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Demographic and Reproductive Characteristics of the Squaretail Coralgrouper (*Plectropomus areolatus*) in Solomon Islands.

Thesis submitted by

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Bachelor of Science (James Cook University)

Postgraduate Diploma of Research Methods (James Cook University)

in August 2017

for the degree of Doctor of Philosophy in Marine Biology

with James Cook University

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To my Parents.

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Jenno with her *Plectropomus areolatus* catch of the day.

Photo courtesy of Stu Cawlker

Abstract

The overall goal of this study was to examine the age-based demographics and aggregating behaviour of *Plectropomus areolatus* in Solomon Islands, so that culturally appropriate management strategies could be developed for this species. To place this work within a regional context I began by examining the abundance patterns of *Plectropomus* species in Australia, Papua New Guinea and Solomon Islands. The analyses show that *P. leopardus* and *P. laevis* dominate the reefs of north-eastern Australia while *P. areolatus* is the most prevalent species in the western Solomon Islands. A more in-depth look at *P. areolatus* abundance was made possible by examining populations at three locations in western Solomon Islands that had experienced different levels of historical fishing pressure. This showed that habitat structure was a greater driver of *P. areolatus* abundance than fishing pressure. The most abundant *P. areolatus* populations occurred in habitats that provided for recruitment (inshore reefs), juvenile growth (lagoonal habitats) adult habitats (barrier reef systems) and spawning sites (well flushed reef passes linking the ocean environment with the lagoonal habitat).

The age-based investigation of the study focused on four locations in western Solomon Islands. Growth analysis revealed that this species is relatively fast growing, with most somatic development taking place in the first quarter of a moderate life-span of 12 years. There were sex-specific differences in growth with males growing faster and reaching larger sizes than females. Patterns of growth varied between study locations, with the variation observed explainable in terms of historical fishing pressure. An investigation of the reproductive biology of *P. areolatus* indicated that the sexual pattern of *P. areolatus* was gonochoristic, which differs from the pattern of protogynous reproductive development previously suggested for this genus. Males pass through an immature bisexual phase before maturing and recruiting into the population. In the western Solomon Islands heavily fished populations reached sexual maturity at an earlier age than lightly fished populations.

A multi-year investigation on the spatial and temporal dynamics of a grouper spawning aggregation was carried out at Ghizo where the brown-marbled grouper, *Epinephelus fuscoguttatus*, camouflage grouper, *Epinephelus polyphekadion*, and squaretail coralgrouper, *Plectropomus areolatus* are known to aggregate. Both *Epinephelus* species aggregated from February to July each year, whereas *P. areolatus* formed aggregations in every month of the year. Aggregations of all three groupers peaked between March and June. Spawning aggregations were tightly linked to the lunar cycle, with peak densities of all species seen several days prior to the new moon, the lunar period when the gonado-somatic index for *P. areolatus* also peaked. *P. areolatus* densities were higher in the shallower depths, with the reverse pattern seen in *Epinephelus* species. A marked drop in mean aggregation densities for *P. areolatus* towards the end of the 5-year monitoring period appears to be due to excessive fishing pressure at this aggregation site. The findings of this research demonstrate that *P. areolatus*, an economically important species in Solomon Islands, is particularly vulnerable to overfishing due to its predicable aggregating behaviour. As a result of this study, management regulations for aggregating groupers are currently being incorporated into the Western Province Fisheries Ordinance and the Solomon Islands 2016 Fisheries Act.

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1 General introduction

1.1 Coral reef fish spawning aggregations

Coral reef fish form aggregations at a number of temporal and spatial scales and for a variety of purposes. This may include feeding schools (grazing parrotfish and surgeonfish, planktivorous fusiliers and trevallies) or aggregations that form primarily for reproductive purposes, in which groupers and snappers are the best examples (Hamilton & Walter 1999, Welsh & Bellwood 2012, Claro & Lindeman 2002). Feeding schools usually form on a daily basis (Johannes & Hviding 2000) and occur over wide areas and that can be readily located over the normal habitats of the groups in question (Welsh & Bellwood 2012). Species that aggregate for reproductive purposes do so on longer time scales, often at predicable locations on the reef and during specific lunar and seasonal periods (Domeier & Collin 1997). When aggregations are restricted to specific sites, these sites often have particular physical features that are thought to facilitate the successful dispersal and/or retention of larvae (Hamner et al. 2007, Hamner & Largier 2012). These reproductive aggregations are generally classified into resident and transient aggregations based on the distance that spawners travel to reach spawning sites. Resident spawning typically takes place within the species normal home range and can occur on a daily basis all year round. Transient spawners usually undertake longer migrations and congregate over a much shorter time period within the year (Domeier & Colin 1997). Species with larger body sizes (>40cm) are more likely to form transient aggregations (Choat 2012).

Fishers often have detailed local ecological knowledge pertaining to the locations, species composition and lunar and seasonal timing of aggregation formation (Robinson et al. 2008). Indeed, for commercial fishes such as groupers and snapper, most aggregations that have been documented and studied by scientists were initially identified from descriptions from fishers (Hamilton et al. 2012). While the predictable nature of these aggregations make them lucrative targets for fishers, it also renders aggregating species susceptible to overfishing (Sadovy de Mitcheson et al. 2013). Fishers target aggregations due to the high catches that can be obtained, and there are numerous examples globally of the negative impacts of excessive fishing pressure on fish spawning aggregations. For instance, the Science and Conservation of Fish Aggregation (SCRFA) database shows that approximately one quarter of exploited reef fish spawning aggregations have experienced reductions in breeding stocks and 4% of all known aggregations have ceased to form (Russell et al. 2014).

Although there are numerous examples of aggregations that have been discovered and exploited (Russell et al. 2014), the wide-spread distribution of coral reefs, the complexity of their habitats and the diversity of reef fish species means that the features that define the location and size of spawning aggregations are often poorly understood (Sadovy & Collin 2012). There is now an increasing recognition that the behaviour of aggregating species and their responses to fishing is best understood by obtaining a comprehensive understanding of aggregating species habitat requirements, life cycles and the extent to which fish populations are exploited during both aggregating and non-aggregating phases. This means that the study of aggregations and the impact of fishing requires an integrated view that links the understanding of spawning aggregations to non-aggregation abundance patterns, habitat structure and the life cycle of the study species. This is especially true for epinephelid groupers which in the western and central Pacific form an important element of the coral reef fisheries (Frisch et al. 2016). The present study recognizes the need to understand the main features that underlie the formation of spawning aggregations. These include; 1) the habitat structure and morphology of reef systems and the degree to which they support grouper aggregations, 2) the impact of and response to different levels of fishing pressure, 3) the importance of monitoring abundance patterns and life history features such as growth rates and longevity as a measure of fishing pressure, and 4) the nature of the reproductive cycle and the environmental signals that determine the timing and duration of aggregations.

1.2 Coral reef fisheries

Coral reef fisheries contribute an estimated 10% of total world marine fishery landings (Russ 1991, Munro 1996, McManus et al. 2000, Sadovy 2005) and support the livelihoods of millions of people (Cinner et al. 2013). Most of the world’s coral reefs are located within developing Indo-Pacific countries, and for these nations coral reef fisheries are an integral part of subsistence and artisanal economies and culture, providing food, livelihoods and incomes for millions of individuals (Sadovy 2005, Aswani et al. 2015). High levels of artisanal and destructive fishing have resulted in overfishing and degradation of many of the coral reef ecosystems worldwide (Hughes 1994, McManus 1996, Munro 1996, Jackson 1997, Hinrichsen 1998, Jackson et al. 2001, Sadovy 2005). Increasing access to global markets for fisheries products from tropical developing countries has increased pressure on high value species, often resulting in severe depletion of stocks and associated habitat destruction (Dalzell et al. 1996, Sadovy et al. 2013). Overfishing, combined with coastal development, climate change and rapid population growth throughout much of the Indo-Pacific is placing unprecedented pressure on the worlds coral reef fisheries (Hughes et al. 2017).

The lack of qualified personnel and scientific data on coral reef fisheries has hindered the establishment of management strategies to monitor and manage important reef fish stocks in most areas of the Indo-Pacific (Johannes 1998). Furthermore, while many Pacific island communities have detailed local ecological knowledge on the status of their fisheries, efforts to access and incorporate this information into formal fisheries management strategies remains the exception rather than the norm (Johannes 1998). Coral reef fisheries are particularly difficult to manage due to their multi-species harvest, multi-gear use and spatial complexity characteristics (Jennings & Lock 1996, Jennings *et al*. 1998). With population growth within Indo-Pacific countries expected to double within the next 30-50 years and increasing access to global markets (Richardson 2015) the pressure on coral reef ecosystems and marine resources will increase enormously. Therefore, there is an urgent need to better understand and sustainably manage coral reef fisheries so that they continue to provide the ecosystem goods and services for the millions of people whom depend on them (Sadovy 2005).

1.3 Environmental and fishing effects on fish assemblage

Several large-scale studies have focused on the relationship between human population (as a proxy for fishing pressure) and their impact on the community structure and diversity of fish stocks on coral reefs (Hawkins & Roberts 2003, Pinca et al. 2012, Taylor 2014). A recurrent theme from these investigations is that anthropogenic activities have a negative impact on fish abundance. For instance, locations with very low or non-existent human populations have been shown to have higher fish densities and biomass compared to locations that have higher human populations and/or are closer to fish markets and communities that are largely dependent on fishing for a living (Cinner & McClanahan 2006, Brewer et al. 2012, Cinner et al. 2013). However, a multi-scale study on parrotfish assemblage structure by Taylor et al. (2015), revealed that localized fishing pressure and biophysical features of the reef were both important factors at a within-island scale, while island geomorphology and species distribution patterns influenced broader between-island scale patterns. This highlights the need for management to have a good understanding of the fundamental effects of island geomorphology (including reef structure) on abundance patterns of target species when factoring in fishing effects (Pinca et al. 2012).

Coral reef fisheries management in Pacific Islands typically deal with reef resources at the scale of 1-10 km^2, which represent the spatial scales of customary ownership (Almany et al. 2015). At these spatial scales knowledge on the habitat requirements of a target species and how this may change at various stages of ontogenetic development (Hamilton et al. 2017) will help better inform management and conservation goals. While scientific studies at small spatial scales may not exist, this information can often be obtained if the appropriate qualitative methods are utilized to document the local knowledge of fishers (Neiss et al. 1999). As well as providing information on the habitat requirements of target species, fishers can also provide information on the relative abundances of reef fish species at different geographies, the locations and timings of spawning aggregations and an historical perspective on the state of reef fish communities (Johannes et al. 2000, Hamilton et al. 2012).

1.4 Groupers

The Epinephelidae are a biologically diverse group made up of 165 species in 16 genera known commonly as groupers, coralgroupers, rock cods, hinds and lyretails (Craig et al. 2012). They are known to be important apex predators playing a major role in structuring coral reef communities (Unsworth et al. 2007). Epinephelids are also known to possess several common biological characteristics such as rarity, long lifespan, relatively slow growth, late effective maturity, protogynous sex change, and the formation of spawning aggregations, which when coupled with their relative ease of capture at spawning aggregation make them particularly susceptible to overfishing (Sadovy 1996, Huntsman et al. 1999, Jennings et al 1999, Morris et al 2000, Pears et al. 2006).

The genus *Plectropomus* is made up of 8 species (Ma et al. 2016) and is mainly confined to the Indo-Pacific region between depths of 2-20m where it can attain lengths between 50-100cm depending on the species (Heemstra & Randall 1993, Lieske & Myers 1994). Members of the genus are closely related to the similar-shaped *Variola* species and are commercially important in tropical fisheries throughout their distribution (Bentley 1999, Ma et al. 2016, Fricsh et al. 2016). A study by Pears (2005) reported that *Plectropomus* species attain higher numbers within coral reefs compared to *Epinephelus* species, which suggests that encounter rates with fishing gear may be higher in this genus. *Plectropomus* species are generally more elongated and less sedentary than other groupers and tend to be observed actively roving the reef system (Sluka & Reichanbach 1995) and this may increase potential encounters with fishing gear. Three species within this genus are regularly sought after in the international Live Reef Fish Food Trade (LRFFT), *P. leopardus, P. maculatus* and *P areolatus* with the *P. leopardus* and *P. maculates* attaining a higher market value than the "medium value" *P. areolatus* (Sadovy et al. 2003).

Much of the research conducted on this genus has taken place in developed countries such as Australia, and has focused largely on *P. leopardus* followed by *P. maculatus,* both important species in recreational and commercial fisheries (e.g. Ferreira & Russ 1992, Samoilys 2000, Adams 2002, Begg *et al.* 2005, Wen et al. 2013). Species within this genus that occur in Pacific Island countries have generally received relatively little attention despite their importance in local fisheries. Past investigators have used the well-known life history parameters of the closely related *P. leopardus* to make conclusions on the *P. areolatus* (see Johannes *et al*. 1999). However, recently, there has been an increasing number of studies that have looked at various life history aspects of *P. areolatus* within the region (Hutchinson & Rhodes 2010, Hamilton et al. 2012, Almany et al. 2013, Rhodes et al. 2014).

1.5 *Plectropomus areolatus* in Solomon Islands

Like many Epinephelids, *P. areolatus* is known to form spawning aggregations throughout the Indo-Pacific (Hamilton et al. 2012, Rhodes et al. 2014, Karkarey et al. 2017). Recurrent fishing pressure on *P. areolatus* spawning aggregations by small and large-scale commercial fisheries has led to a reduction in abundance on reefs in Palau (Johannes *et al* 1999), Pohnpei (Rhodes et al. 2014), Fiji (Sadovy 2004), Papua New Guinea (Hamilton and Matawai 2006, Hamilton et al. 2011) and Solomon Islands (Hamilton et al. 2012). Apart from these reductions in abundance, the impacts of fishing on *P. areolatus* in terms of the size and age at maturity and sex ratio has received little attention (but see Johannes *et al*. 1999, Rhodes et al 2013). Past studies with similar species *P. leopardus* and *P. maculatus* (Ferreira 1993, 1995, Adams 2003) indicate that *P. areolatus* may be capable of protogynous sexual development. However, a recent study on the reproductive development of this species in Micronesia could not find any conclusive evidence of protogyny (Rhodes et al. 2013) which suggests that this species might be gonochoristic. Therefore further investigation into the reproductive biology of this species is warranted.

A recent fish market-based survey that took place over a 13-month period in the national capital of Solomon Islands, Honiara, showed that *P. areolatus* is the most commonly sold grouper species in the national capital of Solomon Islands. The survey also revealed that *P. areolatus* was the 6th most common species to be imported from Western Province (Rhodes & Tua 2016). It accounted for 2.6% of the overall catch that was sourced from Western Province during that period. Compared to other provinces, there were 837 *P. areolatus* sold in Honiara originating from Western Province followed by 25, 23, 6, 0 from the provinces of Central, Malaita, Isabel and Guadalcanal respectively. Whilst other factors are likely to be involved in determining the composition in catches (e.g. frequency of inter-island shipping, dominant type of fishing pressure, gear type commonly used, etc), the increased availability of complex reef habitat suitable for both juvenile and adult life phases is a plausible reason as to why this species makes up an important component of commercial catches from Western Province.

Local fishers detailed local knowledge on *P. areolatus* aggregations in Western Province (Johannes 1988) and a long history of exploiting these aggregations (i.e. Hamilton and Kama, 2004; Hamilton et al. 2012) is another likely reason for high *P. areolatus* landings in this province. The New Georgia island group that makes up the Western Province includes the lagoon systems of Ghizo, Vonavona, Roviana and Marovo. This represents the largest grouping of lagoon systems in Solomon Islands and provides ample habitat for all life stages of this species. Juvenile *P. areolaus* typically recruit into shallow lagoonal patch reefs in close proximity to land (Almany et al. 2013), undergo an ontogenetic migration to deeper lagoonal and outer reefs as adults and form transient spawning aggregations on the outer reef promontories or channel mouths that connect lagoons to the open sea (Rhodes et al. 2011, Johannes 1988, Hamilton and Kama 2004).

The current study is centred on gaining a better insight on the demographic and reproductive patterns of *P. areolatus* in order to make available information that can lead towards the design of meaningful management strategies in Solomon Islands. In order to accomplish this, the study starts off by examining *Plectropomus* abundance in neighbouring tropical reef systems within the Indo-Pacific region and relates this to observed patterns in Solomon Islands, to see how natural and anthropogenic processes may have had an impact on local fish stocks. Further information on the demography (growth rate, longevity) and reproductive (size and age at maturity, reproductive development, spawning aggregations) aspects of *P. areolatus* were collected to elucidate further the potential vulnerability of this species to fishing pressure.

1.6 Structure of thesis

Chapter 2 attempts to understand the important factors driving the population dynamics of *P. areolatus* on coral reefs in Solomon Islands. It does this by examining the level of influence fishing pressure and available reef habitat present on three reef systems in Western Province and how these affect abundance and size structure of fish populations. Equipped with this information, fishery managers can better understand the dynamic variability in fish populations which will help them make better informed decisions.

Chapter 3 conducts an age-based investigation into the demography of *P. areolatus* in Solomon Islands and compares it to regional patterns. It then uses the information to investigate the potential effects that fishing pressure might have on the demographic profile of populations at neighboring reef systems.

Chapter 4 explores the reproductive development of *P. areolatus* in Solomon Islands to shed more light as to where it sits within the diverse range of reproductive pathways observed within Epinephelid species. Getting a better grasp on whether the species displays gonochoristic or hermaphroditic traits is important for determining its vulnerability to fishing pressure which in turn has important implications for management.

Chapter 5 delves further into the reproductive aspect of this species by conducting a detailed multi-year study on the spawning aggregation dynamics of *P. areolatus* in Solomon Islands which was focused on establishing trends in aggregation formation of the species. The information gathered provided insights into the duration of the spawning season (monthly) and effects of lunar phase on timing of aggregation formation. Such information is critical for designing conservation and management measures for spawning aggregations. It also demonstrated the utility of monitoring spawning aggregations to observe the status/health of populations of aggregate spawning species as a fishery management tool.

2 Abundance and size distribution of *Plectropomus areolatus*

2.1 Introduction

Coral reef systems harbor a complex range of marine habitats with diverse fish species assemblages, making them one of the most productive ecosystems in the world (Burke et al. 2011, Fenner 2012). The spatio-temporal heterogeneity of coral reefs ensures that resident fish assemblages can display contrasting patterns in abundance and distribution when examined at various scales. Much of this spatial variation can be explained in terms of the physical and biological attributes of a given location (Mora et al. 2003, Pinca et al. 2012, Taylor et al. 2015). Furthermore, where fishing is present, the selective nature of this activity can also alter the population dynamics of targeted populations (Dulvy et al. 2004, Graham et al. 2005, Gullimont et al. 2014). Gaining an understanding of the influences of environmental and anthropogenic effects on the abundance and distribution patterns of different fish species provides useful insights into the demography and life history of a species, and also allows the formulation of science-based management measures that are aimed at promoting sustainable fisheries (Houk et al. 2012, Taylor et al. 2015).

The Coral Triangle region (Indonesia, Malaysia, the Philippines, Timor-Leste, Papua New Guinea and Solomon Islands) has been reported as having a relatively high number of threatened grouper species (Sadovy et al. 2013). Yet very little information exists on the abundance and distribution patterns of commercially important grouper species in this region. In contrast, developed countries like Australia have extensive information on target species such as the highly sought-after *Plectropomus leopardus* and *Plectropomus maculatus*, which are commonly found within Australia's tropical reef systems (Ferrira & Russ 1992, Samoilys 1997, Zeller & Russ 1998, Adams & Williams 2001, Wen et al. 2013).

The genus *Plectropomus* contains seven recognized species (Ma et al. 2016) and is confined to the Indo-Pacific region, where the majority of species have broad geographical distributions and are associated with well-developed coral reef systems (IUCN 2017). They represent a distinctive group among the epinepheline fishes, as unlike the majority of the epinephelid species they are not ambush predators but actively forage for their primary prey, reef fish, above the substratum (Pears 2005). Five of the recognized taxa are recorded from the Indo-Australian Archipelago region and in Australia, where *Plectropomus* species also achieve their greatest abundances (Frisch et al. 2016). However, both species richness and abundances of *Plectropomus* spp. decline longitudinally to both the west and east of the Indo-Australia-Archipelago (IUCN 2017). Based on the above, the centre of present diversity and abundance of species of *Plectropomus* is identified as extending from the northern Philippines to latitude 30˚S of the Australian continent and is referred to in this current study as the Australia-Indo-Archipelago.

Of the five species within this geographical region, three (*P. areolatus, P. laevis, P. oligacanthus*) are associated with exposed oceanic and offshore continental reefs, especially in the central and western Pacific, with the former two showing very broad geographical distributions (Froese & Pauly 2017). The wide-spread distribution of *P. laevis* and *P. areolatus* appears to be a reflection of their association with oceanic reefs with clear oligotrophic waters, which occur throughout the Indian and Pacific oceans. *P. oligacanthus* also shares similar habitat associations, but is largely restricted to reefs in the Pacific Ocean (Heemstra & Randall 1993). Two species (*P. leopardus* and *P. maculatus*) are more strongly associated with continental margins and inshore fringing reefs, especially *P. maculatus* whose habitat is usually defined by shallow turbid fringing reefs (Craig et al. 2012). The distinctive nature of *P. maculatus* distribution is reflected in its colonization of recently inundated non-reef habitats such as the Gulf of Carpenteria; *P. maculatus* is the only member of the genus to do so. The two additional members of this genus, *Plectropomus punctatus* and *P. pessuliferus*, are largely confined to the central and western regions of the Indian Ocean, although the latter species shows an intermittent distribution in the Pacific (IUCN 2017, Frisch et al. 2016).

There is a tendency to associate differences in reef assemblage between locations to varying levels of historical fishing pressure (McClanahan et al. 2011). Recent work highlights the importance of factoring in varying geomorphologies alongside human impacts when assessing reef fish structure and abundance between islands (Williams et al. 2015, Heenan et al. 2016). Access to geographical data on the distribution of *Plectropomus* (IUCN 2017) provides a framework for examining the abundance of the study species, *P. areolatus,* over a region where it is observed to be more common. It also allows an assessment on the relative importance of habitat structure and fishing pressure within a more localized area of the western Solomon Islands.

The initial purpose of this chapter is to establish spatial patterns of abundance of four species of *Plectropomus* (*P. areolatus, laevis, oligacanthus* and *leopardus*) over a geographical gradient covering 13°of latitude extending from the reefs of eastern and northwestern Australia to the reefs of the western Solomon Islands and eastern Papua New Guinea. Moreover, this sampling gradient covered 3 distinct regions within the Central Indo-Pacific, the Eastern Coral Triangle, Northeast Australian Shelf and Northwest Australian Shelf (Spalding et al. 2007). Thus, the study sought to capture major trends in the geographical abundance patterns of the four dominant species of *Plectropomus* in the region. Previous work has demonstrated that populations of *Plectropomus* are capable of exchanging larvae at this geographic scale (van Herwerden et al. 2006). A secondary purpose of this chapter is to establish the relative importance of habitat structure and fishing pressure in structuring grouper populations, since both have been demonstrated to impact grouper populations (Ferreira 1995, Wen et al. 2013). To examine the relative importance of habitat structure versus fishing pressure local-scale sampling of *P. areolatus* was conducted within the western Solomon Islands, with study sites partitioned among different reef habitats and areas subject to different levels of fishing pressure.

This hierarchical sampling program was developed to satisfy two objectives.

a. Determination of the distribution and abundance patterns of the four main species of *Plectropomus* associated with mid-shelf to offshore reefs in the southwestern Indo-Pacific. An important aspect of this objective was to place the *Plectropomus* species assemblage of the western Solomon Islands into a broader geographical context.

b. Examine the impact of habitat structure and fishing pressure on the abundance and size structure of the primary study species *P. areolatus,* in the Western Solomon Islands.

2.2 Methods

2.2.1 Study Area

The broader-scale investigation on abundance patterns of *Plectropomus* species is focused on an area of the central Indo-Pacific that is referred to in this study as the **Australian-Indo Archipelago** (AIA). This region harbors some of the highest densities and species composition of the *Plectropomus* genus in the world (Figure 2.1). The AIA differs from the Indo-Australian Archipelago in that it includes the marine eco-regions of the north-eastern and western reefs of Australia along with the eastern Coral Triangle (Figure 2.2).

The classification of these marine eco-regions follows that described in Spalding et al. (2007). Reefs surveyed in northwestern Australia were all located approximately 280-320 km offshore from the mainland on the continental shelf. Reefs in the northeastern region were located on mid- and outer continental shelf regions of the Great Barrier Reef, approximately 27-100 km from the mainland. In contrast, reefs surveyed in Papua New Guinea (PNG) and Solomon Islands (SI) were mostly associated with high islands of volcanic origin and were generally situated less than 10 km from shore.

A more detailed investigation was centered on three reef systems located in the western region of Solomon Islands (Figure 2.3 & Figure 2.4). These three reef systems were selected as they represent systems that have been exposed to different levels of historical fishing pressure and have contrasting reef structure. Two reefs systems, Ghizo and Parara, both have an outer barrier reef encompassing a lagoon with a complex network of reefs and associated marine habitat (Figure 2.5). However, the Parara barrier reef is more continuous and encloses a larger lagoonal system compared to Ghizo. In contrast to the above two locations, the reef system at Tetepare is made up entirely of exposed fringing reef habitat, with a total absence of a barrier reef and lagoonal habitat (Figure 2.5). Furthermore, human population density ranged from 0.83/hectare of reef at Ghizo to 0.01/hectare of reef at Tetepare (Table 2.1).

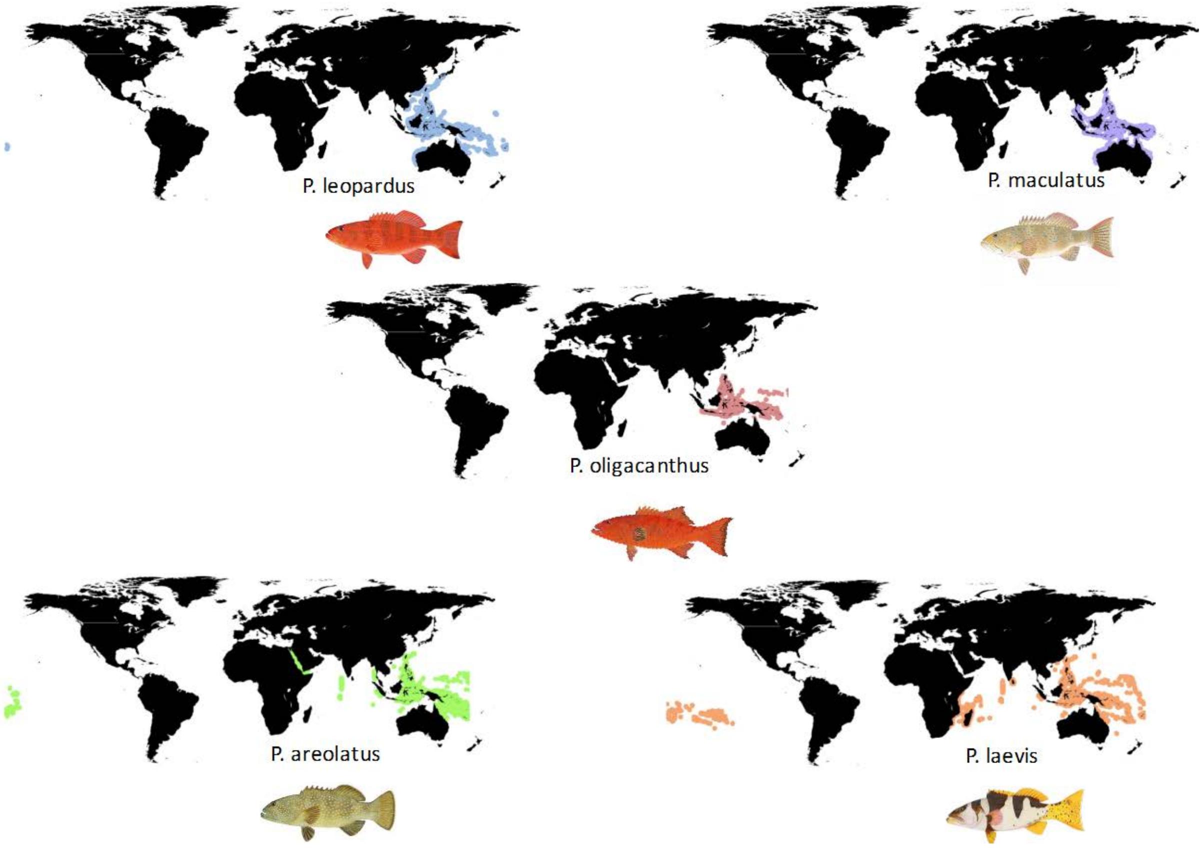


Figure 2.1 Distribution patterns of the five most common *Plectropomus* species within the Indo-Pacific region. Information derived from **IUCN Red List of Threatened Species. Version 2017-1. <www.iucnredlist.org>**

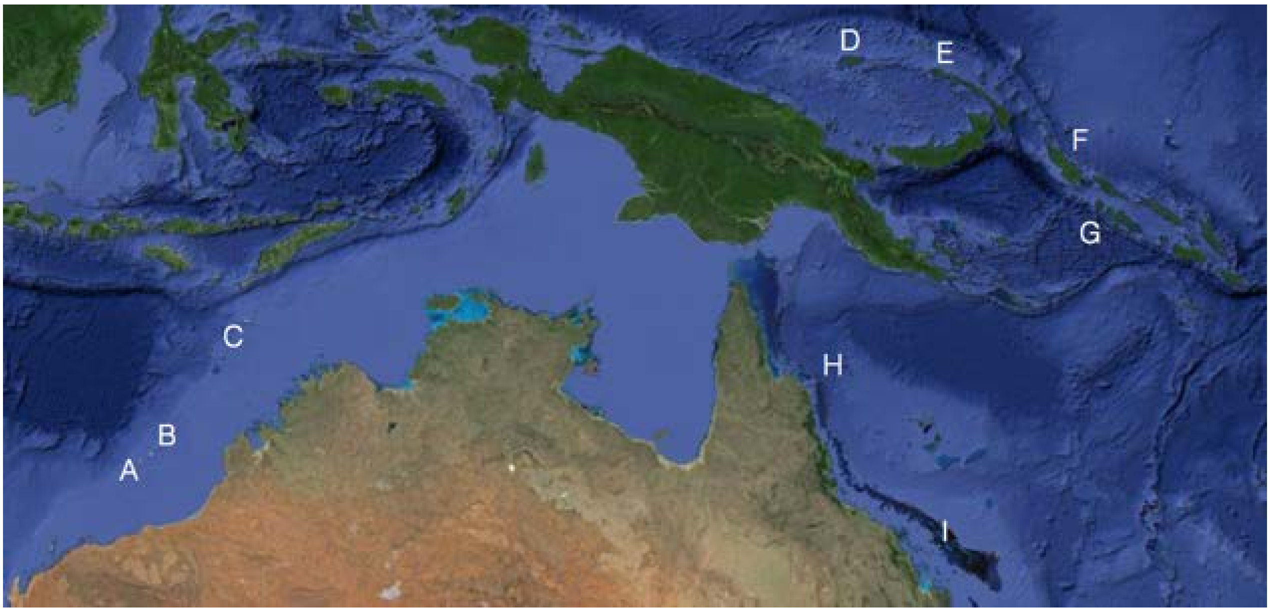


Figure 2.2 The Australian-Indo-Archipelago region. Letters represent the general locations from within which fish surveys were conducted. A) Rowley Shoals (Aust); B) Scott Reef (Aust); C) Ashmore Reef (Aust); D) Manus (PNG); E) Kavieng (PNG); F) Bougainville (PNG); G) Western Solomon Islands; H) Northern GBR (Aust); I) Central GBR (Aust). Image take from Google Earth.

