.84	188.0	9.40	3.28
Achang Reserve	137.9	17.39	13.82	216.7	23.58	2.81
Tumon Bay Reserve	145.9	15.91	14.59	221.5	19.59	12.87
Guam fished areas	138.2	13.82	8.68	215.4	10.78	8.13

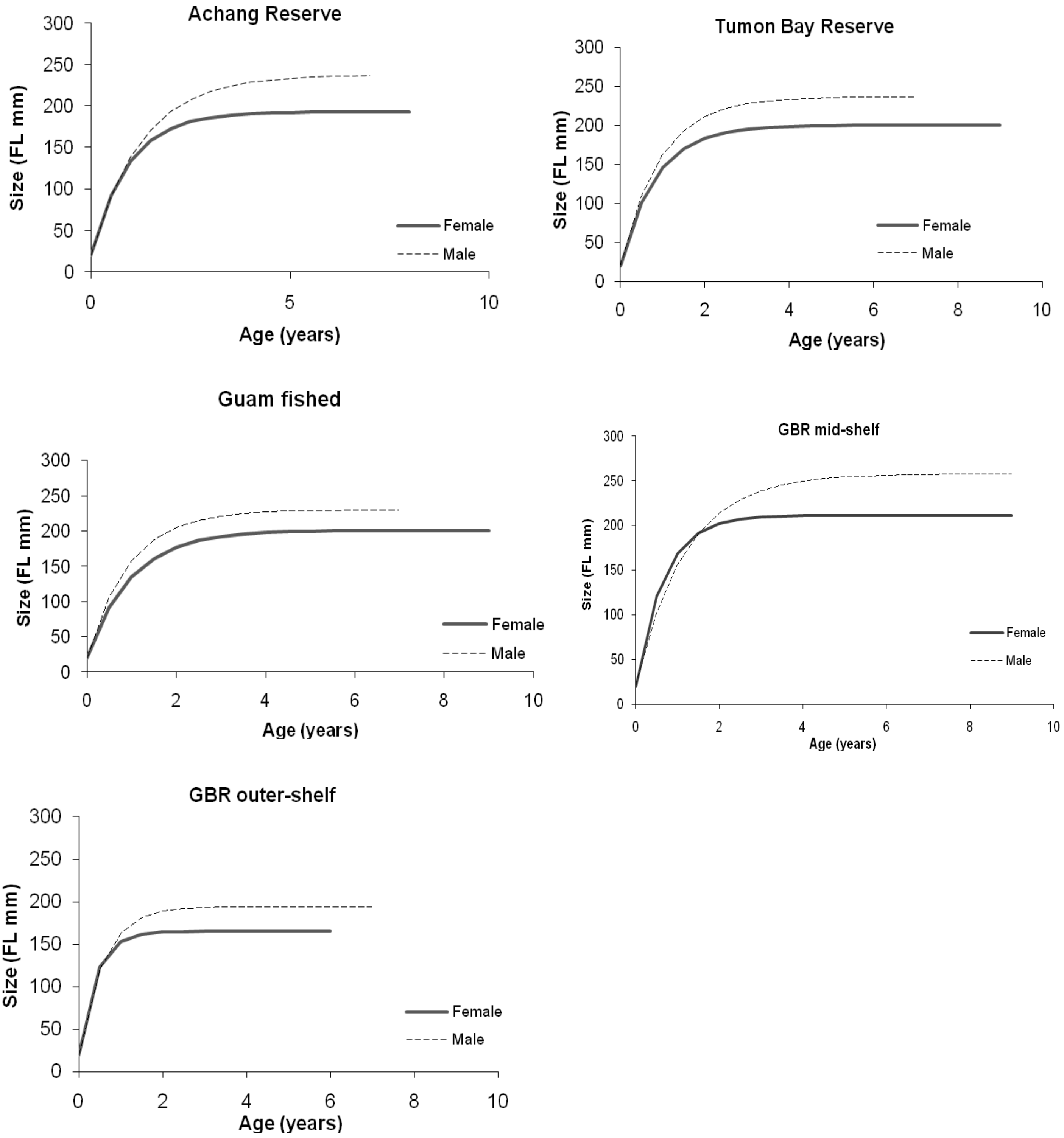


Fig. 4.3: Comparison between female and male *C. sordidus* von Bertalaffy growth curves of populations from Guam and the GBR.

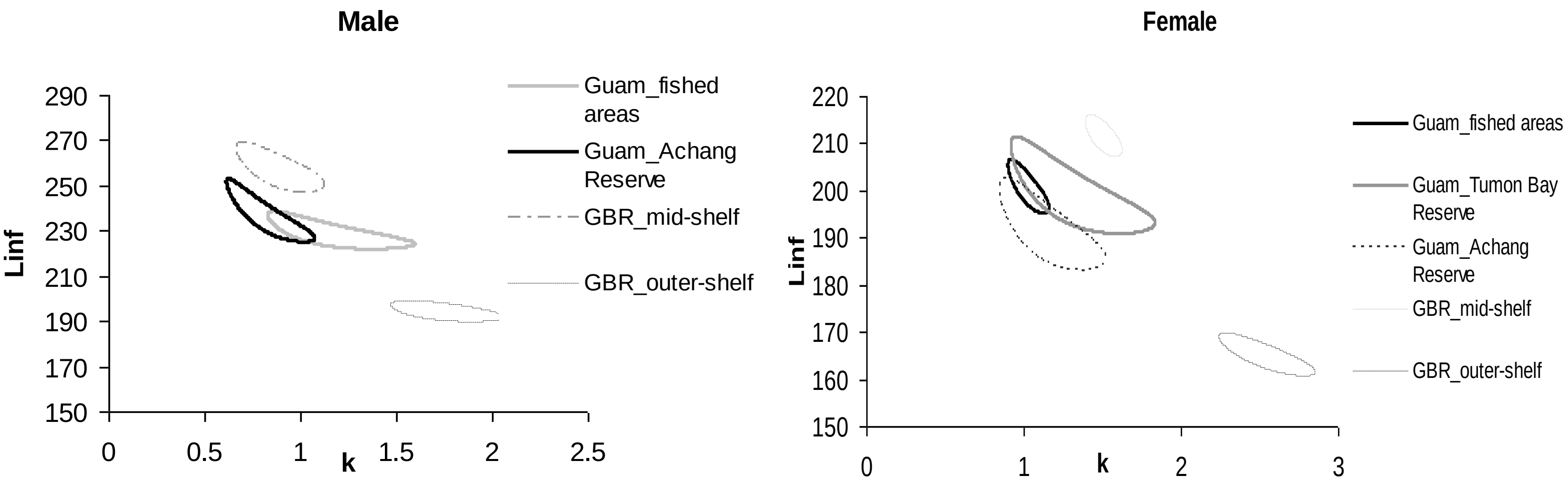


Fig. 4.4: Comparison of 95% confidence interval plots of *C. sordidus* male and female populations from Guam and the GBR.

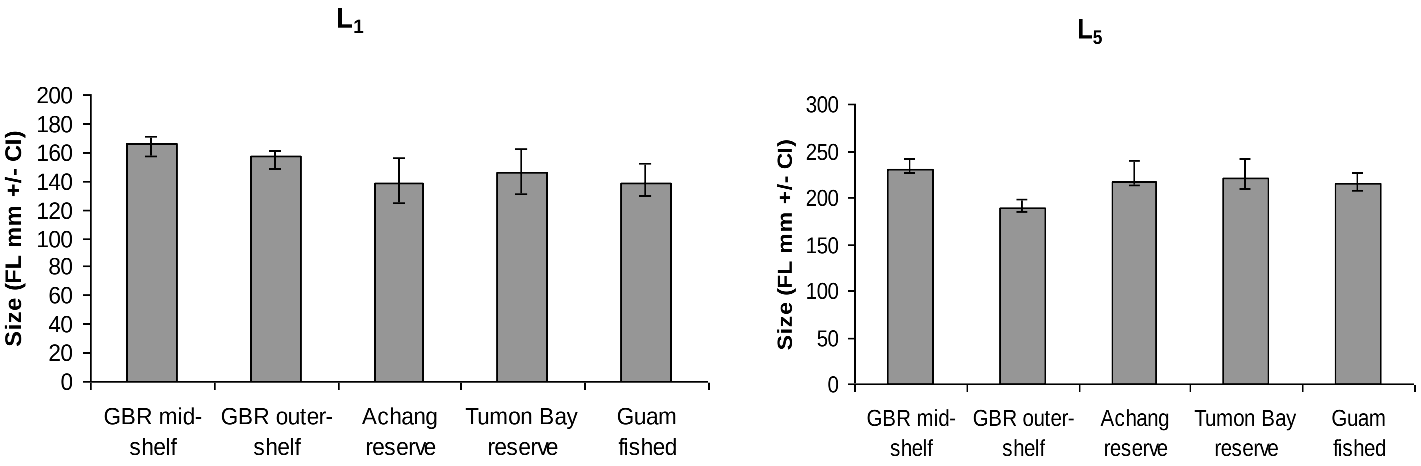


Fig. 4.5: rVBGF parameters L_1 and L_5 (+/- 95% confidence intervals) for each *C. sordidus* population in Guam and the GBR.

Comparisons of gonads

Maturation of *C. sordidus* on outer shelf reefs (GBR) and fished areas (Guam) occurred at smaller sizes than on mid shelf reefs (GBR) and marine reserves (Guam) (Fig. 4.6, 4.7). Plots of gonad somatic indices (GSI) confirmed mature females had reduced fork lengths on outer reefs on the GBR (106 mm) and fished areas (138 mm). The GSI also revealed fifty percent maturation levels were achieved once mature female individuals exceeded 160 mm on the mid shelf reefs (GBR), Achang Reserve, Tumon Bay Reserve and fished areas (Guam); while fifty percent maturation levels were reached once individuals from outer-shelf reefs surpassed 115 mm (Fig. 4.6, 4.7).

Mature female *C. sordidus* gonads from individuals collected on the mid shelf and Tumon Bay Reserve were considerably larger on average (by a factor of three) compared to those collected from outer shelf reefs (Fig. 4.8). Because females from mid shelf reefs and Tumon Bay Reserve developed larger gonads, relatively more energy was invested in reproductive tissue compared to females from other locations. Tumon Bay Reserve also displayed the highest mean gonad somatic index (2.28 +/- 0.46), followed by mid shelf reefs (1.72 +/- 0.113), fished areas (1.32 +/- 0.05), and Achang Reserve (1.19 +/- 0.08); while female individuals from the outer reef population demonstrated the lowest mean gonad somatic index (1.16 +/- 0.04) (Fig. 4.8).

Analysis of gonad weight plots of both female and male gonads revealed that males from Guam fished areas and GBR outer shelf reefs had considerably larger gonads at a younger age compared to reserve areas in Guam and GBR mid shelf reefs (Fig. 4.9).

Plotting of ovary weight onto the relationship between age and body size demonstrated older and larger mature females were relatively more fecund (greater reproductive output) compared to mature females with smaller ovaries (Fig. 4.9).

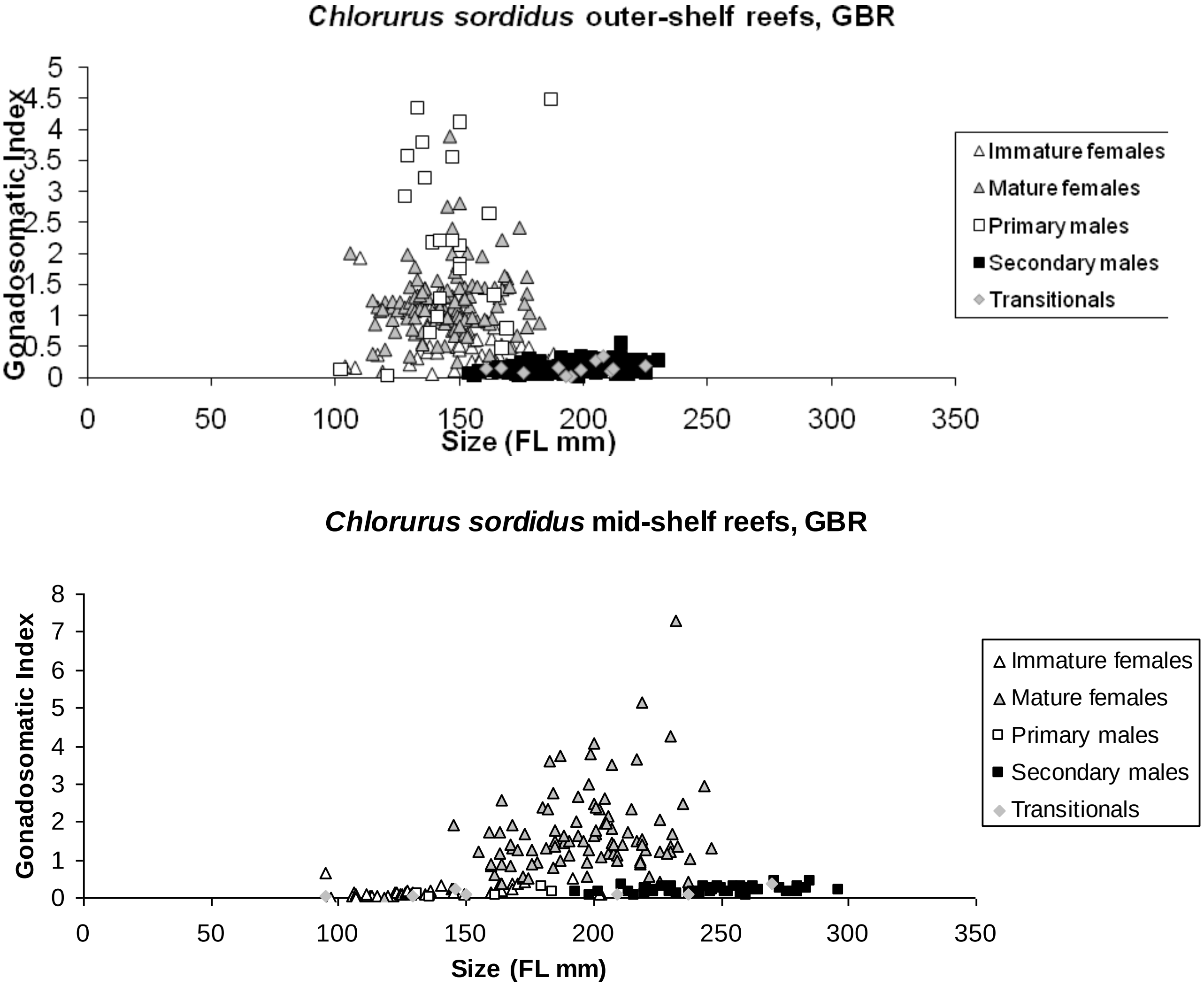
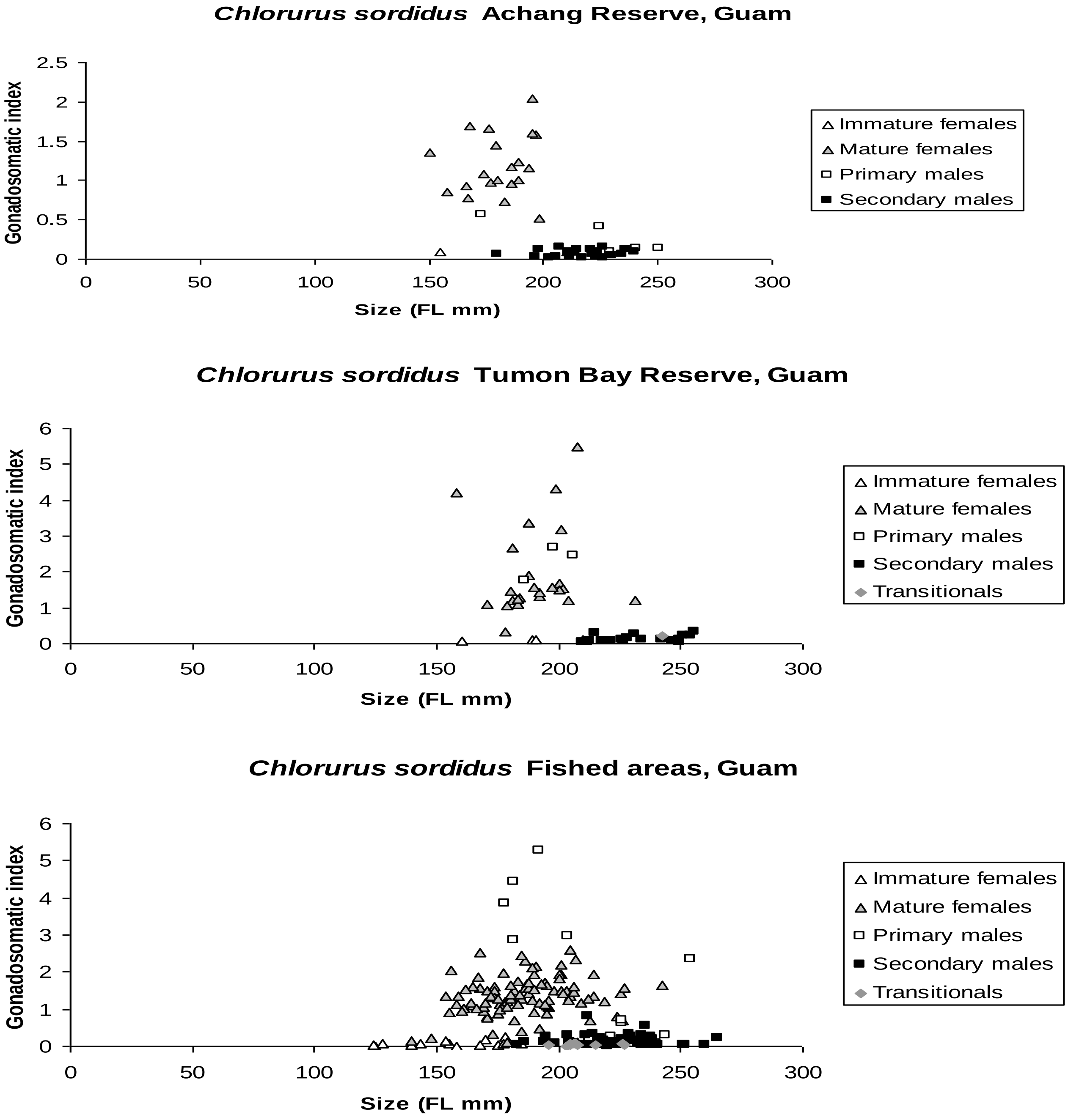


Fig. 4.6: Gonadosomatic index versus fork lengths for the major sexual categories identified by histology for *C. sordidus* population from mid- and outer-shelf reefs, GBR.