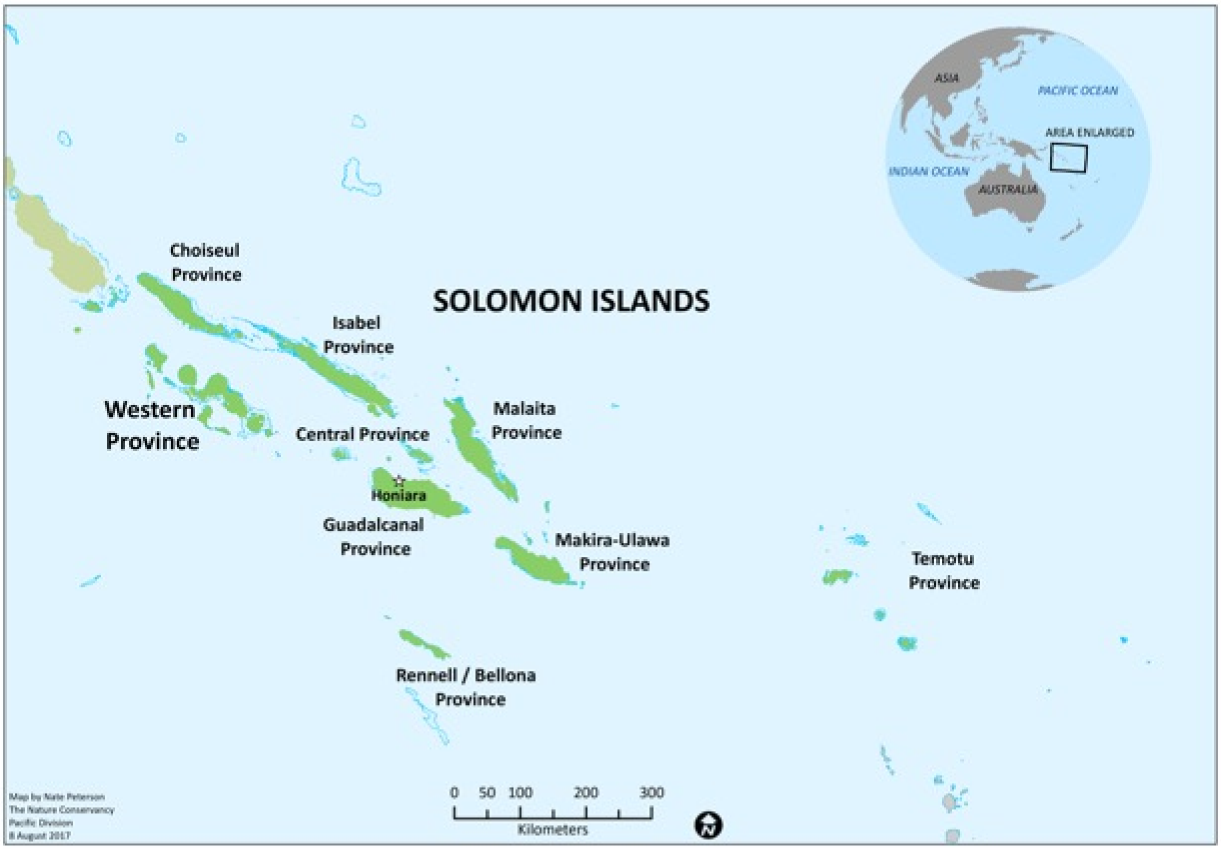


Figure 2.3 Map of Solomon Islands. Western Province is where the study took place in Solomon Islands

Figure 2.4 Map showing the main islands of Western Province, Solomon Islands, and the three study locations. Red outline = Ghizo, Yellow outline = Parara and Orange outline = Tetepare. Image taken from Google Earth.

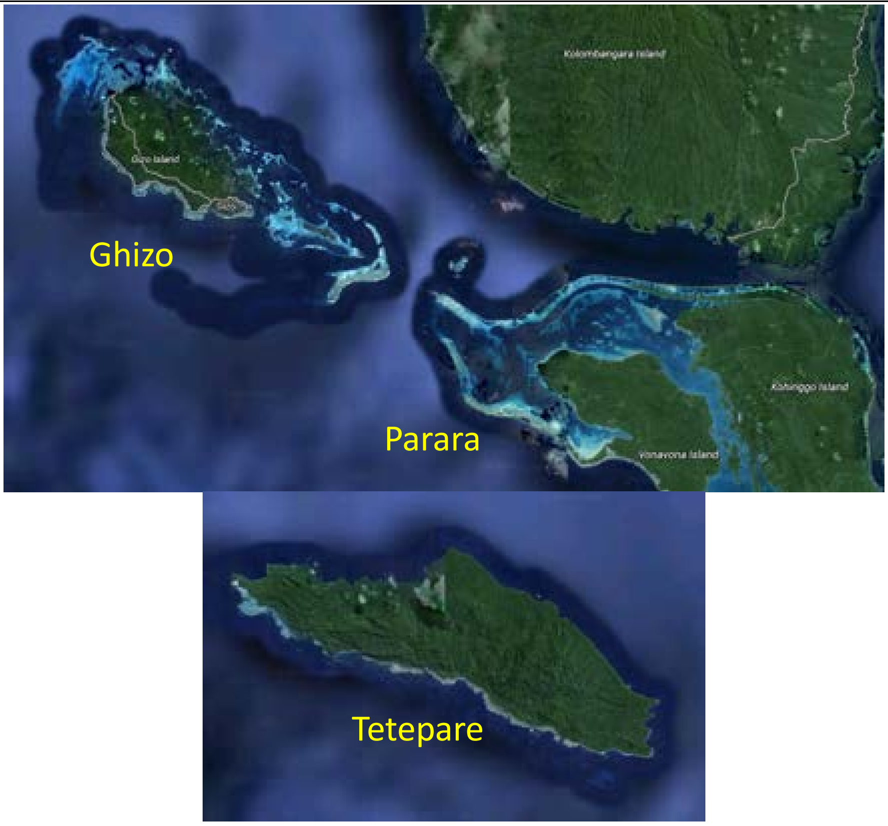


Figure 2.5 Broad marine habitat composition at the three study locations Ghizo, Parara and Tetepare, in Western Province, Solomon Islands. Image taken from Google Earth.

Table 2.1 Reef habitat metrics, human population density and dominant fishery type for Ghizo, Parara and Tetepare in western Solomon Islands.

	Ghizo	**Parara**	**Tetepare**
Overall reef system *(hectare)*	8642	10182	1577
Lagoon system *(hectare)*	3588	5123	0
Patch-reef *Lagoon* *(hectare)*	733	624	0
Barrier reef system *(hectare)*	2420	2686	0
Fore-reef *Exposed Barrier* *(hectare)*	301	209	0
Fore-reef *Exposed Fringing* *(hectare)*	450	43	617
Human population (density [people/hectare of reef])	7177[a] (0.83)	1160[b] (0.11)	10[c] (0.01)
Type of fishing pressure	Small-scale commercial	Subsistence	Very low subsistence

a. taken from 2009 census b. taken from 1999 census and raised by 22% to reflect the overall population increase in Western Province between the 1999 and 2009 census period c. average resident population at field station on Tetepare Island.

A vibrant small-scale reef fish fishery operates within and around Ghizo Island, supplying its urban population. Concerns of excessive fishing pressure reducing stocks have led to the development of plans by NGOs and local government to formally implement a network of small MPAs within the reef system (Liligeto 2011). Historically, fishing pressure within the Parara reef system has been of a subsistence nature. However, increasing demands for fresh seafood from the urbanized fishery in nearby Ghizo is placing added pressure on the marine resources in this reef system. In contrast, the remote location of Tetepare, the establishment of an actively enforced marine reserve (Read et al. 2010) and very low resident population means that fishing pressure has generally been much lower and predominantly of a subsistence nature.

2.2.2 Sampling protocol

Underwater visual census on species of the genus *Plectropomus* was conducted at all sites in this study using the long-swim survey technique developed specifically for surveying large epinphilids by Choat and Pears (2003). This method is particularly suitable for surveying *Plectropomus* species due to their roving nature and scattered distribution. At each site a single observer undertook a 45-min timed swim (except for sites in Papua New Guinea where 20-min timed swims were conducted) on SCUBA along the upper fore-reef habitat. Before each dive, latitude and longitude coordinates were recorded using a hand-held GPS. This was repeated at the end of the dive. All surveys were conducted at 5-12 m of depth and covered approximately 400 m. The numbers of *Plectropomus* present within a 20-m wide belt (10 m either side of the swim-line) were recorded to species-level, resulting in a survey area of approximately 8000 m^2. Length was estimated for each individual in 5-cm size classes. All dives were unidirectional. Data from Solomon Islands was collected by A.T.H. Abundance data for Australia was collected by J.H.C., while The Nature Conservancy collected data from Papua New Guinea (Hamilton et al. 2009, Hamilton et al. 2010), all using similar methods.

As part of the bioregional investigation on *Plectropomus* distribution, a dataset comprised of 212 long-swim surveys (Western Solomon Islands n = 71; Eastern Australia n = 81; Western Australia n = 38; Eastern Papua New Guinea n = 55) was examined using multivariate analyses (Table 2.2). A more focused investigation on the density and size structure of

Plectropomus was carried out within Solomon Islands. In addition to the counts of *Plectropomus* species on Ghizo and Tetepare, a further 21 long swim surveys were conducted specifically for *P. areolatus* within the Parara reef system, adjacent to Ghizo. A total of 92 dives were conducted within these three separate reef systems in Solomon Islands, recording a total of 307 *P. areolatus* individuals (Table 2.2).

Table 2.2 Regional locations and the number of long-swim counts conducted within each location. *UVC surveys at Parara (Solomon Islands) focused solely on *P. areolatus.*

Region	Location	Coordinates	Number of counts
Solomon Islands (SI)	Ghizo	8° 5 S, 156° 49 E	28
	Parara*	8° 10 S, 157° 1 E	21
	Tetepare	8° 44 S, 157° 26 E	43
		total	*92*
Great Barrier Reef (GBR)	Northern GBR	14° 15 S, 145° 18 E	33
	Central GBR	18° 35 S, 147° 24 E	48
		total	*81*
Western Australia (WA)	Rowley Shoals	17° 36 S, 119° 1 E	20
	Scott Reef	13° 56 S, 121° 52 E	6
	Ashmore	12° 15 S, 123° 3 E	12
		total	*38*
Papua New Guinea (PNG)	Manus	2° 5 S, 146° 52 E	11
	Kavieng	2° 37 S, 150° 42 E	18
	Bouganville	6° 13 S, 155° 15 E	26
		total	*55*
		Grand total	288

At all regions, fish counts were conducted along outer/exposed fore-reef habitats on both barrier and fringing reef structures. In general, these outer reefs were exposed to prevailing winds and oceanic conditions. The prevalent fringing reef structure at Tetepare meant that all counts at this location were conducted in exposed fore-reef habitats. Despite the presence of extensive inner-reef habitats at Ghizo and Parara, unfavourable weather conditions hindered attempts to survey inner reefs at both these sites due to reduced visibility during the survey period.

2.2.3 Data analysis

*2.2.3.1 Regional level (*Plectropomus *assemblage)*

Cluster analysis was performed on log(x+1) transformed abundance estimates of the various *Plectropomus* species from each region to examine the level of similarity among regions.

Patterns of community structure were further explored using principal component analysis (PCA) and multi-dimensional scaling (MDS).

*2.2.3.2 Solomon Islands (*Plectropomus areolatus *abundance and size)*

The differences in human population density and historical fishing pressure between the three locations (Table 2.1) provides a useful gradient of reduced fishing pressure as the focus shifts from the urbanized fishery at Ghizo to the more subsistence orientated fishing at Parara then to the very lightly exploited island of Tetepare. In order to examine for possible effects of fishing pressure and reef structure on *P. areolatus* (the most harvested *Plectropomus* species in Solomon Islands), analysis of density and length distribution was conducted for populations at Ghizo, Parara and Tetepare. Length distributions and density estimates were compared among islands using a Kruskal-Wallis one-way analysis of variance on ranks and between habitats at Ghizo using a Mann-Whitney rank sum test, since the data failed the assumptions of normality and equal variance.

2.3 Results

2.3.1 Bioregional distribution patterns

The cluster analysis based on the relative abundance estimates of the four *Plectropomus* species yielded a dendrogram that supports five regional areas (Figure 6). The primary split in the dendrogram revealed a clear partitioning that reflected the latitudinal gradient of sampling with most of the higher latitude reef systems of northeastern and northwestern Australia being distinct from the lower latitude reefs of western Solomon Islands and eastern Papua New Guinea. Within the Australian region three clusters identified as midshelf and outershelf and offshore reefs for northeastern Australia and northwestern Australia were identified with a single northeastern outer reef, NoName, clustering with a northwestern reef. The pattern for the low latitude reefs was more diffuse, with overlap between Solomon Islands and Papua New Guinea sampling localities. A single western Australian reef clustered with Solomon Islands

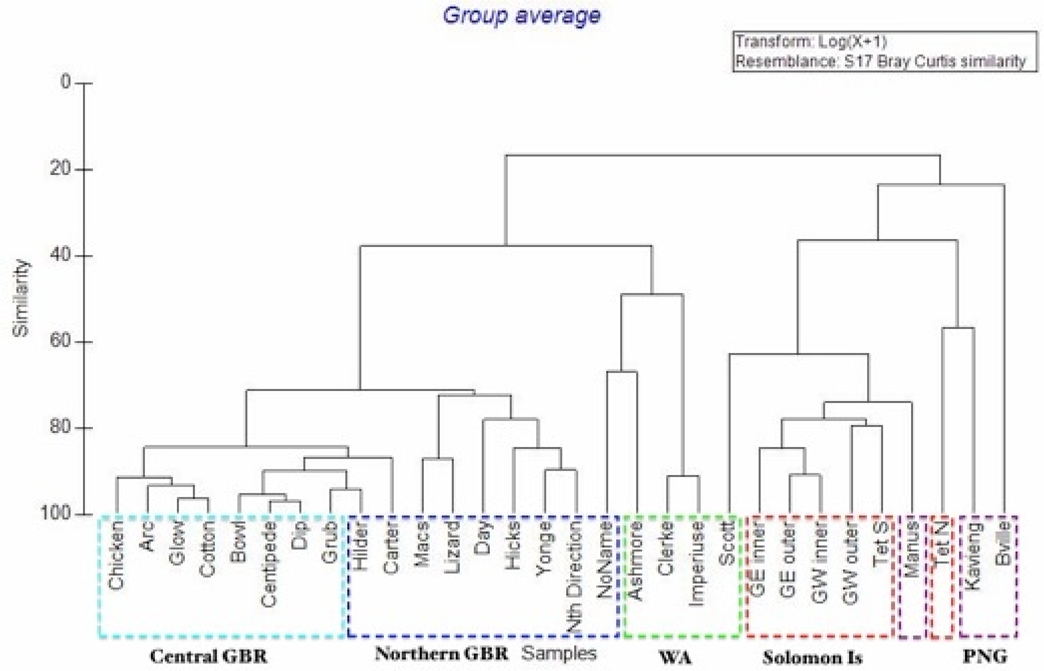


Figure 2.6 Cluster analysis based on relative abundances of four *Plectropomus* species (*P. areolatus, P. oligacanthus, P. leopardus, P. laevis*) within the Australian-Indo-Archipelago (AIA). The different colored boxes reflect the origin of the samples. For example, red boxes reflect samples from Solomon Islands.

Subsequent PCA and MDS analyses supported the observed partitioning of these regions (Figure 2.7). PCA species vectors indicate that the distinguishing feature of the central eastern Australian reefs (i.e central GBR) were a higher abundance of *P. leopardus* and *P. laevis* relative to the other localities, while northwestern Australia, western Solomon Islands and eastern Papua New Guinea were characterized by *P. oligacanthus* and *P. areolatus*. The primary and secondary axis of the PCA axis accounted for 86.6% of the overall variation with PC1 explaining 74.6% (Figure 2.7A). The MDS analysis was confirmatory and identified wide variation in the assemblages of the northwestern Australian reefs and the distinct nature of the Manus (Papua New Guinea) and the Tetepare North (Solomon Islands) assemblages relative to other sites in their region (Figure 2.7B).

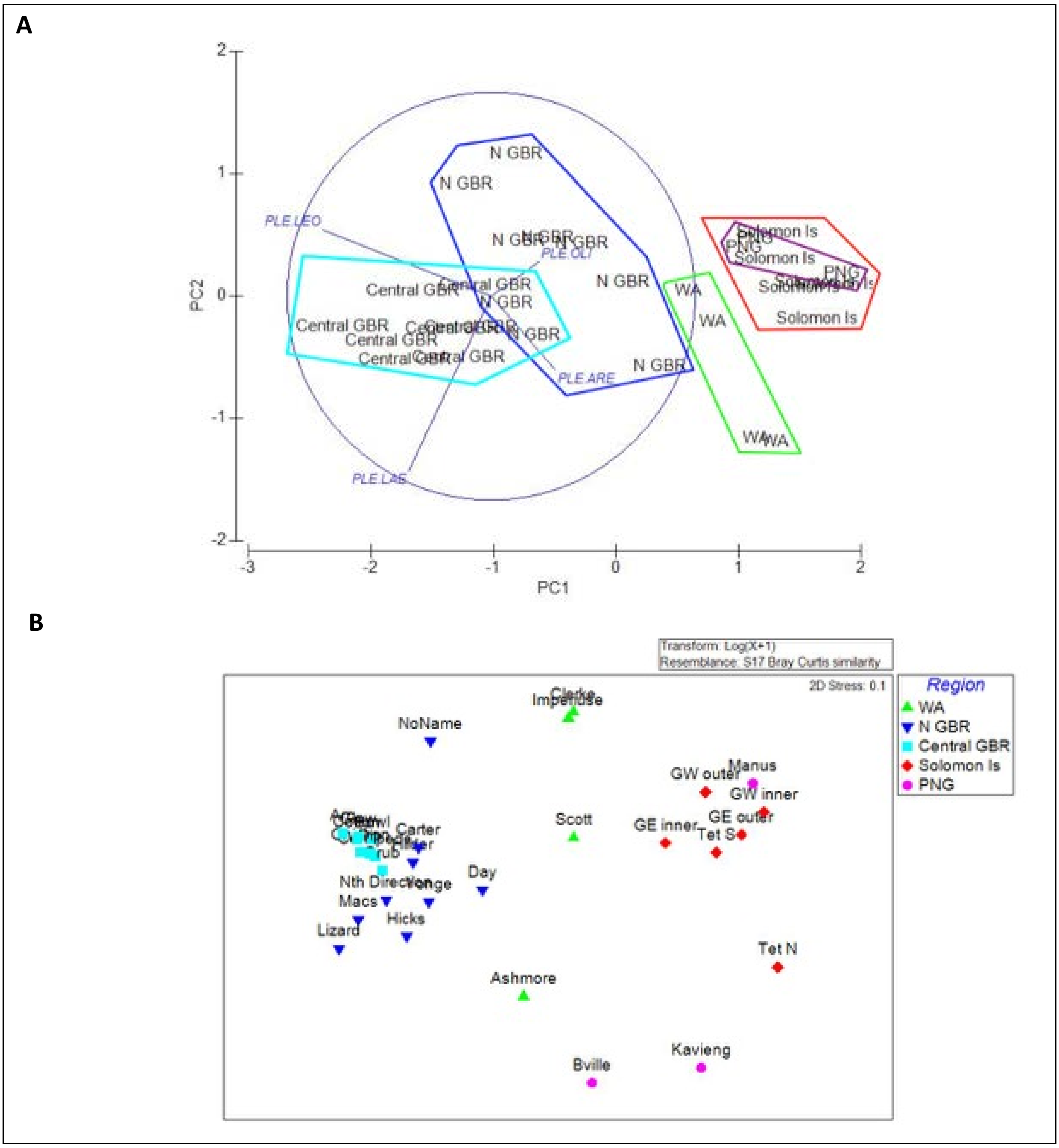


Figure 2.7 A) PCA ordination of the relative abundance of four *Plectropomus* species *(P. areolatus, P. oligacanthus, P. leopardus, P. laevis)* within the AIA with eigenvectors representing each of the four species. B) MDS displaying the level of similarity in species abundance patterns within the AIA.

A breakdown of the locality-specific abundance estimates by species within each region shows the extent to which the outcomes of the multivariate analyses are influenced by species and region-specific patterns of abundances (Figure 2.8). For instance, the grouping of Ashmore (northwestern reef) with NoName (northeastern reef) in the dendrogram appears to be driven by high densities of *P. laevis* relative to other species, while relatively high densities of *P. oligacanthus* explain the grouping of Tetepare North and Kavieng. By far the most abundant species in total was *P. leopardus*. This species achieved maximum abundance on the central and northern GBR where it accounted for 73% and 76% of the total number of *Plectropomus* recorded (Table 2.3). The second-most abundant species in these two regions (and overall study) was *P. laevis*. Both *P. areolatus* and *P. oligacanthus* represent the dominant species in the three remaining regions (WA, SI, PNG), with *P. areolatus* comprising 55% of the *Plectropomus* composition in Solomon Islands while *P. oligacanthus* accounted for 57% in PNG (Table 2.3).

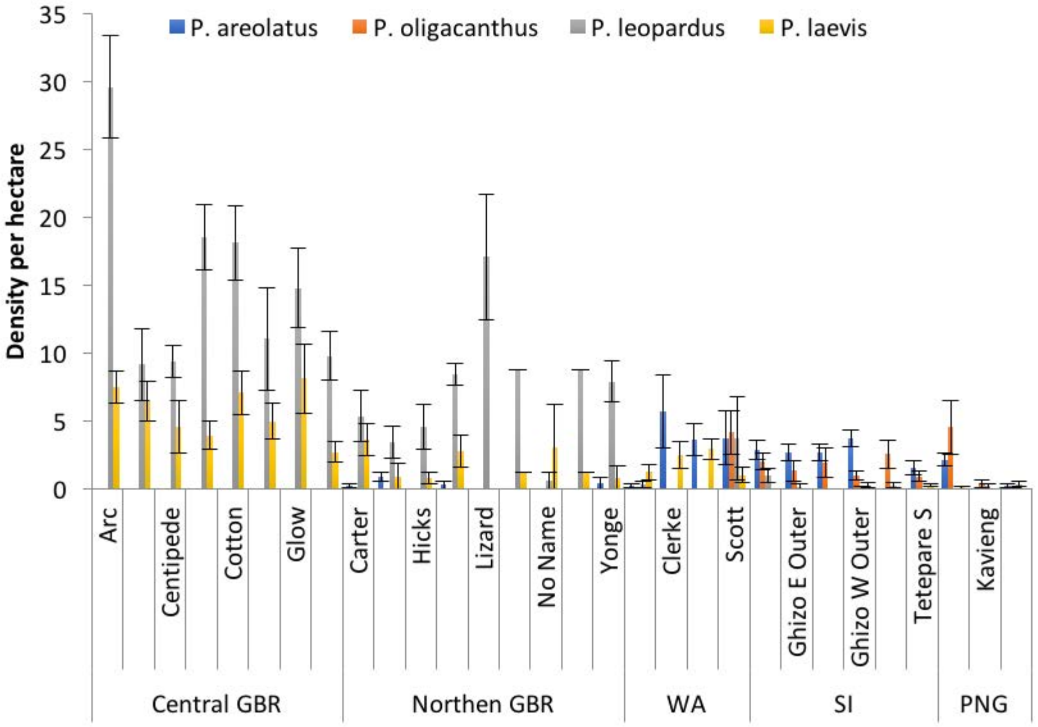


Figure 2.8 Mean densities for each of the four *Plectropomus* species *(P. areolatus, P. oligacanthus, P. leopardus, P. laevis)* throughout the AIA. GBR = Great Barrier Reef, WA = Western Australia, SI = Solomon Islands, PNG = Papua New Guinea.

Table 2.3 *Plectropomus* species assemblage by region. Note. Does not include the *P. areolatus* data from Parara, Solomon Islands.

	P. leopardus	*P. laevis*	*P. areolatus*	*P. oligacanthus*	Total
Central GBR	578 (73%)	218 (27%)	0 (0%)	0 (0%)	796
Northern GBR	190 (76%)	52 (21%)	7 (3%)	0 (0%)	249
Western Aust.	21 (11%)	61 (31%)	93 (48%)	20 (10%)	195
Solomon Is.	19 (7%)	10 (3%)	159 (55%)	102 (35%)	290
PNG	11 (13%)	1 (1%)	24 (29%)	47 (57%)	83
Total	817.2	341.17	281.65	167.98	1613

2.3.2 Effect of habitat on *Plectropomus areolatus* in Solomon Islands

Despite its low human population density and low historical and contemporary fishing pressure, *P areolatus* density at Tetepare was significantly lower than the two more populated locations, while Parara had significantly more fish than Ghizo (Kruskal-Wallis, H = 54.488, df = 2, P < 0.001; Dunn's post-hoc, P < 0.05; Figure 2.9). This suggests that less extensive habitat structure at Tetepare is a more important factor compared to fishing pressure in determining density estimates. In contrast, the similar habitat structures at Ghizo and Parara means that differences in densities between these two sites are much more likely to be due to different levels of fishing pressure (Figure 2.9).

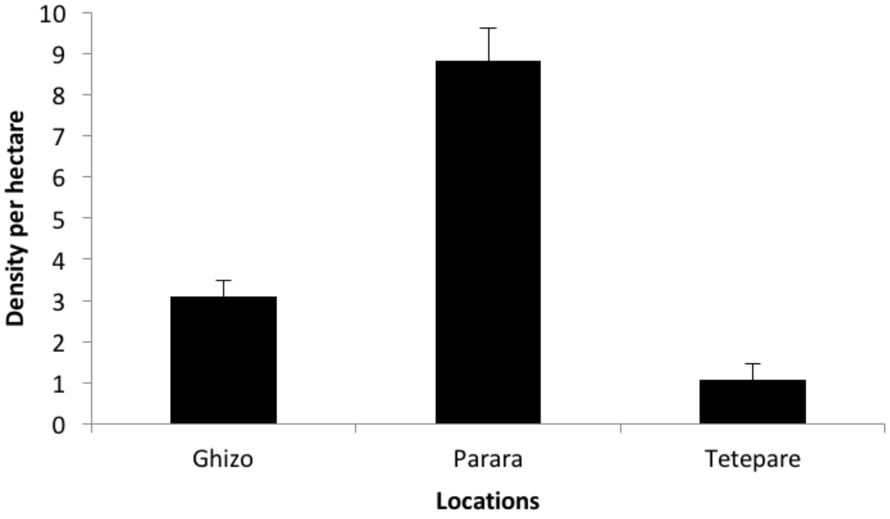


Figure 2.9 Density of *P. areolatus* within outer reef slopes of Ghizo, Parara and Tetepare in western Solomon Islands

2.3.3 Effect of fishing on *Plectropous areolatus* in Solomon Islands

The analysis into population size structure revealed location-specific differences that may relate to fishing pressure. The estimated size structure at Ghizo peaked within smaller modal class (36-40 cm) compared to Parara (46-50 cm) and Tetepare (41-45 cm; Figure 2.10). Size distributions among islands were significantly different (Kruskal-Wallis, H = 51.822, df = 2, P<0.001) and a pair-wise multiple comparison (Dunn's method post hoc test, P < 0.05) revealed Ghizo size structure to be significantly different to Parara and Tetepare. There was no significant difference between the size structure of Tetepare and Parara (Figure 2.10). A reduction in size structure in Ghizo is most likely a consequence of the extended exposure of coralgrouper populations to the small-scale commercial fishery supplying the urban and surrounding communities of Ghizo.

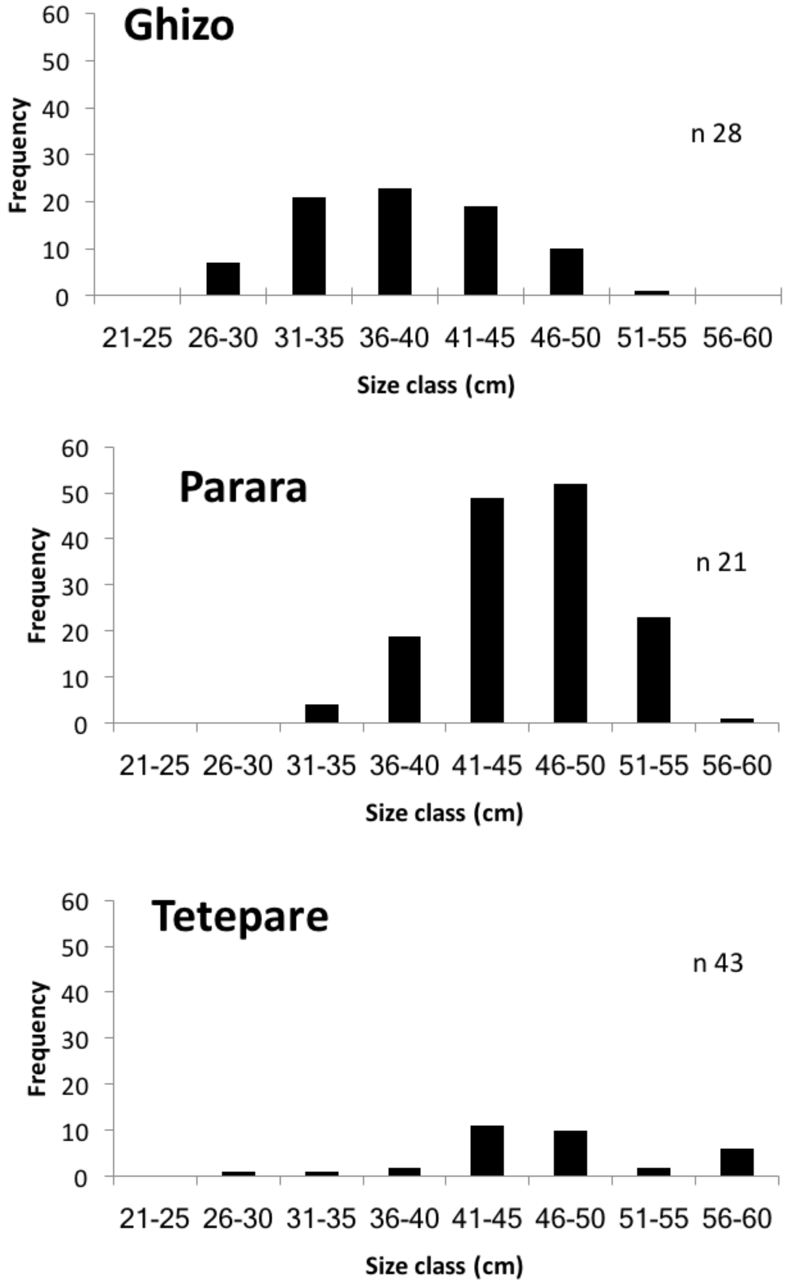


Figure 2.10 *P. areolatus* size structure between outer reef slopes of Ghizo, Parara and Tetepare in western Solomon Islands

2.4 Discussion

This study demonstrates that abundance patterns of *Plectropomus* species varies on a regional scale. Global distribution maps of *Plectropomus* identified an area here described as the Australian-Indo-Archipelago as the centre of diversity and abundance of this genus (IUCN 2017). Four core species (*P. areolatus*, *P. laevis*, *P. leopardus*, and *P. oligacanthus*) were used for distributional analysis. A notable feature was the presence of all four species in the tropical high latitude reef systems of the Australian continental shelf. Regional analysis of species abundance patterns revealed that the *Plectropomus* assemblages associated with the Australian continental shelf reefs were clearly differentiated from the low-latitude assemblages on the reef systems of the Solomon Islands and Papua New Guinea.

Multivariate analysis and plotting of locality-specific abundance patterns revealed a complex pattern of geographic distribution with the northeastern Australian reefs dominated by *P. leopardus* and *P. laevis*, with *P. areolatus* as the dominant species in high-latitude reef systems of western Australia and in the reef system of western Solomon Islands and eastern PNG. In the latter reef systems, *P. oligacanthus* also contributed to the abundance patterns. A second feature revealed by both the multivariate analysis and locality-specific abundance plots was the high level of variation in species abundance patterns within both regions.

Analysis of the regional patterns revealed two important features of *P. areolatus*; i) It was widely distributed within the Australian-Indo Archipelago which mirrors the broad global distributional range of this species; ii) Within each regional distribution there were marked differences in abundance of *P. areolatus* on individual reefs. This occurred in both the northwestern Australia and western Solomon Islands regions and contrasted strongly with the patterns seen in the northeastern Australian region.

Two processes have been implicated in variation in local abundance patterns in epinephelids. Firstly, members of the genus *Plectropomus* and epinephelids generally are subject to high levels of fishing that have major impacts on local abundances (Sadovy de Mitcheson et al. 2012). Secondly, it is also clear that many reef fish species, including *Plectropomus* spp., have specific habitat requirements with respect to recruitment and spawning sites (Bonin et al. 2009, Wen et al. 2013, Hamilton et al. 2017). For instance, in Manus Province, Papua New Guinea, the vast majority of juvenile *P. areolatus* are located on sheltered inshore patch reefs adjacent to mangroves within barrier reef lagoons, highlighting the importance of these habitats as recruitment sites for *P. areolatus* (Almany et al. 2013). Consequently, adult *P. areolatus* are generally found to be more abundant on coral-rich barrier reef slope habitats adjacent to inner lagoon environments (Hamilton et al 2012; Hutchinson & Rhodes 2010) often adjacent to reef passes and promontories which are the main locality for spawning aggregations (Chapter 5).

As fishing can have major impacts on *P. areolatus* spawning aggregations (Hamilton & Matawai, 2006; Hamilton et al. 2012) the expectation was that the variation in local abundance patterns for *P. areolatus* would be driven primarily by fishing pressure. Within the western Solomon Islands fishing pressure is assumed to be greatest in areas of high human population density and have active fish markets, a metric that is commonly used in the evaluation of fishing effects (Brewer et al. 2013a, Cinner et al. 2013). However, reef habitat structure has been shown to have a major impact on the local abundance of reef fishes including *Plectropomus* (Almany et al. 2013, Wen et al. 2013, Weeks 2017). For this reason it was necessary to use a sampling design that took into account both fishing pressure and habitat structure.

The presence of a large remote island with an active marine reserve, Tetepare, provided a comparison for *Plectropomus* abundance patterns on reefs subject to fishing. Ghizo, with the highest human population in the western Solomons, supports a reef fishery with both commercial markets and subsistence fishing (Liligeto 2011). However, Tetepare differs with Ghizo and Parara in terms of habitat structure. Both Ghizo and Parara are characterised by substantial areas of lagoonal environment which are surrounded by a barrier reef system. Their inner lagoonal environment is made up of networks of patch reef, seagrass and mangrove habitats. In comparison, Tetepare lacks a barrier reef system and supports very small areas of in-shore habitats such as seagrass and mangroves.

The more complex reef systems of Ghizo and Parara had higher densities of fish compared to the remote and protected reef system of Tetepare. This suggests that habitat structure is playing a more important role in determining population structure than anthropogenic factors at this site. A gross analysis of the geomorphology between the two locations suggests that contrasting patterns in reef structure and specific habitat features was likely to be the influencing factor in fish abundance rather than human density (i.e. fishing pressure). It has been shown that certain physical and biotic features associated with a particular reef area can affect the distribution and abundance of species (Sluka et al. 2001).

Inshore areas that are comprised of mangroves, seagrass beds, patch reefs and estuarine areas are known to play an important "nursery" role in the early stages of the life-cycle of grouper species (Craig et al. 2012, Rhodes 2012a,b, Waldie et al. 2016). Whereas, more exposed outer reefs are known to be preferred by adult members of grouper species (Sluka et al. 2001). Therefore, locations with complex reef structures which contain habitats that are important for both juvenile and adult phases of a species life-cycle can be expected to have higher population numbers compared to locations that have less essential habitat available. An increasing number of broad-scale studies have highlighted the important role that habitat and environment have in structuring abundance patterns of fish species (Williams et al. 2015) and have demonstrated why it is important to take these factors into consideration when assessing potential effects of fishing (Taylor et al. 2015). Indeed, the importance of considering interconnected seascape habitats is increasingly recognized by fisheries scientists, managers and conservation planners (Weeks 2017). For example, a study by Wen et al. (2013) demonstrated that networks of marine protected areas (MPAs) only achieved their objective of increasing adult fish abundances when MPA networks included good recruitment habitat along with adult habitat.

A fishing effect is nevertheless evident at Ghizo, and appears to be the primary factor influencing the smaller maximum sizes and lower densities observed within the Ghizo reef system compared to Parara. Most reef fisheries tend to target more desirable larger-bodied predatory species. Investigations on the effects of fishing have concluded that fishing can affect the size and structure of reef communities (Jennings & Kaiser 1998, Martin et al. 2017). It has therefore been suggested that data on changes in the size structure of a population can be a useful proxy for determining the abundance-biomass effects of a fishery (Graham et al. 2005). Given the active commercial fishery in Ghizo and high human population density, it is reasonable to assume that truncated size-frequency distribution of *P. areolatus* in the Ghizo fishery is a result of high fishing pressure at this site.

In summary, within the area of greatest species diversity and abundance (the Australian-Indo-Archipelago), the *Plectropomus* genus shows clear geographical trends in species distribution and abundance, with *P. areolatus* occurring in a wide range of habitats within each geographical region. Fishing has important effects on the abundance of *Plectropomus* generally and *P. areolatus* specifically. However, comprehensive sampling within the western Solomon Islands confirms that reef habitat also has significant effects on abundance independent of fishing pressure. Any evaluation of fishing that does not take location and habitat structure into account runs the risk of providing inaccurate estimates of the influence of human activities on target species.

3 Age and Growth of *Plectropomus areolatus*

3.1 Introduction

The use of age-based approaches to obtain information on growth rates, longevity and age-specific mortality has long been part of fisheries-related research in higher latitude regions. In contrast, it has only been in recent decades that age-based techniques have increasingly been used in lower latitude tropical fisheries. Historically it was widely assumed that obtaining reliable age estimates from otoliths of tropical reef fish species was problematic due to the lack of distinct seasonal shifts in temperature that were thought to be responsible for producing annual increments (Munro 1983, Campana and Neilson 1985, Fowler 1995). However, a rapidly growing body of work on tropical species has verified the validity of obtaining age estimates from sectioned otoliths in reef fishes for age-based demographic assessments (Ferreira & Russ 1994, Choat et al. 1996, Pilling et al. 2000, Choat and Robertson 2002, Choat et al. 2009). Validation methodologies have included tetracycline marking of otoliths and more recently, bomb carbon dating techniques (Francis et al. 1992, Choat et al. 2006, Andrews et al. 2015).

Tropical fish species are assumed to have a higher population turnover rate (i.e. faster growth, higher natural mortality and reduced longevities) compared to fishes in more temperate waters, and these life history parameters suggest that tropical reef fishes may be more resilient to overfishing than their temperate counterparts (Choat et al. 2009). However, a growing body of work has revealed that tropical species can display extended lifespans that correspond to low natural mortality rates. For instance, lifespans in excess of 30 years have been found in commercially harvested families such as Lutjanids (Newman et al. 1996), Acanthurids (Choat and Axe, 1996), scarine labrids (Hamilton & Choat 2012, Andrews et al. 2015) and epinepheids (Mosse and Davies 2007). Therefore, the presumption that tropical reef species should be relatively resilient to fishing pressure may not hold true for all species and underlies the importance of attaining accurate information on demographic parameters of targeted species for proper management of tropical reef fish stocks.

Growth in tropical reef fishes is characterized by rapid initial growth that decreases at a later adult stage when energy resources begin to be invested into maturation processes (Choat and Robertson 2002). The pattern of growth amongst these species is complex and can differ significantly between and within taxa. For instance, within the Epinephelidae family, species of the genus *Plectropomus* generally display an indeterminate growth profile, where body size continues to increase throughout the life-span of species (Ferreira & Russ 1992, Williams et al. 2008, Heupel et al. 2010), however, members of the closely related *Cephalopholis* genus have been shown to have a determinate growth pattern and with much longer life spans, where minimal somatic development takes place for the majority of their life-span (Mosse and Davies 2007). A deterministic growth profile often results in a de-coupling of the size and age relationship and leads to the concentration of age classes within a limited size range (Taylor 2008).

Investigations into population dynamics of tropical reef fish have increasingly documented substantial demographic and life history variation at multiple scales. Variation in life history characteristics is likely to be influenced by a range of ecological, environmental and anthropogenic influences specific to each location (Jones 1987, Hart and Russ 1996, Gust 2002, Law 2000, Hilborn and Minte-vera 2008). Furthermore, where populations are exposed to fishing pressure, the selective nature of fishing practices, which usually results in the disproportionate removal of older and larger individuals, will also have an effect on growth rates, size structure, and longevity of targeted species (Russ 1991, Russ and Alcala 1998, Hamilton et al. 2007, Jennings et al. 2009). In species that display sex-specific growth (such as protogynous spp), the removal of larger individuals (usually males) may lead to an imbalance in the operational sex ratio which could result in reduced overall reproductive output for a population (Beets & Friedlander 1999, Rhodes & Sadovy 2002a,b, Robinson & Samoilys 2013). This may have serious implications for management through subsequent recruitment failure.

Gathering information on the age-based demographic parameters of reef fish species is fundamental for understanding population dynamics, and is a necessary prerequisite for assessing populations and designing meaningful management practices. The primary goal of this chapter is to investigate demographic parameters of *Plectropomus areolatus* populations from similar habitats in Solomon Islands that have been exposed to different levels of fishing. The study then compares data from this region to datasets from the Red Sea, northwestern Australia, Torres Straits and Micronesia to examine broader regional patterns in growth and longevity of *P. areolatus*. Due to the geographic spread of locations, it is expected that some spatial variation will occur as a result of differences in environmental conditions and historical fishing pressure.

3.2 Method

3.2.1 Sampling locations

Samples of *P. areolatus* were collected from four locations in the western Solomon Islands (Ghizo, Parara, Roviana, Marovo) via both fishery-dependent and independent methods. Data for Roviana and Marovo was collected in 2002 and for Ghizo and Parara between March 2008 to December 2010. The distance between locations varied from 3-120 km (Figure 3.1). The fisheries that target the Parara reef system are largely of a subsistence nature, with limited small-scale commercial fishing to supply the nearby urban population of Ghizo. Fish samples were obtained from Parara by purchasing from local fishers and by research spearing. Approximately 67% of the Parara samples were obtained from a known *P. areolatus* FSA. The Ghizo reef system is heavily exploited to support a centralized fish market in Gizo Town (Aswani & Sabetian 2009). Fish samples were obtained from Ghizo by sampling the Gizo fish market, purchasing directly from local fishers outside of the market and research spearing (note spelling difference between reef system and town). Approximately 40% of samples collected originated from known *P. areolatus* FSAs within the Ghizo reef system.

Fish samples were obtained from Roviana by purchasing from a local fisher from Munda who first discovered and exploited a large *P. areolatus* aggregation site from the mid-1990s onwards (Hamilton et al. 2012). Approximately 90% of the Roviana samples were obtained from this FSA. At the time that the Roviana samples were collected from this aggregation and the surrounding reefs were lightly exploited. Samples were obtained from Marovo by purchasing from local fishers supplying a local fish buying centre in Seghe. Similar to Roviana, approximately 90% of the Marovo samples were obtained from a known *P. areolatus* aggregation site (Toata Molea, *personal communication*). This FSA has been heavily exploited since the early 1980s by both spearfishers and the Live Reef Fish Food

Trade operations (Johannes 1988, Donnelly et al. 2000). Both Roviana and Marovo have much larger lagoon systems compared to the smaller lagoons of Ghizo and Parara. The primary study locations therefore results in a pairing of similar reef configurations (i.e. Ghizo:Parara and Roviana:Marovo) that have been exposed to different levels of historical fishing pressure (Figure 3.1 and Table 3.1).

Figure 3.1 The four primary study locations, Ghizo, Parara, Roviana, Marovo in the Western Province of Solomon Islands.

Table 3.1. Environmental setting and historical fishing levels of each location from Solomon Islands

Location	*Reef system*	*Fishing level*	*Lat & Long*
Ghizo	Small lagoon	High	8° 5 S, 156° 5 E
Parara	Small lagoon	Low	8° 10 S, 157° 1 E
Roviana	Large lagoon	Low	8° 20 S, 157° 14 E
Marovo	Large lagoon	High	8° 29 S, 157° 58 E

3.2.2 Age and growth analyses

All individuals in the datasets were measured (mm Fork Length FL) and weighed to the nearest gram. Otoliths were removed and stored in pairs in culture plates. One otolith from each pair was weighed to the nearest 0.1 mg and stored in a separate culture plate to be aged. The remaining otolith of each pair was stored away as backup. Each otolith was mounted on the edge of a glass slide by melting thermoplastic glue (Cyrstal Bond^{TM}) onto the slide via a hotplate so that the nucleus was sitting approximately on the edge with half the otolith protruding off the edge of the slide. The slide was then held perpendicular to the grinding plate and the otolith was ground close to the nucleus.

The otolith was then removed after reheating and re-positioned in the middle of the slide in an upright position, with the flat grounded edge glued to the slide surface with Crystal Bond^{TM}. The otolith was subsequently grounded with the slide held parallel to the grinding plate until a thin section of the otolith was produced with visible opaque bands. This sectioned piece of the otolith was then covered with a few drops of Crystal Bond^{TM} to enhance the visibility of the bands when counting. Otolith slides were then read using a stereomicroscope with transmitted light. Sectioned otolith samples were read three times in succession. Any differences in estimates of >2years or difficulties in reading otoliths were noted and expert advice was sought from experienced workers. In all cases the final two readings were very similar therefore the average of these two readings was taken to indicate the age of the individual. In addition, existing data for the Red Sea, northwestern Australia (WA), Great Barrier Reef (GBR), Torres Straits and Pohnpei were obtained to facilitate a comparison of demographic patterns in *P. areolatus*. These represent sub-samples from both published (Red Sea (DeRosier 2009), Pohnpei (Rhodes et al. 2013) and Torres Straits (Williams et al. 2008) and un-published (northwestern Australia) datasets.

In order to compare the patterns of fish growth, it is necessary to describe the pattern of growth mathematically. There exists a large literature on growth equations and many plausible equations that can describe the general features of fish growth (Enberg et al. 2008). The most popular of these is the von Bertalanffy growth equation (VBGF) which is represented by the formula:

$$L(t) = L_{\infty}\{1 - \exp[-K(t-t_0)]\}$$

where $L(t)$ is the estimated mean length at age t, L_{∞} is the mean asymptotic length, K is a growth coefficent and t_0 is the theoretical age at which fish length is zero (used to estimate time at settlement). A higher value of *K*, suggests a faster rate the fish is estimated to grow and reach L_∞. The VBGF was chosen for this exercise since it provided the best fit to size-at-age data according to the parameter estimates of the Schnute (1981) growth function. However, the validity of the above VBGF parameters for statistical comparisons has been questioned therefore a re-parametised version of the VBGF (rVBGF) is increasingly being used to compare growth (Francis 1988, Trip et al. 2008, Taylor and Choat 2014). The rVBGF is represented by the following formula:

$$L(t) = L\,(\tau) + \frac{\big(L(\mu)\text{-}L(\tau)\big)\left[1 - r^{2\frac{t\text{-}\tau}{\mu\text{-}\tau}}\right]}{1 - r^2}$$

where $r = \frac{L(\mu)\text{-}L(\omega)}{L(\omega\text{-}L(\tau)}$ and $L\,(t)$ is the average size-at-age t to be predicted by the model, provided that $L(\tau) < L(\omega) < L(\mu)$ and $(L(\mu)\text{-}L(\omega) \neq \big(L(\omega)\text{-}L(\tau)\big)$. Growth is compared using the 3 parameters $L(\tau)$, $L(\omega)$ and $L(\mu)$ that represent mean body size at 3 designated ages (τ, μ and ϖ). For this study I used $L(\tau)$ = 2 years, $L(\omega)$ = 5 years and $L(\mu)$ = 8 years when comparing between locations and sexes.

Representation of all size (and age) classes is an important consideration when modeling growth. Due to the under-representation of young individuals for some locations where FSAs were predominantly sampled, growth curves were constrained to settlement sizes of 50 mm based on estimates obtained from Papua New Guinea and Pohnpei (Rhodes et al. 2013). This was done when calculating parameters for both the conventional VBGF and the rVBGF for all curves. 95% confidence regions (ellipses) were produced for the rVBGF parameters $L(\tau)$ and $L(\mu)$ to compare growth.

Potential differences in the size and age of populations were tested using a One-Way ANOVA with location as a fixed factor followed by a Tukey post-hoc test. Longevity (T_{max} = mean maximum age) was calculated from the mean age of the oldest 25% individuals for each location. Mean maximum size (L_{max}) was calculated as the mean length of samples used to calculate longevity. A Kruskal-Wallis test was used to compare T_{max} and L_{max}. In addition, 95% confidence regions were generated around these two parameters and plotted for comparison between sub-samples of published data-set from the region. All statistical tests were done using SigmaPlot and R.

Age-based catch curves of Beverton and Holt (1957) and Pauly (1984) were used to estimate the instantaneous rate of total mortality. This method assumes that recruitment rates on each reef remains constant. The natural logarithm (*Ln*) of the number of fish (frequency) in each age class was plotted against their corresponding age in completed years and Z (total mortality) estimated from the descending slope. Z = F (fishing mortality) + M (natural mortality). Any year classes to the left of the age frequency mode were excluded since sampling procedures likely under-sampled smaller fish. Z values were compared between locations using a modified t-test (Taylor and McIlwain 2010).

3.3 Results

3.3.1 Population structure – Western Solomon Islands

A combined total of 907 *P. areolatus* samples were collected from Ghizo (49%), Parara (22%), Roviana (9%) and Marovo (20%) in western Solomon Islands (Table 3.2). In 13 samples otoliths were damaged and unable to be processed. Age structure displayed both unimodal and bimodal distributions with strong mode classes of 3 years (Ghizo, Roviana, Marovo) and 4 years (Parara) (Figure 3.2). Individuals ranged in age from 0.57 years (Parara) to a maximum age of 12 years (Parara and Roviana). Mean age varied significantly between locations (ANOVA, $F_{3,\ 891}$ = 28.130, p = <0.001). Parara registered significantly higher mean age compared to Ghizo, and Marovo but ages were not significantly different from Roviana (Table 3.3). No significant differences occurred between Ghizo and Roviana while Marovo registered significantly lower mean age compared to all other locations (Tukey's HSD $p<0.05$).

Table 3.2 Demographic information of *P. areolatus* between from locations within western Solomon Islands, northwestern Australia (WA), Torres, Strait, Pohnpei and Red Sea. L_2, L_5, L_8 are the rVBGF parameters for size-at-age 2, 5 and 8 years L_∞ represents the mean theoretical asymptotic length, *K,* describes the rate at which the individual will reach the asymptotic length, t_0 is theoretical size at age zero, *Z* is the mortality rate, S is survivorship and n is sample size.

Locality	L_2	L_5	L_8	L_∞	*K*	t_0	R^2	*Z*	*S (%)*	*n*
Ghizo	295	429	466	481	0.42	-0.26	0.29	**0.61**	**42**	431
- male	295	413	441	494	0.46	-0.18	0.25	-	-	172
- female	313	448	482	450	0.47	-0.25	0.24	-	-	306
Parara	288	417	454	468	0.42	-0.27	0.28	**0.38**	**39**	199
- male	330	447	470	476	0.54	-0.21	0.20	-	-	68
- female	295	399	420	426	0.53	-0.24	0.21	-	-	124
Roviana	329	466	500	511	0.47	-0.22	0.30	**0.37**	**45**	78
Marovo	329	461	493	502	0.48	-0.22	0.48	**0.99**	**39**	187
Rowley (WA)	294	432	472	489	0.41	-0.27	0.30	0.75		255
Scott (WA)	276	415	462	482	0.37	-0.30	0.33	0.74		165
Torres St	410	523	538	541	0.66	-0.15	0.14	0.39		409
Red Sea	344	476	505	513	0.50	-0.20	0.22	0.53		101
Pohnpei	350	440	451	453	0.68	-0.17	0.13	0.44		282

Table 3.3. Size and age range of samples, mean size and age and the mean age of oldest 25% of the population (T_{max}) and the mean size of the oldest 25% (L_{max}) of *P. areolatus* collected from locations within western Solomon Islands, Western Australia, Torres, Strait, Pohnpei and Red Sea.

Locality	Size range	Mean Size	L_{max}	Age range	Mean Age	T_{max}
Ghizo	170 - 552	387.98	477.15 (2.17)	0.6 - 10	4.2 (0.09)	6.1 (0.14)
- male	329 - 552	457.24	504.86	3 - 9	5.7	6.3
- female	170 - 552	396.01	496.82	1 - 10	4.3	6.2
Parara	155 - 560	390.20	477.88 (.4.17)	0.57 - 12	4.9 (0.16)	6.9 (0.33)
- male	390 - 560	452.79	506.79 (3.24)	3 - 12	4.2	8.5 (0.26)
- female	166 - 550	363.55	454.68 (2.85)	0.57 - 10	4.2	6.2 (0.19)
Roviana	260 - 660	433.40	539 (12.54)	2 - 12	4.5 (0.24)	6.4 (0.16)
Marovo	205 - 694	397.34	465.70 (7.64)	1 - 8	3.3 (0.08)	4.4 (0.20)
Rowley	262 - 590	427.35	491.97 (3.75)	2-11	5.3 (0.1)	6.5 (0.16)
Scott	227 - 539	382.77	460.34 (5)	1-9	4.3 (0.12)	6 (0.20)
Torres St	301 - 645	495.60	583.25 (1.33)	1-12	5.0	7.7 (0.10)
Red Sea	240 - 570	420.50	504.40 (2.47)	1-12	3.7	5.8 (0.23)
Pohnpei	130 - 599	424.40	530.59 (1.62)	0.31-12	5.1	5.6 (0.12)

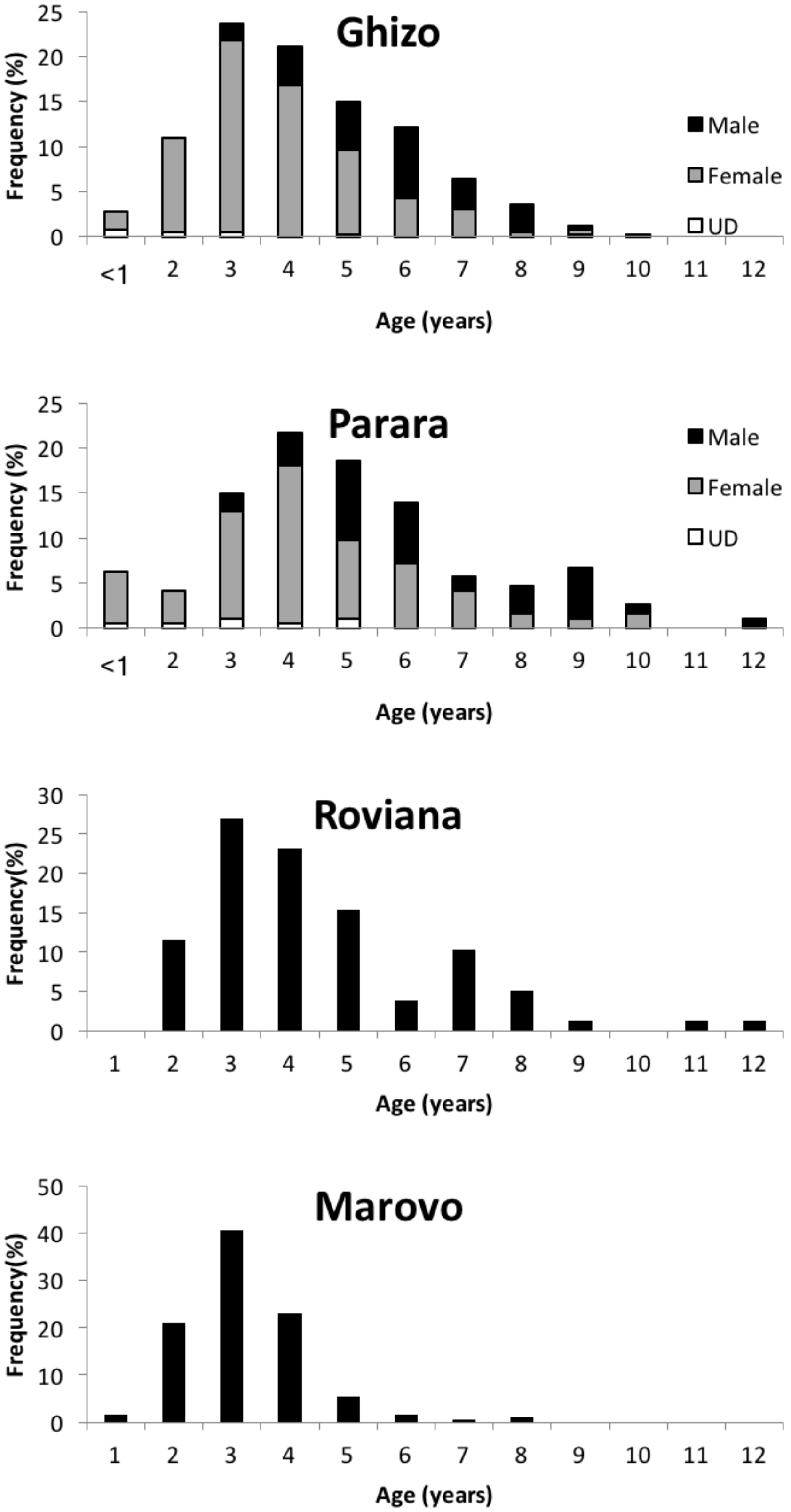


Figure 3.2 Age distributions of *P. areolatus* from locations in Solomon Islands. No sex-specific information was available for the locations Roviana and Marovo. NB: Scales on the Y-axis differ between graphs for comparison purposes. UD: undetermined sex.

Distribution of fish size was similar in that it was unimodal for all locations with strong modal classes of 351-400 mm (Ghizo and Marovo) and 401-450 mm (Parara, and Roviana) (Figure 3.3). A maximum size of 694 mm was recorded at Marovo, which is 4 cm less than the reported maximum length (Heemstra and Randall 1993). Mean size was found to vary significantly between locations (ANOVA, $F_{3,\ 894} = 8.891$, $p = <0.001$). Roviana had significantly higher mean sizes compared to the other locations (Tukey's HSD, $P<0.05$). No significant difference was identified between Ghizo, Parara and Marovo.

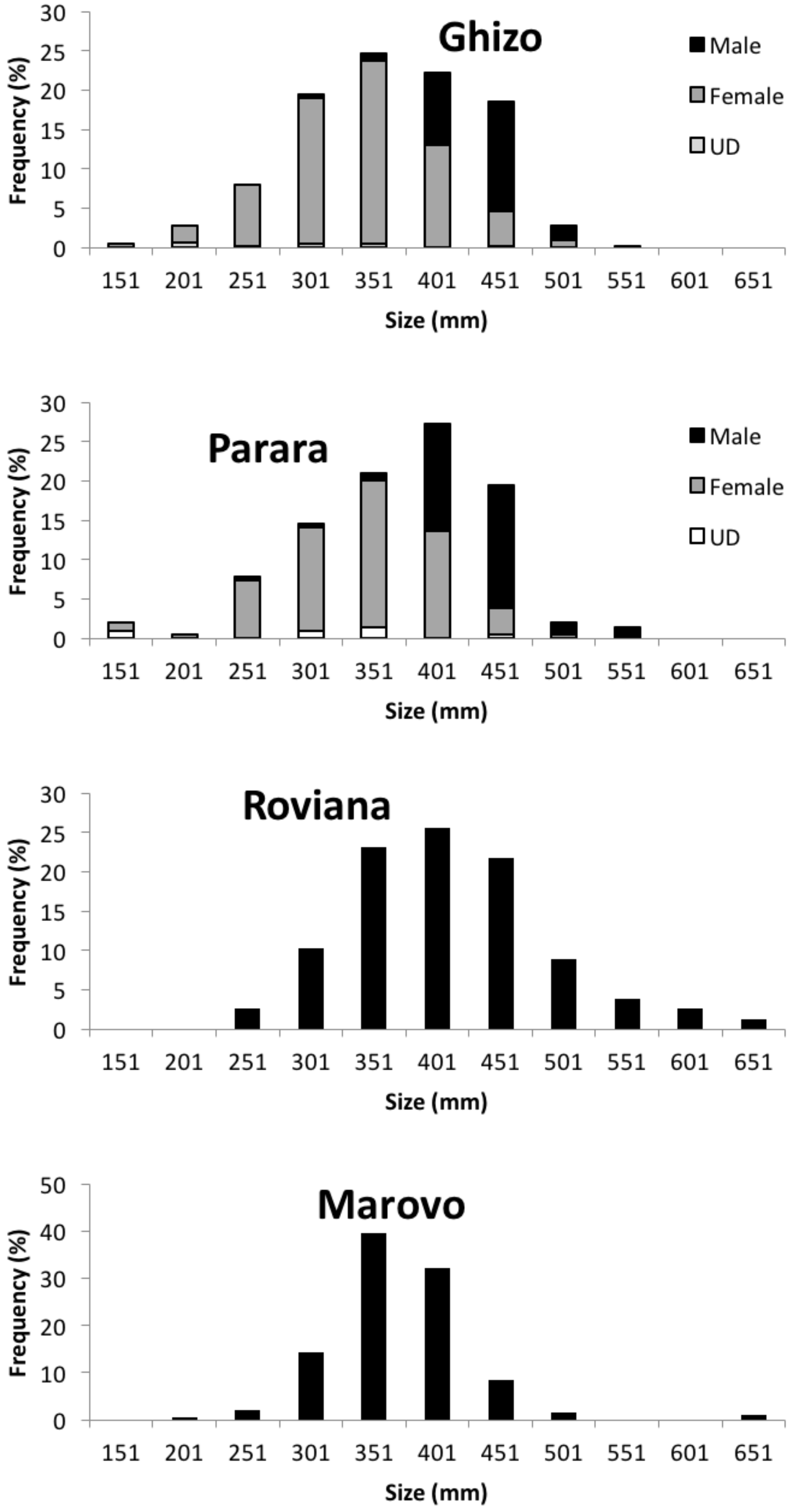


Figure 3.3 Size distributions of *P. areolatus* from locations in Solomon Islands. No sex specific information was available for the locations Roviana and Marovo. NB: Scales on the Y-axis differ between graphs for comparison purposes. UD: undetermined sex.

3.3.2 Growth

There was substantial variation observed in the size-at-age of *P. areolatus* for all four locations (Figure 4). The use of the von Bertalanffy Growth Function in analysing the data generated an indeterminate growth pattern that was consistent throughout the study locations and is generally characteristic of *Plectropomus* growth. The majority of fish growth took place within the initial few years of observed lifespans providing growth curvature estimates (K) that ranged from 0.42-0.48 (Table 3.2). Asymptotic length (L_{inf}) ranged from 468 – 511 TL mm at maximum size while values of hypothetical ages at which length is equal to zero (t_0) were all negative ranging from -0.22 to -0.26 (Table 3.2). The rVBGF parameters L_2, L_5 and L_8 revealed size ranges of 288 – 329 TL mm at 2 years of age, 417 – 466 TL mm at 5 years of age and 454 – 500 TL mm at 8 years of age, respectively (Table 3.2).

There was a general partitioning of growth trajectories between locations with Ghizo and Parara sharing similar growth characteristics. Roviana and Marovo displayed faster initial growth that later translated into larger adult sizes compared to the other locations (Figure 3.4 and 3.5A). A comparison of these trends to regional datasets (Red Sea, Pohnpei, northwestern Australia and Torres Strait) demonstrated similarities in the growth curves between Roviana and Marovo and that of the Red Sea. Initial growth in Pohnpei was similar to Roviana, Marovo and the Red Sea but asymptotes much earlier resulting in adult sizes that are comparable to Parara in Solomon Islands. Northwestern Australia locations followed similar growth profiles to Ghizo and Parara. Torres Strait displayed the fastest growth rate of the regional comparison and achieved larger adult sizes (Figure 3.5A and Table 3.2).