Chlorurus sordidus Achang Reserve, Guam

Chlorurus sordidus Tumon Bay Reserve, Guam

Chlorurus sordidus Fished areas, Guam

Fig. 4.7: Gonadosomatic indices versus fork lengths for the major sexual categories indentified by histology for *C. sordidus* populations in Guam.

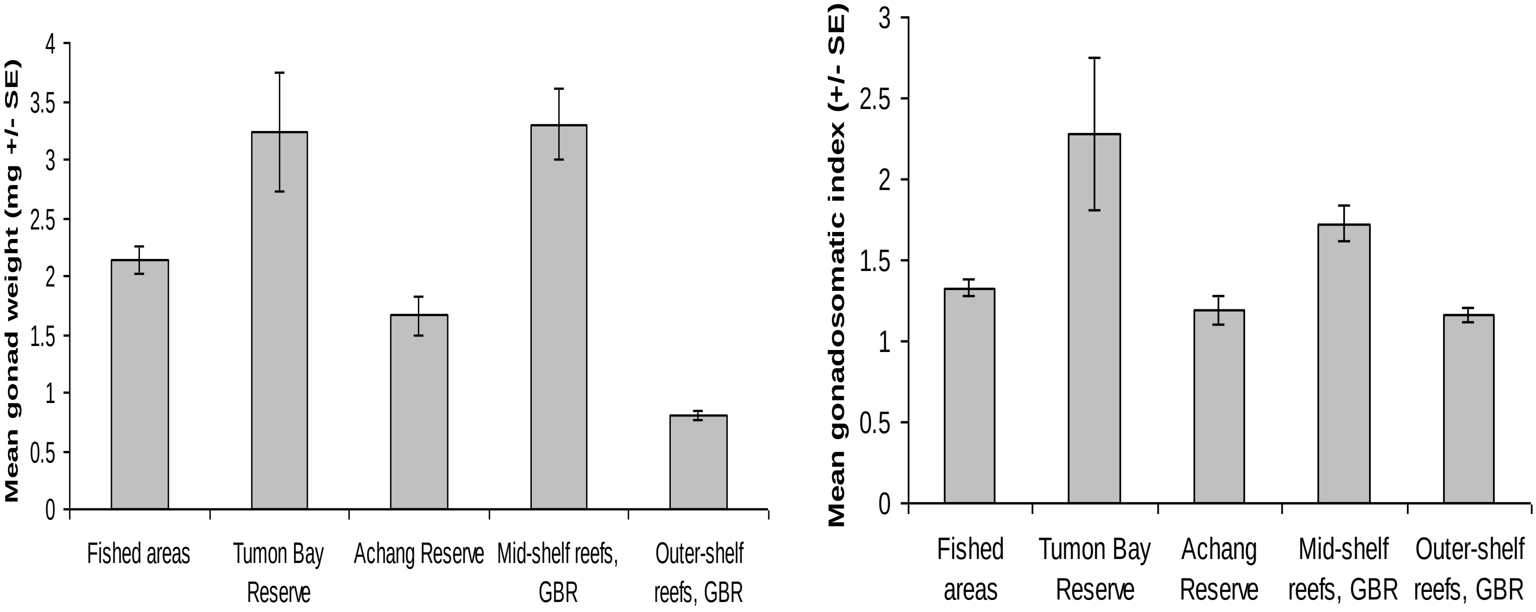


Fig. 4.8: Mature female mean gonad weights (mg +/- SE) and mean gonad somatic indices (+/- SE) for *C.sordidus* populations from both Guam and GBR sample locations.

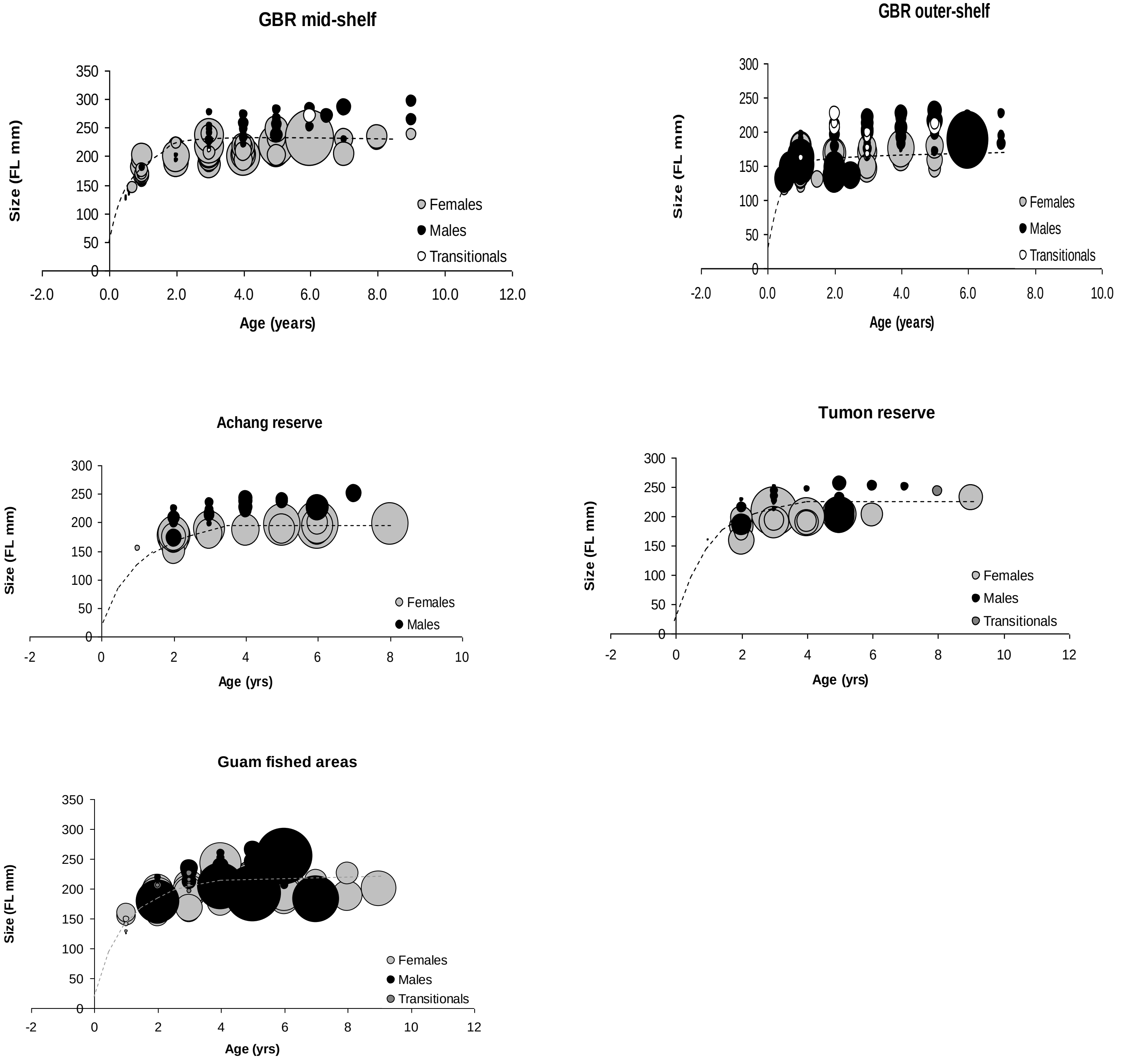


Fig. 4.9: Size-at-age of female and male *C. sordidus* showing relative ovary and testis weight (circle size) as a measure of reproductive output in Guam and the GBR. Growth curves (von Bertalanffy Growth Function; VBGF) is shown and represented by dashed lines.

Comparisons of maturity and sex change

Age and size at 50% maturity were estimated for female *C. sordidus* from populations in Guam and the GBR (Table 4.8). Both mid and outer shelf females reached 50% maturity at younger ages compared to all locations in Guam (Fig. 4.10). Tumon Bay reserve had the oldest age at 50% maturity estimated at 1.9 years [95% CI 2.05 - 1.76]. Size at 50% maturity was slightly different across Guam and mid shelf reef populations (Fig. 4.10). The smallest estimated size at maturity was from outer shelf reefs, with a calculated size at 50% maturity of 113.4 mm [120.3 - 96.4].

Age and size at 50% sex change were also estimated for secondary male *C. sordidus* from populations in Guam and the GBR (Table 4.9). Secondary males from Guam and outer shelf reefs all represented similar age at 50% sex change (Fig. 4.11). Mid shelf secondary males reached 50% sex change roughly 1 year older to all other males [2.9 years; 3.2 - 2.6]. Size at 50% sex change of secondary males showed slight differences across populations (Fig. 4.11). The smallest estimated size at sex change was from secondary males from outer-shelf reefs, with a calculated size at 50% sex change of 173.3 mm [183.2 - 168.7].

Table 4.8: Results of female maturity (age- and size- at 50% maturity) for *C. sordidus* populations in Guam and the GBR +/- confidence intervals (CI).

Female maturity						
Location	**Age at 50% Maturity (years)**	CI +	CI -	**Size at 50% Maturity (FL mm)**	CI +	CI -
GBR mid shelf	0.9	0.06	0.05	157.8	15.78	8.02
GBR outer shelf	0.3	0.02	0.04	113.4	6.86	17.01
Achang reserve	1.5	0.14	0.07	154.1	1.95	30.87
Tumon Bay reserve	1.9	0.09	0.19	141.4	13.43	13.58
Guam fished	1.0	0.06	0.06	149.5	15.02	11.10

Table 4.9: Results of male *C. sordidus* populations for age- and size- at 50% sex change +/- confidence intervals (CI).

Secondary males: timing of sex change						
Location	**Age at 50% sex change (years)**	CI +	CI -	**Size at 50% sex change (FL mm)**	CI +	CI -
GBR mid shelf	2.9	0.29	0.29	223.8	13.77	5.59
GBR outer shelf	1.9	0.19	0.19	173.3	9.93	4.60
Achang reserve	1.9	0.19	0.16	185.6	13.09	5.39
Tumon Bay reserve	2.0	0.19	0.21	213.3	21.77	21.15
Guam fished	2.1	0.21	0.17	200.8	14.17	5.22

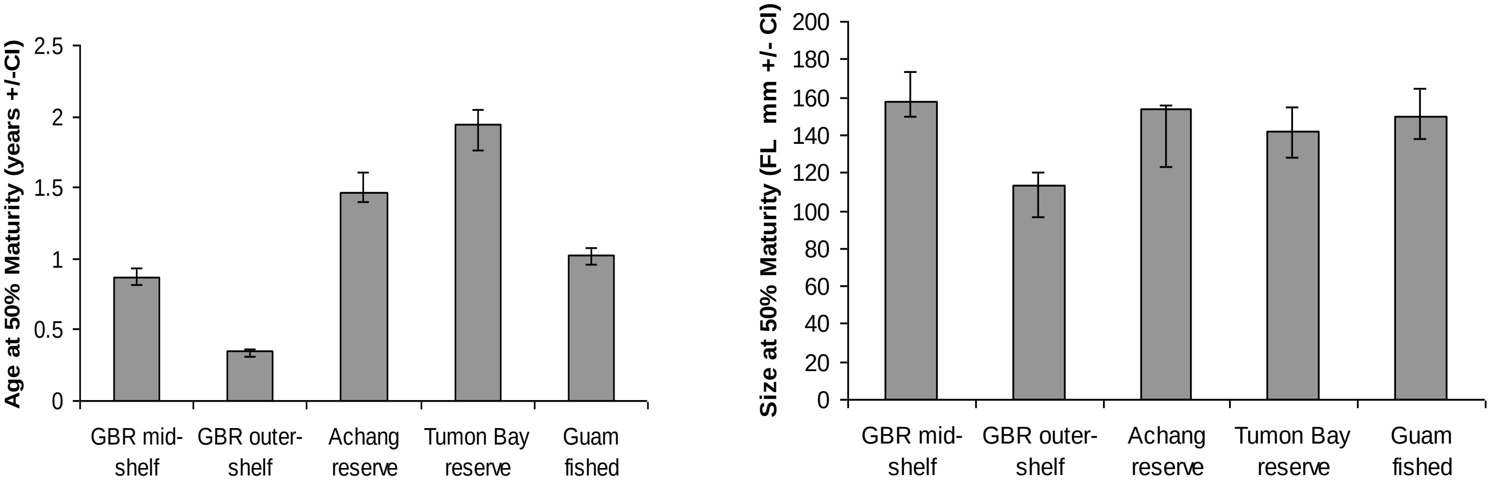


Fig. 4.10: Age and size at 50% maturity for female *C. sordidus* from populations in Guam and the GBR.

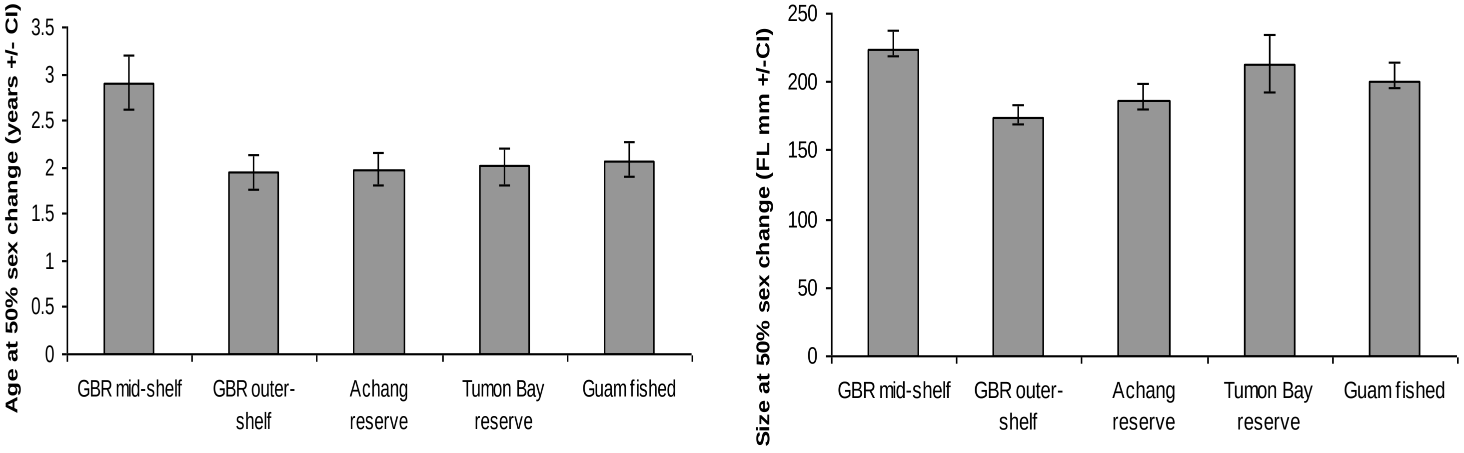


Fig. 4.11: Age and size at 50% sex change of male *C. sordidus* from populations in Guam and the GBR.

Comparisons of protogynous sex reversal

Chlorurus sordidus was confirmed to display protogynous sex reversal and the presence of transitional sex changing individuals was observed at several locations sampled, although mid shelf reefs and reserves had fewer transitional sex changers compared to outer-shelf reefs and fished areas. All transitional individuals were functional males and displayed terminal color phase, signifying functional sex change precedes color changes in this scarid species. Sex reversal was also observed to occur over a wide range of ages and sizes. Terminal phase (TP) males showed considerable differences in size between mid and outer reefs on the GBR by almost 55 mm (Fig. 4.12). While only slight variation was detected across Guam locations. TP males from mid shelf reefs were older by almost 1.5 years compared to all other populations observed (Fig. 4.12)

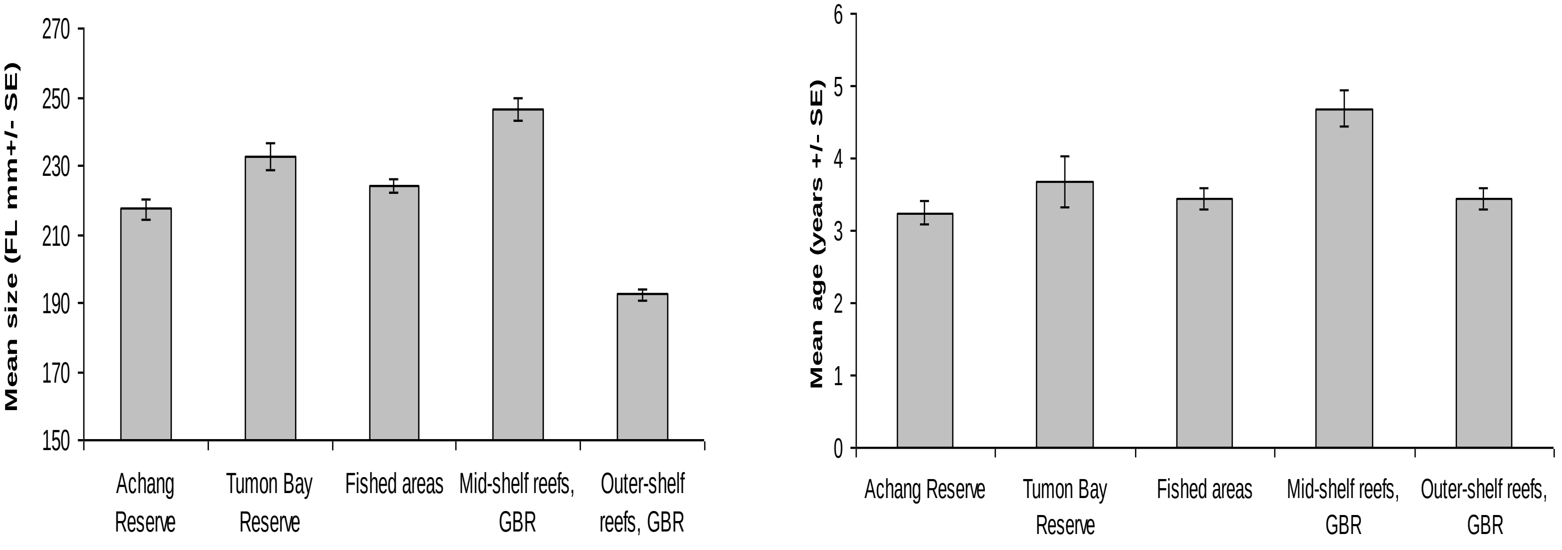


Fig. 4.12: Mean terminal phase male size (FL mm +/- SE) and age (years +/- SE) for *C. sordidus* populations in Guam and the GBR.

4.4 Discussion

This study explores the impact of habitat, geographic location and fishing on four demographic variables: longevity, growth rate, age and size at maturity and timing of sex change of two populations of *Chlorurus sordidus* at two locations, Guam and the Great Barrier Reef (GBR). Although adequate samples of the study species were collected from each location, it was not possible to achieve a balanced design in which marine reserves and habitat category were orthogonal. However, it was possible to measure the magnitude and direction of demographic variation at each geographic locality in the absence of fishing pressure. *C. sordidus* is protected from fishing by marine reserves in Guam and is not a targeted species on the GBR. Moreover as the species was unfished on the GBR the pattern of demographic variation associated with different habitats could be assessed in the absence of human disturbances. This studyreveals that both broad scale (geographic) and local scale (habitat differences) had a profound effect on the population biology of this species, with natural variation in life history parameters in this species masking the effects of fishing activities.