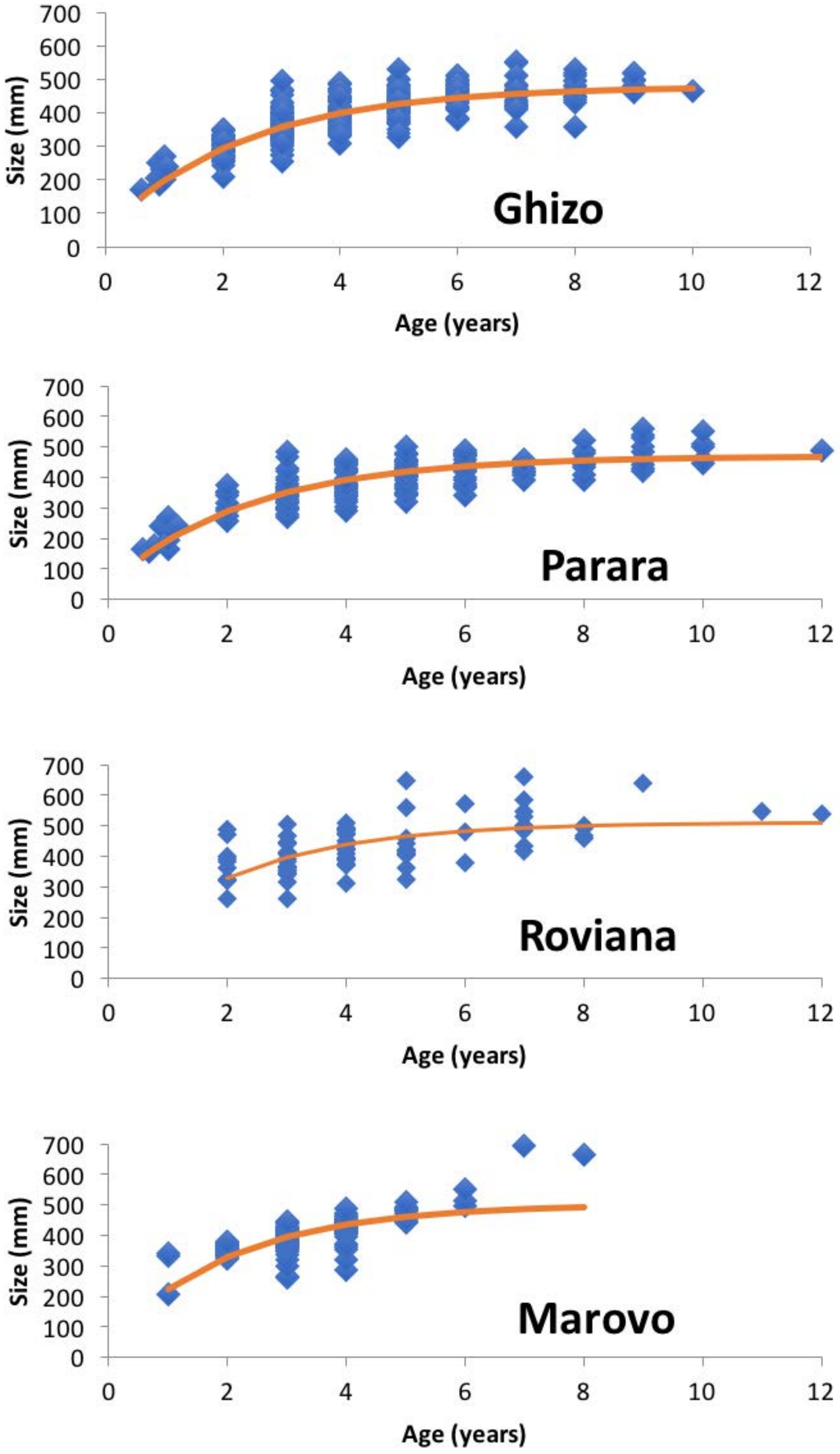


Figure 3.4 Size-at-age data for *P. areolatus* from populations within four locations from the Western Solomon Islands.

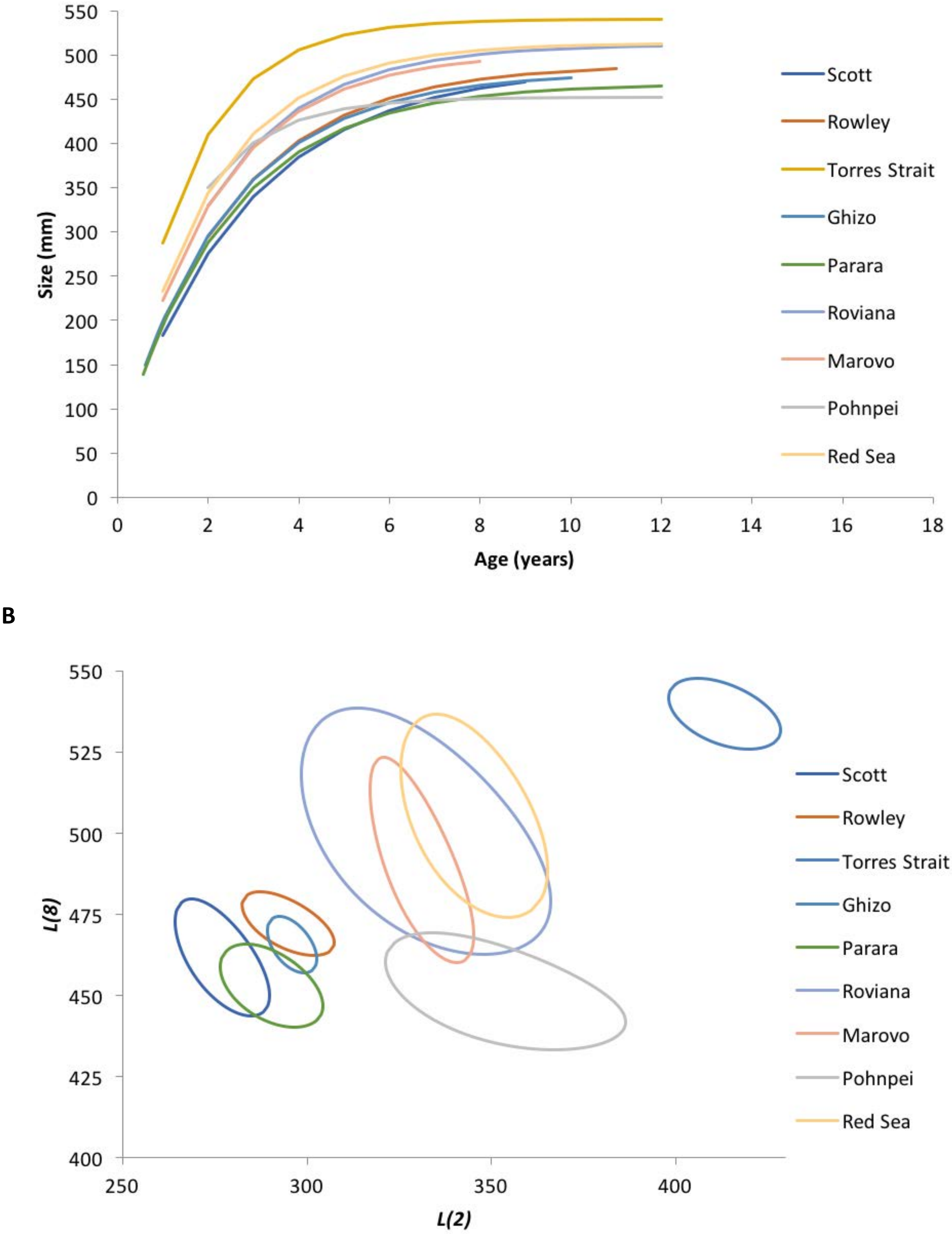


Figure 3.5 A) Von Bertalanffy growth function (VBGF) generated from size-at-age data for the four primary locations in Solomon Islands and from other regional datasets, B) Comparison of the 95% regions of the rVBGF parameters L_2 and L_8 from the above growth curves.

The L_2/L_8 95% confidence ellipses formed a grouping of ellipses based on the observed growth trajectories. As expected, the separation in the 95% confidence ellipses of the first group was largely explained by smaller mean size-at-age-2 (L_2) (Figure 5B). While locations in the second group generally reached larger mean size-at-age 8 (L_8). Both the L_2/L_8 95% confidence ellipses for GBR and Torres Straits separated on their own from both of the above groups, although there was some similarity between GBR L_2 confidence region to Roviana, Marovo, Red Sea and Pohnpei while the confidence ellipse for Torres Strait spans a similar range to the upper L_8 region of the Roviana, Marovo and Red Sea ellipses.

There were clear differences in growth patterns between sexes within populations from Solomon Islands (Ghizo, Parara) with males displaying faster initial growth and larger adult sizes compared to females (Figure 3.6A & 3.77A). Subsequently, an inspection of the L_2/L_8 95% confidence ellipses revealed a clear separation of the female and male ellipses in Solomon Islands (Figure 3.6B & 3.7B).

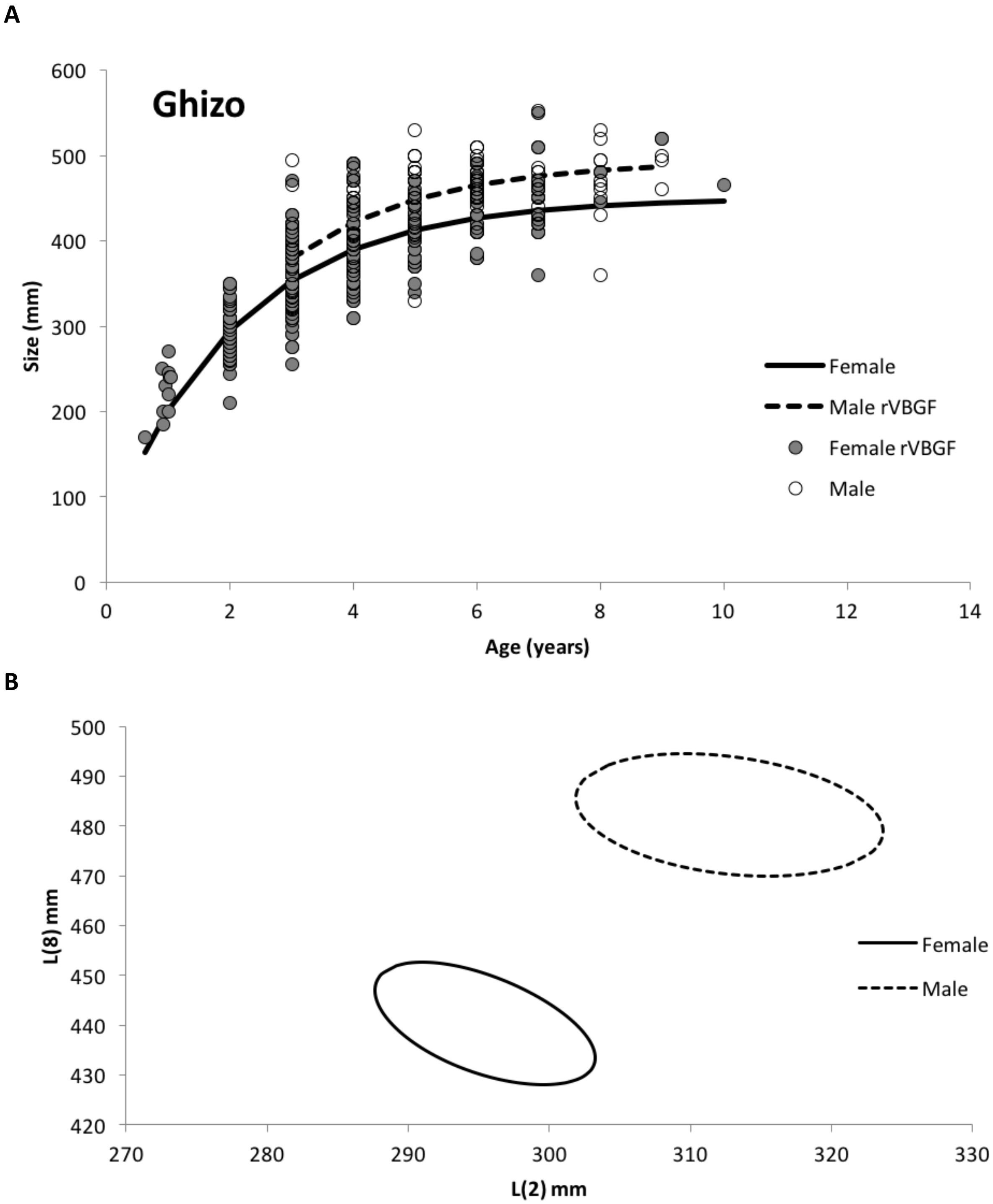
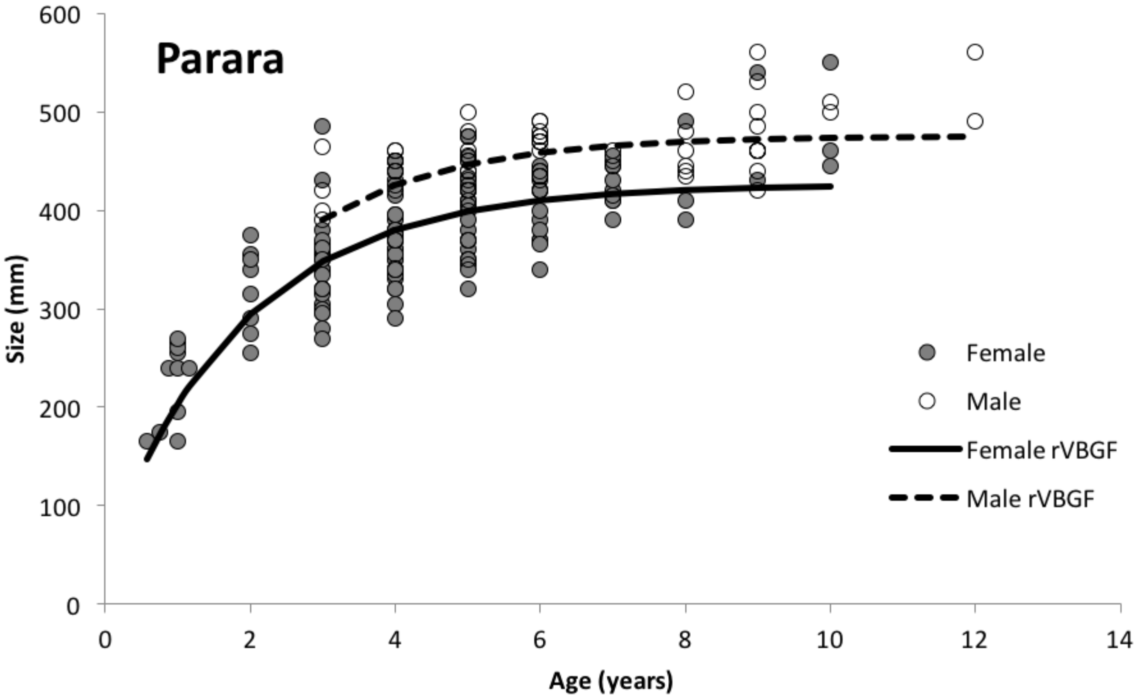


Figure 3.6 A) Sex-specific VBGF growth curve fitted to size-at-age data for Ghizo, Solomon Islands, B) 95% confidence regions for each sex from Ghizo.

A



B

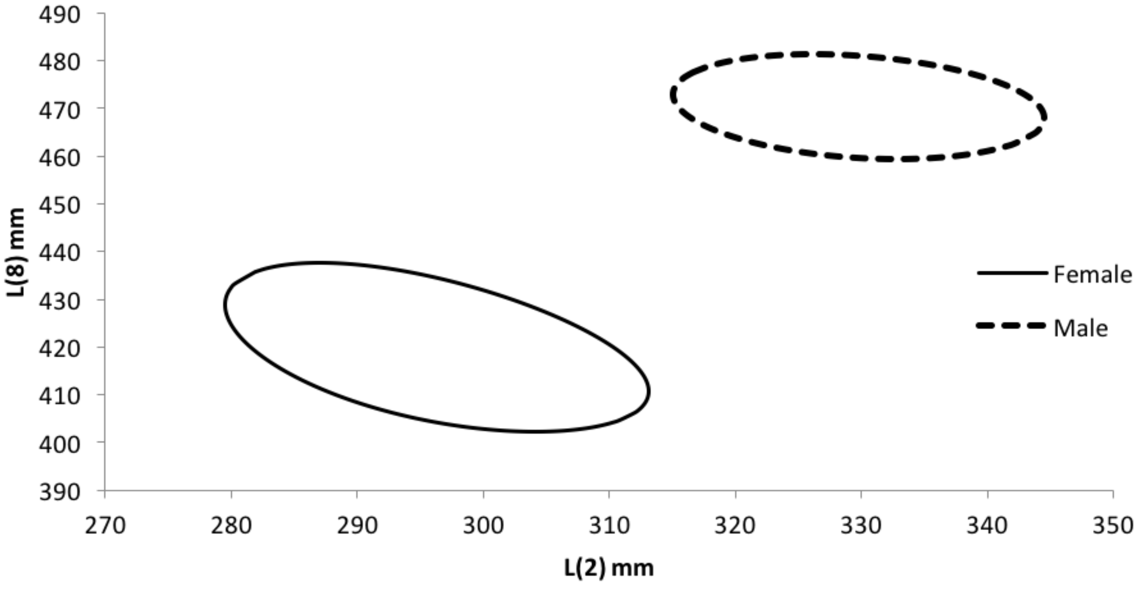


Figure 3.7 A) Sex-specific VBGF growth curve fitted to size-at-age data for Parara, Solomon Islands, B) 95% confidence regions for each sex from Parara.

3.3.3 Maximum age, longevity and mean maximum size

The oldest maximum ages recorded from the four study sites ranged from 8 years (Marovo) to 12 years (Roviana and Parara) (Table 3). Similarly, longevity (T_{max}) was greatest for Parara and lowest for Marovo with a range of 6-7.3 years (Table 3). There was a significant difference in T_{max} between locations (Mann-Whitney H = 49.326, df = 3, P = <0.001). All locations had significantly higher T_{max} compared to Marovo (Dunn's Method P<0.05) with no differences between the remaining three locations.

Mean maximum size (L_{max}) was greatest for Roviana and lowest for Marovo with a range of 466 – 539 TL mm (Table 3.3). There was a significant difference between L_{max} of the four locations (Mann-Whitney H = 55.715, df = 5, P = <0.001). A pair-wise comparison confirmed Roviana has higher significant L_{max} compared to all three locations while Ghizo and Parara had significantly higher L_{max} compared to Marovo (Dunn's method P <0.05). The lower T_{max} and L_{max} in Marovo is a result of the truncated age structure (Figure 3.2).

A comparison of the T_{max}/L_{max} confidence regions for the study sites revealed a similar spread of T_{max} and L_{max} values for Ghizo and Parara, however Marovo (lower T_{max}) and Roviana (higher L_{max}) each separated away on their own (Figure 3.8). When compared with other regional locations the confidence region of Roviana was more similar to Pohnpei and Red Sea although all three locations had similar spread of T_{max} values to Ghizo, Parara and the northwestern Australia locations. Both Torres Straits and GBR separated from the rest by L_{max} while GBR separated more strongly by T_{max} (Figure 3.8). The large confidence region of the GBR is due to the small data-set used in the comparison (Table 3.2).

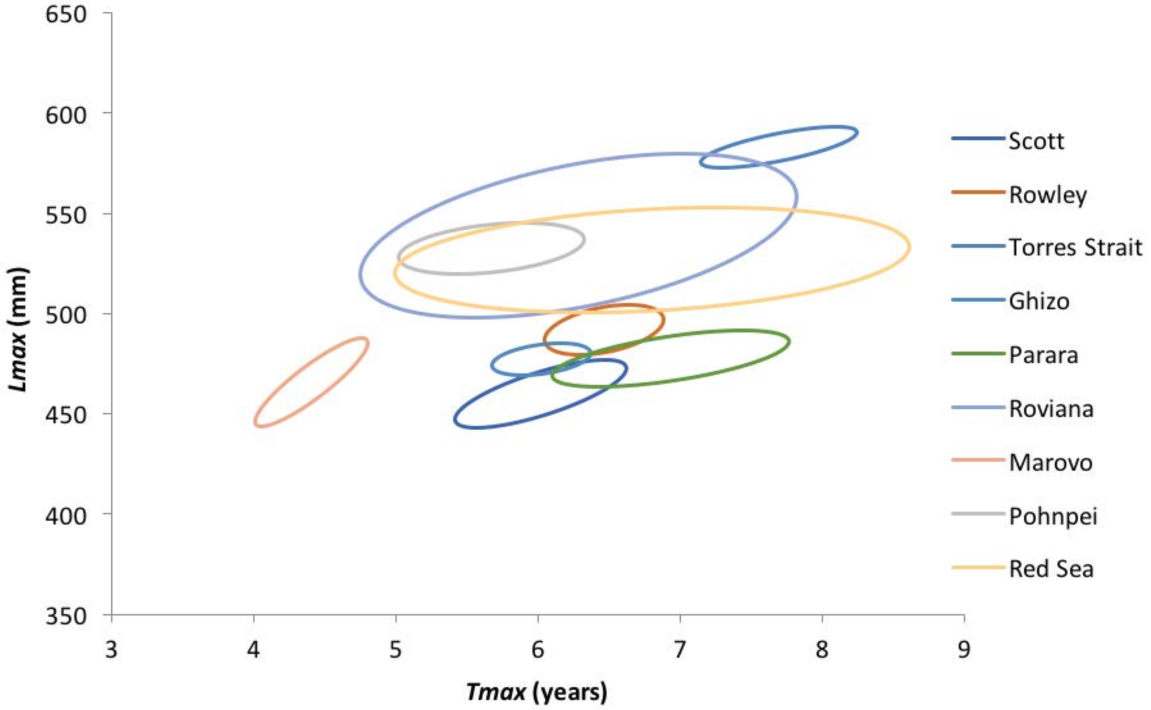


Figure 3.8 Comparison of L_{max} and T_{max} 95% confidence regions for the four primary study locations in Solomon Islands and from available regional datasets.

3.3.4 Mortality

Log-linear regressions of the age-frequency data revealed differences in mortality (Z) and survivorship (S) estimates between the four study locations (Figure 3.9). Estimated mortality rates were highest at Marovo (0.99 yr^{-1}) and lowest in Parara (0.38 yr^{-1}) and Roviana (0.37 yr^{-1}), corresponding to 37%, 68% and 69% annual survivorship, respectively (Table 3.2). Estimates of Z for Parara differed significantly to Ghizo (*t* = 2.26, P = 0.048, df = 14). Similarly, estimates of Z for Roviana were also significantly lower compared to Marovo (*t* = -4.77, P = 0.002, df = 14).

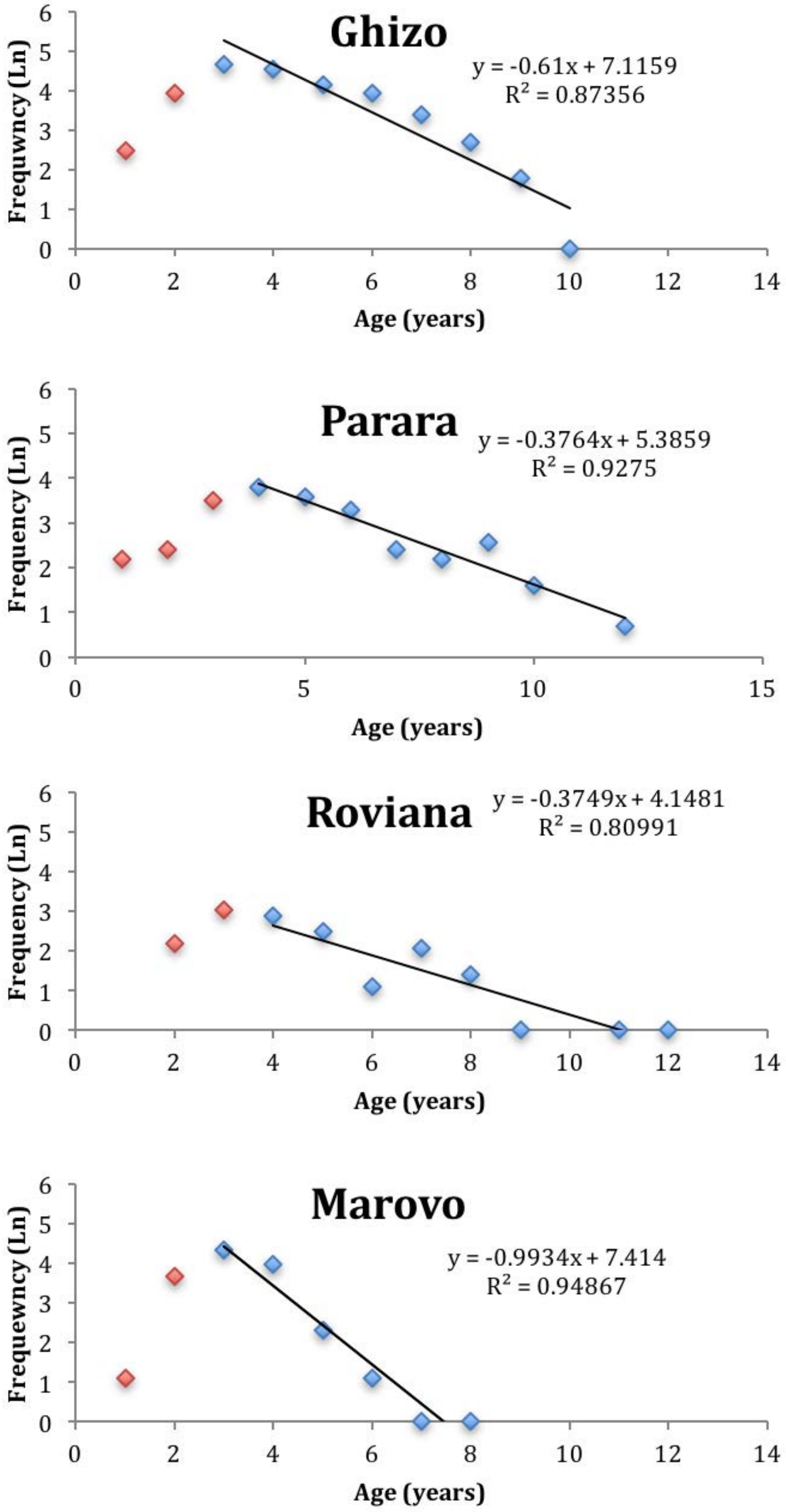


Figure 3.9 Age-based catch curves providing *Z* estimates for *P. areolatus* from locations in Solomon Islands. Red dots indicate samples not included in the regression.

3.4 Discussion

This chapter provides further insight into the general life history characteristics of *P. areolatus* as well as revealing interesting variation in the demographic parameters of longevity (T_{max}) and mortality rates (Z) between populations at large (latitudinal) and small (within country) scales. Latitudinal shifts in longevity was apparent with the Torres Strait and Rowley Shoals population displaying higher longevity compared to the lower latitude populations of Pohnpei and Solomon Islands. While within Solomon Islands, differences in age structure and mortality rates were present with populations from Ghizo and Marovo displaying truncated age structures and higher mortality rates compared to populations from Parara and Roviana. Varying levels of historical fishing pressure between these locations in Solomon Islands is likely to be the primary factor driving the observed differences. Similar broad and fine-scale differences have been described for other reef fish populations (Trip et al. 2008). Sex-specific growth was present in Solomon Islands with males growing faster and attaining larger size

In general, the growth parameter of this species is similar to that of other plectropomids (Ferreira & Russ 1992, 1994; Choat & Robertson 2002, Williams et al. 2008, Heupel et al. 2008). At all locations, *P. areolatus* registered a continuous growth pattern with most somatic development taking place during the first 2-3 years of its lifespan. The range of maximum ages in Solomon Islands (8-12 years) is similar to those reported for other locations. A recent study on *P. areolatus* collected from commercial fisheries in the Red Sea reported maximum age estimate of 9 years (DesRosier 2011). In Micronesia, *P. areolatus* are estimated to reach 12 years of age (Rhodes et al. 2013). While in the Torres Straits, *P. areolatus* achieves a maximum age of 14 years (Williams et al. 2008).

A comparison of the VBGF growth curve between locations in western Solomon Islands reveals substantial difference in their growth trajectories. For example, while there is very little difference between Ghizo and Parara there is a clear distinction between these two locations to the datasets from Roviana and Marovo. When compared to regional datasets, there appears to very little difference between Ghizo and Parara to the northwestern Australia locations of Scott and Rowley. In contrast, the higher initial phase growth and larger adult body sizes found in the larger lagoon systems (Roviana and Marovo) more closely reflect the pattern of growth found in the Red Sea (DesRosier 2011). Growth in Pohnpei (Micronesia) differed in that it was characterized by faster initial growth, similar to that observed in Roviana and Marovo, but with an adult size comparable to the other 2 locations in Solomon Islands. This corresponds with the higher growth coefficient (0.68) and lower asymptotic size (459 mm) published based on the complete data-set for the species in Micronesia (Rhodes et al. 2013). Interestingly, the Torres Strait population appears to undergo distinctly faster initial growth rate and generally reach a larger adult size. Similar variation in demographic parameters of reef fish populations have been documented on several scales ranging from within-reef systems to between ocean systems (Meekan et al. 2001, Gust et al. 2002; Robertson et al. 2005, Ruttenberg et al. 2005).

The variations in the patterns of growth seen in the western Solomon Islands is likely due to two possible factors. Firstly, the faster growth rates and larger adult sizes observed at Roviana and Marovo could be an artifact of predominantly sampling fish from FSAs. Faster growing individuals could be expected to join the spawning population earlier than slow growing individuals in the same cohorts. Furthermore, because spawning aggregations are predominantly made up of mature fish, the mean size of fish captured at FSAs is likely to be larger than catches from surrounding reefs where adults, subadults and juveniles form a component of the catch.

Alternatively, the Roviana and Marovo populations may have different levels of food availability (Clifton 1995, Gust et al. 2002), enabling *P. areolatus* in these regions to undergo accelerated growth to a comparatively larger adult size, thereby making it less prone to predatory pressures. Marovo and Roviana lagoons encompass large extensive networks of patch reefs and mangrove ecosystems that receive regular external nutrient input from terrestrial runoff. This contrasts with the smaller lagoonal systems of Ghizo and Parara. Therefore, variation in growth observed may be a product of differences in the physical environmental (i.e. productivity and food availability) and effects of anthropogenic activities (i.e fishery extraction) at each location.

Populations with higher densities are likely to experience a reduction in overall growth and size compared to those with lower densities due to density-dependent factors (e.g. competition for food and habitat) (Casselle et al. 2011). On the GBR, populations with higher densities have been shown to harbour smaller size and younger age structures (Gust et al. 2002). It was suggested that increased competitive interactions were responsible for the observed demographic patterns. However, similar patterns were not observed in the Galapagos and Solomon Islands where species with faster growth and larger body sizes resided in higher density populations that were exposed to more abundant and favorable food supply (Hamilton 2004, Ruttenberg et al. 2005). Although density data for Ghizo and Parara is available (Chapter 2) additional data on the density of *P. areolatus* from Roviana and Marovo alongside information on predation pressure, productivity and resource availability for all locations would be required to further examine just how important density-dependent processes maybe in driving the observed differences.

Fishing pressure can alter the population demography of reef fishes by reducing the abundance of target species and selectively removing larger sized individuals (Halpern & Warner 2002, Pauly et al. 2002). Where age is size-related, intensive fishing pressure can result in the alteration of the age structure of harvested populations. Mean age from more heavily fished locations (Ghizo and Marovo) was consistently lower compared to less heavily fished locations (Parara and Roviana). Despite sharing similar growth trajectories to Parara and Roviana, the lower mean age estimates observed in populations from Ghizo and Marovo, respectively, are likely to be a result of long established artisanal fisheries within those two locations. Indeed, mortality rates (Z) at heavily fished locations in Solomon Islands were consistently higher compared to more lightly fished locations.

The discrepancy in growth rates between sexes in Solomon Islands is similar to that observed for the same species in Micronesia with males tending to have higher growth rates and overall body size (Rhodes et al. 2013). Such growth characteristics are commonly observed in species that undergo sexual transition (Choat & Robertson 2002). It has been suggested that increased growth occurs following the period of sexual transition resulting in a growth spurt during the male phase. This is hypothesized to occur due to the lower costs of producing sperm that allow extra energy to be directed to somatic development (Wootton 1985). An alternative theory based on a study on *P. maculatus* by Adams and Williams (2001) proposes that faster growing females (larger initial sizes) are more likely to undergo sex-change to a male either before or after female maturity. However, gonochoristic species are also known to display sex-specific growth in which males attain faster growth than females (Moore *et al.* 2007). Furthermore, recent life history investigations on *P. areolatus* have not provided conclusive evidence of sex-reversal (Williams et al. 2008, Rhodes et al. 2013). In light of this, a detailed analysis into the reproductive biology of this species is warranted and is the focus of the next chapter.

4 Reproductive Biology of *Plectropomus areolatus*

4.1 Introduction

The reproductive biology of the Epinepheline groupers is quite diverse and generally encompasses gonochoristic or protogynous hermaphrodites (Smith 1965, Shapiro 1987, Sadovy & Colin 1995, Sadovy 1996, Fennessy & Sadovy 2002). Gonochoristic development, (as observed with *Epinephelus striatus* (Sadovy & Colin 1995), *E. polyphekadion* (Rhodes & Sadovya) and *E. maculatus* (Rhodes et al. 2016)) is the recruitment of males or females directly from an immature juvenile stage with no further sex change in their life history. Protogynous hermaphroditism, or protogyny (change sex from mature females to matrure males at an older and larger size) is reportedly the most prevalent reproductive pathway in epinephelid species (Sadovy 1996, Rhodes & Sadovy 2002a). Furthermore, two forms of protogyny, monandric and diandric, are currently recognized. The former describes the transition from a mature female to a mature male (secondary male) and the latter describes development directly into a male from an immature juvenile stage (primary male) or from a mature female (Sadovy & Shapiro 1987, Fennessy & Sadovy 2002, Sadovy & Domeier 2005b).

Past studies have shown that some epinepheline groupers possess several biological characteristics (rarity, long lifespan, relatively slow growth, late effective maturity and protogynous sex change) which when coupled with their tendency to a) form predictable spawning aggregation and b) be easily caught at spawning aggregation, can make them particularly susceptible to being overfished (Sadovy 1996, Huntsman et al. 1999, Jennings et al. 1999, Morris et al. 2000, Pears et al. 2006). In general, fishing has a direct impact on abundance, size and age structure, growth and reproduction of a target species. Such impacts are accentuated when fishing takes place on spawning aggregations, with potentially serious consequences if fishing pressure is of an intense commercial scale (Sadovy de Mitcheson 2016).