For any fish species, longevity, growth rate, age and size at maturity and timing of sex change will all influence future generations. Interrelationships among these traits are predicted that natural selection will optimize trade-offs among them, thereby maximizing an individual’s fitness in a particular environment (Roff 1992, Stearns 1992). Age at maturity is an especially important life history trait (Belk 1998). Studies have shown a significant correlation between age at first reproduction and both mortality and growth rates in local populations (Alm 1959, Roff 1984, Beverton 1987, Charnov 1993, Sadovy 1996). Timing of maturation presents a tradeoff between the demands of reproduction, growth and survival in response to local conditions. Moreover, under increased mortality regimes, a reduction in age at maturity is generally observed. This is because if the individual waits to grow first they may die and never reproduce. Subsequently, to maximize an individual's fitness and reproductive output, "optimal" age and sizes at which an individual will undergo maturation should occur earlier (Stearns & Koella 1986, Kozlowski 1992, Stearns 1992).

Differences in population dynamics occurred on the GBR between mid and outer shelf habitats. *C. sordidus* on outer shelf reefs had decreased longevity and growth rate, timing of sex change was earlier and matured at younger ages and smaller sizes when growth was reduced compared to mid shelf populations. Gust *et al* (2002, 2004) attributed the higher mortality rates on exposed reefs to a greater abundance of predators, which resulted with populations with higher turnover rates with changes in reproductive output as a consequence. Higher turnover also influenced survival and longevity patterns of individuals. Cowen (1990) reported a similar trend of reduced growth and earlier maturation in reef fish under high mortality and suggested fish allocated more energy towards earlier or more intensive reproduction at the expense of somatic growth.

Reduced longevity and growth rates, as well as, declined timing of sex reversal and age and size at maturity are common outcomes for many marine fish following selective harvesting (Law 2000). No significant differences in longevity, growth and timing of sex reversal were observed for *C. sordidus* populations between harvested areas and reserve areas in Guam. An increase of recruitment of smaller individuals in reserve areas may explain why no differences were detected in other demographic characteristics of *C.*

sordidus between fished and unfished areas. However, individuals from areas exposed to fishing matured at a younger age and had a reduced growth rate relative to populations from marine reserves. Earlier maturation under exploitation is well documented (Beacham 1983, Jørgensen 1990, Rjnsdorp *et al*. 1991, Reznick 1993, Trippel 1995). Demographic consequences of life history change have also been reported for the commercially fished Atlantic cod (Hutchings 1999, 2005). Exploitation has caused a decline in 50% maturity from 6.5-7.0 years to approximately 5.0-5.5 years (Hutchings 2005) as well as reductions in growth rate (Sinclair *et al*. 2002, Swain *et al*. 2007).

Many studies of demographic variation in life histories have demonstrated biogeographic effects (latitudinal trends) that can be attributed to environmental conditions. The most common explanations are Bergmann's Rule and the Temperature Size Rule ("Hotter is Smaller" hypothesis), which describe relationships between body size and maturation with latitudes (Bergmann 1847, Kingsolver & Huey 2008). In many fish, larger body size under cold conditions at higher latitudes is coupled with delayed maturation at a larger body size (Atkinson 1994, Angilletta 2009). In this study, delayed maturation was observed for all populations in Guam compared to lower latitude location of the GBR. However, life history characteristics of longevity, growth, body size and timing of maturation did not follow this prediction.

Conclusion:

By comparing fish from Guam and the GBR, this study sought separate natural variation from anthropogenic changes in *C. sordidus* populations. This study suggests that small parrotfish species in Guam are not at all affected by fishing. Changes in growth patterns and longevity were very different in GBR compared to Guam, which was attributed to higher turnover rates produced by predators. However, in Guam there are virtually no predators to cause such differences. This study also showed differences in the social mating systems between populations. In parrotfish, large terminal phase males (secondary males) are territorial and generally pair-spawn with visiting females, while small initial phase males (primary males) are non-territorial and group-spawners. This study found differences in social mating system of *C. sordidus* populations. Pair-spawning generally consists of many large female to small male gonad ratios. However, in *C. sordidus* populations from fished areas (Guam) and outer shelf reefs (GBR), we are seeing considerably large male gonads compared to females, which may be explained by group spawning, when the social mating system breaks down. When the mating system breaks down, it may be modified where individual males start competing with each other, because there becomes a lot of opportunity for male-male competition, larger male gonads may mean higher sperm production.

Chapter 5: Comparative analysis of maturation patterns of the protogynous parrotfish *Scarus psittacus*

5.1 Introduction

Protogynous fishes are excellent study species with respect to reproductive biology as sex reversal provides an additional variable, the timing of sex change, for the analysis of reproductive performance. Both timing of maturation and timing of sex reversal are key factors in an individual's reproductive success. Both traits are highly plastic and have evolved to maximize reproductive value given the constraints of the local environment (Warner *et al*. 1975, Charnov & Bull 1977, Cowen 1990).That is an organism should mature and change sex at a size (or age) that would maximize its reproductive potential relative to its lifetime. The optimal size and age at which this occurs may not be set within a species (Charnov 1982), but is dependent upon local conditions that affect mortality regimes and resource availability.

Both the timing of maturation and timing of sexual transition can be very complex traits because of the association with both mortality and growth (Gust 2004, Munday *et al*. 2004). In order for an individual to mature, a trade off in growth may be observed to ensure success of future generations at the expense of growing to an ideal size. Growth may also influence patterns of sex change in protogynous species, especially when sex change is socially controlled and only the largest individuals in a social group change sex (Francis 1992). For short lived species a problem occurs between maturation and sex change. Under increased mortality, short-lived species are faced with the dilemma of whether to mature and reproduce as a female or to be a male via sex change.

Diagnosis of the sexual ontogeny of some parrotfish species has proven to be complex. Some species have separate sexes while others undergo sex reversal. The presence of two male pathways in many scarine labrid species further complicates the diagnosis of sexual ontongeny (Choat & Robertson 1975). Depending on mating system of the population, some males will develop directly from a juvenile gonad (primary males) while other males will develop as the result of sex reversal of females (secondary male) (Munday *et al.* 2006). The diagnosis of sexual ontogeny is important for establishing the schedules of maturation and sex reversal for the analysis of reproductive function. Histological examination of gonad structure must cover all stages of sexual development and be associated with demographic information on the relationship between size, age and sexual identity.

Much of fisheries theory has been developed with respect to long-lived species, due to the harvested population composed of a wide range of age classes so that any effects of fishing are spread across a number of cohorts. However, very few studies have looked at how fishing will influence short-lived species. Short-lived species are unlikely to be influenced by the same processes as long-lived species, primarily because of their ability to turnover very quickly. But how will this increased turnover affect individuals with respect to schedule of sexual transition and age at maturity? This study will use *Scarus psittacus* to compare patterns of maturation and sexual transformation to determine if such patterns are comparable with species of greater life expectancies. Information derived from otoliths and gonads is essential to determine growth rates, life spans and reproductive parameters of reef fishes, and allow the comparisons between species/populations and localities. For this study, otoliths and gonads were used to measure growth, longevity and maturation of the scarid, *Scarus psittacus*, between two demographically distinct locations, the Great Barrier Reef (hereafter GBR) and Guam to analyze three objectives:

1) To compare populations of the same species with different habitat requirements.
2) To compare populations of the same species between two locations, Guam and the GBR, to identify any biogeographic effects.
3) To determine to what extent fishing effects influence species life history variation.

Scarus psittacus (Forsskål, 1775), the common parrotfish (or palenose parrotfish), has a size range between 10-20 cm and maximum reported age of 5 years (Randall *et al*. 1990, Choat *et al*. 1996). *Scarus psittacus* is a diandric, protogynous hermaphroditic species with two developmental pathways for males. Some males develop directly from a juvenile gonad (primary males) while other are the result of sex-changing functional females (secondary males). *S. psittacus* has two colour phases: a brightly coloured terminal-phase (TP) and a drab initial-phase (IP). Initial phase individuals represent females and primary males, while terminal phase individuals can be either secondary males or primary males that have transformed to the bright terminal phase.

5.2 Methods

Study location

A total of 110 individuals were sampled from Guam (13°28’N, 144 °45’E), with 42 individuals collected from fished areas and 68 collected in marine reserves, between

March and May 2010 (see Fig. 4.1). *S. psittacus* was also collected on mid and outer shelf reefs of the GBR, where a total of 70 individuals were sampled from Lizard Island (14˚40´S, 145˚28´E) between January 1996 and January 2000 (see Fig. 2.1b). It is important to note that while samples were taken almost a decade apart and that the time variation could have the potential to confound the comparison, continued monitoring of the GBR has proved little to no change in the environment between the times the samples were collected. This allowed me to focus entirely on spatial variation.

Fish were collected by hand spearing from each location. It was made sure that the samples taken represented the size structure at each site. This usually entailed extra effort at the fished sites, as larger fish were harder to spear. However, despite the heavy fishing pressure this is an abundant fish, so while the larger fish were somewhat more difficult it was possible to sample them. Each individual's fork length (FL), standard length (SL), total weight (TW), and gutted weight (GW) were measured and recorded to the nearest millimeter and gram, respectively. Sagittal otoliths were removed, cleaned, washed in ethanol, and stored to dry before ageing. Whole gonads were removed and placed in FAAC, a formalin-based fixative (4% formaldehyde, 5% glacial acetic acid, 1.3% calcium chloride dehydrate) before histological investigation of reproductive status. Gonads were also weighed to the nearest milligram. Gonadosomatic indices (GSI) were calculated for each individual as the gonad's percent contribution to total body weight.

Age determination

Annual ageing was achieved using sagittal ototliths. Each ototlith was examined and read at least twice for verification of incremental bands representing annuli. Putative anual increments were used to estimate age. Ageing process followed the techniques described in Choat *et al* (1996). See Chapter 2 for further details of otolith ageing.

Modelling of growth

Growth of *S. psittacus* was estimated for all populations sampled by examination of the relationship between size (Fork Length, FL) and age. Size-at-age data were fitted by using both the von Bertalanffy Growth Function (VBGF) and Franci's (1988) re-parameterized equation of the von Bertalanffy Growth Function (rVBGF). The rVBGF parameters estimated for *S. psittacus* were $L(1)$ and $L(3)$, generating estimates of mean body size-at-ages one and three years. For further details of growth modeling refer to Chapter 2.

Estimates of longevity and adult body size

Mean maximum age T_{max} (longevity) and mean maximum body size L_{max} (adult body size) were calculated for each *S. psittacus* population from the 20% oldest and largest individuals. One way Analysis of Variance (ANOVA) were then used to determine locality differences in mean age and size of both female and male *S. psittacus.* The model tested the effects of location (a fixed effect), using mean age/size as replicates in this broad scale analysis. Prior to the ANOVA calculations, the assumption of homogeneity of variances was examined using box plots of residuals and log10 (X+1) transformations were used to remove heterogeneity of variances as required.

Age- and size-at-maturity

Gonad histology was performed for *S. psittacus*. Complete details of histological processing of gonad samples are described in Chapter 2. Sexual identity was assessed based on the criteria developed in Chapter 2. Age- and size-at-maturity were estimated by calculation the age and size at which 50% of females were mature (proportion of mature females relative to the total number of females within each age or size class) (Williams *et al*. 2008). The logistic function used for estimating age- and size-at-maturity is described in Chapter 2. 95% confidence intervals (CI) were also estimated for each parameter value of age-at-maturity (*T50*) and size-at-maturity (*L50*) using a bootstrapping procedure (Moore *et al*. 2007), also described in Chapter 2.

Age- and size-at sex change

A logistic regression approach was used to estimate age and size at which 50% of sex changing females undergo sex reversal (Williams *et al.* 2008). The logistic function used for calculating age- and size-at-maturity was:

$$P_a = [\, 1 + e^{[-\ln(19)(a - a_{50}) / (a_{95} - a_{50})]}]^{-x}$$

Where P_a is the proportion of sex changing females in age or size class a, x is the observed frequency of males within each age or size class, a_{50} is the age or size at which 50% of sex changing females have changed sex, and a_{95} is the age or size at which 95% of sex changing females have changed sex. Parameters evaluated for this study were age-at-50% sex change T_{50}, age-at-95% sex change T_{95}, size-at-50% sex change L_{50}, and size-at-95% sex change L_{95}. Age classes were based on one year increments and size classes were based on 50mm increments. For each of the above paramters, 95% confidence intervals (CI) were estimated using a bootstrapping procedure, where the data was randomly re-sampled 1000 times with replication (Moore *et al*. 2007).

Analysis

A Principle Component Analysis (PCA) was performed in this study to explore the variation in life history traits across locations, Guam and the GBR, sampled. Variables were categorized according to the type of information provided. Six information categories were identified: (i) longevity (mean T_{max}), (ii) growth rate (Linf), (iii) primary males (as a percentage of the population), (iv) age at maturity (T_{mat}), (v) age at sex change ($T_{sex\ change}$) and the (vi) percentage of life span as individual reached at 50% L_{inf}. Variables were checked for the presence of skewed distributions across locations using pair-wise correlation plots (Draftsman plots), but no transformations of the life history variables were required.

5.3 Results

Growth, longevity and body size

All *Scarus psittacus* populations demonstrated continuous growth over the age classes sampled and represented indeterminate growth patterns (Fig. 5.1). The growth patterns of reserve areas in Guam and mid shelf reefs on the GBR were relatively uniform with these two locations demonstrating comparable $L\infty$ values. Similarly, both fished areas (Guam) and outer shelf reefs (GBR) represented lower $L\infty$ values (Table 5.1), however outer-shelf reef populations achieved the smallest asymptotic size compared to other populations. Both GBR populations revealed higher *k* values, which indicated *S. psittacus* populations converge on their asymptotic size more rapidly, compared to the Guam sites (Table 5.1). Although it is important to note this does not necessarily mean they grow more rapidly. The growth comparison between locations (Fig. 5.1) also shows slight differences between *S. psittacus* populations between reserve and fished areas in Guam, as well as significant differences between populations across mid and outer shelf reefs.

Length-at-age data of *Scarus psittacus* from rVBGF varied between each location (Fig. 5.2). Achang Reserve populations displayed a higher L_1 (137.7 mm; +10.9753, -6.8866) compared to fished area populations (Fig. 5.2, Table 5.2). Similarly, populations from mid shelf reefs demonstrated a higher L_1 compared to outer shelf reef populations (Fig. 5.2). For length at age 3 (L_3), there were considerable differences between areas in Guam, with *S. psittacus* populations from Achang Reserve reaching a significantly larger size at age 3 compared to populations from fished areas (Fig. 5.2, Table 5.2). However, the calculated length at age 3 was relatively uniform for both GBR locations (Table 5.2).

Table 5.1: von Bertalanffy Growth function results for *S. psittacus* populations across four locations.

Location	**Growth function (L_∞) (FL mm)**	**Growth function (*k*)**
fished, Guam	192.6	0.87
reserve, Guam	218.4	0.81
mid shelf,GBR	218.2	1.08
outer shelf,GBR	156.9	1.82

Table 5.2: Re-parameterized von Bertalanffy growth parameters for *S. psittacus* with Confidence Intervals.

Location	**L_1 (FL mm)**	**CI+**	**CI-**	**L_3 (FL mm)**	**CI+**	**CI-**
fished, Guam	108.8	10.88	5.44	163.2	7.65	3.74
reserves, Guam	137.7	10.98	6.89	210.5	9.63	5.26
mid shelf, GBR	148.1	8.32	7.41	192.6	9.29	4.33
outer shelf, GBR	132.9	6.78	5.01	193.5	9.68	4.12

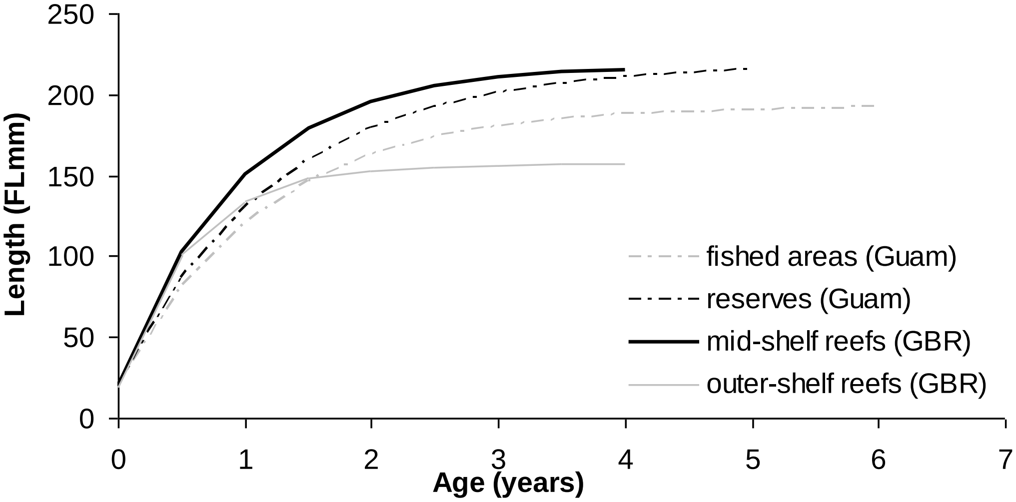


Fig. 5.1: Comparison of VBGF growth curves of *S. psittacus* populations in Guam and the GBR.