Recently, studies have highlighted that larger and older females have a more significant contribution to egg production than younger and smaller individuals (Birkeland & Dayton

2005, Hixon et al. 2014). For instance, female fecundity has been shown to increase exponentially with size (Rochet 2009) while eggs produced by older and larger females have a better chance of surviving the larval phase compared to their younger and smaller counterparts (Stige et al. 2017). These studies suggest that energy may be primarily invested towards somatic growth at younger immature or early maturity stages before switching over to reproductive functions at an older age. Consequently, a reduction of mature reproductive individuals and optimal sex ratios affects recruitment levels due to reductions in spawning potential of the population (Sadovy 1996, Coleman et al. 1999, Huntsman et al 1999). Modelling suggests that intraspecific socially mediated adjustment for the effect of fishing (earlier age at sexual maturity of females, earlier transition from mature female to mature male) was unlikely to compensate effectively and that protogynous populations were more likely to experience overfishing than for similar gonochoristic populations (Huntsman & Schaaf 1994).

Understanding the sexual pattern of groupers (and other species) is a necessary step in designing and implementing suitable management measures. For instance, protogynous species are thought to be more susceptible to selective forms of fishing compared to gonochores (Erisman et al. 2008, Sadovy de Mitcheson 2016). The typical bimodal size distribution of sexes observed in protoynous species means that harvesting techniques that focus on either lower or uppers ends of the size structure may disproportionately remove a given sex. In species that display sex-specific growth rates, size-selective fishing may lead to an imbalance in the optimal operational sex ratio of a population which can in turn lead to a reduction in the overall population size and reproductive output (Sadovy 1996, Coleman et al. 1996).

Apart from the inclusion of known spawning aggregations within marine protected areas (Hamilton et al. 2012) no other management measures specific to *P. areolatus* has been implemented in Solomon Islands due in part to the lack of biological information available on this species in Solomon Islands. As such, the objectives of this chapter are to:

a. Determine the reproductive biology of *P. areolatus* and provide data on the sexual pattern, timing of sexual maturity, male recruitment and reproductive periodicity;

b. Examine how different levels of fishing may have affected reproductive parameters of *P. areolatus* populations in Solomon Islands.

Information obtained through this study will be important in determining further management options for this species such as minimum size limits and temporal sale and fishing bans.

4.2 Methods

4.2.1 Study area

Data for this study was collected from Ghizo and Parara, two adjacent reef systems in the central region of Western Province (Chapter 2 and Figure 4.1). The Ghizo reef system is made up of a thin intermittent barrier reef structure of Ghizo Island that stretches approximately 36 km from the northwestern end down to the southeastern end encompassing a small lagoon system. There is a striking difference in reef development on the opposite side of the island where it is characterized by fringing reefs and offshore platform reefs. A vibrant small-scale reef fish fishery operates within and around Ghizo Island, supplying the township of Gizo (note difference in spelling). Concerns of overfishing have led to the development of plans by NGOs and local government to formally implement a network of small MPAs within the reef system (Liligeto 2011). The Parara reef system consists of a continuous barrier reef with well-developed coral growth that forms an effective barrier around the western-most extremity of Vonavona Lagoon. An expansive network of patch reefs is located within the lagoon. Historically, fishing pressure within the Parara reef system has been of a subsistence nature. However, increasing demands for fresh seafood from the urbanized fishery in nearby Ghizo is placing added pressure on the marine resources in this reef system. Spawning aggregations of reef fishes, including squaretail coralgrouper, are known to occur within both reef systems.

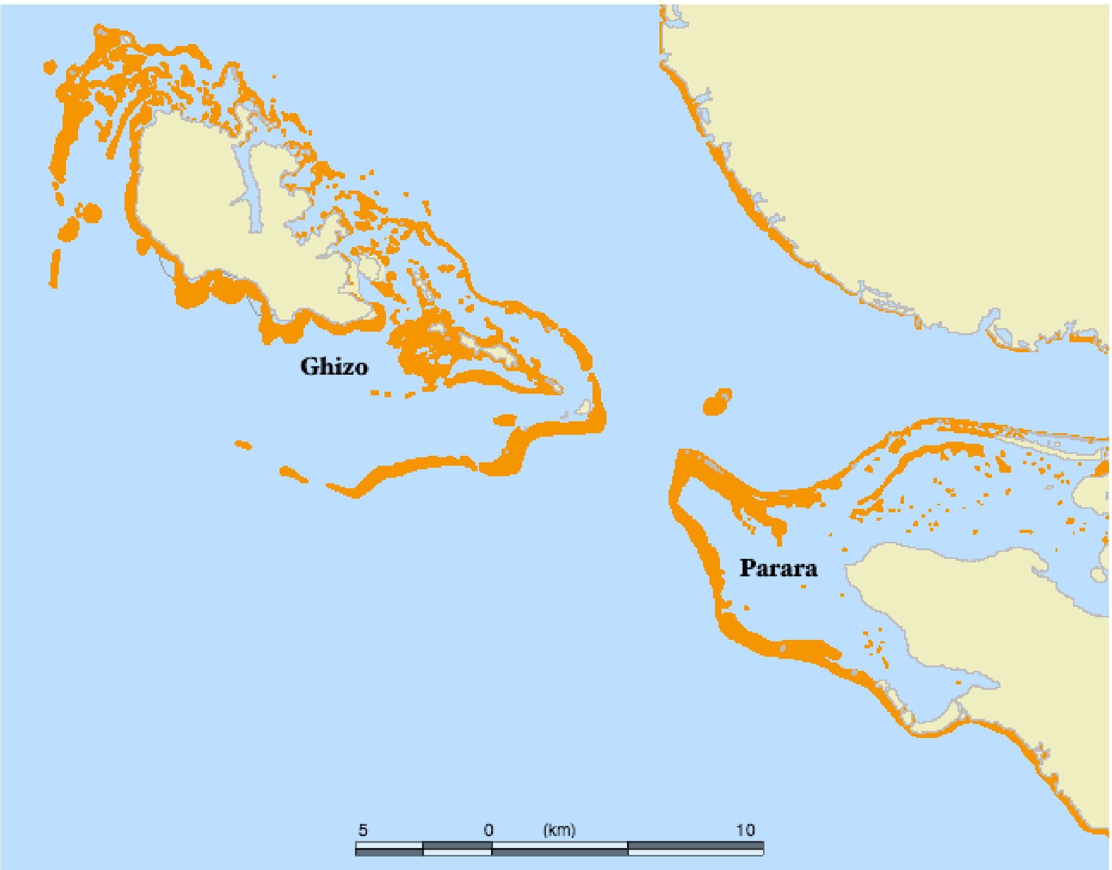


Figure 4.1 Location of study area in the central region of Western Province, Solomon Islands. The orange colour represents the reef system and the light brown colour is island/land mass.

4.2.2 Collection of samples

Sampling of *P. areolatus* occurred between the months of January-November over a four year period (2008-2011) and yielded a total of 625 gonads of which 69% were collected from Ghizo and 31% from Parara using both fisheries-dependent and fisheries-independent methods. Samples were attained from breeding populations at spawning sites and non-breeding populations on reefs outside of spawning periods. All fish samples were measured to the nearest millimeter (fork length, FL) and weighed to the nearest gram. All available gonads were weighed to the nearest 0.1 gram (g) and immediately stored and preserved in vials filled with FAACC (4% formaldehyde, 5% acetic acid, 1.3% calcium chloride) prior to transportation back to the laboratory.

4.2.3 Gonad analysis

Difficulties in accurately sexing all stages of gonads macroscopically meant that histological techniques were used in the lab to determine the sex (male or female) and subsequent reproductive stages of both sexes. Portions of tissue 3-5 mm thick were dissected from the medial region of each gonad, dehydrated with alcohol and embedded in paraffin wax. Thin sections (5µm) of the gonad were then removed and mounted on slides before being stained with Mayer's haemotoxcylin and Young's eosin-erythrosin (Winsor 1984). The different stages of oocyte development were classified according to stages described by West (1990) as follows: *Stage 1*- chromatin nucleolar stage; *Stage 2*- perinucleolar stage; *Stage 3*- yolk vesicle formation; *Stage 4*- vitellogenic stage; *Stage 5*- hydration. These stages were then categorised according to descriptions of gonadal morphology modified from Samoilys and Roelofs (2000), Adams (2002) and Pears et al. (2006). Classification of the different stages of spermatogenesis was adapted from Rhodes and Sadovy (2002a).

4.2.4 Sexual pattern

Individual gonads were examined for the possible presence of anatomical and functional hermaphroditism following criteria in Sadovy de Mictcheson & Liu (2008). Sex-specific size- and age-frequency distributions for each location were constructed to examine the extent of overlap between females and males. Mann-Whitney nonparametric tests were used to compare median size and age of mature males and females both within and between the two locations. The sex ratio of mature females and males at each location was examined for any deviation from a balanced sex ratio of 1:1 using Chi-square (X^2) goodness of fit test (Wootton 1998). Bisexual individuals as described below were not included in the comparison.

4.2.5 Size and age-at-maturity

Gonado-somatic indices (GSI) were calculated using the formula: GSI = 100 x (gonad weight/body weight). GSI values of each sex were used to represent gonadal development and were plotted onto to size distribution to explore size-based reproductive capacity at both locations. In addition, estimates of size and age-at-maturity for females were obtained by plotting the proportion of mature females (F2-F5) vs immature females (F1) against the relevant length and age classes. This was accompanied by fitting a logistic regression function to the data using the maximum likelihood method (Moore et al. 2007). The same approach was used to calculate the timing of male recruitment by comparing the proportions of females and males by size class. The extent of any overlap in the size range between the two sexes is taken to be the period at which males are likely to appear in the population.

4.2.6 Spawning season

The timing and frequency of spawning season was established by plotting GSI of reproductively active individuals according to their month of collection (pooled between years). It is expected that an increase in GSI will occur when gonads, especially ovaries, increase significantly in size and weight according to spawning schedules. In addition, the proportion of each reproductive phase for females and males was plotted by month of collection to examine the ovarian and testicular development patterns throughout the year and the degree of spawning activity occurring in each month.

4.3 Results

4.3.1 Gonad development

Examined gonads had a bilobed formation consisting of cylindrical structures (lobes) of similar length that were detached at the anterior of the gonad and for most of the gonad length, and connected posteriorly near the urogenital opening. The gonad structure was supported within the body cavity by a network of mesenteries, ligaments, arteries and veins which were attached along the length of the gonad.

F1 (immature) inactive female: n = 111

Ovaries of immature females were small and weighed an average of 1.44 g (+/- 0.18 S.E). The gonads generally had thin walls and contained mostly oogonium and previtellogenic (Stage 1 & 2) oocytes closely packed within the lamellae depending on the development stage (Figure 4.2A).

F2 (resting) mature inactive female: n = 87

Gonads were typically comprised of early growth oocytes but with increased presence of cortical alveolar stage (Stage 3) oocytes. The majority of gonads had thick gonad walls, scattered presence of muscle bundle and had a mean weight of 7.40 g (±1.02 S.E.) (Figure

4.2B). Spermatocytes were observed within cysts in 25 gonads belonging to F2 individuals ranging in size from 335 mm to 520 mm.

F3 (ripe) mature active female: n = 136

Gonads had increased mass with an average weight of 34.63 g (±1.83 S.E.). The traverse diameter of gonads was larger than earlier gonad stages and the lamellae contained yolk globule stage oocytes. Primary growth oocytes were also present indicating varying oocyte development rates with the gonad (Figure 2C).

F4 (hydrated) mature active female: n = 80

The gonads were undergoing the final stages of oocyte maturation. Overall oocyte diameter increased as lipid droplets and yolk globules coalesced and proceeded to hydrate. Some scattered primary growth oocytes were present in a few of these gonads (Figure 2D). Mean gonad weight was 67.66 g (± 4.69 S.E.).

F5 (post-spawn) mature active female: n = 7

Post-spawn – All oocyte development stages present except for hydrated oocytes. Atretic vitellogenic oocyte commonly present alongside muscle bundles along with intra-lamellar debris and cytoplasmic strands.

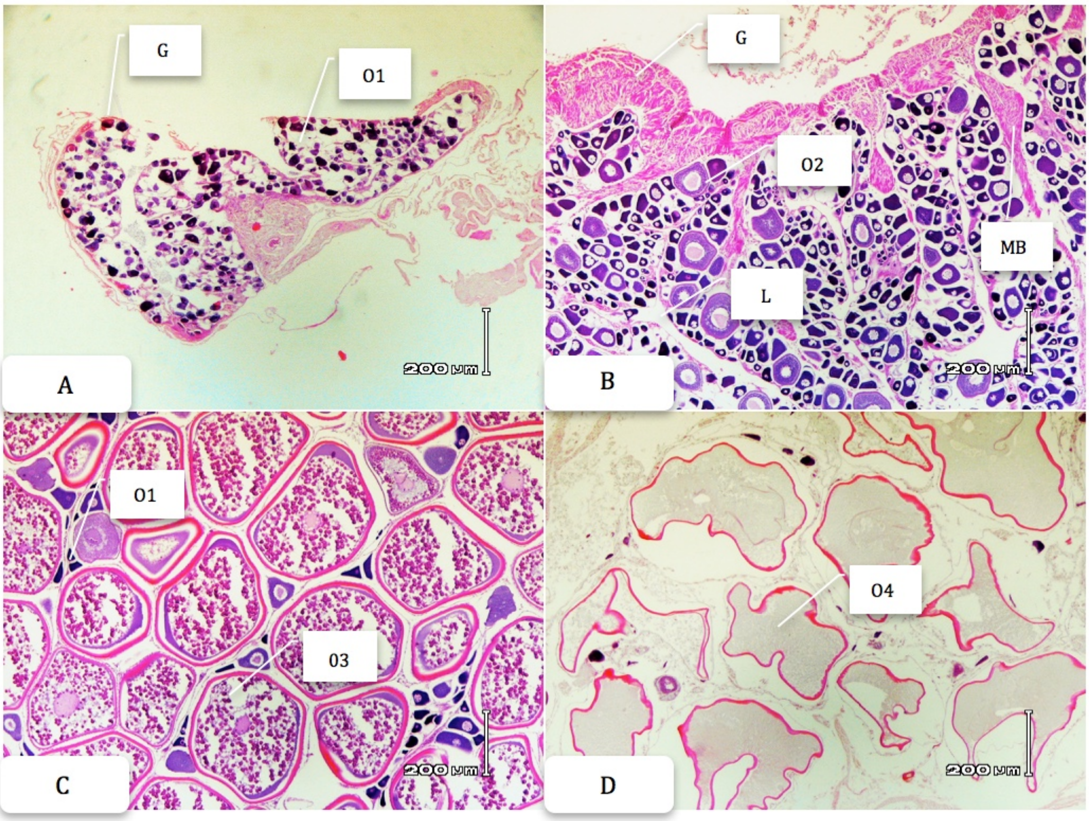


Figure 4.2 Histological sections from female *Plectropomus areolatus* gonads collected in western Solomon Islands. (A) Section from a 1-year old immature female (F1) showing thin gonad wall (GW) and tightly packed Stage 1 oocytes (O1). (B) Section from 3-year old resting female (F2) showing thick gonad wall, muscle bundles (MB), lumen (L) and Stage 3 oocytes (O3). (C) Section from a 6-year old ripe female (F3) with Stage 1 & 3 oocytes. (D) Section from 7-year old spawning female (F4) with Stage 4 oocyte (O4).

Inactive bisexual (B): n = 20

Gonads were similar in appearance to immature female gonads but were classified as inactive bisexual as they contained both early spermatogenic tissue and pre-vitellogenic oocytes within the gonad lobules (Figure 4.3). In all cases Stage 1 & 2 oocytes dominated the lobule area (>75%). The condition of these gonads was clearly of a non-functional state, i.e. had not previously spawned (Fennessy and Sadovy 2002), and were found in fish ranging in size from 165 mm to 395 mm. Nine of these gonads belonged to individuals below the female size at 50% maturity (L_{m50}).

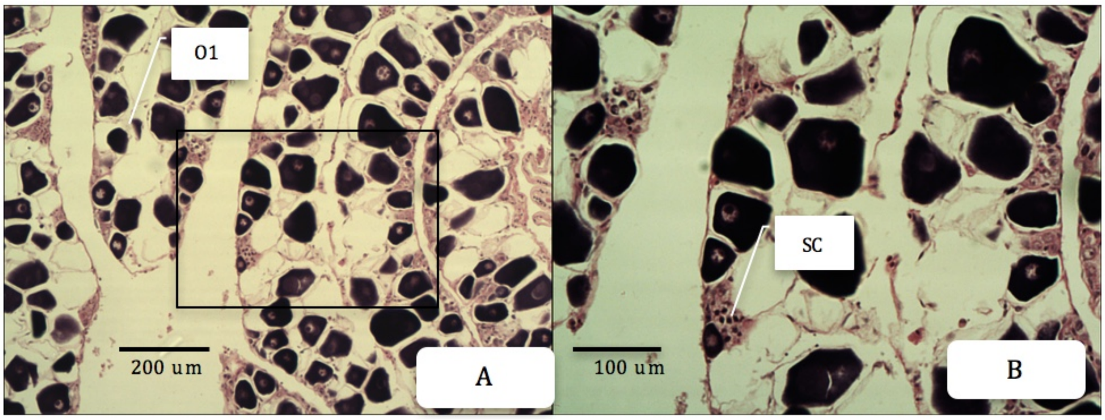


Figure 4.3 Histological sections from an A) inactive bisexual 2-year old *Plectropomus areolatus* showing distinctive features of a F1 gonad. B) Enlarged section of A showing presence of spermatocytes.

M1 inactive mature male: n = 16

Gonad appeared to be in an inactive/dormant state. Varying stages of early spermatogenesis was abundant in the form of spermatogonia and spermatocytes (Figure 4.4A). Gonads were either in a disorganized state, suggesting prior spawning activity, or appeared as if they were in an extended state of rest.

M2 mature, active male: n = 16

Most stages of sperm development present. Spermatids and spermatozoa dominate the seminiferous lobules but have not entered the sperm sinuses and duct (Figure 4.4B). Primary growth oocytes can be present.

M3 mature, active male: n = 147

Individuals are defined as being in a spawning-capable stage. Seminiferous lobules have increased in mass and are filled with spermatozoa. Spermatozoa have entered sperm sinuses and ducts. Early stages of spermatogenesis was rare (Figure 4.4C).

M4 mature, active male: n = 3

Testes in a state of disarray. Seminiferous lobules have separated. Spermatozoa largely absent from sperm sinuses and ducts. Gonad lobules have significant muscle bundles (Figure 4.4D).

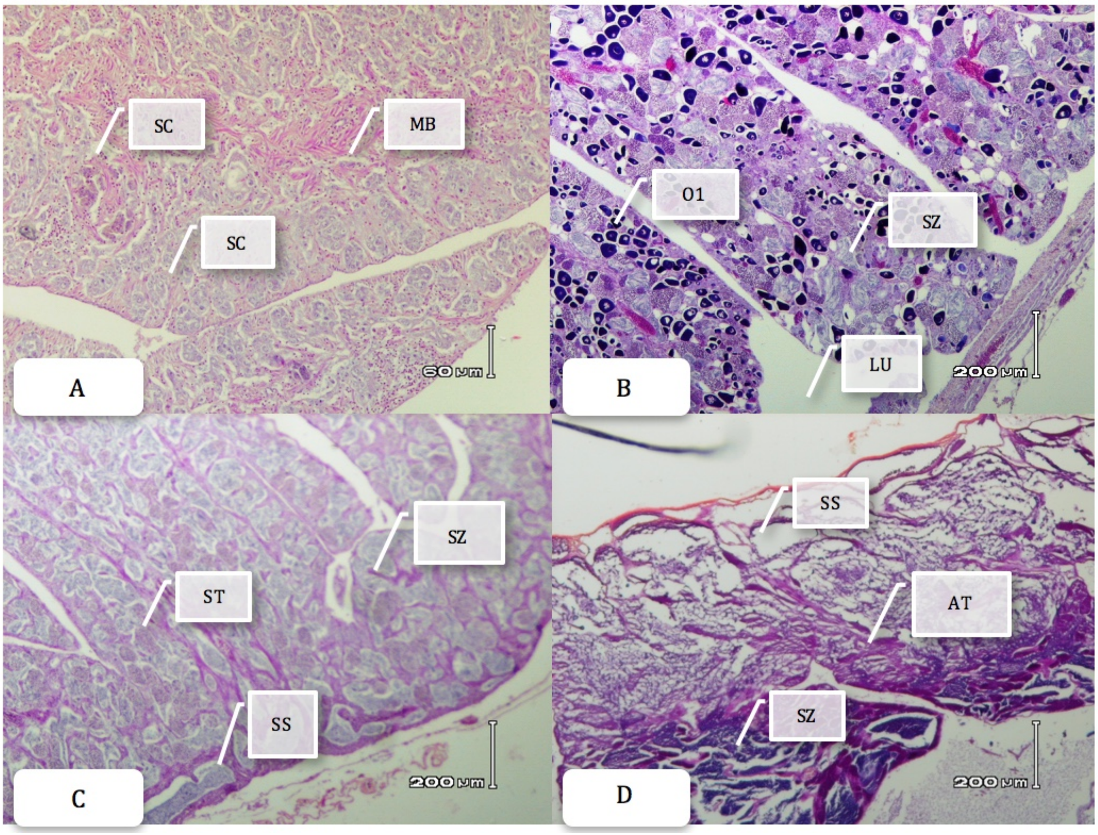


Figure 4.4 Histological sections from male *Plectropomus areolatus* gonads collected in western Solomon Islands. A) section from a 9 year old inactive male (M1). B) Section from 5-year old ripe male (M2) with spermatozoa (SZ) scattered though out gonad. C) Section from a 3-year old spawning capable male (M3) showing sperm sinus (SS) filled with SZ. Spematids (ST) and SZ dominate gonad. D) Section from a 6-year old spent male (M4). Testes in a state of disarray with atresia of tissue (AT)

4.3.2 Population structure and sex ratio

The degree of overlap in size and age structure between sexes was considerable at both locations (Figure 4.5 & 4.6). All sex-specific distributions were unimodal except for males at Parara, which had a bimodal age distribution (Figure 4.6b). Female modal size class was 351 mm at both locations as opposed to males, which was 451 mm TL. The modal age class for females was 3 and 4 compared to 6 and 5 years for males at Ghizo and Parara, respectively. The number of mature females at Ghizo was significantly greater than the number of mature males (2.18:1, n=331, x^2 = 44.967, P < 0.001). In contrast, the sex ratio at Parara was closer to a 1:1 ratio with the number of mature females not differing significantly from the number of mature males (1.29:1, n=142, x^2 = 2.035, P = 0.154).

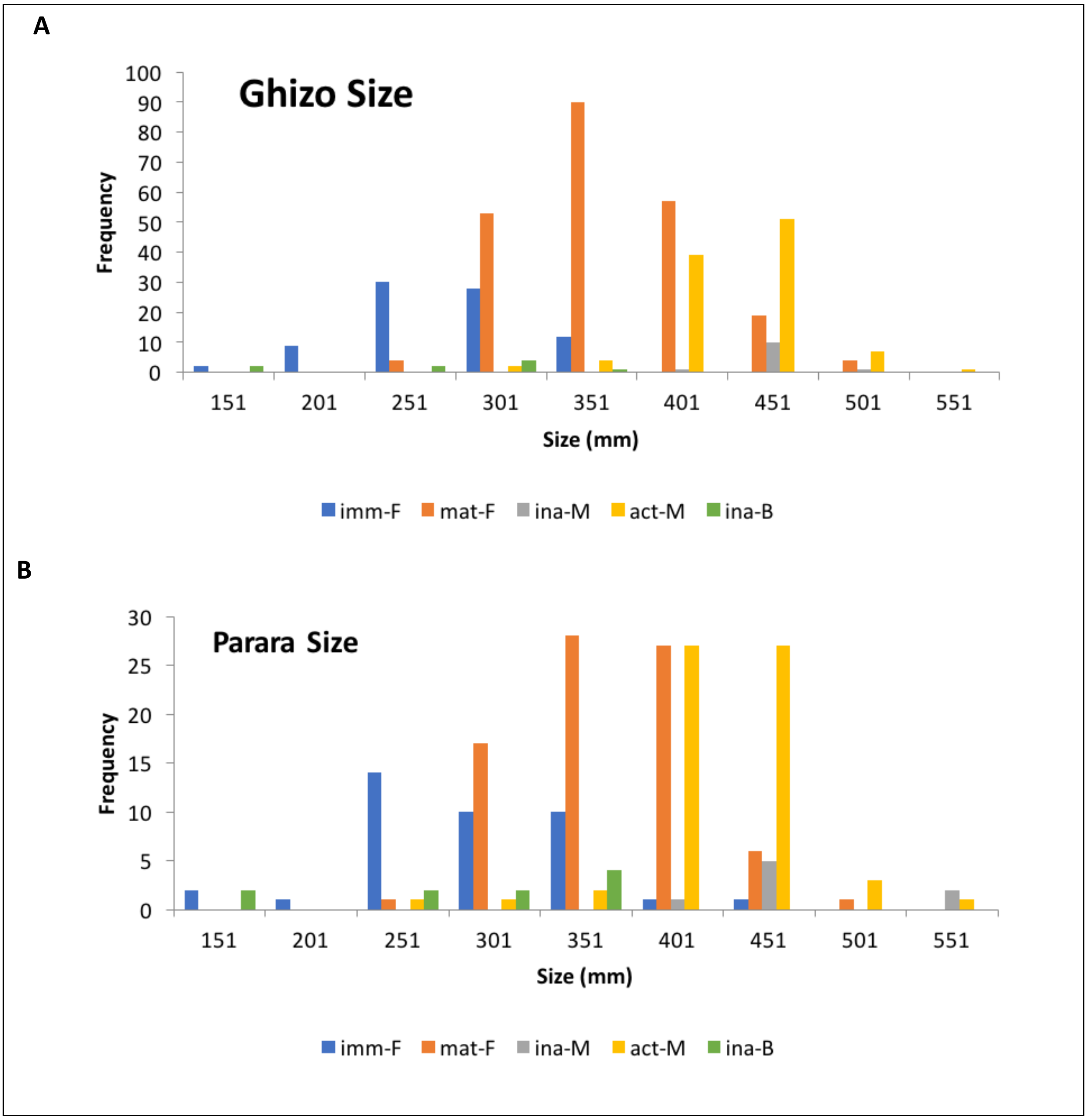


Figure 4.5 Size-frequency distributions at (a) Ghizo and (b) Parara, for immature female (blue), mature female (orange), inactive male (grey) and active male (yellow) *Plectropomus areolatus* in Western Province.

A comparison of the median sizes of mature female and males revealed significant differences within Ghizo (Mann-Whitney U-statistic = 3009.500, T = 2850.500, P < 0.001) and Parara (Mann-Whitney U-statistic = 829.500, T = 6021.500, P <0.001) with males attaining higher median values.

Figure 4.6 Age-frequency at (a) Ghizo and (b) Parara for immature female (blue), mature female (orange), inactive male (grey) and mature male (yellow) *Plectropomus areolatus* in Western Province.

Similarly, comparison of the median ages of female and males also revealed significant differences for Ghizo (Mann-Whitney U-statistic = 5183.500, T = 22832.5, P < 0.001) and Parara (Mann-Whitney U-statistic = 1671.500 , T = 5038.500, P = 0.002). There was no significant difference between the median size (Mann-Whitney U-statistic = 2971.500 , T = 4924.500, P = 0.399) and age (Mann-Whitney U-statistic = 2680 , T = 5494, P = 0.11) of males between locations. Female median sizes were not significantly different (Mann-Whitney U-statistic = 7988.500 , T = 12946.500, P = 0.181) between locations, however, females at Parara had a significantly higher median age (Mann-Whitney U-statistic = 5453, T = 15087, P <0.001).

4.3.3 Gonado-somatic index and seasonal spawning pattern

Female GSI increased substantially after the 300mm mark driven by the presence of active individuals (Figure 4.7 & 4.8). Two hundred and twenty eight females (74% of mature females) with microscopic evidence of being in a “reproductively active” state were collected between the months of February and October (Figure 9A) with gonads weighing as much as 16% of body weight and a mean of 5.48 % (± 0.24 S.E.). Active male gonads (M2-M4) on the other hand, accounted for 27% of gonads and averaged 1.91% (± 0.09 S.E.) of body weight. However, two active males in the lower end of the male size distribution (350 mm and 370 mm) attained high GSI values (9.61% and 7.64% respectively), which were comparable to those of active females of similar sizes (Figure 7B). Both males were collected from the Ghizo spawning site. The GSI value of active females was significantly greater than that of active males (Mann-Whitney U statistic = 6361.000, T = 20222, P < 0.001).

There was an obvious seasonal trend in GSI values taken from reproductively active individuals over a 9-month period. Mean active female GSI increased substantially from 2.19% in February to 6.17% in March, before peaking at 6.65% in April (a 3-fold increase) (Figure 4.9A). The GSI values then gradually decreased from April to to September. This was in contrast to the male GSI trend, which displayed a very gradual increase in GSI between March and May (1.61-1.98%) and reaching a maximum of 3.08% in June and again in August (2.89%) before returning to “pre-peak” levels by September (Figure 4.9A).

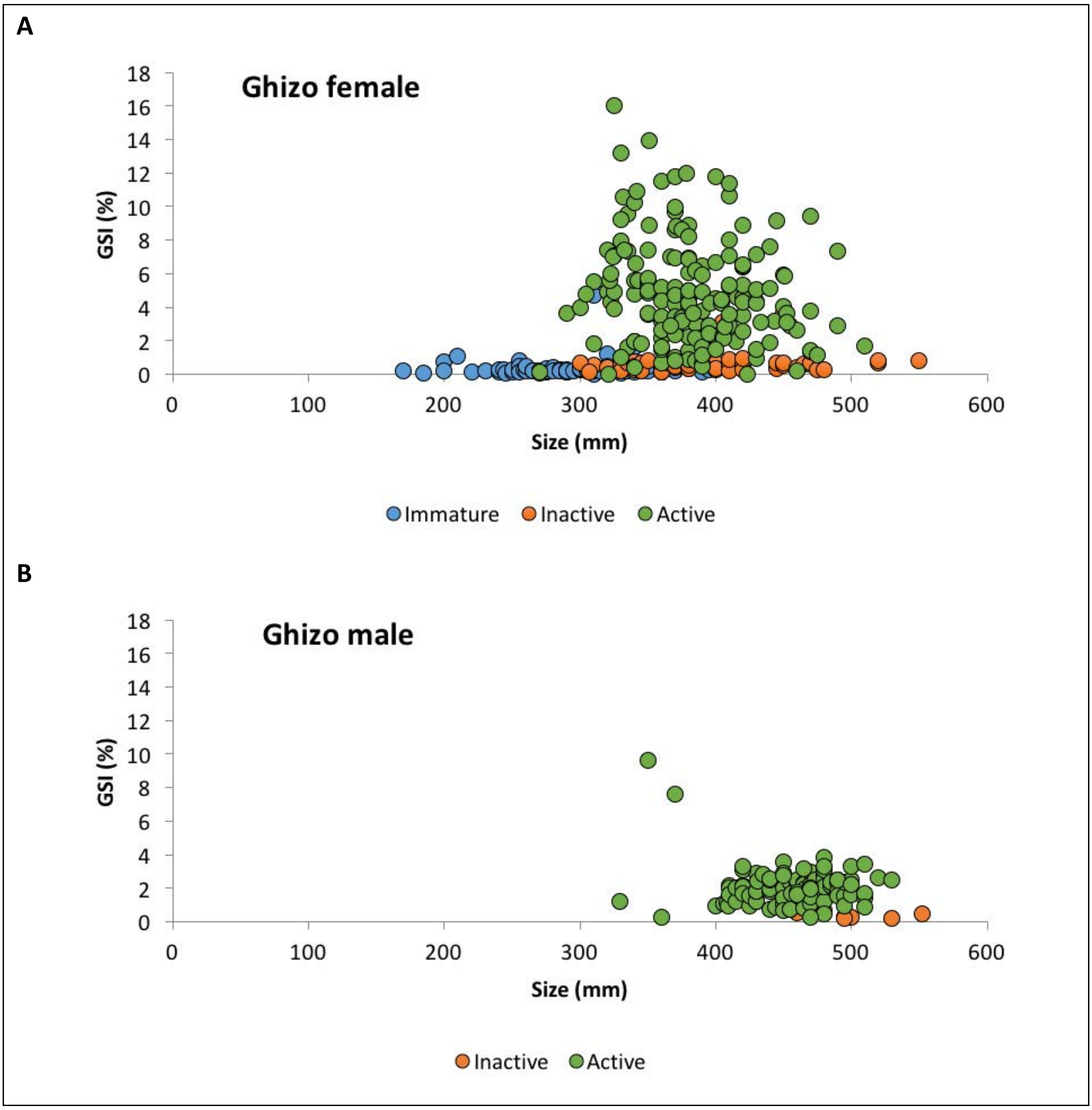


Figure 4.7 Gonado-somatic index (GSI) values for squaretail coralgrouper (*Plectropomus areolatus*) collected at Ghizo, Solomon Islands for (a) immature, mature inactive and mature active females and (b) mature inactive and mature active males

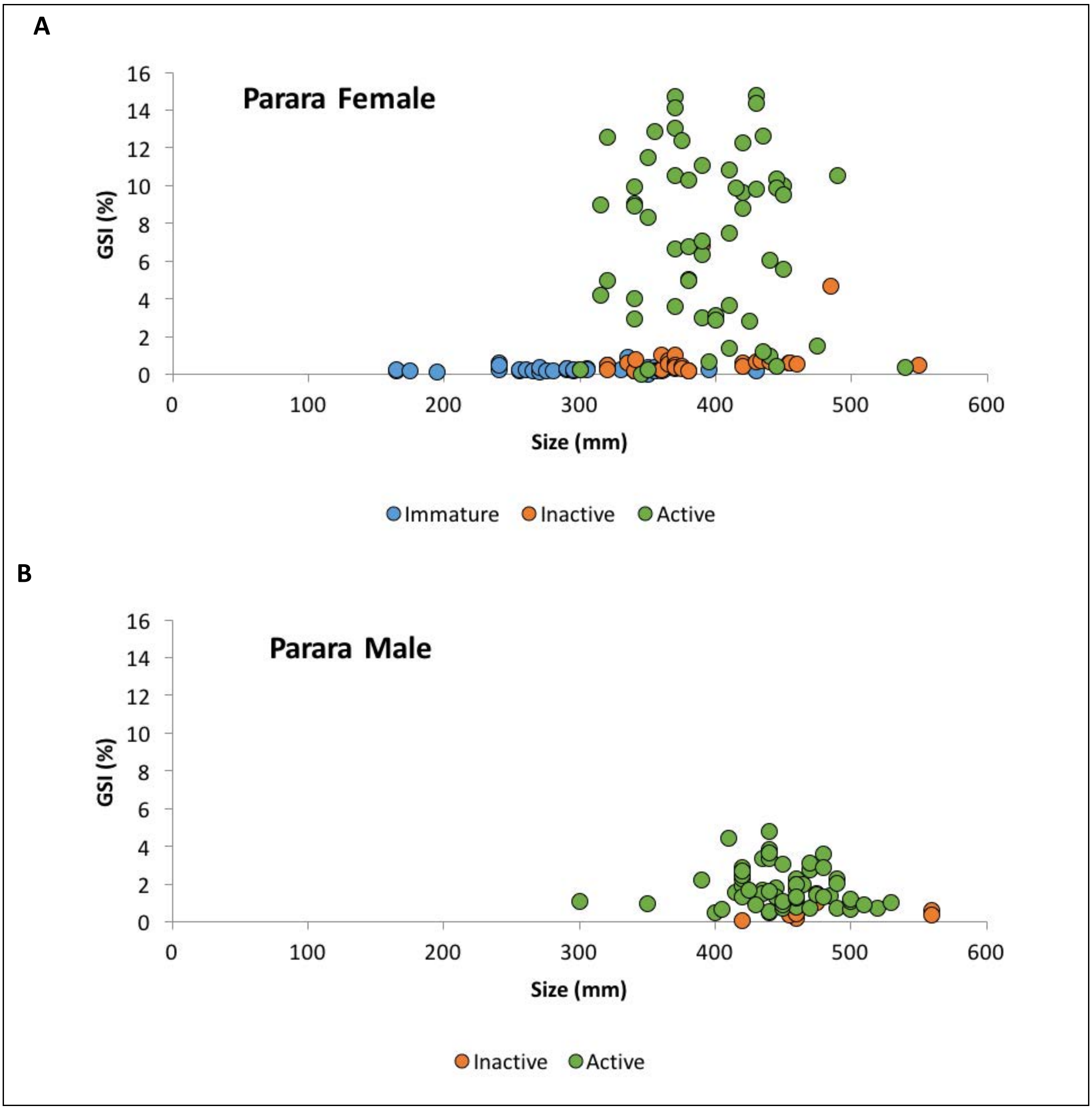


Figure 4.8 Gonado-somatic index (GSI) values for squaretail coralgrouper (*Plectropomus areolatus*) collected at Parara reef system, Solomon Islands for (A) immature, mature inactive and mature active females and (b) mature inactive and mature active males

Although immature females (F1) and inactive females (F2) were present throughout most of the monthly samples, females with active ovaries (F3-F5 stages) were present in substantial numbers in samples collected between the months of March and July, further indicating that the majority of spawning activity takes place during these months (Figure 4.9B).

However, the collection of reproductively active females also occurred in the latter months of the year, suggesting that some spawning may also occur outside of peak reproductive months. Except for the month of September, reproductively active males (M2-M4) dominated more than 70% of testes samples between March and October (Figure 4.9C).

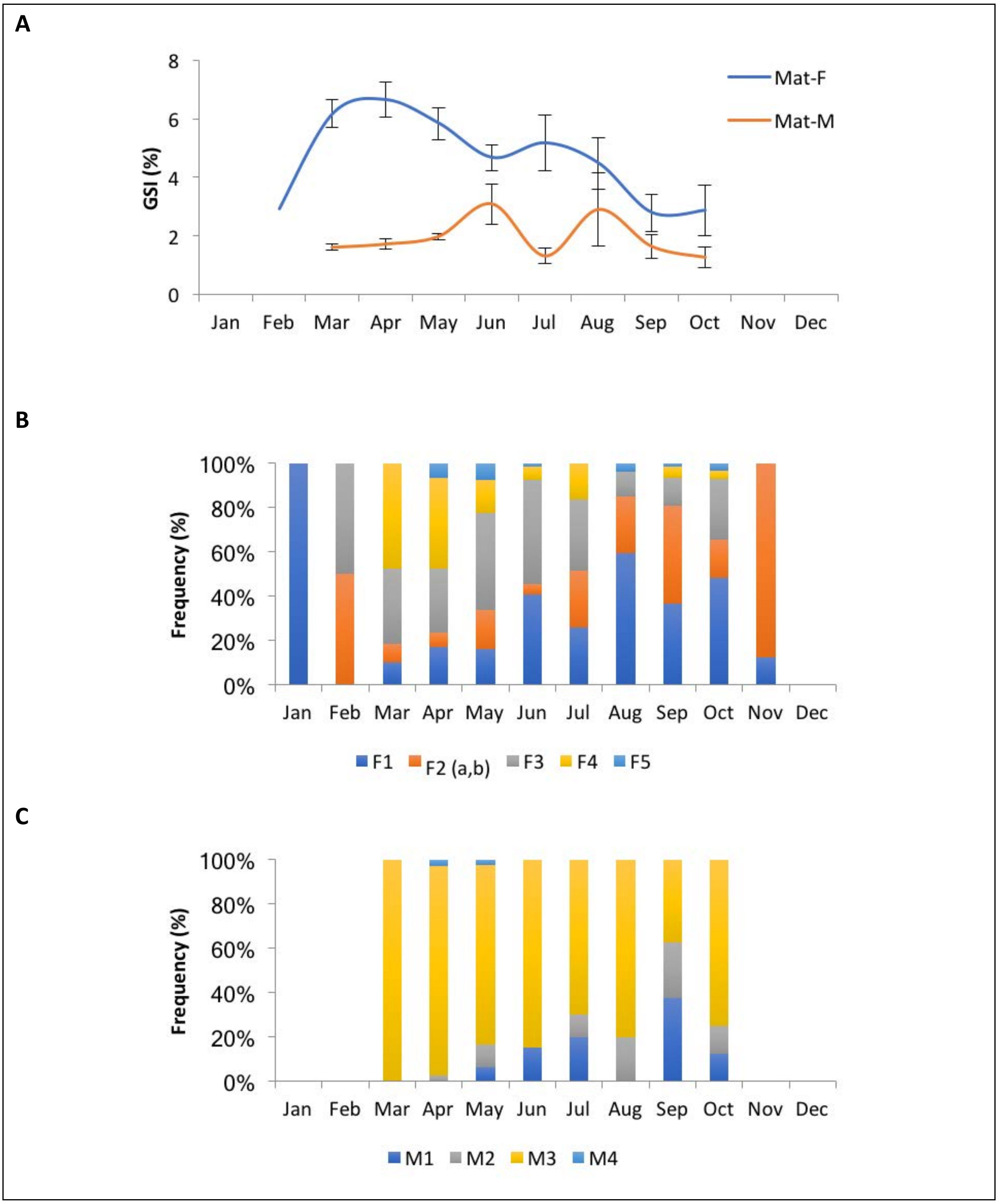


Figure 4.9 A) Mean gonadosomatic index (GSI) values for mature active female and male squaretail coralgrouper (*Plectropomus areolatus*) collected from Ghizo and Parara, western Solomon Islands. All GSI collected for this study were pooled to display monthly over a 12-month period. Vertical bars denote standard errors. Various reproductive stages of all B) females and C) males pooled by month. F1 - immature female; F2 –

resting female; F3 – ripe female; F4 – hydrated female; F5 – spent female; M1 – resting male; M2 – ripe male; M3 – spawning ready male; M4 – spent male.

4.4 Size and age-at-maturity and male recruitment

The minimum size at sexual maturity (L_m) for females was 270 and 300 mm for Ghizo and Parara, respectively, and 2 years of age at both locations. In Ghizo, females first reached 50% maturity at 321.6 mm (L_{m50}) and 2.6 years (T_{m50}) achieving 95% maturity at 399.7 mm (L_{m95}) and 4.2 years of age (T_{m95}) (Figure 4.10 and Table 4.1).

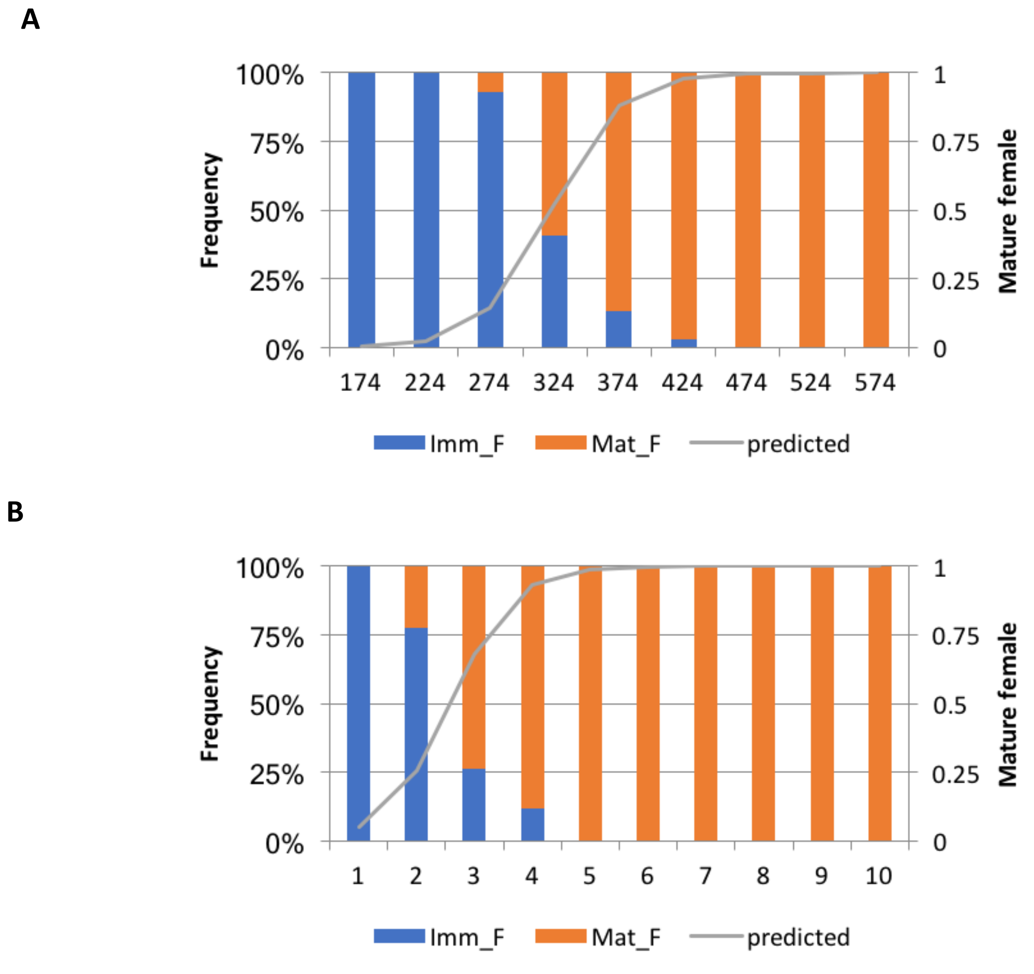


Figure 4.10 A) Size at 50% maturity and B) Age at 50% maturity for female squaretail coralgrouper (*Plectropomus areolatus*) collected from Ghizo reef system, Solomon Islands. Blue bars: immature females, Red bars: mature females.

Table 4.2 Reproductive parameters of female squaretail coralgrouper (*Plectropomus areolatus*) in western Solomon Islands. T_{m50} = age at 50% maturity, T_{m95} = age at 95% maturity, L_{m50} = size at 50% maturity and L_{m95} = size at 95% maturity.

	T_{m50} (yrs)	T_{m95} (yrs)	L_{m50} (mm)	L_{m95} (mm)
Ghizo	2.6	4.2	321.6	399.7
Parara	3.4	5.1	337.9	448.5

In Parara, 50% maturity in females occurred at 337.95 mm (L_{m50}) and 3.4 years (T_{m50}) and subsequent 95% maturity at size 448.5 mm (L_{95}) and age 5.1 years of age (T_{95}) (Figure 4.11 and Table 4.1). Males first reached maturity (L_m) at 329 mm (Ghizo) and 350 mm (Parara) and at Age 3 for both locations (Figure 4.5 & Figure 4.6).

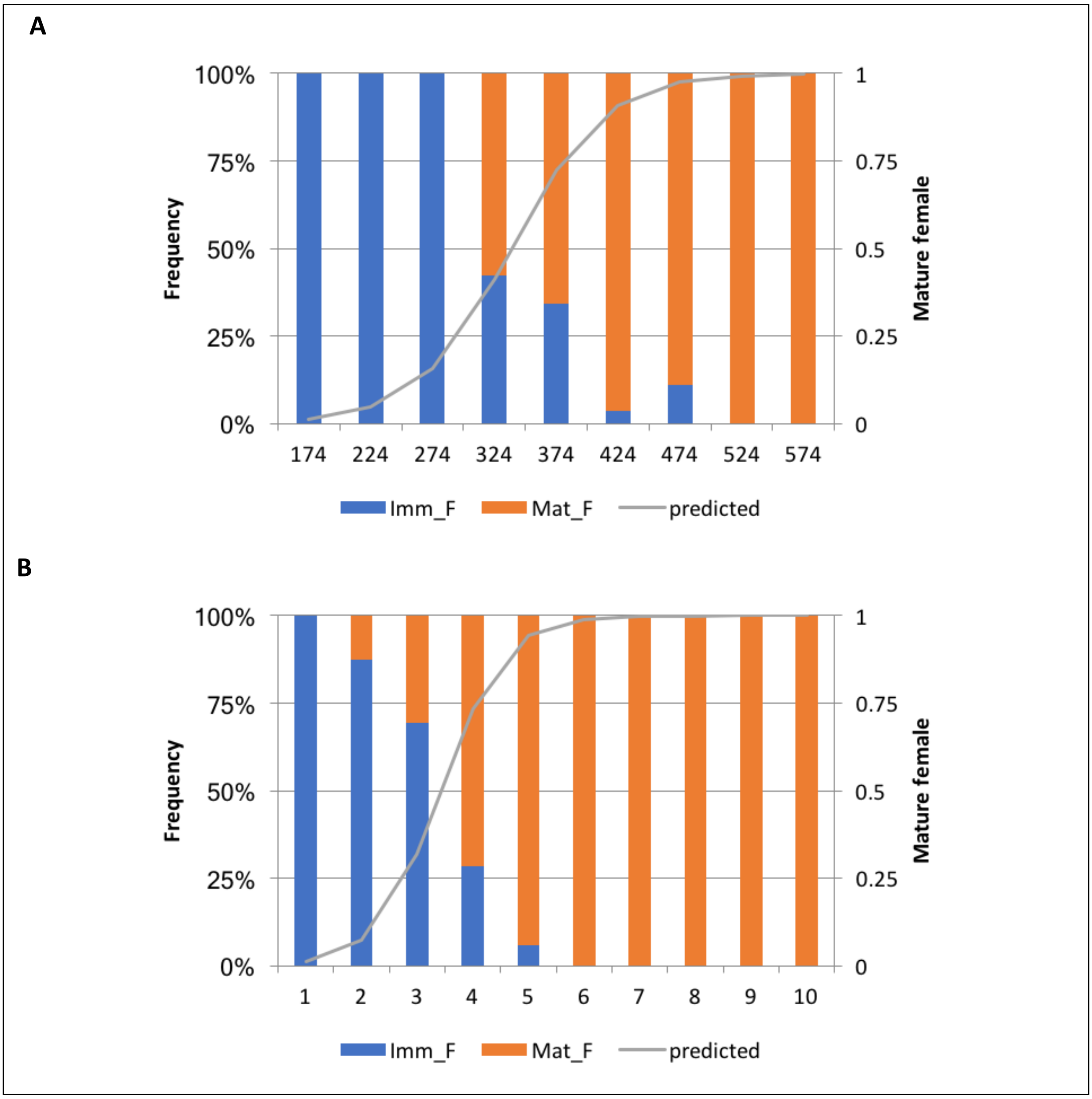


Figure 4.11 A) Size at 50% maturity and B) Age at 50% maturity for female squaretail coralgrouper (*Plectropomus areolatus*) collected from Parara reef system, Solomon Islands. Blue bars: immature females, Red bars: mature females,

Parara registered significantly higher T_{50}/T_{95} estimates compared to Ghizo (Figure 4.12). Even though Parara registered slightly higher L_{50}/L_{95} the overlap in confidence intervals of the maturity estimates between locations meant there is very little difference (Figure 4.13).

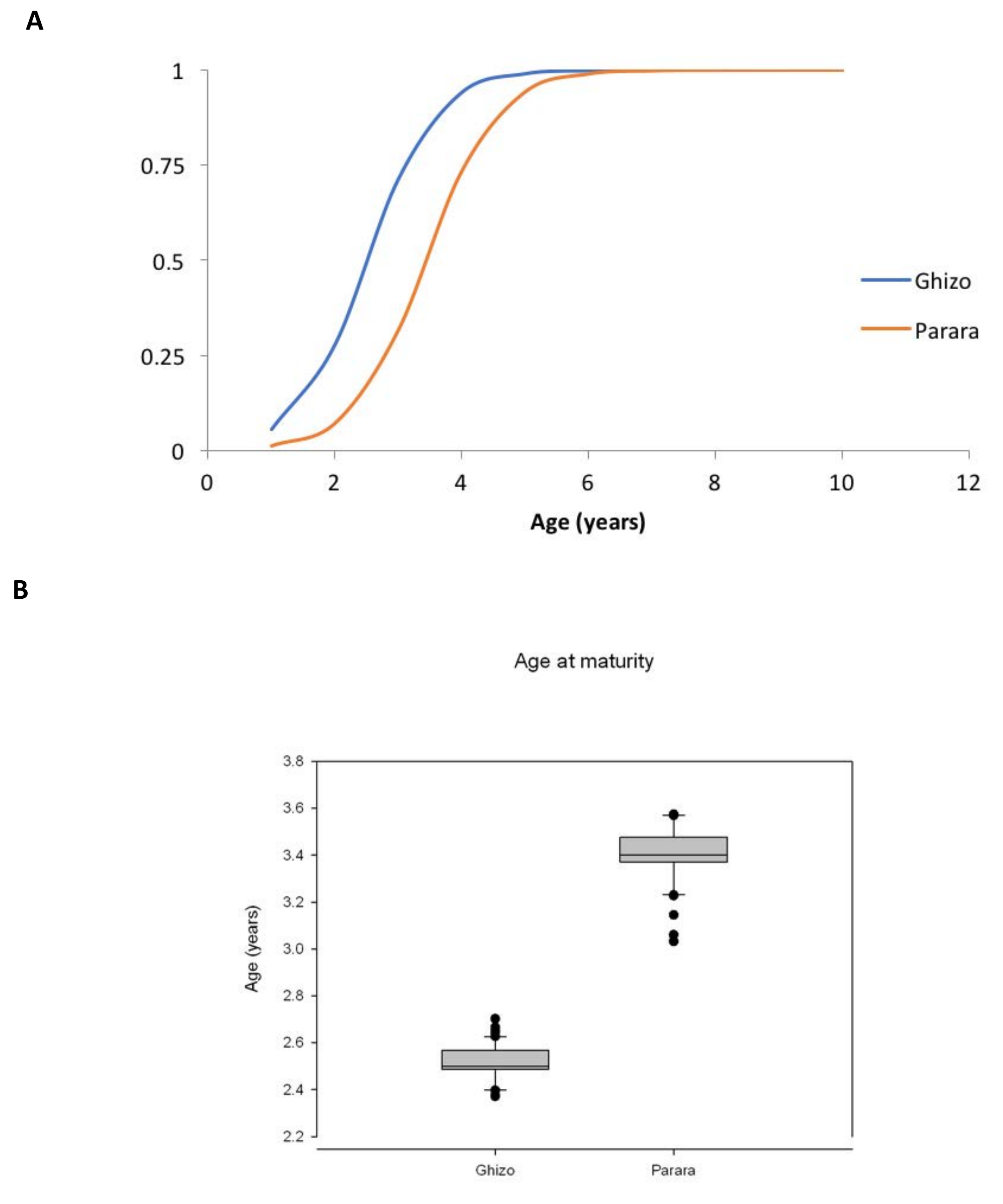


Figure 4.12 A) Comparison of the age at 50% female maturity (T_{m50}) for squaretail coralgrouper (*Plectropomus areolatus*) from Ghizo (blue line) and Parara (red line). B) Boot strapped estimates of T_{m50} for Ghizo and Parara.

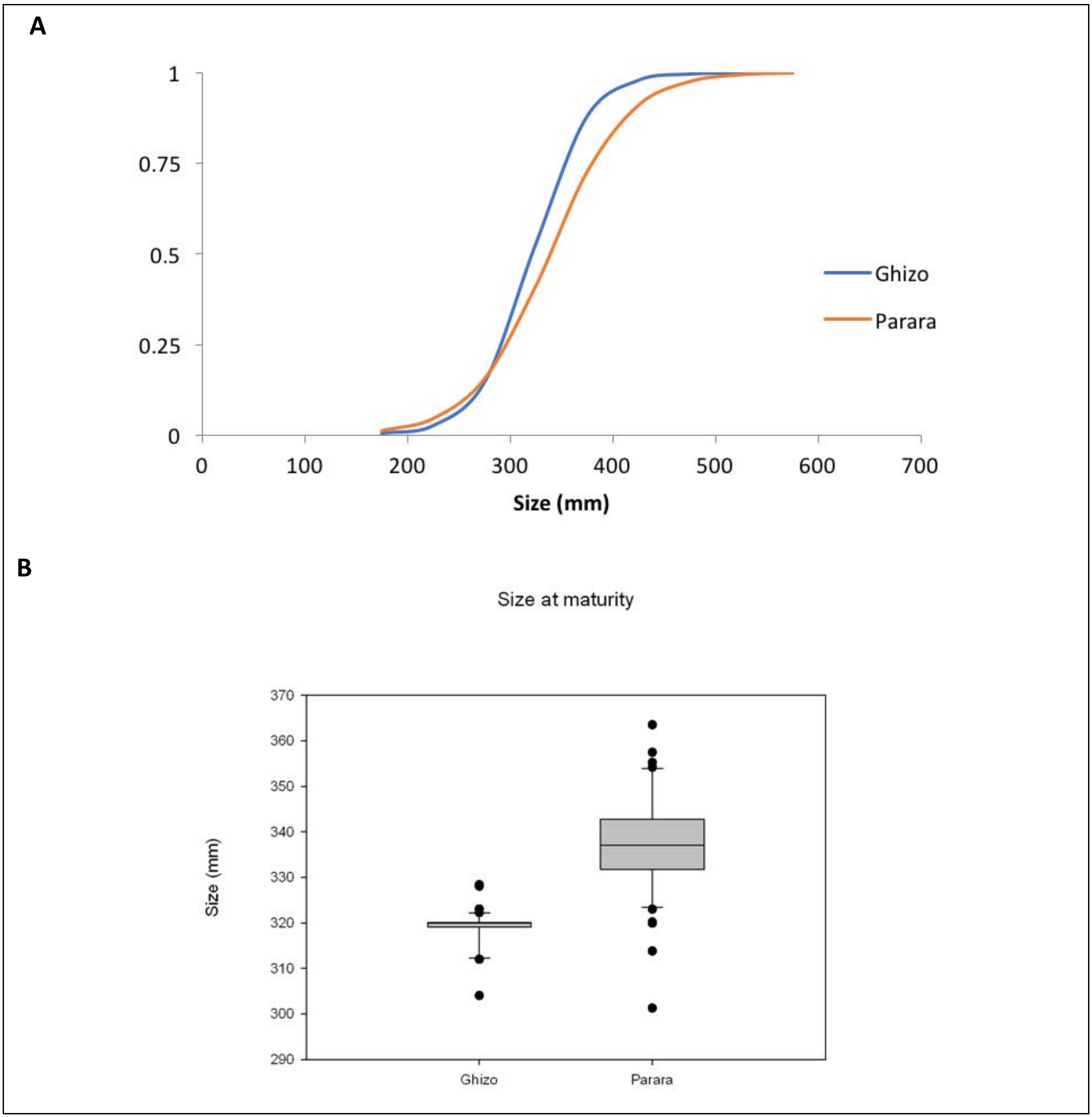


Figure 4.13 A) Comparison of the size at 50% female maturity (Lm50) for squaretail coralgrouper (*Plectropomus areolatus*) from Ghizo (blue line) and Parara (red line). B) Boot strapped estimates of Lm50 for Ghizo and Parara.

The size at which 50% of the population is made up of males (P_{50}) was estimated at 444.84 mm and 430.11 mm for Ghizo and Parara, respectively (Figure 4.14). Based on the broad overlap in the size and age distribution of sexes, male recruitment is likely to occur between a size range of 329-550 mm and an age range of 3-9 years at Ghizo, and similarly, between a size range 300-550 mm and an age range 3-10 years for Parara. Note: samples that were classified as either “inactive males” or bisexuals occurred within these ranges.

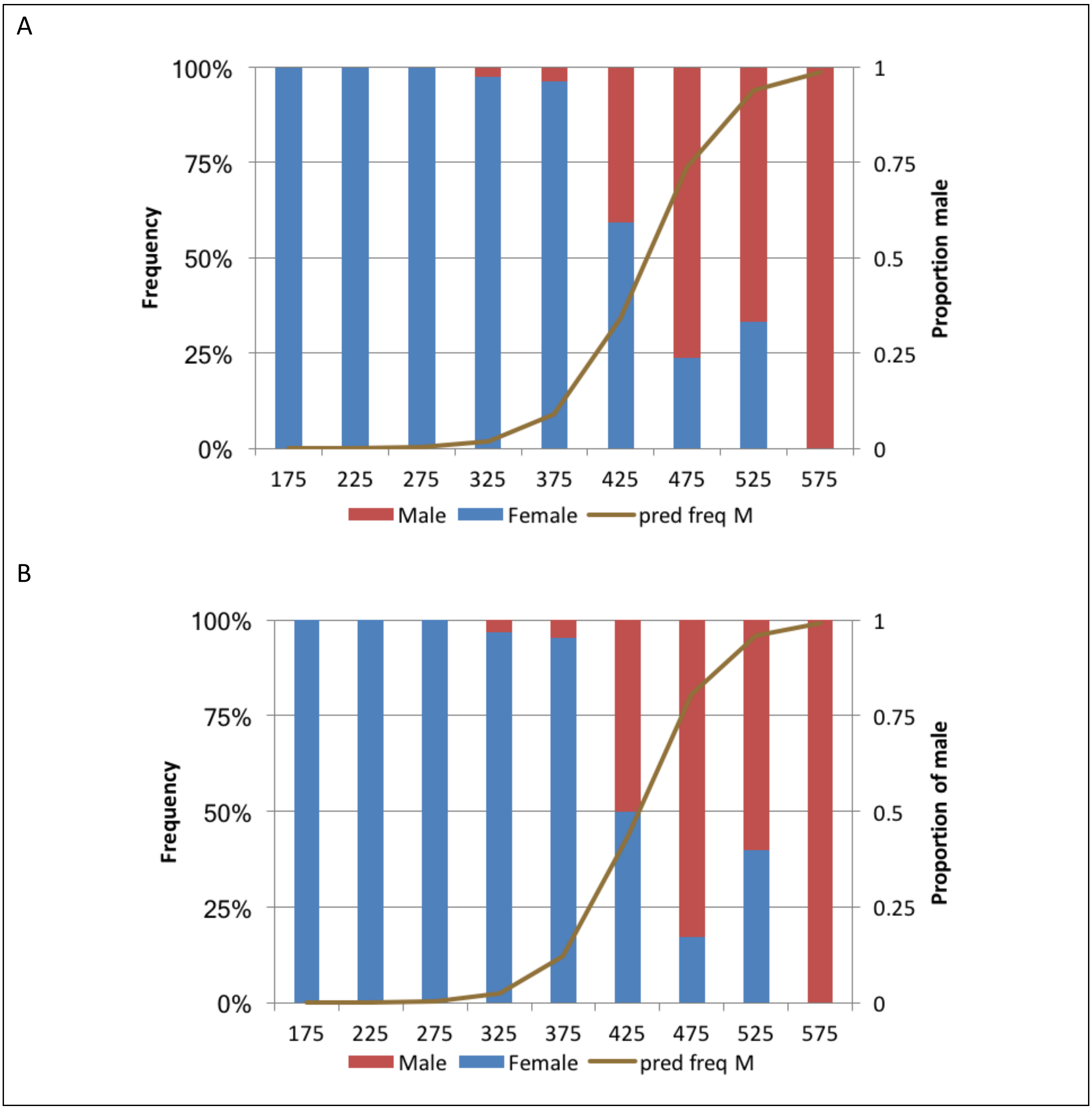


Figure 4.14. The size at which more then 50% of the *Plectropomus areolatus* population are males (P_{50}) in Gizo (A) and Parara (B).

4.5 Discussion

Based on the observed morphological features and chronological sequence in gonad development, it is suggested that sexual development in *P. areolatus* is essentially gonochoristic (primary males) in nature, with potential for diandry development. Size and age frequency distribution were bimodal at both locations, however at Parara sex-specific modal age classes were much more closely grouped together compared to Ghizo. No males were recorded at sizes and ages below female maturity. However, individuals with gonads containing both early stage female and male reproductive cells (inactive bisexuals) were recorded in sizes and ages before and after female maturity. GSI and gonad histology indicate that peak reproductive season was between March and July but with some spawning occurring in later months.

All *P. areolatus* testes examined in the current study retained an ovarian-like lumen while most had sperm sinus structures visible, traits regularly observed in Epinephine species. The retention of the lumen structure limits the use of this feature in distinguishing whether an individual is a primary or secondary male (Sadovy and Shapiro 1987, Hamilton et al. 2008). In contrast, there is a clear distinction in the testes structure of other protogynous species (e.g. labroids) between those testes that have been derived from an immature phase (primary males) to those that have developed from a functional female stage (secondary males) (Reinboth 1967). Of the five criteria listed for defining protogynous species (Sadovy & Shapiro, 1987, Sadovy de Mitcheson & Liu 2008), the presence of transitional gonads, i.e. those containing atretic vitellogenic oocytes alongside proliferating spermatogenic activity, provides the most conclusive evidence for the classification of a species as a protogynous hermaphrodite (Mackie 2000, Sadovy de Mitchesen & Liu 2008). Previous investigations of the reproductive biology of *Plectropomus* species have confirmed, via the presence of transitional individuals, monandric (*P. laevis*: Adams 2002) and diandric (*P. maculatus*: Ferreira 1993, 1995; Adams 2003; *P. leopardus*: Ferreira 1995) modes of protogynous hermaphroditism.