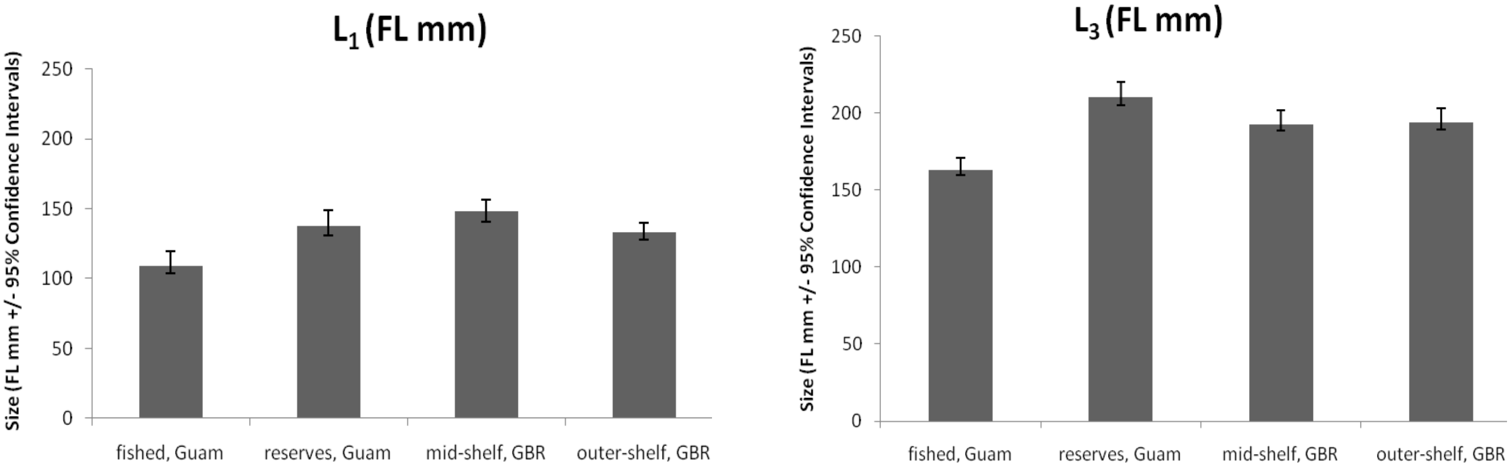


Fig. 5.2: Re-parameterized von Bertalanffy growth function parameters L_1 and L_3 (+/- 95% confidence intervals) for each *Scarus psittacus* population in Guam and the GBR.

Variation occurred in age and size of both male and female *S. psittacus* populations from each location (Table 5.3, Table 5.4). Males from Guam locations demonstrated similar ages, while slight differences were observed between sizes (Table 5.3). On the other hand, males from the GBR locations revealed considerable differences in both age and size. Male populations on the outer shelf were younger and smaller compared to populations on the mid shelf (Table 5.3). Substantial variation in both age and size was also exemplified for females between the four locations. Females were much older and larger from fished areas compared to reserve areas (Table 5.4). Comparison between the GBR locations revealed female populations from outer shelf reefs were smaller (133.1 mm) and younger (1.2 years) compared to mid shelf reef populations (160.8 mm: 1.6 years). Results from the one-way ANOVA revealed that both mean age and length for males and females were significantly different between each location sampled (Table 5.5).

The maximum recorded age for *S. psittacus* was 6 years. Maximum longevity varied at a geographic scale (between Guam and GBR); however maximum longevity of male individuals was identical for both Guam locations [4 years] and uniform between GBR locations (Table 5.3). Male populations from outer-shelf reefs displayed a considerably smaller calculated maximum size compared to mid-shelf reef populations [193.3 mm: 251 mm]. For females, maximum longevity on the mid-shelf reefs (GBR) was 3 years, which was around one and a half years older than female populations from outer shelf reefs. Females from fished areas had an older calculated maximum life span compared to those from reserve areas [Table 5.4]. Although the calculated maximum size for female individuals showed the mid shelf population being larger compared to outer shelf population, females from fished areas were significantly larger with a maximum size of 192.8 mm compared to 162.3 mm from reserve areas (Table 5.4). Results from the one-way ANOVA revealed the significance of both maximum longevity and maximum size for males and females between each location (Table 4.4).

Table 5.3: Represents the mean age (years), mean size (FL mm), 20% longevity (years) and 20% adult size (FL mm) of male *S. psittacus* from four locations.

Location	**Mean Age (years)**	**Mean size (FL mm)**	**20% Longevity (years)**	**20% Adult Size (FL mm)**
Fished areas	2.9	194.4	4	226.8
Reserve areas	3.1	186.2	4	222.7
Midshelf-GBR	2.3	204.5	3	251
Outershelf-GBR	1.5	145.3	3.3	193.3

Table 5.4: Represents the mean age (years), mean size (FL mm), 20% longevity (years) and 20% adult size (FL mm) of female *S. psittacus* from four locations.

Location	**Mean Age (years)**	**Mean size (FL mm)**	**20% Longevity (years)**	**20% Adult Size (FL mm)**
Fished areas	2.9	159.3	4.8	192.8
Reserve areas	2.1	139.2	3.3	162.3
Midshelf-GBR	1.6	160.8	3	193
Outershelf-GBR	1.2	133.1	2.5	174

Table 5.5: One-way ANOVA results comparing mean age (years) and mean size (FL mm) of male and female *S. psittacus* populations from Guam and the GBR. (* P<0.05: **P<0.01: ***P<0.0001)

Sex	**Dependent variable**	**Source of variation**	**DF**	**MS**	**F**	**p**
Male	Size (FL mm)	Location	3	12213	12.392	0.000002***
		Residual	59	986		
Female		Location	3	2987	5.850	0.002**
		Residual	56	511		
Male	Age (years)	Location	3	10.9729	15.4370	0.00000***
		Residual	59	0.7108		
Female		Location	3	9.4576	10.4433	0.00002***
		Residual	56	0.9056		

Table 5.6: One-way ANOVA results comparing maximum age (years) and maximum size (FL mm) of oldest male and female *S. psittacus* individuals from populations in Guam and the GBR. (* P<0.05: **P<0.01: ***P<0.0001)

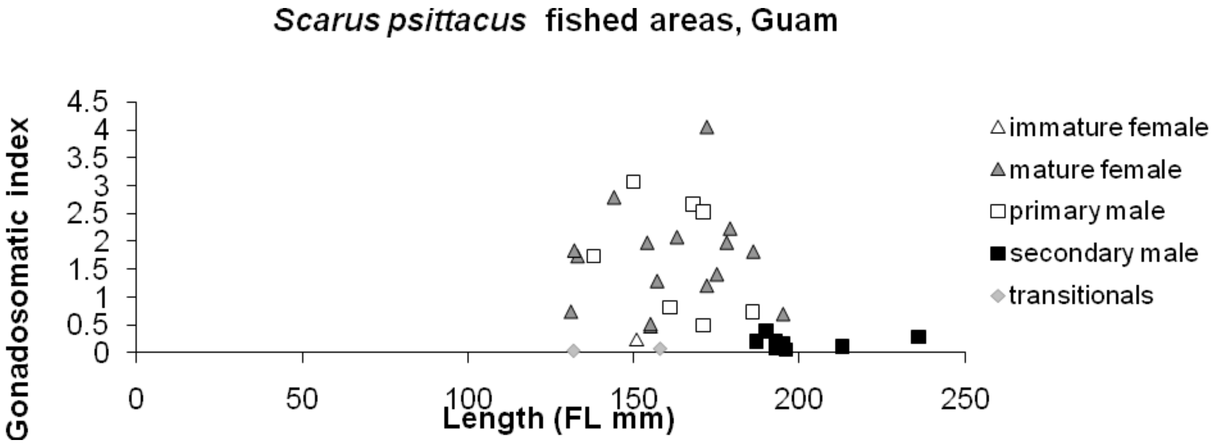
Sex	**Dependent variable**	**Source of variation**	**DF**	**MS**	**F**	**P**
Male	Maximum Adult Size (FL mm)	Location	3	1660	8.383	0.005**
		Residual	9	198		
Female		Location	3	704.5	2.470	0.14
		Residual	8	285.2		
Male	Maximum Longevity (years)	Location	3	0.7756	2.5385	0.12
		Residual	9	0.3056		
Female		Location	3	3.0000	4.0563	0.05*
		Residual	8	0.7396		

Comparison of gonads

Gonadosomatic index plots revealed patterns of distribution of sizes of fish of different sex. Maturation in *S. psittacus* on the outer shelf (GBR) occurred at smaller sizes and younger ages compared to mid shelf (GBR) and both reserve and fished areas in Guam (Fig. 5.3, 5.4). Plots of gonad somatic index (GSI) confirmed mature females had reduced fork lengths on outer shelf reefs [100 mm]. The GSI plots also revealed fifty percent maturation levels were achieved once mature female individuals exceeded 130 mm on the mid shelf (GBR), fished areas (Guam) and reserve areas (Guam) (Fig. 5.3, 5.4).

Mature female *S. psittacus* gonads from individuals collected on fished areas (Guam) were considerably larger on average (almost twice the size) compared to those collected from reserve areas (Fig. 5.5). Both GBR locations were found to have similar gonad weights. Because females from fished areas (Guam) developed larger gonads, relatively more energy was invested in reproductive tissue compared to females from other locations. Mature females from Fished areas (Guam) also displayed the highest mean gonad somatic index [1.68+/- 0.23], followed by outer shelf reefs [1.46 +/- 0.19]; while female individuals from both reserve areas (Guam) and mid shelf reefs demonstrated the lowest mean gonad somatic index [0.995 +/- 0.190: 1.05 +/- 0.12] (Fig. 5.5).

Analysis of gonad weight plots of both female and male gonads revealed that males from all locations have considerably larger gonads, however, male occur at younger ages (1 year) on mid and outer shelf reefs compared to Guam locations (Figure 5.6). Plotting of ovary weight onto the relationship between age and body size demonstrated older females had a relatively larger ovaries and were comparatively more fecund (greater reproductive output) compared to mature females with smaller ovaries (Fig. 5.6).



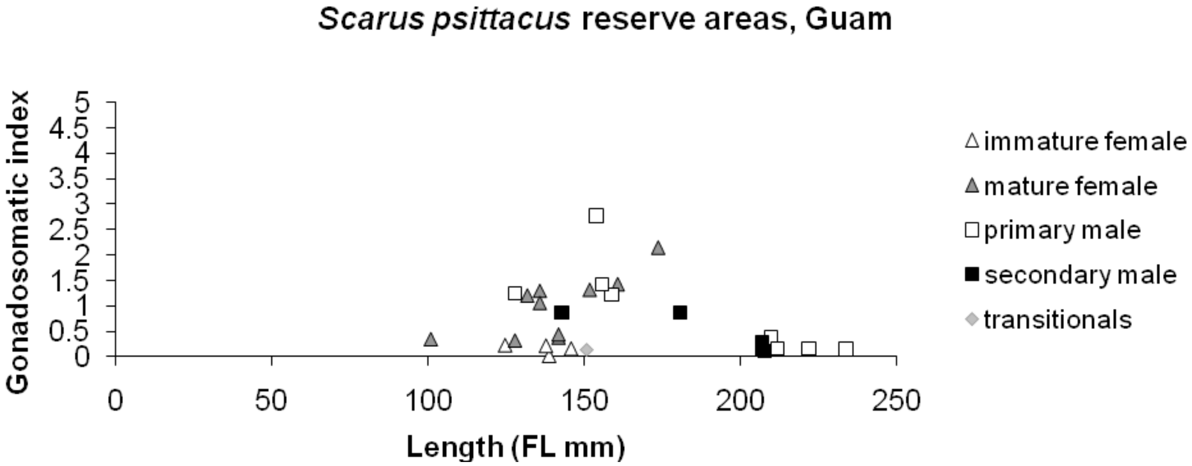
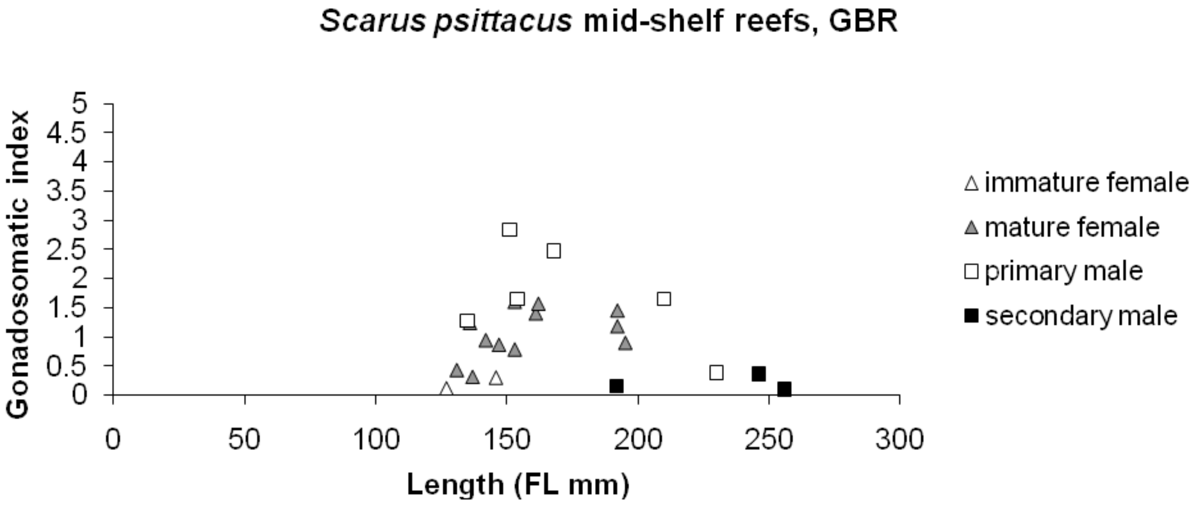


Fig. 5.3: Gonadosomatic indices versus fork lengths for the major sexual categories indentified by histology for *Scarus psittacus* populations between fished are reserve areas in Guam.



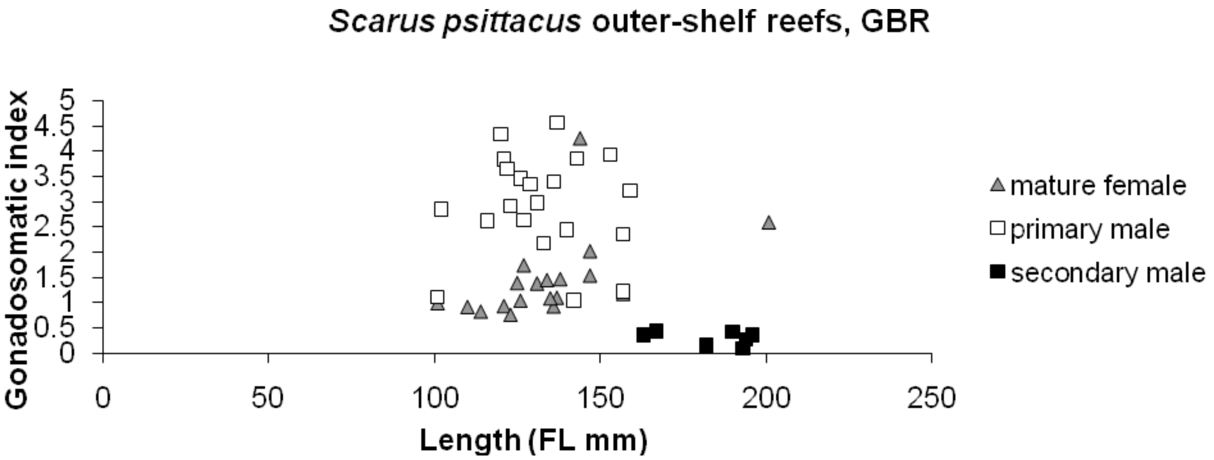


Fig. 5.4: Gonadosomatic indices versus fork lengths for the major sexual categories identified by histology for *Scarus psittacus* population from mid and outer shelf reefs, GBR.

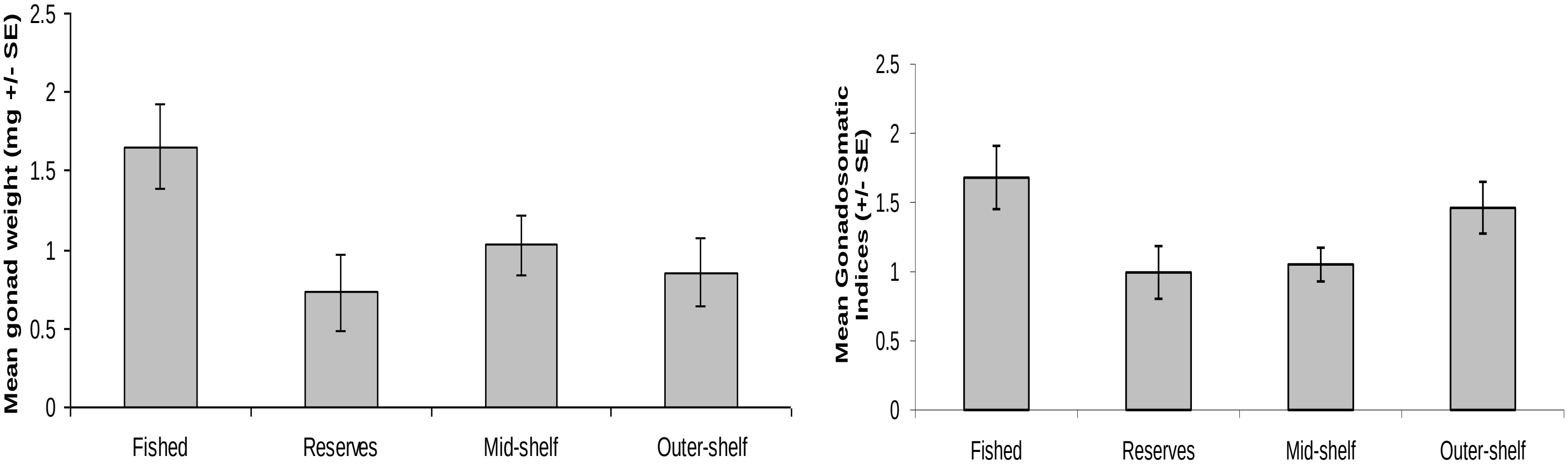


Fig. 5.5: Mature female mean gonad weights (mg +/- SE) and mean gonadosomatic indices (+/- SE) for *Scarus psittacus* populations from both Guam and GBR sample locations.