However, despite the extensive nature of the sampling design (collecting a broad size distribution of samples over an extended temporal period) meeting one of the requirements for the investigation of sexual development in fishes (Sadovy & Shapiro 1987), no conclusive evidence of female-to-male sex-reversal was present for *P areolatus.* Prior studies on reef fish reproductive biology have reported that transitional individuals generally represent a small proportion of sampled datasets (Sadovy & Shapiro 1987, Munday et al. 1997, Mackie 2000). This suggests that the anatomical transformation of the gonad from one functional sex to the other is likely to be a relatively rapid process (McGovern et al. 1998, Bean et al. 2003). Furthermore, the timing of species-specific sex transition is said to vary throughout the year with some indication that it occurs after the spawning season (Shapiro 1987, Ferreira 1995, Siau 1994, Chan and Sadovy 2002, Frisch et al. 2007). Although it is possible that sampling effort may have missed individuals undergoing sex-reversal in the wild, recent investigations from the eastern Torres Straits and Micronesia were also unable to provide firm evidence of hermaphroditism (Williams et al. 2008, Rhodes et al. 2013).

The presence of gonads containing both primary female and male cells with no signs of prior spawning (inactive bisexuals) has been reported in both gonochorous and protogynous species (Adams 2003, Liu & Sadovy 2004, Hamilton et al. 2008). In this study, inactive bisexuals occupied the same size and age range as immature females. A similar finding was observed in the gonochoristic *Epinephelus striatus* (Sadovy & Colin 1995). Although no immature males were recorded, the overlap of the above immature/inactive stages with the distribution of mature/active stages of both females and males suggests that development into mature functional sexes is complete by a size and age of 400 mm FL and 4 years.

Early spermatogenic cells observed within gonads of mature females are likely to be remnants of an earlier inactive bisexual stage (i.e. mature females can develop from both an immature female gonad and a bisexual gonad). This Similarly, the presence of chromatin nucleolar and perinucleolar oocytes in the testes of mature males (n = 13) is suggested to be the result of an earlier transition through a bisexual stage. The lack of males below the size and age of female maturity is in contrast to other gonochoristic and diandric species (Fennessey and Sadovy 2002, Moore et al. 2007). In the case of *P. areolatus* in Solomon Islands, our findings suggests that male development maybe suppressed during early life stages until reaching a threshold of some sort related to the metabolic and/or behavioral requirements of a male phase.

The higher male growth rates observed in the age-based analyses (Chapter 3) implies that individuals capable of becoming males invest more energy into early somatic development (during the bisexual stage) at the expense of reproductive development. An extended bisexual phase would allow individuals the opportunity to assess which sex is likely to provide the most reproductive success before committing to either for the rest of their lives. In other words, the bisexual stage in this species may represent a stage from which either female or male development takes place depending on some flexible form of social control governing sex ratio (Sadovy & Shapiro 1987, Sadovy & Colin 1995, Vincent & Sadovy 1999).

This would explain why males are entering the population at an older age – not having reproduced as a female first - but waiting until they're bigger so they can reap the reproductive rewards of entering the population at a larger size for a given age. The occurrence of small (young) males with comparatively high GSI levels suggests that some males may choose to mature earlier rather waiting before reaching a larger size. This typically occurs in situations where alternative reproductive strategies such as streak/sneak spawning behaviour occurs (Warner 1984, Taborksy 1994). However, the limited number of males with this feature observed in this study calls for further investigation on spawning behavior in this species.

The bimodal population structure present in Ghizo and, albeit less distinctly for age, at Parara, with a female bias towards the lower end and a male towards higher end of size/age structures, is similar to that reported for *P. areolatus* in Micronesia (Rhodes et al. 2013) and Torres Straits (Willams et al. 2008) and is a commonly reported feature in protogynous epinephelids including other *Plectropomus* species (Ferreira 1995, Adams 2003). Furthermore, the significantly female-biased sex ratio at Ghizo is typical of epinephelid species (Moe 1969, Shapiro 1987) and has been reported for *P. areolatus* in the eastern Torres Strait (Williams et al. 2008). The non-significant female bias in the Parara population is more in line with what would be expected of species in which males and females both develop directly from an immature stage (gonochoristic) or from dual male development pathways (i.e. diandric) (Adams et al. 2000).

Although bimodal distributions and sex ratios can be influenced by the timing of sampling efforts and spatial movement of species, a more plausible explanation for the observed differences in population structure and sex ratio observed maybe attributed to different levels of historical fishing pressure at the two reef systems. Higher fishing pressure on the Ghizo reef system over a longer period of time (Chapter 2) could have selectively removed faster growing, larger and older individuals (i.e. this generally being males). This would have modified the size/age population structures and increased female sex ratio. Ferreira (1995) provided a similar conclusion based on observed differences in *P. leopardus* sex ratios between Townsville and Lizard Island populations.

The maturity schedule from both locations appears to be reflective of their respective growth patterns observed in the age-based analyses (Chapter 3). It is possible that slightly faster growth and earlier maturity estimates from Ghizo may reflect in part higher fishing pressure on the Ghizo reef system. This may also explain why there was a significantly lower age for females at Ghizo. Although the size-at-maturity estimates for Ghizo (314 mm) and Parara (327 mm) were less than that reported for *P. areolatus* in Micronesia (366 mm), the age-at-maturity estimates at Ghizo (2.5 years) and Parara (3.2 years) were older than Micronesia (2.3 years) (Rhodes et al. 2013). Although sex-reversal is not reported, the size at which more than 50% of the sample were males in this study (444.8 mm and 430.1 mm for Ghizo and Parara respectively) is substantially less than that recorded in Micronesia (494 mm) and the eastern Torres Strait (549 mm) (Williams et al, 2008, Rhodes et al. 2013).

The collective presence of oocytes in various stages of development in the ovaries of individual *P. areolatus* suggests that the pattern of gonadal development in female squaretail coralgrouper is asynchronous and indicates that females have the capacity to partake in multiple spawning events both within and between the last lunar quarter phase of a single spawning season. This notion conforms with findings from studies on the movement patterns of the *P. areolatus* in Micronesia and *P. leopardus* on the GBR where individuals were recorded returning from spawning aggregations at the same site in consecutive months (Zeller 1998, Rhodes & Tupper 2008). The higher mean female GSI during the months of March-July, implies that the majority of *P. areolatus* spawning activities take place over a 5-month period. The elevated GSI pattern was driven by the increased presence of active and hydrated female individuals. This pattern is consistent with results from monthly fish surveys conducted at spawning sites that have recorded increased fish densities over a 4-5 month period each year in western Solomon Islands (Chapter 4; Hamilton et al. 2012). However, the capture of females with hydrated oocytes between August and October coupled with the strong representation of mature testes that were in an advanced stage of spawning readiness (spermatozoa in sperm duct and sinuses) between March and October, suggests that some level of spawning activity may also occur outside of peak reproductive months.

Despite a lack of field observations documenting actual spawning behaviour in the current study*, P. areolatus* males displayed high levels of aggression towards other “interested” males during the last lunar quarter and this behaviour intensified 3-4 days before new moon. In most conditions, smaller-sized males were effectively chased away by a larger male. Sperm competition theory, the contest between sperm from rival males for fertilization of an ovum, predicts that male species which participate in a paired-mating system, will invest little energy in sperm production (resulting in smaller testes) and more into territorial behaviour. In contrast, those species which engage in group spawning i.e two or more males/female in a spawning event, will invest more into sperm production (i.e. bigger testes) and less into resource defense (Sadovy and Colin 1995). In such behavioral interactions, an increased male body size provides greater competitive advantage over smaller males (Warner 1984). When combined with the dominant male presence in larger size classes observed in this study, these behavioral traits provide tentative indications of a polygynous mating system, through which a larger male pair-spawns with several females. However, the relatively high mean GSI of males, 1.9%, suggests that this species may be capable of participating in both pair-spawning and group-spawning behavior. Indeed, *P. areolatus* has recently been observed undertaking both pair-spawning and group-spawning techniques in an unfished spawning aggregation located in a remote archipelago off the south-west coast of India (Karkarey et al. 2017). Although no such observations were made in this study, the presence of some smaller *P. areolatus* males with high GSI values (7-9%) that are comparable to active females suggests that *P. areolatus* maybe capable of undertaking various mating strategies (e.g. sneak spawning, pair spawning, group spawning) in order to maximise reproductive success (Marques & Ferreira 2011).

The results presented here point to *P. areolatus* being a functionally gonochoristic species whereby mature males recruit into the population at a larger size. This has important implications for management as the targeted removal of larger individuals can potentially impact on the overall reproductive output of the population. However, certain biological characteristics of *Plectropomus areolatus* are similar to those observed in protogynous species suggesting this species maybe capable of diandric male development. Future efforts that undertake a broader geographic sampling regime would be essential to investigate this further.

5 Spawning aggregation dynamics of *Plectropomus areolatus*

5.1 Introduction

Fish stocks associated with coral reefs provide a valuable source of protein and income for coastal communities throughout the tropics and subtropics. Many fish, including a number of commercially important species (e.g. snappers, groupers, emperors) form spawning aggregations at predictable times and places (Choat 2012). As a result, these aggregation sites are lucrative targets for fishers, with catch from aggregations often an important component of subsistence and commercial fisheries (Sadovy de Mitcheson & Erisman 2012, Erisman et al. 2015).

In almost all cases, the targeting of fish spawning aggregations (FSAs) has been characterised by a "boom and bust" scenario, with several well-documented examples of decreases in spawning populations due to excessive targeting of their FSAs (Johannes 1998, Sadovy 2005, Sadovy & Domeier 2005a, Sadovy de Mitcheson et al. 2012, Erisman et al. 2015, Stump et al. 2017). Heavy fishing on FSA of some species, such as the Nassau grouper (*Epinephelus striatus*) in the Caribbean and western Atlantic, has led to several aggregations becoming economically extinct, with other historical aggregations no longer forming (Sadovy & Domeier 2005a, Aquilar-Perera 2007, Sadovy de Mitcheson et al. 2012). Similarly, marked depletions of epinephelid FSAs in Palau in the early 1980s were attributed to an increase in fishing pressure by the Southeast Asia-based Live Reef Food Fish Trade (LRFFT) (Johannes et al. 1999; Sadovy et al. 2003). Similar impacts have been noted for grouper FSA in Pohnpei, Papua New Guinea and Solomon Islands, with commercial fishers targeting FSAs in order to supply local markets and the LRFFT (Rhodes and Sadovy 2002a, Hamilton & Matawai 2006, Hamilton et al. 2012, Rhodes et al. 2011, Rhodes et al. 2014).

FSA represent a critical phase in the life history of aggregating species, since most, if not all, reproduction occurs during these gatherings (Sadovy & Domeier 2005a). Heavy fishing of FSA typically results in the progressive reduction in abundance of larger individuals within a population (Koslow et al. 1988, Birkeland 1997, Overzee & Rijnsdorp 2015). The removal of larger individuals in a population has important consequences for fishery management, since smaller individuals are less fecund (Birkeland and Dayton 2004). It has also been shown that quality of larvae produced by older females is of a superior quality to younger females increasing the chances of survival (Berkeley et al. 2004, Stige et al. 2017). A study on groupers on the Great Barrier Reef, Australia, also reported that smaller and younger females were less sexually active than larger and older individuals (Pears et al. 2006), suggesting that a decrease in reproductive individuals may affect recruitment levels due to the reductions in spawning potential of the population (Sadovy 1996, Coleman et al. 1999, Huntsman et al 1999). Furthermore, in species where there are sex-specific differences in growth and adult body sizes, the removal of individuals within certain size or age classes may negatively affect the sex ratio, which can also reduce reproductive output (Koenig et al. 1996, Vincent & Sadovy 1998, Johannes et al. 1999, Coleman et al. 1999, Oversee & Rijnsdorp 2015).

In the Western Pacific, three grouper species (Brown-marbled grouper *Epinephelus fuscoguttatus*, Camouflage grouper *E. polyphekadion* and Squaretail coralgrouper *Plectropomus areolatus*) commonly form FSA that often overlap temporally during at least a portion of their respective spawning seasons and in areas proximate to each other (Rhodes & Sadovy 2002, Sadovy 2005, Craig et al. 2011, Hamilton et al. 2012). The occurrence of the timing and location of most of these FSA is common knowledge among local fishing communities who have traditionally depended on them for subsistence and more recently artisanal purposes. Continuing population growth and the spread of the cash economy has intensified subsistence and commercial fishing activities at FSAs in recent decades (Johannes 1988, Hamilton et al. 2012, Robinson 2015, Waldie et al. 2016). This has placed FSAs of these grouper species under increasing threat of overexploitation (Hamilton et al. 2012). Predictable transient FSAs are also likely to display hyperstability (Sadovy and Domeier 2005a, Erisman et al. 2011, Sadovy de Mitcheson and Erisman 2012), where catch per unit effort (CPUE) is maintained as abundance declines (Hilborn and Walters 1992), hence creating an illusion that the present catch rates are sustainable. Hyperstability can be pronounced in coral reef fish that form predicable aggregations and may result in dramatic collapses (Hamilton et al. 2016).

In order to assist in the design of workable management regimes to conserve these critical spawning events, an increasing body of work in the region is examining the dynamics of

FSAs (Johannes et al. 1999, Rhodes and Sadovy 2002b, Hamilton et al. 2011; Hamilton et al. 2012; Rhodes et al. 2012, Bijoux et al. 2013, Rhodes et al. 2014, Robinson et al. 2008, Waldie et al. 2016). In Solomon Islands, a study conducted by Hamilton et al. (2012) represents the only detailed assessment of a grouper FSA in the country.

This chapter summarizes the temporal aggregation patterns of *Plectropomus areolatus* (Squaretail coralgrouper), *E. fuscoguttatus* (Brown-marbled grouper) and *E. polyphekadion* (Camouflage grouper) in the Gizo region by assessing underwater visual census (UVC) information that was collected from a spawning aggregation site over a 5-year period in the Western Province of Solomon Islands. I also report in detail on reproductive information directly related to the daily, lunar and seasonal timing of spawning behaviour in *P. areolatus,* drawing on both UVC surveys and fisheries dependent data that I collected from fishers who were targeting FSA sites. Together with the earlier work (Hamilton et al. 2012), the findings presented here may enable the design of FSA management strategies for Solomon Islands that are suitable for consideration and adoption by coastal communities and regulatory authorities.

5.2 Methods

5.2.1 Environmental setting

This chapter is based on work conducted within the Ghizo and Parara reef systems of the Western Province (refer to Figure 4.1 in Chapter 4). Both systems play important roles in the supply of fresh protein and income to surrounding coastal communities. The Ghizo reef system supports an active commercial fishery, which supplies the centralized fish market in Gizo town (Rhodes & Tua 2017) and to a lesser extent also provides fresh fish to Honiara, the capital of Solomon Islands (Brewer 2011). The Gizo fish market is the largest of its kind in Western Province, with reef fish species making up the majority of catch sold locally (Bennett et al. 2014). In contrast, the Parara reef system has traditionally supported a more subsistence-orientated fishery with the fresh fish consumption of resident communities estimated at approximately 111 kg/person/year (Pinca et al. 2009). However, due to its close proximity to Ghizo, the reef system is becoming more exposed to commercially oriented fishing practices both from resident and non-resident fishers that supply the Gizo Town fish market. Both of these reef systems support FSAs for a range of species including groupers. The location and timing of these FSAs are well known to local fishers who are attracted to them because of the high catch per unit of effort (CPUE) they provide. This is evident in the sudden increase of certain aggregation spawners at the Gizo Town fish market during certain lunar phases when spawning aggregations are known to form. Harvesting at these FSAs is typically conducted by night-time freediving spearfishers who use flashlights as a source of illumination, however spearfishing and hand-line fishing also takes place during daylight hours.

5.2.2 Site description

One FSA within each of the above reef systems was examined, but for logistical reasons intensive sampling was only feasible at the Ghizo site. The location of the FSA site in Ghizo (Site A) is well-known to local communities and has been frequented by subsistence and artisanal fishers from Ghizo and surrounding islands for at least the past thirty years. The site is located on the seaward edge of a reef promontory on the northwestern tip of the barrier reef system (Figure 5.1). Three species of groupers form overlapping aggregations at the site. Exploratory dives conducted in April and May 2008 confirmed that *P. areolatus* primarily aggregates within 5-15 m depth, while *E. polyphekadion* and *E. fuscoguttatus* generally occur between 15-40 m. The aggregation area stretches over approximately 250 m of lateral reef area. The Parara site (Site B) also occurs along the seaward side of a barrier reef, situated between a reef promontory and a deep channel (submerged barrier reef) (Figure 5.1). Of the above three grouper species, only *P. areolatus* is known to form significant spawning aggregations at the Site B. These *P. areolatus* aggregations typically form along approximately 600 m of reef between depths of 7 to 25 m.

Sheltered within the barrier reef systems where the two spawning sites are located are complex lagoon systems made up of a mosaic of patch reefs, seagrass and mangrove habitats. Although the Parara reef system (including lagoon) is larger, the barrier reef has less pronounced promontories and reef passes/channels compared to Ghizo (Table 5.1). However, because both FSA sites are located next to promontories or channels, they both experience high levels of water movement driven primarily by changes in the daily tidal cycle. This hydrological feature is also observed at two well-known smaller *P. areolatus* FSA sites located close to promontories and channels within the Ghizo reef system (Figure 5.1).

Figure 5.1. Figure showing the location of fish spawning aggregation sites within the Ghizo (Site A) and Parara (Site B) reef systems in Western Province, Solomon Islands.

Table 5.1 Some physical features of the Ghizo and Parara barrier reef systems in Western Province, Solomon Islands. Area data obtained from Millennium Coral Reef Mapping (www.imars.usf.edu).

	Ghizo	**Parara**
Overall reef system (hectare)	8,642	10,182
Lagoon system (hectare)	3,588	5,123
Patch-reef *Lagoon* (hectare)	733	624
Barrier reef system (hectare)	2,420	2,686
Fore-reef *Exposed Barrier*	301	209
Fore-reef *Exposed Fringing*	450	43
No. of deep water barrier reef passes	7	1

5.2.3 Data collection

The fisheries independent underwater visual census (UVC) monitoring data (fish counts) presented in this chapter is focused on the three above mentioned grouper species and was collected from Site A over a 5-year period. The fisheries-dependent reproductive information reported on here focused on *P. areolatus* and was obtained between March 2008 and May 2011 using two approaches. Firstly, I collected gonads of *P. areolatus* that were on sale at the central Gizo fish market. And secondly, I accompanied local spearfishers that were specifically targeting both FSAs at the Ghizo and Parara sites and removed the gonads of *P. areolatus* that were captured during my visits. Gonads were removed and stored in preservative for later microscopic examination (see Chapter 4 for details).

5.2.3.1 Underwater monitoring of spawning aggregation

In order to record the seasonal reproductive (or aggregating) patterns for the three grouper species at Ghizo, a baseline assessment was implemented that involved monthly surveys between April 2009 and June 2011 (Hughes et al. 2012). Using information collected from this 27-month period, further surveys that focused on the period surrounding the peak spawning months were conducted in the first half of the year for another 2 consecutive years resulting in a 5-year dataset (Hughes et al. 2012). To effectively sample the aggregation within safe SCUBA diving limits, a sampling protocol was designed that utilised two fixed transects. Both transects run the length of the horizontal distribution of the spawning aggregations along two depth profiles. The first transect measured 150 m by 20 m (3000 m^2) and was installed along a 10-m depth contour to primarily sample the shallow-water portion of the *P. areolatus* aggregation. The second transect measured 250-m by 20-m (5000 m^2) and was installed along a 25-m depth to effectively sample the combined *E. fuscoguttatus* and *E. polyphekadion* aggregations, including the deeper portion of the *P. areolatus* aggregation. The outer boundaries of all transects were all marked by steel rebars installed at 25-m intervals to aid divers in collecting data within the transect area. All dives were conducted by a pair of divers. Fish counts were shared between two divers with Diver 1 recording *P. areolatus* and Diver 2 recording *E. fuscoguttatus* and *E. polyphekadion*.

In order to identify the initiation and cessation of the aggregation within a given spawning month, daily sampling of fish numbers commenced in April 2009 on the day of full moon, and continued up until 2 days after new moon (danm) (18-day period) in order to examine the trend in daily aggregation build-up. A similar sampling effort was repeated in June and July of the same year but focused on 10 and 5-day periods, respectively (7 and 3 days before new moon (dbnm), day of new moon and 2 danm) to further validate the peak and cessation of spawning activities (Table 5.2). Using the information collected from these sampling exercises, the monitoring protocol for the remainder of the baseline assessment mostly concentrated within the 3-day period before new moon of each month in subsequent surveys (Table 5.2).

Table 5.2. Lunar days on which transects were surveyed during each month that monitoring was conducted at Site A in Gizo, Western Province, Solomon Islands. Lunar day 0 = New Moon.

	Lunar days UVC conducted at FSA																	
	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	-1	-2
Apr 09	✓			✓		✓		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
May 09																		
Jun 09									✓	✓	✓	✓		✓	✓	✓	✓	✓
Jul 09													✓	✓	✓	✓	✓	✓
Aug 09												✓	✓	✓	✓	✓		
Sep 09													✓	✓	✓	✓		
Oct 09														✓	✓			
Nov 10													✓	✓				
Dec 10													✓	✓	✓	✓		
Jan 10														✓	✓			
Feb 10															✓	✓		
Mar 10													✓		✓	✓		
Apr 10														✓	✓	✓		
May 10														✓	✓			
Jun 10														✓	✓			
Jul 10														✓	✓			
Aug 10															✓	✓		
Sep 10														✓	✓			
Oct 10														✓	✓			
Nov 10														✓	✓			
Dec 10														✓	✓			
Jan 11																		
Feb 11														✓	✓			
Mar 11														✓	✓			
Apr 11														✓	✓			
May 11														✓	✓			
Jun 11														✓	✓	✓		
Apr 12														✓	✓			
May 12														✓	✓			
Jun 12													✓	✓	✓			
Jul 12												✓	✓	✓	✓			
Feb 13													✓	✓				
Mar 13													✓	✓				
Apr 13													✓	✓				
May 13														✓	✓			
Jun 13														✓	✓			
Jul 13														✓	✓			
Aug 13														✓	✓			

5.2.3.2 Reproductive composition and Gonado-somatic index

In order to verify whether the above aggregating patterns reflected reproductive activity, gonads of both female and male *P. areolatus* were histologically examined. Samples presented in this chapter were obtained during the different lunar phases, with the greatest sampling intensity between the last quarter and new moon (Table 5.3). In addition, gonado-somatic indices (GSI) were pooled by sex for both females and males that were reproductively active firstly by lunar phase and secondly over the 12-day period before new moon temporal scales. Individuals that were not reproductively active (i.e. immature and resting stages) were not included in these analyses. See Chapter 4 for a description on histology methods and how GSI was calculated.

Table 5.3 The various months and lunar phases on which *P. areolatus* gonads were collected from FSA sites and non-FSA sources around the Ghizo and Parara reef systems of Western Province, Solomon Islands.

Year	Month	1Q+	FM+	3Q+	NM+	FSA	Non-FSA	Total
2008	March		3	42	5	47	3	50
	April	1	8	21		30		30

	May	21	1	73	3	98		98
	June	7	25	11	8	2	49	51
	July		8	15	4	9	18	27
	August	13		5	4	4	18	22
	September	22	15	23	12	7	65	72
	October			18	9	5	22	27
2009	January							
	February							
	March			23		23		23
	April			36		36		36
	May			8	6	14		14
	June			19		19		19
	July		8	6		5	9	14
	August	7		2		2	7	9
	September	14		5		2	17	19
	October		5				5	5
	November							
	December							
2010	January				2		2	2
	February							
	March							
	April	7		12	3	14	8	22
	May		4	30		25	9	34
	June		9	2		4	7	11
	July							
	August		2	1			3	3
	September	14		5				
	October		5			8	1	9
	November						8	8
	December							
2011	January				2		2	2
	February			1		1		1
	March							
	April				15	15		15
	May			6	12	18		18
	Total	**92**	**94**	**397**	**58**	**388**	**253**	**641**

5.2.3.3 Sub-surface sea temperature monitoring

To determine if FSA formation correlated with temperature, sub-surface temperature profiles for the surrounding waters of Ghizo Island were recorded on two separate occasions. Both involved installing waterproof HOBO Pro V2 (Onset Computers, Bourne Massachussetts, USA) loggers at approx. 20 m depth. The first set of temperature data was collected between January 2008 and September 2009 and the second set between August 2011 and November 2012 as part of the current study.

5.3 Results

5.3.1 Annual seasonality and depth preference

Grouper aggregation patterns at Ghizo differed between the three species. *E. fuscoguttatus* was present over a 4-5 month period, with peak months falling between March and July (Figure 5.2A). *E. polyphekadion* formed aggregations over a 3-4 month period with peak months occurring on April and May. Overall *E. polyhekadion* had lower densities compared to *E. fuscoguttatus* (Figure 5.2B). Unlike the two *Epinephelus* species, *P. areolatus* formed aggregations year-round. For all three species, the month of peak aggregation density overlapped with the other two species, which generally occurred between the months of March and June each year (Figure 5.2C).

Depth-related differences in core aggregation densities were also identified among species. *E. fuscoguttatus* aggregated at higher densities within the deeper transect during the spawning season (ANCOVA, $F_{(1,\ 7)} = 54.119$, $P < 0.001$) (Figure 5.2A). This pattern was also observed with *E. polyphekadion,* which registered higher densities within the deeper transect (ANCOVA, $F_{(1,\ 7)} = 47.28$, $P < 0.001$) (Figure 5.2B). In contrast, *P. areolatus* aggregated in greater densities along the shallower transect (ANCOVA, $F_{(1,\ 7)} = 10.24$, $P = 0.01505$) (Figure 5.2C).

A

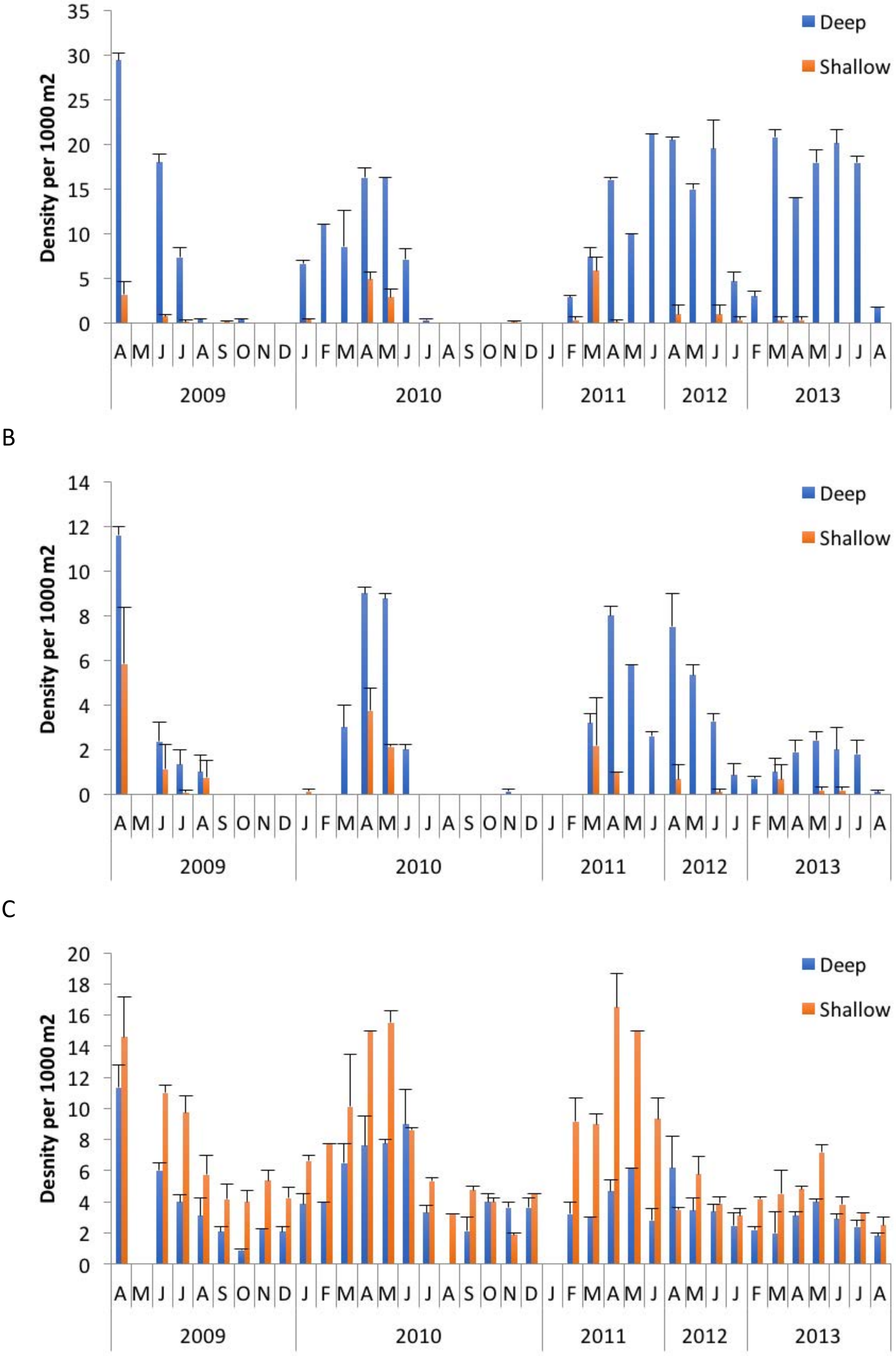


Figure 5.2 Seasonal patterns of abundance for A) *Epinephelus fuscoguttatus*, B) *Epinephelus polyphekadion,* C) *Plectropomus areolatus* over a 5-year period. Note scale on Y-axis differs for data presentation purposes.

5.3.2 Inter-annual variation in aggregation densities during the peak period

In general, *E. fuscoguttatus* maintained relatively stable aggregation densities on the deep transects during the peak spawning period (March -June) over the 5-year period. The only statistical difference in density between years for *E. fuscoguttatus* (One-way ANOVA, $F_{(4, 31)} = 4.893$, $P < 0.004$) occurred between the 2009 and the 2010/2011 seasons ($P<0.05$) (Figure 5.3A). *E. polyphekadion* showed significant inter-annual differences within the deeper transect (Kruskal-Wallis, df = 4, H = 12.402, P=0.015), which are explained by differences between the 2009 and 2013 seasons and the 2012 and 2013 seasons ($P<0.05$) (Figure 5.3B). No significant differences were recorded for either *E. fuscoguttatus* (Kruskal-Wallis, df = 4, H = 7.415, P = 0.115) or *E. polyphekadion* (Kruskal-Wallis, df = 4, H = 9.366, P = 0.53) densities within the shallow transects between years.

There was a drop in in aggregation densities for *P. areolatus* at the Ghizo FSA over the 5-year period with significant differences within the shallow transect (One-way ANOVA, $F_{(4, 21)} = 11.837$, $P <0.001$) and deep transects (One-way ANOVA, $F_{(4, 20)} = 14.572$, $P <0.001$). Pair-wise tests identified no differences in the shallow transect among the first three years (2009, 2010, 2011) and the latter two years (2012, 2013). However, there was significant difference between the initial three years and the final two years (Tukey, $P<0.05$). Within the deep transect, mean densities in both the 2009 and 2010 seasons differed significantly in density to the 2013 season (Tukey, $P<0.05$). No significant differences in density were observed in the deep transect between the final three years (Figure 5.3C).