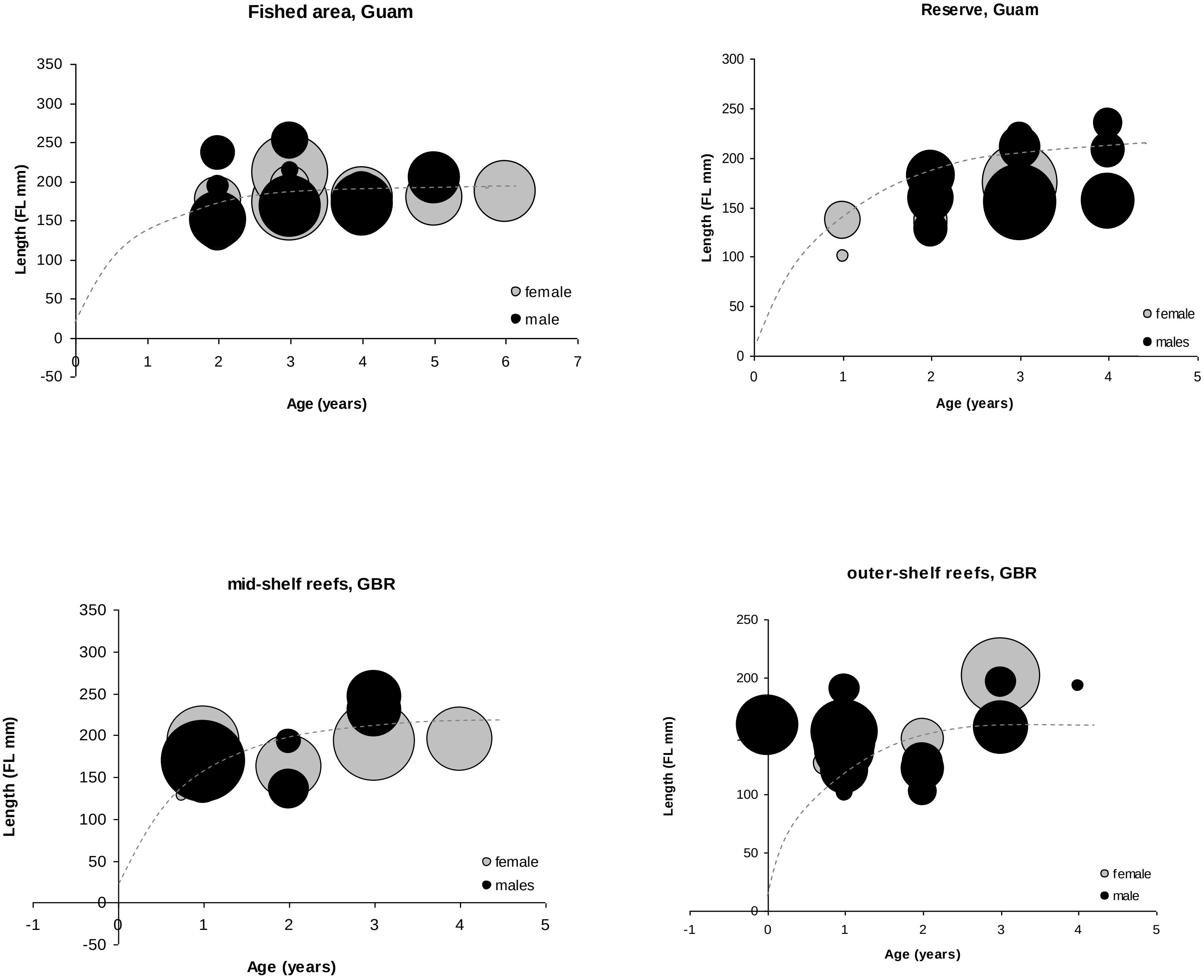


Fig. 5.6: Size-at-age of female and male *Scarus psittacus* showing relative ovary and testis weight (circle size) as a measure of reproductive output in Guam and the GBR. Growth curves (von Bertalanffy Growth Function; VBGF) is shown and represented by dashed lines.

Comparisons of maturity and sex change

Age and size at 50% maturity were estimated for female *Scarus psittacus* from populations in Guam and the GBR (Table 5.7). Both fished and reserve areas reached maturity at much older ages compared to GBR locations (Fig. 5.7). Reserve areas and fished areas reached maturity at very similar years [1.9:1.9]. Outer shelf reef females reached maturity at a significantly older age (almost doubled) [1.4 years] compared to mid shelf reef females [0.9 years] (Fig. 5.7). Size at 50% maturity showed considerable variation between Guam locations and slight variation between GBR locations (Fig. 5.7). The smallest estimated size at maturity was from reserve areas in Guam, with a calculated size at 50% maturity of 105.8 mm [119.2 – 95.3]. Comparison of variance estimates around the values of size-at-maturity across populations of *S. psittacus* suggested that females matured at similar body sizes across two geographically separated locations, Guam and the GBR (Fig. 5.9 A). In contrast, comparison of the variance associated with parameters of age-at-maturity between *S. psittacus* populations revealed that females matured significantly later in both Guam locations relative to those living in either of the GBR locations (Fig. 5.9 A).

Age and size at 50% sex change was also estimated for secondary male *Scarus psittacus* from populations in Guam and the GBR (Table 5.8). Secondary males from both localities in Guam and mid-shelf reefs all represented similar age at 50% sex change, while outer-shelf secondary males reached 50% sex change roughly 1 year older compared to all other males [2.9 years]. Size at 50% sex change of secondary males showed slight differences across populations (Fig. 5.8). The smallest estimated size at sex change was from secondary males from reserve areas, with a calculated size at 50% sex change of 150.4 mm [160.0 – 142.9]. Comparison of variance estimates around the parameter values of size-at-sex change amongst *S. psittacus* populations suggested that females undergo sex change to males at similar body sizes between reserve areas in Guam and outer reefs on the GBR and between fished areas in Guam and mid shelf reefs on the GBR (Fig. 5.9 B). In contrast, evaluation of the variance associated with parameters of age-at-sex change revealed that females change sex to males at an older age on outer-shelf reefs (GBR) relative to all other locations (Fig. 5.9 B).

Table 5.7: Results of female maturity for age- and size- at 50% maturity *S. psittacus* populations in Guam and the GBR +/- confidence intervals (CI).

Female maturity						
Location	**Age at 50% maturity (years)**	CI +	CI -	**Size at 50% maturity (FL mm)**	CI +	CI -
reserve, Guam	1.9	0.09	0.13	105.8	13.41	10.49
fished, Guam	1.9	0.23	0.17	154.1	0.96	18.85
mid shelf, GBR	0.9	0.06	0.12	129.5	6.47	12.71
outer shelf, GBR	1.4	0	0	121.5	0.05	0

Table 5.8: Results of male *S. psittacus* populations for age- and size- at 50% sex change +/- confidence intervals (CI).

Secondary males: timing of sex change						
Location	**Age at 50% sex change (years)**	CI +	CI -	**Size at 50% sex change (FL mm)**	CI +	CI -
reserve, Guam	2.1	0.21	0.10	150.4	9.58	7.52
fished, Guam	2.0	0.19	0.11	188.4	9.42	8.68
mid shelf, GBR	1.9	0.2	0.18	179.6	35.93	6.87
outer shelf, GBR	2.9	0.26	0.29	162.0	10.67	13.23

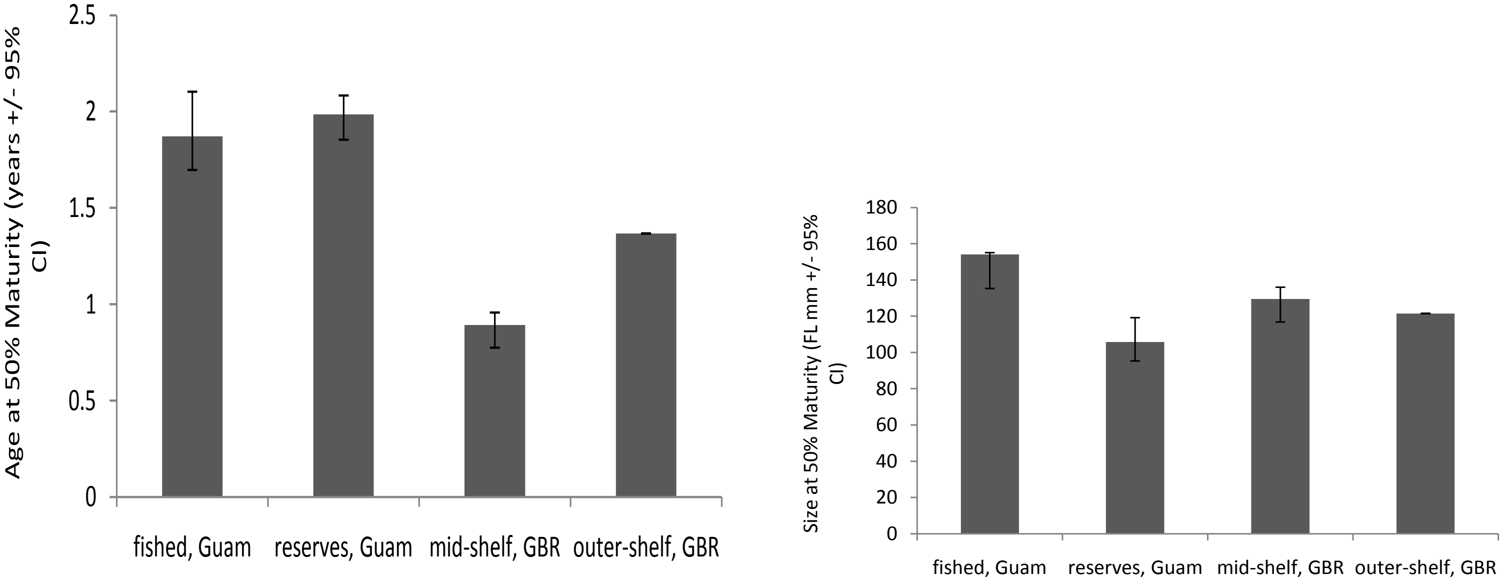


Fig. 5.7: Age and size at 50% maturity for female *S. psittacus* from populations in Guam and the GBR.

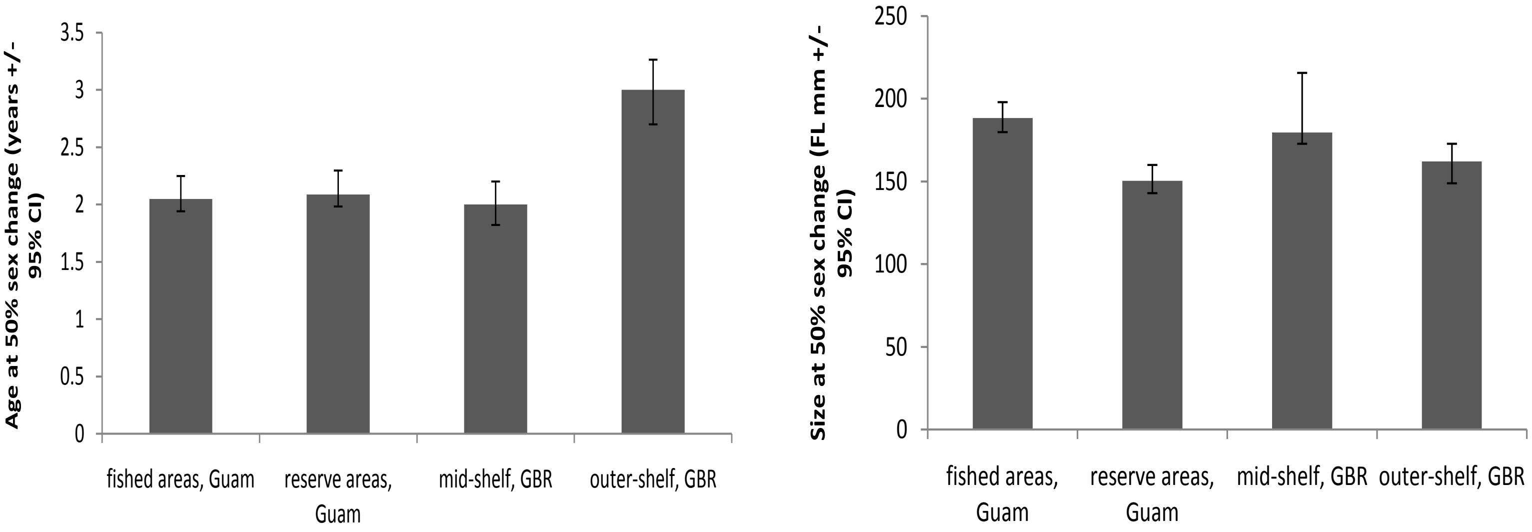


Fig. 5.8: Age and size at 50% sex change of *S. psittacus* populations in Guam and the GBR.

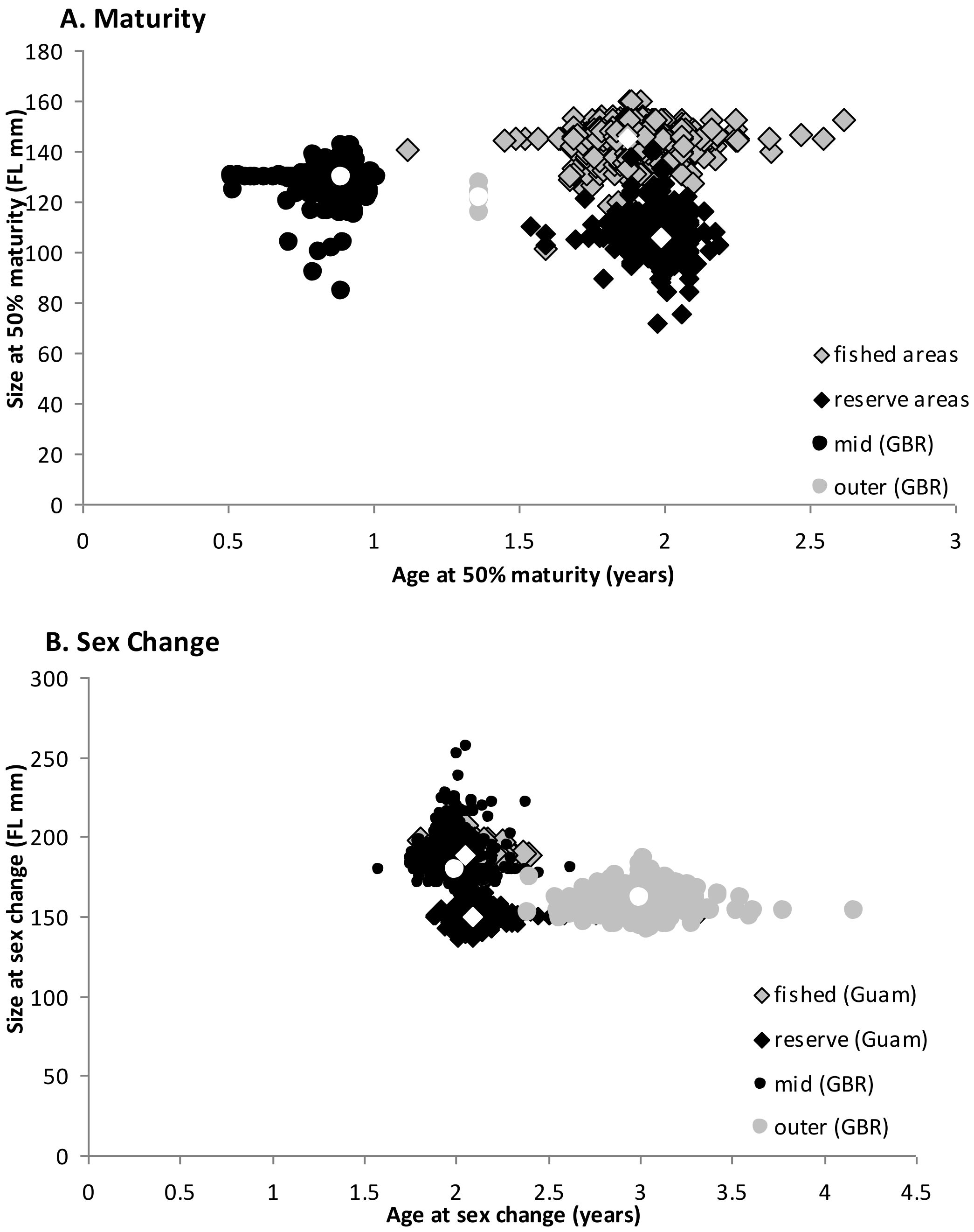


Fig. 5.9: Relationship between size and age at female maturity (A) and size and age at male sex change (B) in *S. psittacus* between Guam and the GBR. White symbols show bias-adjusted mean parameter values and black and gray symbols show bootstrapped variance estimates around each parameter.

Comparison between assemblages

The percent sexual composition of *S. psittacus* populations was compared between all localities (Fig. 5.10) and revealed that females were more abundant in fished (50%), reserve (55%) and mid shelf reefs (60%). In contrast, primary males were the most prominent on outer shelf reefs over females (45% to 40%). Secondary males were least abundant in reserve areas (18%), mid shelf reefs (10%) and outer shelf reefs (10%).

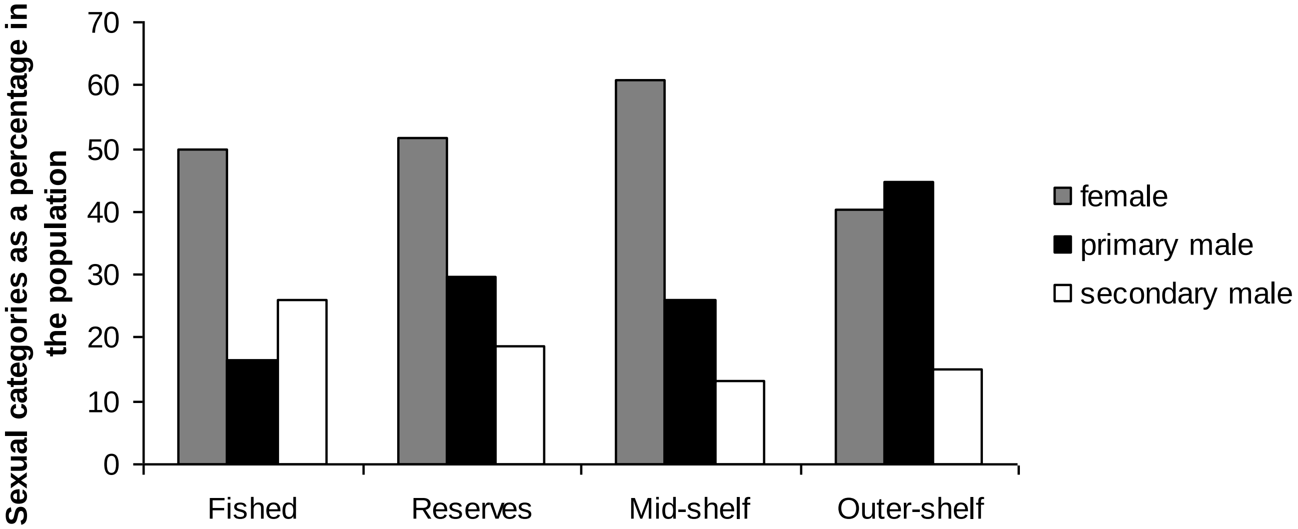


Fig. 5.10: Compares the occurrence of female, primary male and secondary male *S. psittacus* from populations in fished and reserve areas in Guam and mid- and outer-shelf reefs on the GBR.

5.4 Discussion

Three main conclusions can be made from this analysis. First, broad scale comparison of demographic characteristics revealed differences in growth pattern, age structure, maturation and sex change of *S. psittacus* occurred between Guam and the Great Barrier Reef populations. Populations in Guam were found to have slow initial growth, maximum longevity of males and females were older, reached maturity at older ages and changed sex at larger sizes compared to populations from the GBR. This confirms the "Hotter is smaller" rule which states fish living in warmer temperature waters (lower latitudes) will represent faster initial growth, short life spans, mature and change sex at younger ages and smaller sizes (Kingsolver & Huey 2008, Angilletta 2009). However, it is important to note that all populations demonstrated the same life span.

Secondly, differences in demographic characteristics in growth, age structure, maturation and sex change of *S. psittacus* occurred at a habitat scale. Population from outer shelf reefs on the GBR represented a smaller final body size, significantly different growth curve, younger ages for both male and female longevity, matured and changed sex at older ages compared to *S. psittacus* populations on mid shelf reefs. Differences in growth, size and age structure may reflect density dependent effects. Studies have shown a higher density of parrotfish on outer reefs (Gust *et al*. 2001, Gust *et al.* 2002) which can result in intra-specific abundance (crowding) and increased competition for resources (Jones 1986, Sebens 1987). As food availability is strongly associated with growth, increased competition for limited resources may limit the food intake per individual and result in reduced somatic growth (Rijnsdorp 1994, Helser & Almeida 1997).

Such growth differences between mid and outer shelf positions could also reflect differences in the timing of maturation and sex change. Maturation in many individuals is often accompanied by a decrease or cessation of growth (Bernado 1993) fish maturing at earlier ages can compromise future growth by allocating more energy towards reproductive tissue at the expense of somatic tissue (Schultz & Warner 1991, Jennings & Phillips 1992). Therefore, earlier maturation was expected for populations on outer shelf reefs, however, the results confirmed the opposite, populations matured at significantly older ages on outer barrier reefs compared to mid barrier habitats.

The distribution of sizes of fish of different sex oberserved from the GSI plots also provided some interesting insight into the dynamics of sex change in this species. The size-advantage model of sex change predicts that for a given social organization, the range of sizes at which sex change occurs should be fairly narrow, with little overlap between the size of females and the size of males (Clifton & Rogers 2008). This pattern, where all females reach a certain size and then change sex was observed for populations from mid shelf reefs (GBR) and reserve areas (Guam). But populations with large amonts of overlap in the sizes of males and females (suggesting females forego sex change) have been observed (for outer shelf reefs (GBR) and fished areas (Guam)) and this may be due to high predation of males (Clifton & Rogers 2008).

Lastly, differences in demographic characteristics were examined between fished and unfished (reserve) locations in Guam. *Scarus psittacus* makes up 20% of the total parrotfish caught (by weight) in the inshore reef fishery in Guam (DAWR unpublished data). *S. psittacus* populations from fished areas displayed a reduced somatic growth, differences in age structure and both timing of maturation and sex change. Although there were differences between fished and reserve areas, these differences were not strong. This suggests habitat and recruitment variation play a more significant role in population dynamics of parrotfish rather than fishing (Jennings *et al.* 1999).

This study provides a comprehensive analysis of demographic characteristics and contributes to a better understanding of demographic variation of a scarine labrid species at three levels: locality (broad scale), habitat (local scale) and the potential impacts of fishing pressure. This study illustrates that demographic characteristics examined of *Scarus psittacus* are significantly influences by habitat, which was evident on cross shelf comparison of the Great Barrier Reef. Demography was also strongly influenced at a broad geographic scale, when comparing populations between Guam and the GBR. Although fishing effects on demographic characteristics of *S. psittacus* were minimal, future studies should be carried out for other species and families to better understand anthropogenic influences.

Chapter 6: General Discussion

This thesis examined demographic and reproductive parameters of coral reef fish in order to assess the impacts of fishing, habitat and geographical influences. This was accomplished by examining variation in demography and reproductive characteristics of parrotfish species with respect to environmental effects, broad scale variation between Guam and the GBR and local scale variation (habitat effects), as well as the potential impacts of fishing. Knowledge of how demography and reproductive characteristics vary in coral reef fishes is important for two reasons. First, because coral reef fish have a wide distribution, information on demographic characteristics is important in understanding reef fish ecology. Second, coral reef fish are under increasing fishing pressure, and details of their demography and reproductive traits will provide useful information for management plans.

Information on demography and reproductive characteristics in the literature is predominately focused on temperate fish (but see Robertson & Warner 1978). However, to date there are few demographic studies on coral reef fish due to the complexity of environment influences, where reef fish are more impacted by habitat shifts. Studies have found temperate species to be long lived, slow growing to a large final adult size and late maturing, with these life history traits characteristic of cold water environments (Roff 1984) . In contrast, coral reef environments are complex, with the presence of many different habitat types in one location. The demography and life history traits of coral reef fish will not only differ between species groups, but will also vary within a group which is dependent on which habitat type the species is located. Therefore, management strategies in place for temperate fishes should not be applied to coral reef fish.

Parrotfish are a complex group, mainly because of their reproductive characteristics. This thesis provides evidence that we can use to start to distinguish differences in life history characteristics within this group. Evidence of a clear effect on size was demonstrated within the parrotfish group. For a large species, *Chlorurus microrhinos*, similar patterns of growth and life span occurred at a local scale. However, for all small species considerable differences in growth and life span for fish occupying outer reef habitats compared to mid reefs on the GBR. This finding was very important, especially when we consider the potential effects of fishing on population biology of parrotfish species. Since all larger parrotfish species have been essentially fished out, the fisheries are now targeting smaller species.

The analysis in this thesis provides evidence of consistent differences in growth patterns linked to particular life history characteristics. Species with indeterminate growth patterns had a higher proportion of primary males in the population than species with asymptotic growth. Species with asymptotic growth (*Scarus frenatus*, *Scarus niger* and *Chlorurus sordidus*) attained an asymptotic size very quickly (within 3 to 5 years) and spend much of their life span (often >80%) at that size. In contrast, species with indeterminate growth (*Chlorurus microrhinos* and *Scarus psittacus*) invest in somatic growth throughout much of their life span and will reach half their growth late (often >40%). This data is similar with observations of acanthurids (asymptotic growth) and reef gobies (indeterminate growth) (Choat & Axe 1996, Hart & Russ 1996, Hernaman & Munday 2005).

Although this thesis provides information on growth and life spans of parrotfish, more importantly it provides information on reproductive parameters. Information on maturation, specifically age at maturity, and reproductive parameters can be useful tools in understanding the responses of fish to any influence. A general trend in maturation and sexual transformation occurred at a local scale across the scarine labrids. We distinguished parrotfish populations matured at younger ages, as well as, changed sex earlier on exposed (outer) reef habitats compared to populations sampled from mid shelf habitats. Similar findings of earlier maturation and sex change were reported for *Scarus frenatus* and *Chlorurus sordidus* between mid and outer reefs on the GBR by Gust (2004) and it was suggested that increased mortality rates and reduced growth of populations on outer shelf reefs lead to maturation of younger and smaller individuals.

Comparative analysis of life history characteristics between species revealed species with similar growth patterns and life spans have contrasting demographic patterns. Both *Chlorurus sordidus* and *Scarus psittacus* are short lived species with high turnover rates, very abundant and have high recruitment rates. However, timing of maturation and sexual transformation revealed different outcomes between species. *C. sordidus* populations matured at younger ages and changed sex earlier on outer shelf reefs compared to mid shelf reefs, while the opposite was observed for *S. psittacus* populations. This suggests that *S. psittacus* does well in exposed areas, where there is less competition for resources for *Scarus psittacus* in outer reefs compared to *Chlorurus sordidus.*

What I have been able to do with the analysis in this thesis is to comment on the effects of fishing. First, it seems that for small parrotfish natural effects are just as big as fishing effects. Other studies have shown weak fishing effects in response to abundance, size and species richness in parrotfish (Russ & Alcala 1989, Russ & Alcala 1998, Jennings *et al*. 1999) and suggest habitat and recruitment variation play a more significant role in population dynamics of parrotfish.

Second it seems direct effects of fishing are not so obvious. The fishing effect on *Chlorurus sordidus* and *Scarus psittacus* was not nearly as pervasive as what was expected. Although populations in fished areas were smaller, had reduced growth, matured earlier and changed sex earlier, such differences were minimal when compared to differences observed for natural variation of demographic traits. However, substantial empirical evidence is available for changes in size structure, growth rates, longevity and age at maturity for many exploited populations, such as the North Atlantic cod (Beacham 1983, Sinclair et al. 2002, Barot et al. 2002, 2004, 2005, Olsen et al. 2004), plaice (Rijnsdorp 1993, Grift et al. 2003, 2007), and Atlantic silverside (Conover & Munch 2002). All of these studies have shown direct effects of fishing to select for smaller sizes, reduced growth, shorter life spans and earlier maturation. One problem that may have influenced the results is that in Guam parrotfish are heavily targeted and this makes it hard to detect any fishing effects.

Future directions

While this thesis provides important data on growth, longevity and reproductive parameters of parrotfish species, more research is needed to understand the relationship between the three demographic traits. Also, further research on potential influences of fishing on parrotfish species should be considered. It may be that the location chosen, Guam, has more of a habitat influence that overshadows any potential impacts of fishing. Therefore, other locations in the Indo Pacific that target parrotfish may be beneficial to look at.

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Appendix:

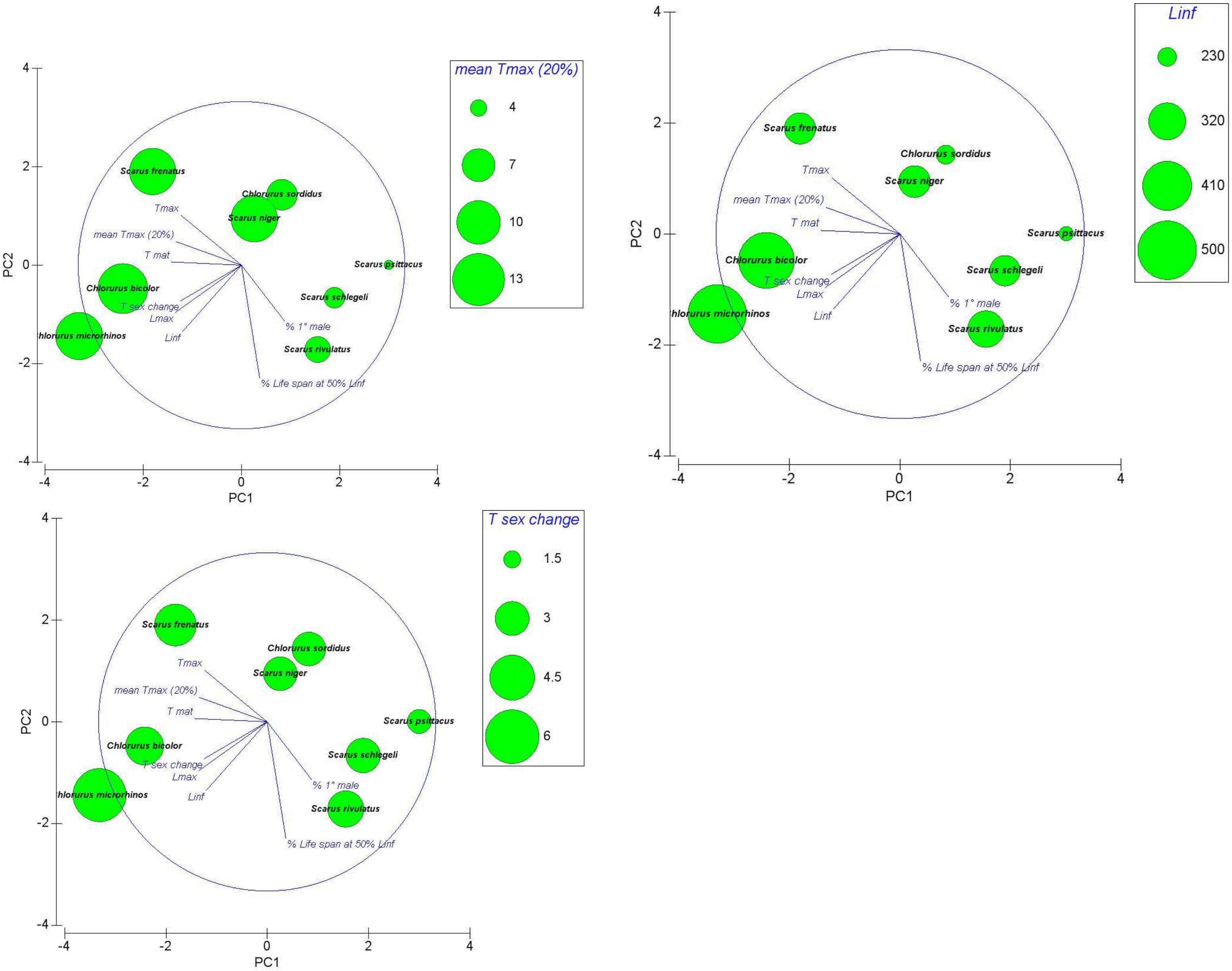

Fig. 1: PCA ordination of life history parameters of eight parrotfish species from the GBR, showing eigenvectors of life history variables and the shape of gradients for mean longevity (T_{max}) (top left panel), growth function L_{inf} (top right panel) and age at sex change ($T_{sex\ change}$) (bottom left panel). Bubble size represents gradients from lowest to highest values of mean life span, growth and age at sex change.

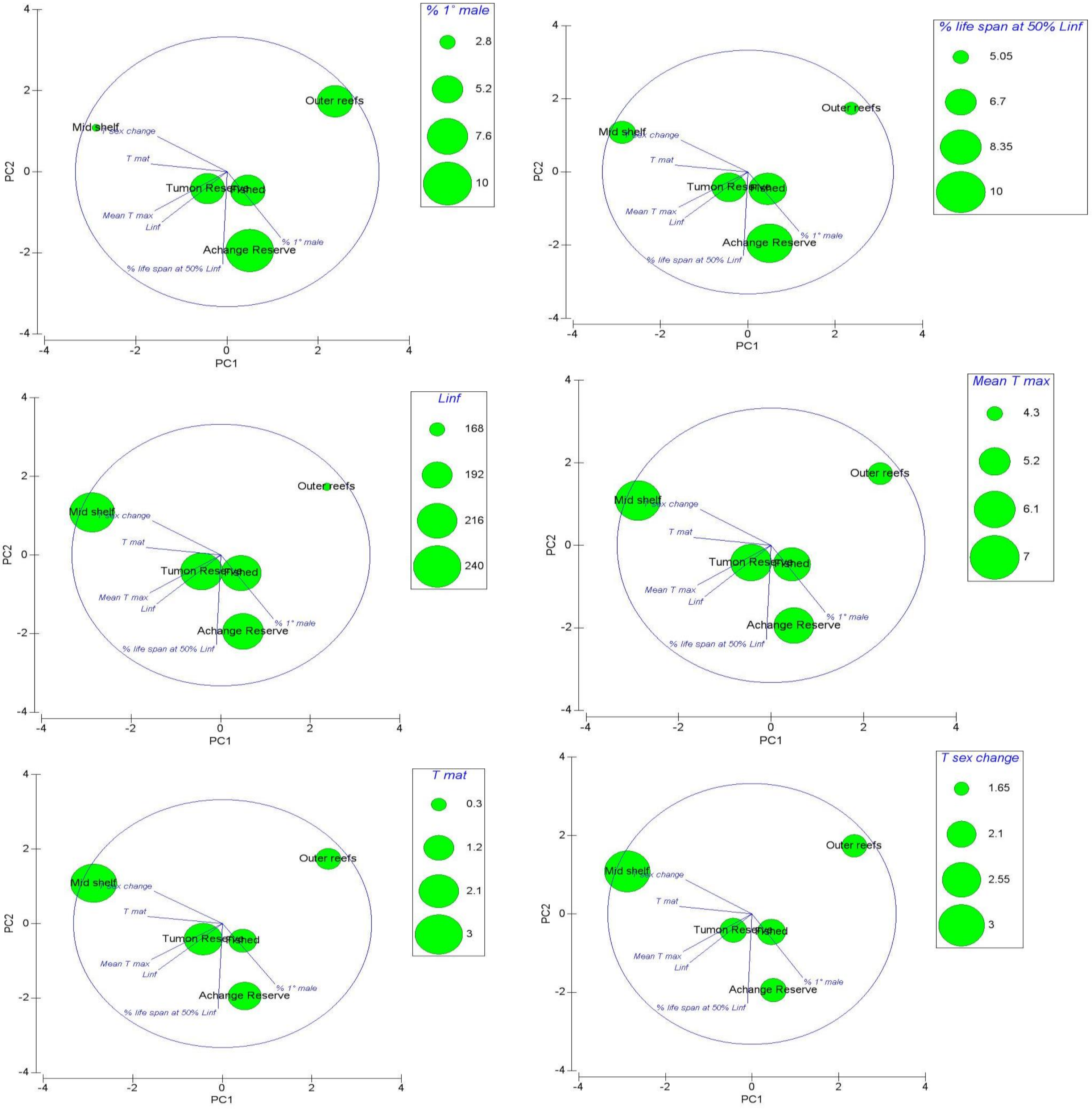

Fig. 2: PCA ordination of life history parameters of *C. sordidus* from mid and outer shelf reefs on the GBR and fished and reserve areas in Guam.

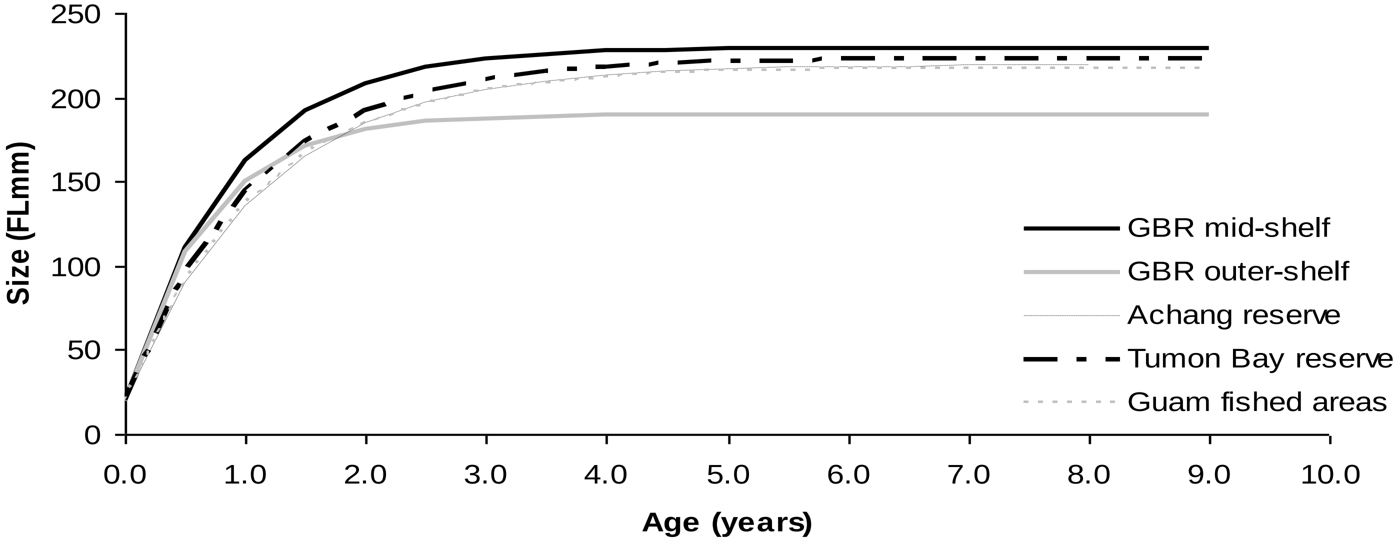

Fig. 3: Von Bertalanffy Growth Function (VBGF) curves for populations of *C. sordidus* from Guam and the GBR.

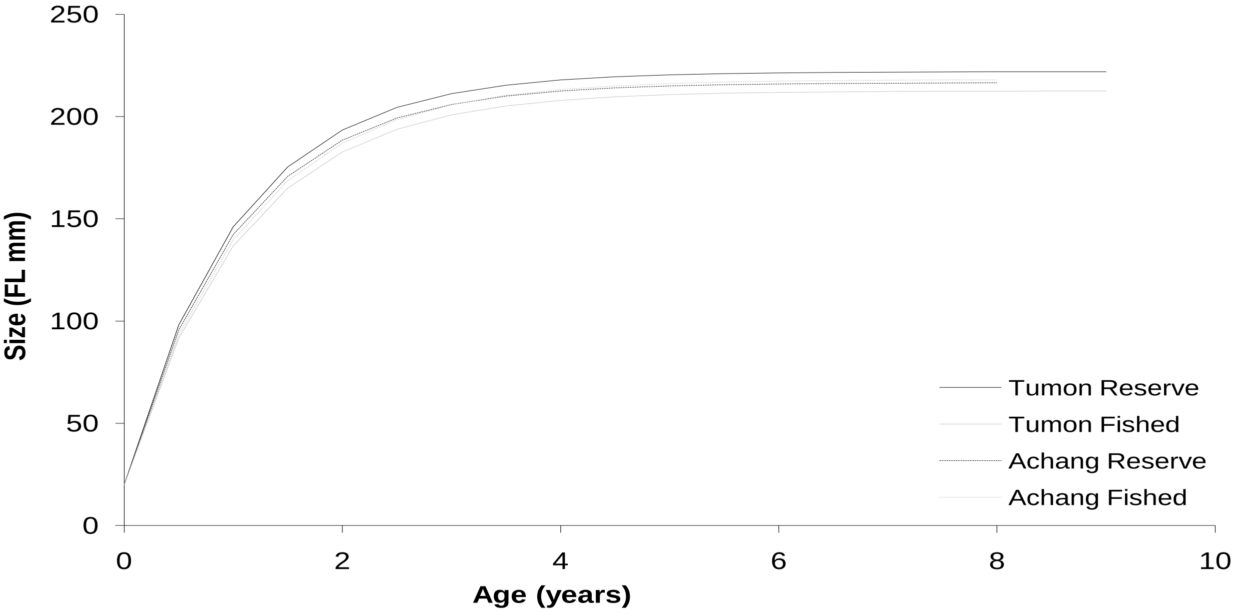

Fig. 4: Preliminary analysis of growth rate between two reserve areas, Tumon Bay and Achang, with adjacent fished areas. Similar patterns were found when combined fished areas.

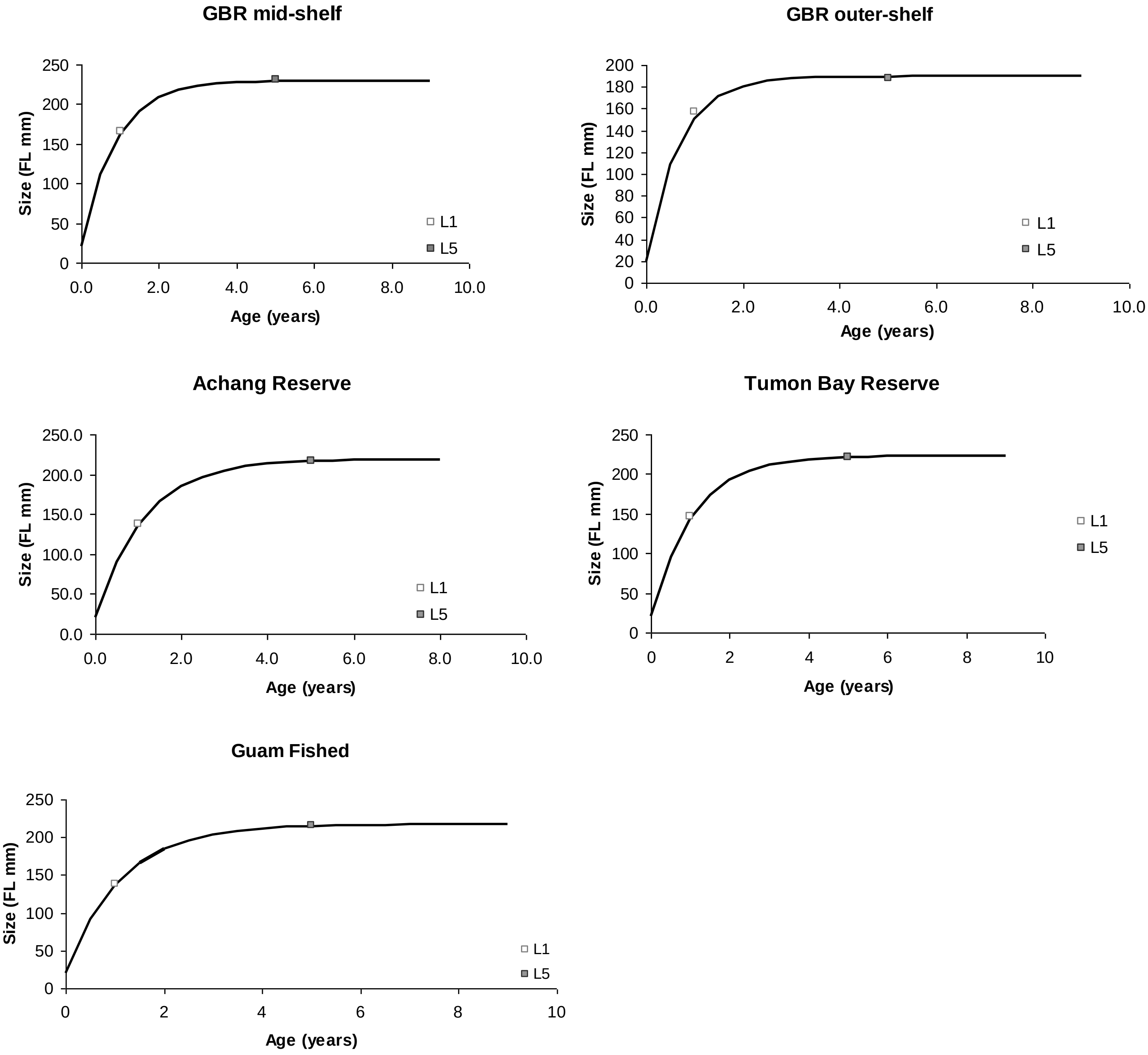

Fig. 5: rVBGF parameters L_1 and L_5 for each *C. sordidus* population in Guam and the GBR.

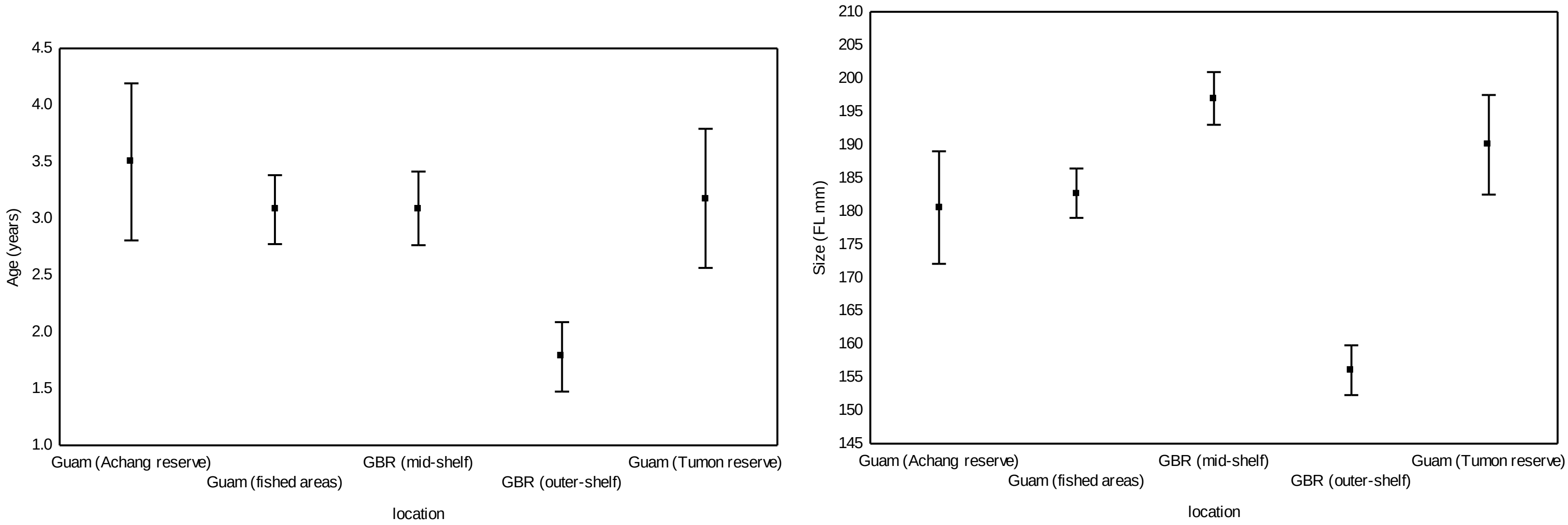

Fig. 6: Mean ages and sizes of female *C. sordidus* from reserve and non-reserve locations in Guam and across shelf positions in the GBR.

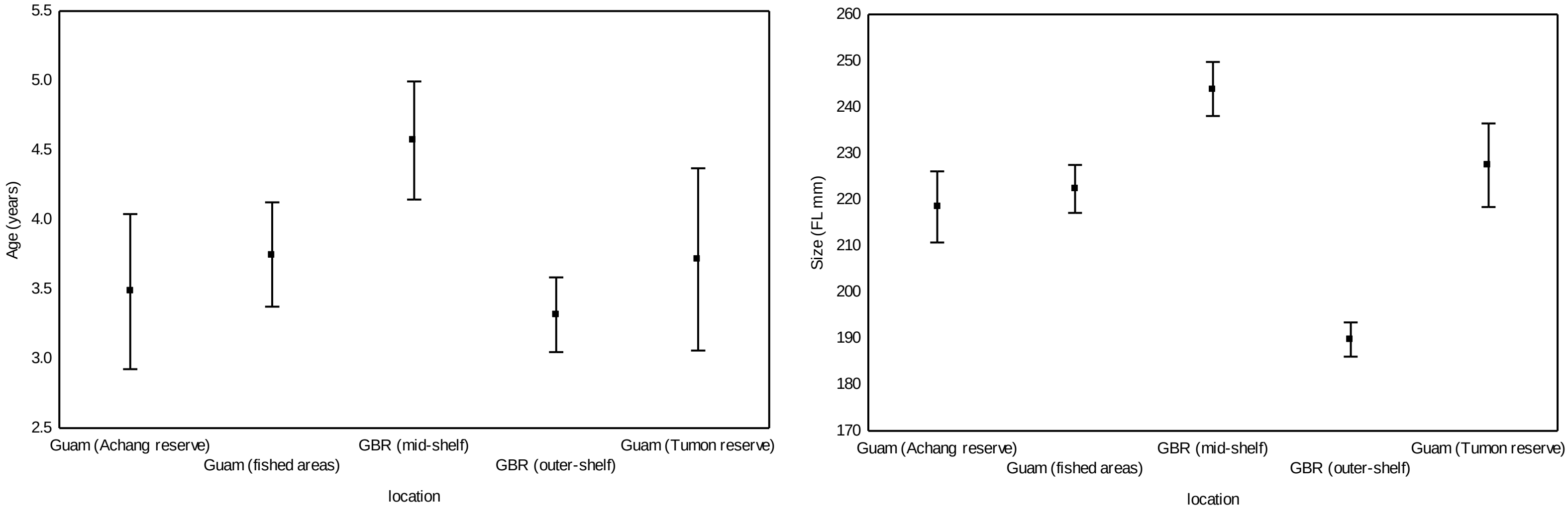

Fig. 7: Mean ages and sizes of male *C. sordidus* from three locations in Guam and across shelf positions in the GBR.

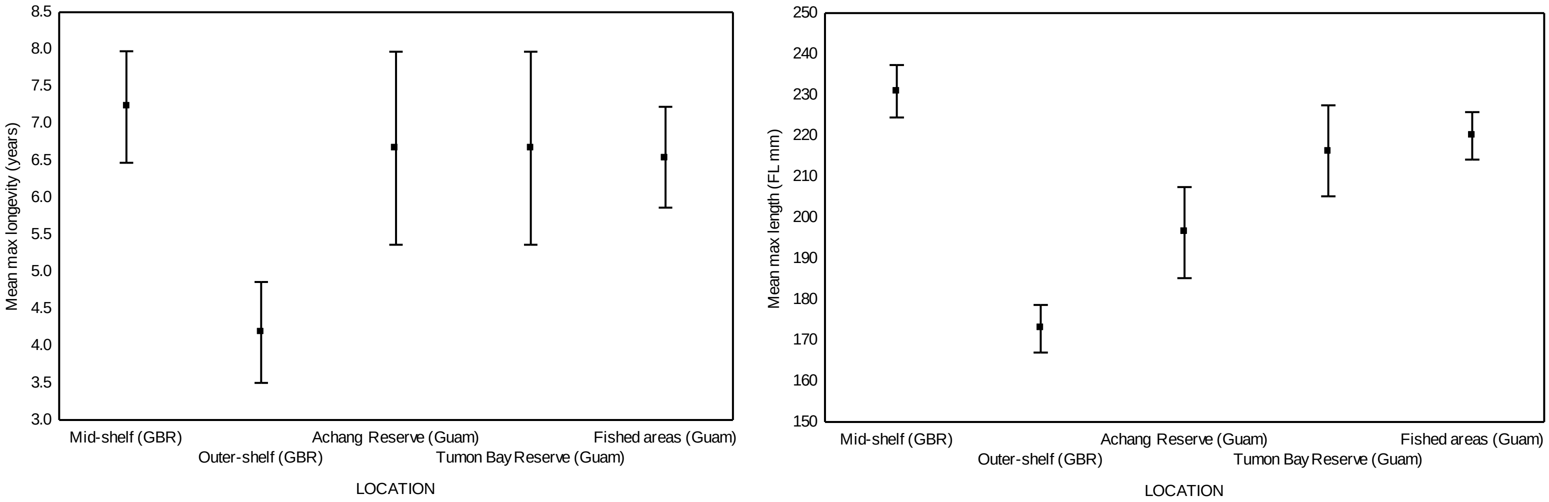

Fig. 8: Mean maximum age and size for female *C. sordidus* populations from Guam and the GBR.

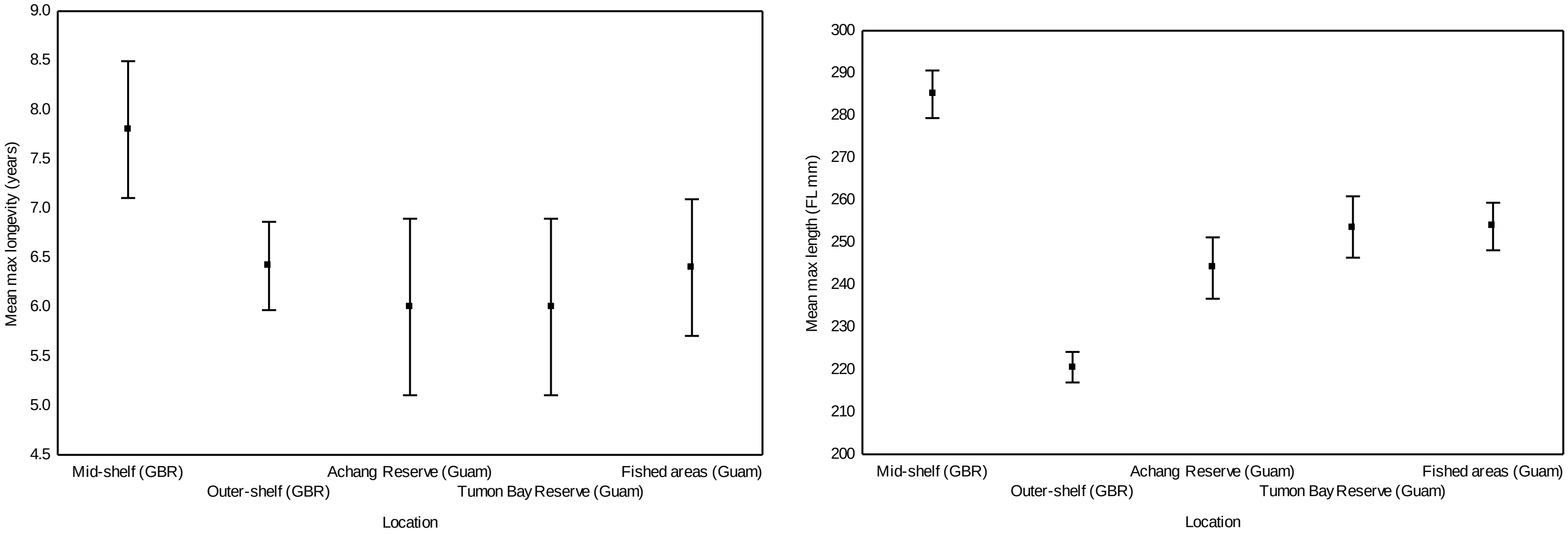

Fig. 9: Mean maximum longevity and length for male *C. sordidus* populations from Guam and the GBR.

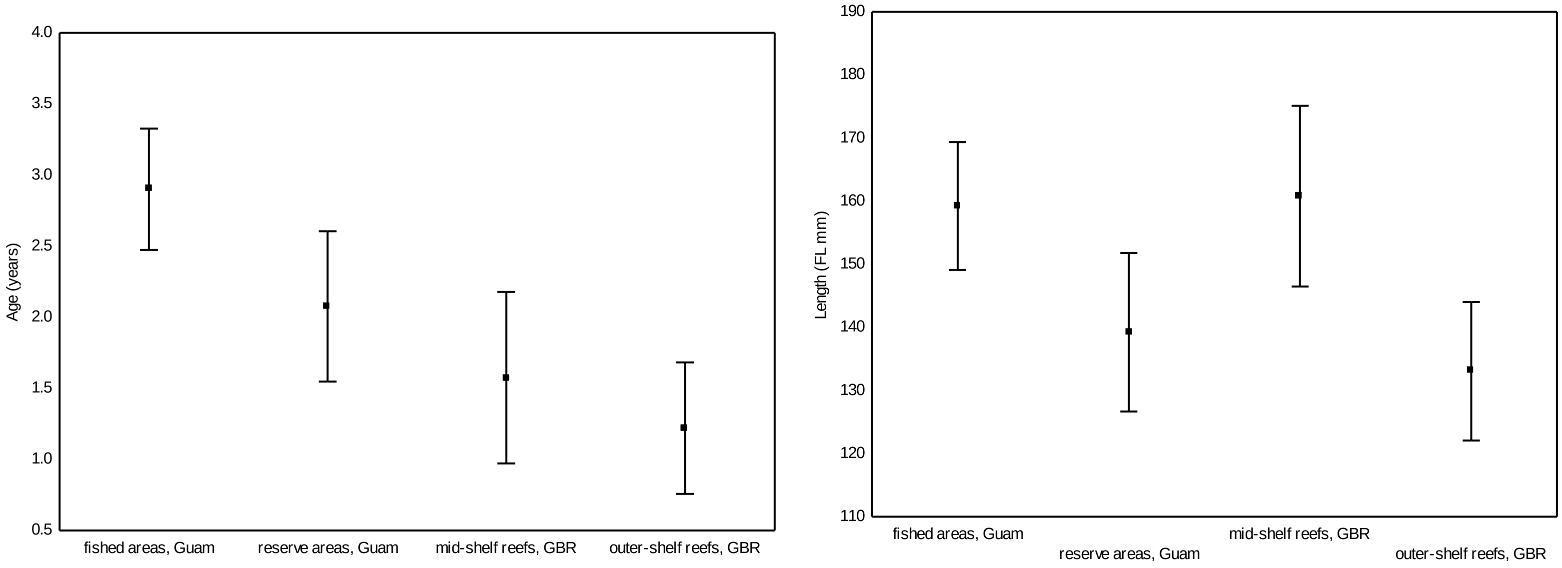

Fig. 10: Mean age and adult size of female *S. psittacus* populations from Guam and the GBR.

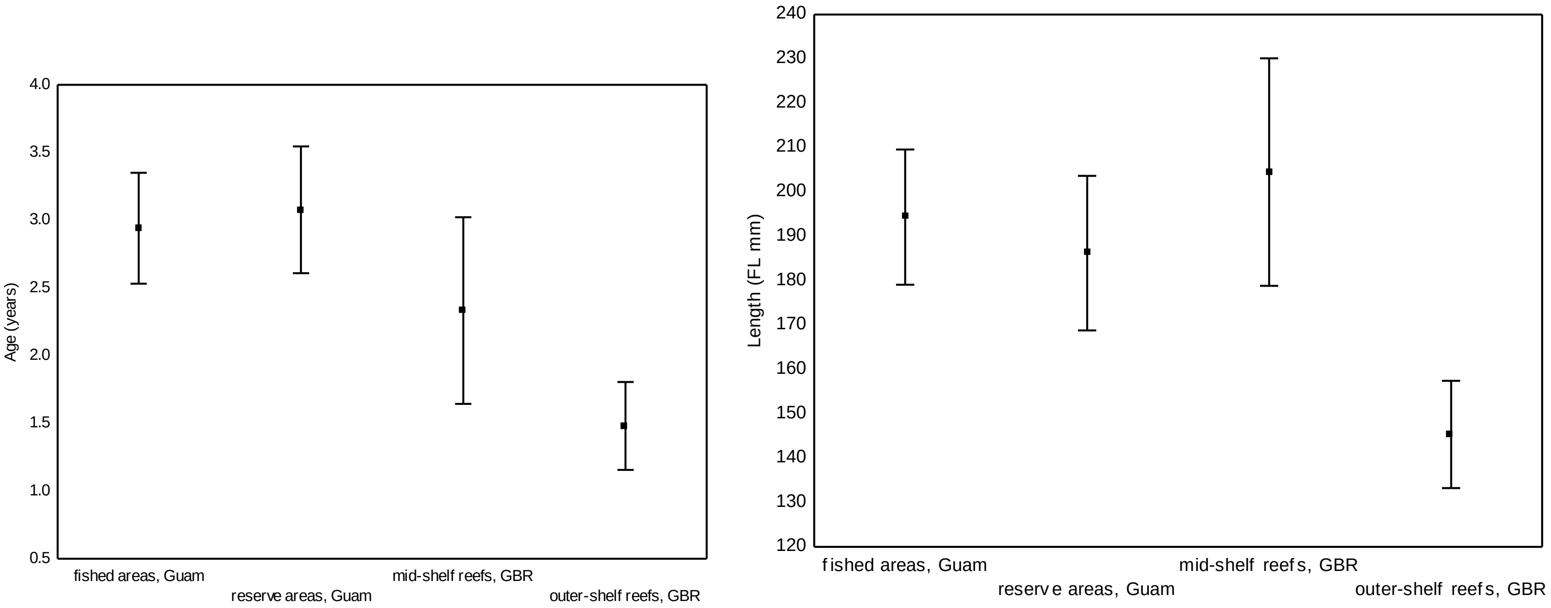

Fig. 11: Mean age and size of male *S. psittacus* populations from Guam and the GBR.

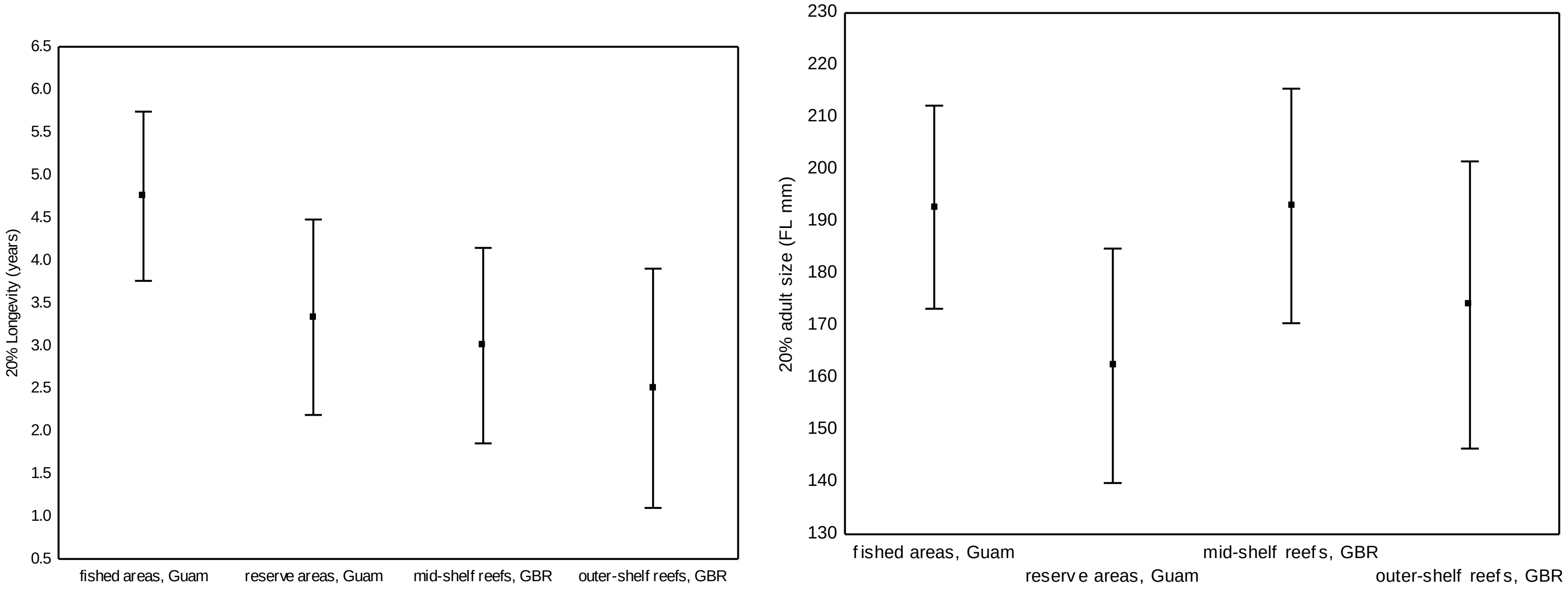

Fig. 12: Maximum longevity and adult size of female *S. psittacus* populations between Guam and the GBR.

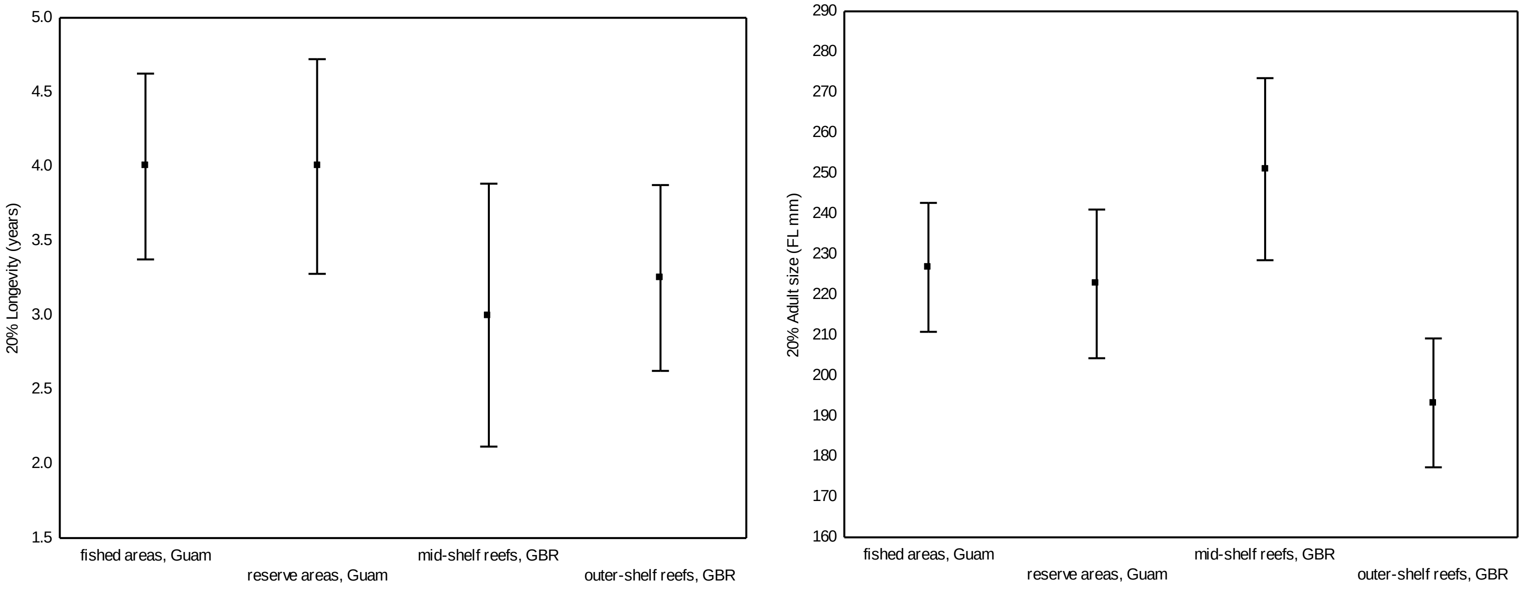

Fig. 13: Comparison of maximum longevity and adult size of male *S. psittacus* populations from Guam and the GBR.

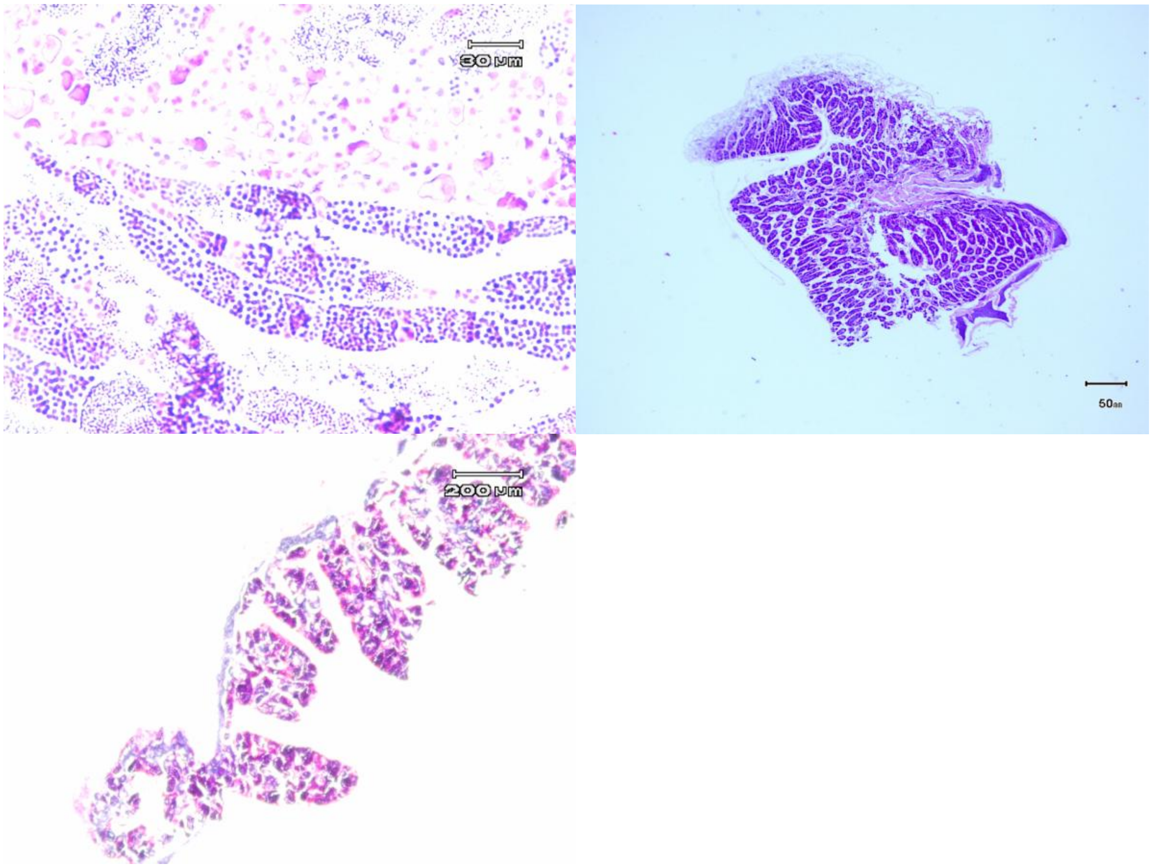

Fig. 14: Histological photos of male *C. sordidus* gonads, with classifications of: top left transitional phase, top right primary male phase and bottom left secondary male phase.

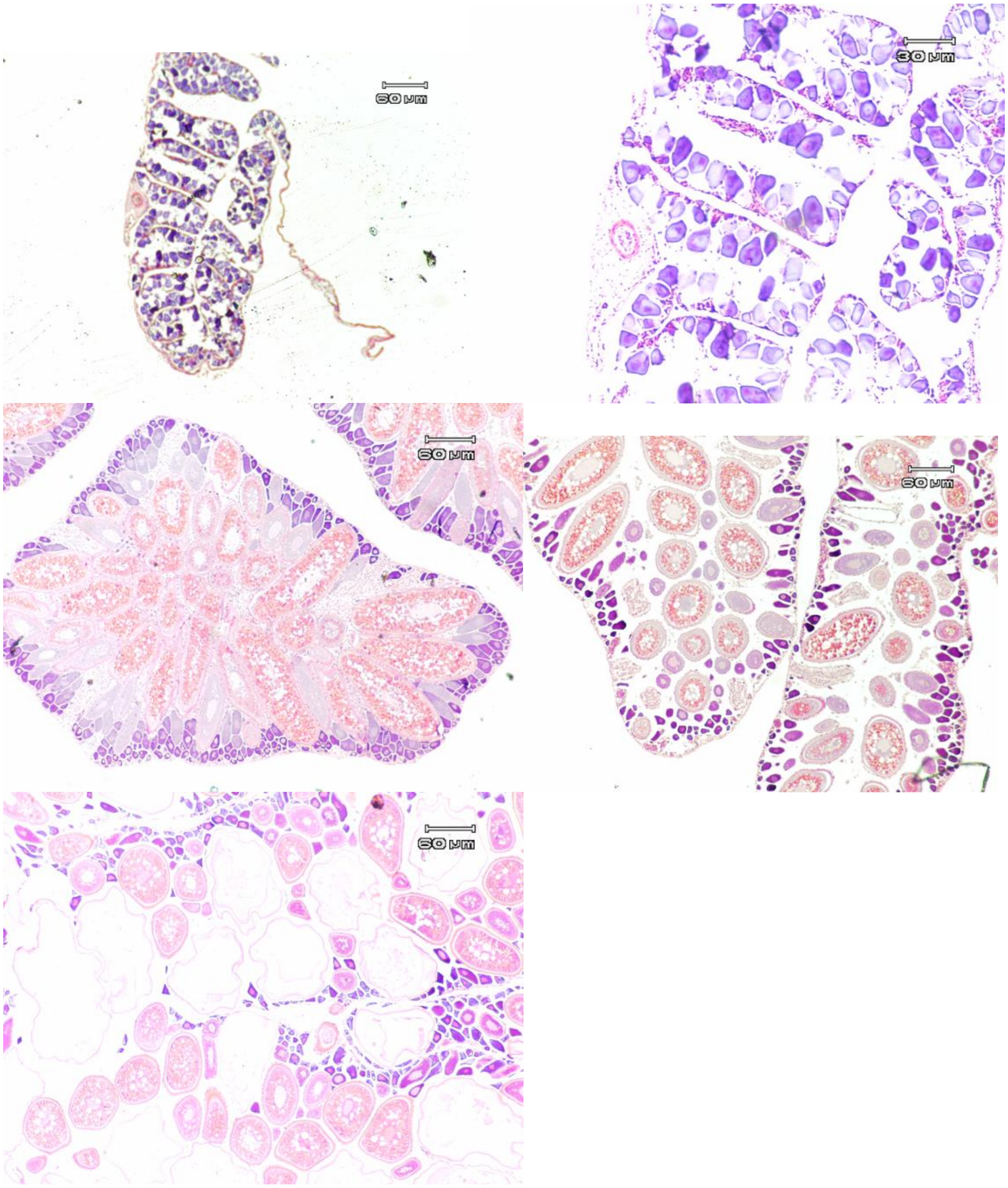

Fig. 15: Histological classification of female *C. sordidus* gonads. Top left shows immature female phase, top right mature resting phase, middle left mature ripe phase, middle right mature spent phase and bottom left mature hydrated phase.