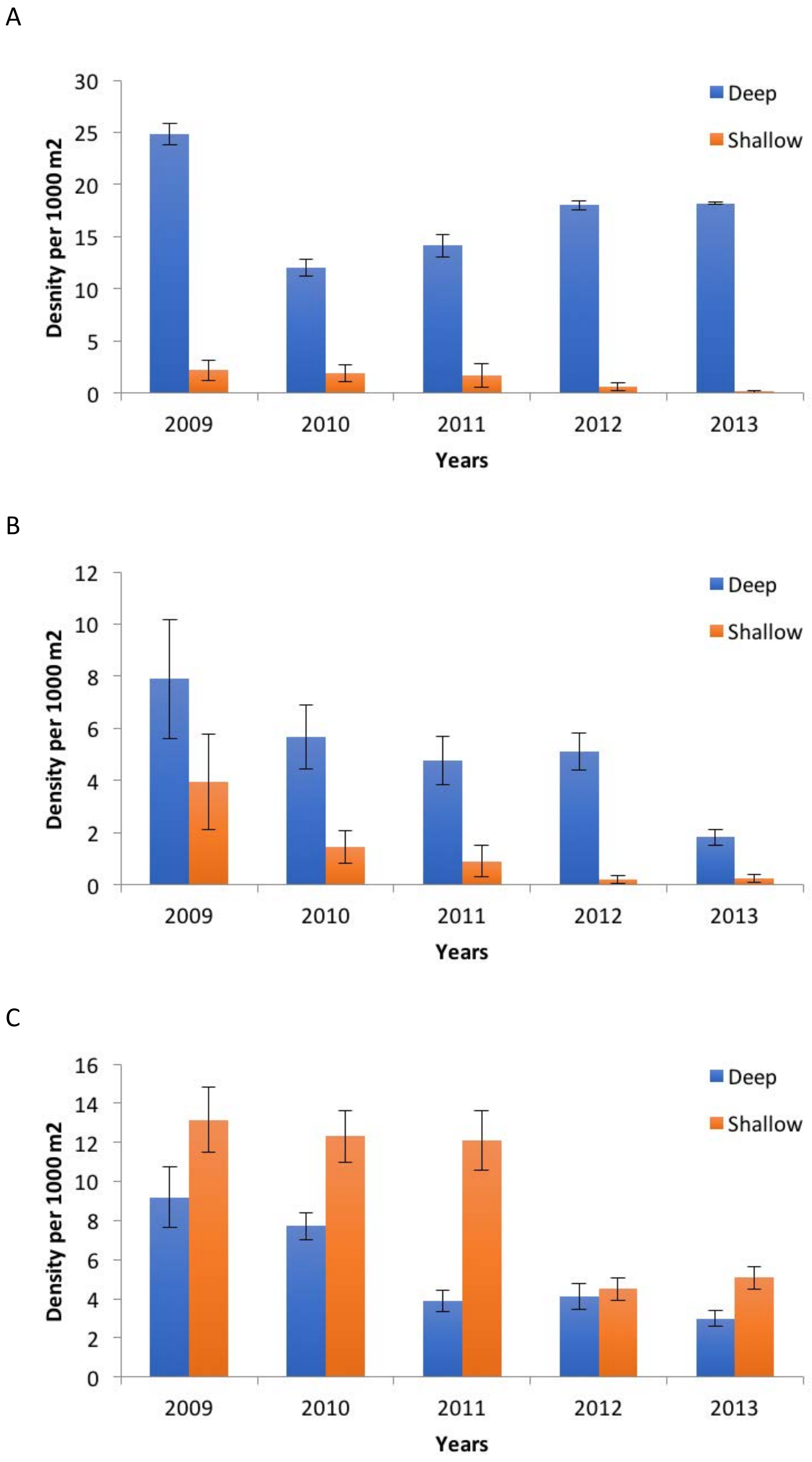


Figure 5.3 Mean densities during peak months (March-June) of A) *Epinephelus fuscoguttatus*, B) *Epinephelus polyphekadion,* C) *Plectropomus areolatus* over a 5-year period. Note scale on Y-axis differs for data presentation purposes.

5.3.3 Daily aggregation build-up

The mean density for all three grouper species at the FSA site gradually increased over a 15-day period before the new moon lunar phase with numbers peaking in the final six days of the last quarter lunar period. A subsequent decline was in progress by the day of new moon with aggregation numbers reduced to non-reproductive levels 2 danm (Figure 5.4).

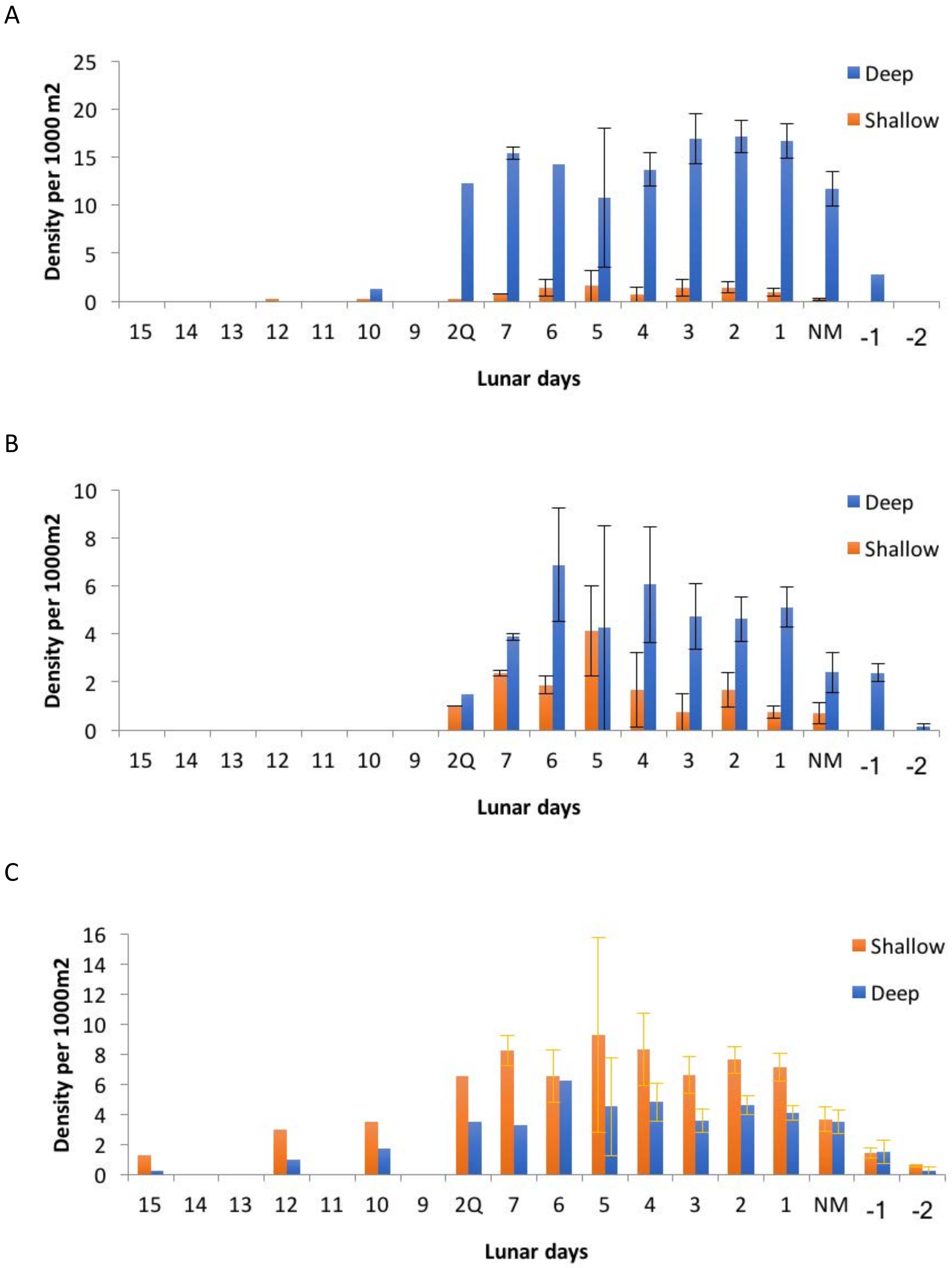


Figure 5.4 Mean density of A) *Epinephelus fuscoguttatus*, B) *Epinephelus polyphekadion,* C) *Plectropomus areolatus*) at the Ghizo fish spawning sggregation site with data pooled over a 18-lunar day period. 2Q = 2nd lunar quarter, NM = New moon. Note scale on Y-axis differs for data presentation purposes.

5.3.4 Gonado-somatic index and reproductive condition

There were obvious differences in reproductive activity when female *P. areolatus* GSI was pooled by the different lunar periods. The mean female GSI showed an increasing trend from the 1st quarter moon period onwards, with a peak in the last quarter (Figure 5.5A), which was a result of an increased presence of reproductively active females, especially those with hydrated oocytes (Figure 5.5B). The significant differences in GSI values between the lunar periods (Kruskal-Wallis, H = 95.190, *df* = 3, P<0.001), was revealed by pair-wise comparison to be between the 3Q+ and the 1Q+/FM+ lunar periods and also between the FM+ and 1Q+ lunar periods (Dunn's Multiple Comparison, P <0.05). Male GSI patterns remained relatively constant (1.16%-1.98%) with no significant differences between lunar periods (Kruskal-Wallis, H = 6.445, *df* = 3, P = 0.092) (Figure 5.5A).

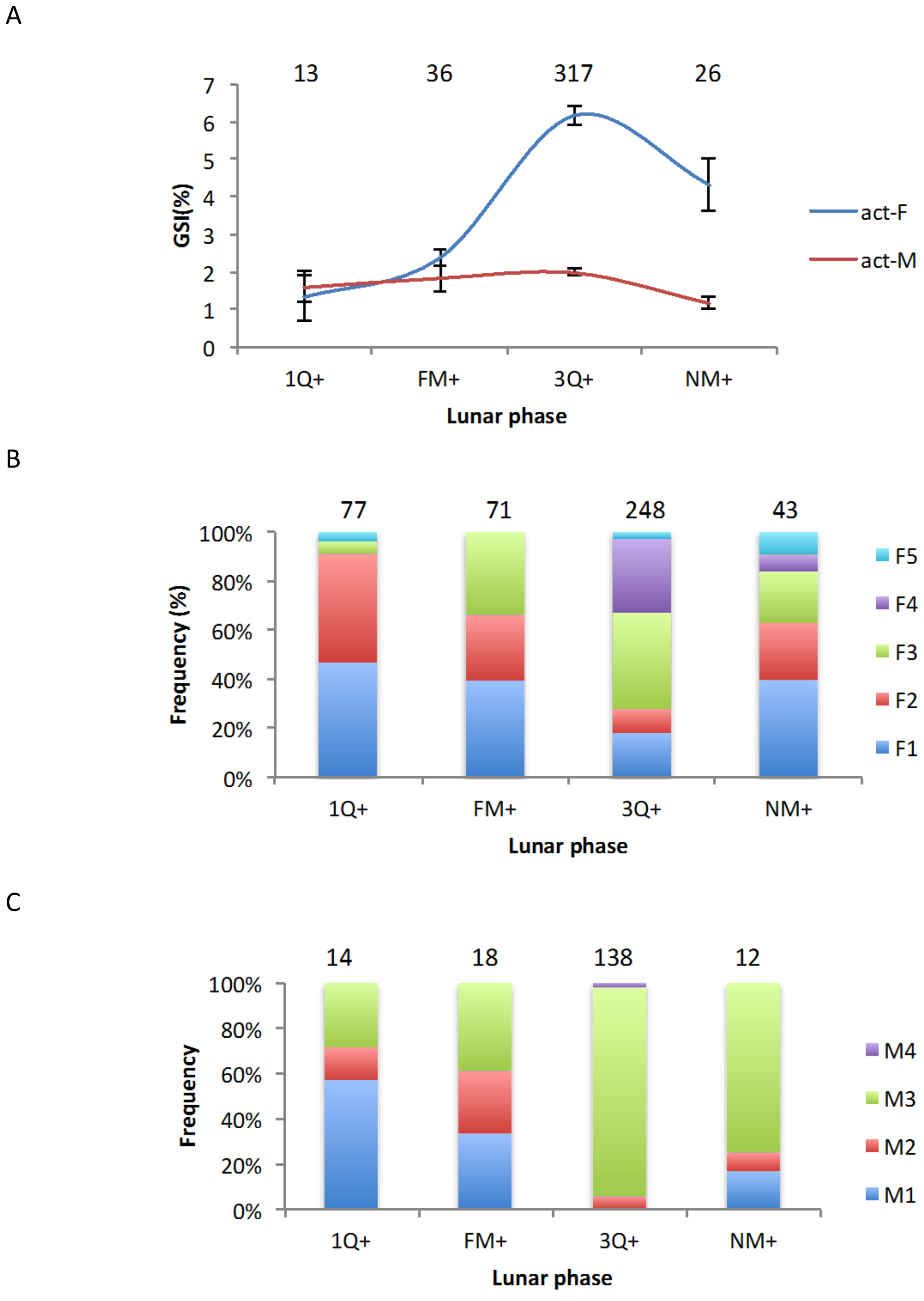


Figure 5.5 A) Gonado-somatic Indices for reproductively active females and males pooled by lunar phase. B) Reproductive composition of all female samples pooled by lunar phase, C) Reproductive composition of all male samples by pooled lunar phase. Numbers above charts represent sample size. F1 - immature female; F2 – resting female; F3 – ripe female; F4- hydrated female; F5 – spent female; M1 – resting male; M2 – ripe male; M3 – spawning ready male; M4 – spent male.

Intensive histological sampling at the FSAs in the two weeks prior to new moon during the peak spawning periods enabled me to examine the pattern of GSI in detail. Female GSI values remained relatively steady during the 10-5 dbnm period (GSI = 2.22-3.46%). During the 4 dbnm there was a notable increase in mean GSI values with a peak (7.95) occurring 2 dbnm (Figure 5.6A). This was explained by the increased presence of reproductively active females that had hydrated oocytes (F4) (Figure 5.6B). A decline to non-reproductive levels appeared to be in progress by new moon. Male GSI patterns varied between (0.31-2.8%) with a peak occurring 2 dbnm (Figure 5.6A). Reproductively active males, especially those with sperm sinuses and ducts filled with spermatozoa (M3), dominated the reproductive composition of males over the 12-days before new moon (Figure 5.6C) and during different lunar periods (Figure 5.5C). This is similar to the pattern observed in the monthly composition of males (Chapter 4).

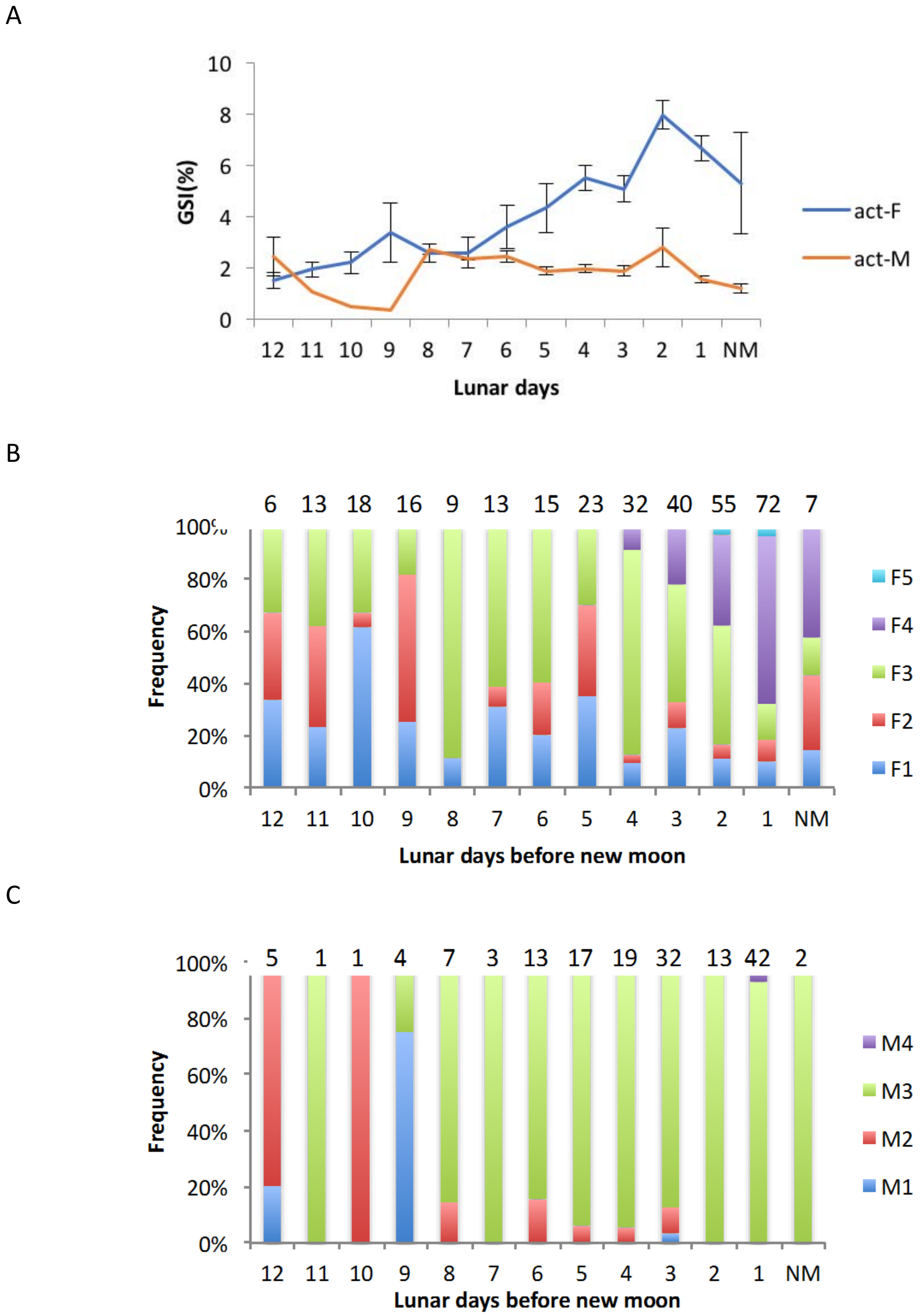


Figure 5.6 A) Gonado-somatic Indices for reproductively active *P. areolatus* females and males pooled by lunar day over the 12-day period before new moon. B) Reproductive composition of all female samples pooled by lunar day and, C) Reproductive composition of all male samples by pooled lunar day. Numbers above bars represent sample size. F1 - immature female; F2 – resting female; F3 – ripe female; F4- hydrated female; F5 – spent female; M1 – resting male; M2 – ripe male; M3 – spawning ready male; M4 – spent male.

5.3.5 Reproductive composition of aggregating *Plectropomus areolatus*

Histological results revealed that not all individuals present at a spawning aggregation site were in a mature or reproductively active state (Figure 5.7). Of the 276 samples collected from both spawning sites during the third lunar period of the peak spawning months, immature individuals (both immature females and bisexuals) accounted for 7% of the overall sample whilst mature inactive females made up 3% (Table 5.4).

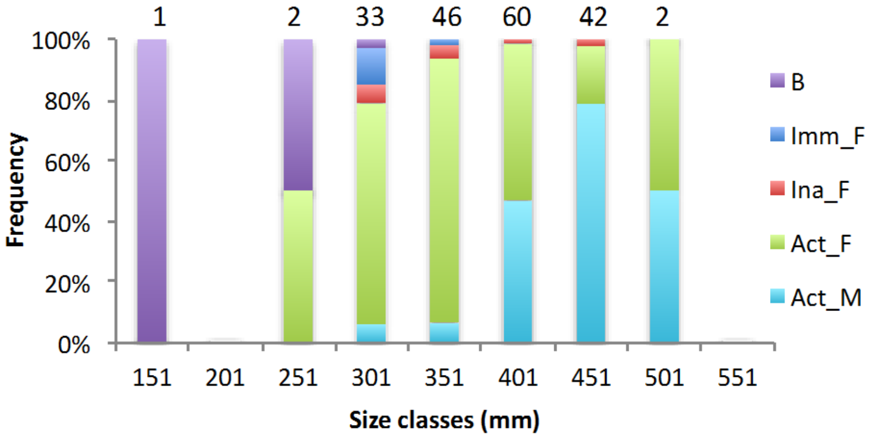


Figure 5.7 Reproductive composition of individuals sampled from the Ghizo FSA site. B = bisexual, Imm_F = immature female, Ina_F = mature inactive female, Act_F = mature active female, Act-M = mature active male. Numbers above bars represent sample sizes for each size class.

Table 5.4. Combined reproductive composition of individuals sampled from populations at spawning sites in Ghizo and Parara during the third lunar quarter period of the peak spawning months (March – June).

N = 276	Immature female	Bisexual	Inactive female	Active female	Active male
%	5	2	3	50	41

5.3.6 Sub-surface sea temperature profile

Sub-surface water temperate in the Ghizo region generally ranges between 28.5-30.5 ^{o}C over the year (Figure 5.8). Warmer water temperature usually occurs between November and June with peaks occurring between December and March. Despite the fact that the peak aggregation period occurs during warmer months of the year, months with peak temperature do not correlate with timing of months with peak fish density at FSAs.

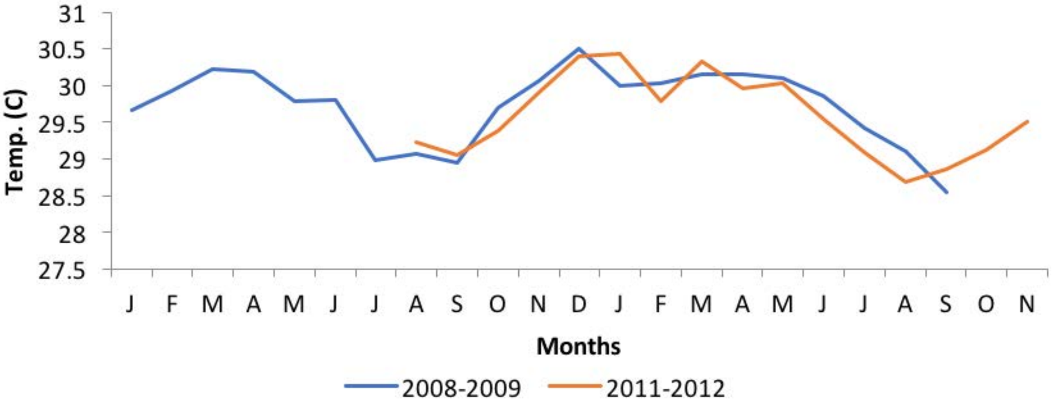


Figure 5.8 Annual sub-surface temperature profile for Ghizo coastal waters. Blue line indicates data collected over a 20-month period in 2008 & 2009. Red line indicates data collected over a 16-month period in 2011 & 2012.

5.4 Discussion

Temporal patterns of *E. fuscoguttatus*, *E. polyphekadion* and *P. areolatus* FSAs were examined as part of a long-term monitoring study. Further insight into the timeline of reproductive activities for *P. areolatus* was made possible by conducting histological analyses of gonads and examining patterns in gonado-somatic index.

The temporal patterns in aggregation formation displayed by the two *Epinephelus* species are typical of transient-type spawning aggregations (Domeier 2012) and characteristic of medium-bodied to large epinephelid species. *E. fuscoguttatus* formed peak aggregations (>10 fish/1000 m2) over a 4-5 month period seasonally with smaller aggregations occurring immediately before and after this period. This is similar to other regionally based studies on *E. fuscoguttatus* that have reported spawning seasons of 3-5 month durations (Johannes et al. 1999, Robinson et al. 2008, Rhodes et al. 2012). Furthermore, the shorter spawning season observed for *E. polyphekadion* is also typical of trends observed for this species in other locations in the Indo-Pacific (Rhodes and Sadovy 2002, Robinson et al. 2008). In nearby Roviana Lagoon, *E. fuscoguttatus* also had longer spawning seasons compared to *E. polyphekadion* (Hamilton et al. 2012). The year-round aggregation formation of *P. areolatus* is a familiar pattern for this species. Studies in Palau (Johannes et al. 1999), Papua New Guinea (Hamilton et al. 2011) and at Roviana Lagoon (Hamilton et al. 2012) have all described monthly aggregation formation for this species. However, Rhodes and Tupper (2008) report that in Pohnpei this species forms FSA only during a 5-month period.

Although, the year-round aggregation formation of *P. areolatus* is a trait more commonly associated with resident spawners, it is still unclear whether spawning for *P. areolatus* occurs during all months of the aggregation period.

Fish density at the Ghizo site for all three species were greatest between the months of March and May. This is similar to aggregation patterns observed at sites in Marovo lagoon for *P. areolatus* (Johannes 1988). However, peaks in aggregation densities are known to occur earlier in the year (January-March) for Roviana lagoon (Hamilton et al. 2012). Therefore, although aggregation formation appears to take place during warmer months for Ghizo and Roviana, the fine-scale spatial differences in peak aggregation periods between these two localities suggests that temperature is likely to be part of a suite of environmental cues that help to co-ordinate the spawning behavior of this group of fishes. For instance, in Pohnpei, although peak aggregation densities occur within similar months to Ghizo and Roviana, this period is characterized by rising water temperatures from seasonal lows (Rhodes and Sadovy 2002, Rhodes and Tupper 2008, Rhodes et al. 2012). Therefore, more comprehensive investigations into the proximal environmental cues leading to aggregation formation is required to help elucidate which factors influence their timing.

A clear link has been noted in the timing of specific lunar phases and the formation of spawning aggregations for certain species (Sadovy 1996, Heyman et al. 2005) with the particular lunar phase known to vary between regions for some species (Rhodes and Sadovy 2002b, Pet et al. 2005). Aggregation formation of the three species in this study occur just prior to the new moon phase of the lunar cycle, which is similar to patterns observed in Palau (Johannes et al. 1999) and in Roviana (Hamilton et al. 2012). However, in Indonesia, these species are known to form aggregation on the full moon, with the exception of a couple of months when *P. areolatus* was also recorded to form aggregations during the lead-up to new moon (Pet et al. 2005). An intensive monitoring effort by Hamilton et al. (2012) recorded daily densities at the spawning aggregation site over a 39-day period and found that fish numbers increased between full moon and new moon, an identical pattern to what I have reported for the Ghizo region.

The presence of hydrated oocytes' within the ovarian lamellae of *P. areolatus* females captured at the FSAs during the 4 days before and on the day of new moon (5-day period) provides direct evidence that the FSAs reported on here had formed for the purpose of spawning (Sadovy et al. 2003, Rhodes & Sadovy 2002a) and likely spawned in the lead up to new moon. Numerous indirect spawning signs such as courtship behaviors, colour change and acts of aggression also became more prevalent at the FSAs during the last lunar quarter. The evidence of a strong lunar component to spawning in *P. areolatus* differs markedly to *P. leopardus* on the Great Barrier Reef where hydrated females were present during all moon phases, indicating that spawning is not restricted to a particular lunar period for this genus (Ferreira 1995).

The fact that a small percentage of individuals that were collected from FSAs during peak spawning periods were comprised of mature resting (inactive) females and younger immature individuals is interesting. It is possible that the inactive females were using this period to assess the operational sex ratio present before investing energy into production of gametes. Similarly, immature individuals at the FSA maybe using the opportunity to determine which sex to develop into in order to improve reproductive success in later adult years. Furthermore, the presence of immature individuals at spawning aggregations suggests that social learning maybe an important component to the future re-occurrence of aggregations through the passing down of site and timing information from older individuals to new recruits. If this is the case then the loss of older adults may impact on the ability of new recruits to find aggregation sites (Sadovy & Domeier 2005a).

A gross analysis of the various physical attributes of the Ghizo and Parara reef systems provides some indication of what features appear to be important in identifying the potential location of a particular site for mass reproductive purposes. As described in Chapter 2, the presence of a barrier reef, which encompasses a complex lagoonal system are important elements in the ecology of *P. areolatus* as both provide crucial habitat for larval settlement and ontogenetic development (see contributions in Arreguín-Sanchez et al. 1996, Largier 2003, Almany et al. 2013). All the known FSA sites within the Ghizo and Parara reef system share similar geomorphology in that they are located on or close to a barrier reef promontory that drops off into the deep waters of the Vela Gulf and Ferguson Passage, respectively. Despite a lack of detailed investigation into the physical near-shore oceanographic patterns at these areas, their shared geomorphological features suggest that they are also exposed to similar oceanographic conditions (e.g. Heyman and Kobara 2012).

A common observation at these locations is the formation of nearshore eddies especially during rising or falling tides when water movement is greatest. Although it is likely that some eggs and larvae may get ejected out into off-shore hydrodynamic systems, recent work suggests that the formation of eddies generated by reef promontories can play an important role in the retention of larvae near natal reefs (Hamner et al. 2007, Ezer et al. 2010, Beldade et al. 2016).

Due to its tendency to form significant shallow water aggregations *P. areolatus* is the most vulnerable of the three species to free diving spearfishing, especially at night (Hamilton et al. 2012). At night this species is easily caught as it does not flee from an approaching spearfisher with a handheld spotlight. In fact, local spearfishers specifically target spawning aggregations at night and during the early hours of the morning because of the ease at which this species can be caught. A couple of spear-fishermen working as a team have been observed removing the equivalent of 30 *P. areolatus* hr^{-1} from a spawning aggregation site. Daytime hook and line fishing in Pohnpei yielded about 7 fish hr^{-1} by comparison (Rhodes pers comm).

During the course of the 5-year monitoring period, the number of *P. areolatus* within both the shallow and deep transects became substantially reduced. Local variation in levels of recruitment, growth, natural mortality or movement patterns may be responsible for the observed reduction. However, the fact that Site A is commonly targeted by subsistence and artisanal spearfishers means that fishing pressure is likely to be a strong contributing factor. Indeed, at two other known and heavily fished *P. areolatus* FSAs in Gizo, aggregation numbers are now much lower than a decade ago (personal observation), providing additional support that overfishing may be a key driver in the declines observed at Site A.

The result from this study supports observation made elsewhere in the region that have described the tendency for *E. fuscoguttatus*, *E. polyphekadion* and *P. areolatus* to form overlapping spawning aggregations. It is clear that the fish present at these aggregations are particularly vulnerable to fishing activities, especially by spearfishing. In order to protect these breeding stocks it is strongly recommended that spatial closures that encompass fishing spawning sites are enacted and accompanied by a temporal sales ban on aggregating species during their spawning seasons. In theory, a sales ban will a) help to discourage the poaching of breeding stocks of fish from spawning sites that are already afforded protection within management plans and b) provide protection to breeding stocks at sites that are yet to be included in management strategies designed to protect fish spawning aggregations. It is acknowledged that the wide-spread and complex geographical nature of Solomon Islands will make enforcing such regulations challenging. Therefore, focusing management efforts on urbanized centers with active fish retailing facilities would be an important first step. For instance, the centralized nature of the fish market in Ghizo presents a useful opportunity for management authorities to enforce a sales ban. If actively enforced, such management measures should help protect fish spawning aggregations both within the Ghizo reef system and at neighboring reef systems such as Parara. That said, it is important to bear in mind that seasonal patterns can and do differ between locations. As part of continued efforts to improve our understanding on the dynamics of FSAs in Solomon Islands, local fisher knowledge surveys are being planned in 2017/2018 to examine the distribution, status and seasonal patterns of fish spawning sites around the New Georgia island group in Western Province.

6 General Discussion

6.1 General distribution patterns

Observations of the regional distribution patterns of the *Plectropomus* reveal that apart from two species located on the western edge of the genus range, the centre of distribution is situated within the Coral Triangle region with most species associated with habitats found within the reef systems adjacent to high Islands or continental shores. *Plectropomus areolatus* and *P. laevis* are the most widely distributed of the *Plectropomus* species but unlike *P. laevis* the distribution of *P. areolatus* does not extend to the atoll systems of the southeastern Pacific or the south western Indian Ocean (southern Seychelles). The habitat distribution of *P. areolatus* at biogeographic scales can be summarized as strongly associated with coastal ecosystems that support complex reef systems. Behavioral patterns of the genus highlight the fact that they are distinctive to the majority of Indo-Pacific groupers in that they are not ambush feeders but are actively seen roving about the substratum (Pears 2005).

A more focused inspection of *Plectropomus* species distributions and relative densities was made possible in this study by examining fish abundances from outer reef slope habitats within the Australian-Indo Archipelago. The analyses were based on the four dominant *Plectropomus* species found within this region: *P. areolatus*, *P. laevis, P. leopardus* and *P. oligacanthus*. The relative species composition of *Plectropomus* differed markedly within the Australian-Indo Archipelago region, with distinct clusters of *Plectropomus* species identified at northwestern Australia, north-eastern Australia (central and north GBR), eastern Papua New Guinea and western Solomon Islands.

The species composition of these regions were characterized by *P. leopardus* and *P. laevis* at the GBR regional localities, *P. areolatus* at the northwestern Australian and western Solomon islands and *P. oligacanthus* at the eastern Papua New Guinea reefs. Two important patterns emerged from this analysis. Firstly, there was a strong latitudinal trend in abundance with the higher latitude populations of the GBR providing some of the highest abundances (25 fish/hectare) achieved by epinephelids. Secondly, a high level of variation in *Plectropomus* abundance was present within and between regional datasets which cannot be attributed solely to fishing pressure despite the fact that *Plectropomus* species are targeted by small scale, regional and international fisheries throughout their range.

6.2 Impacts of habitat and fishing on *P. areolatus* abundance

To better understand how fishing pressure and habitat structure influence the abundance of *P. areolatus,* detailed surveys were carried out in Western Solomon Islands at sites that contained varying degrees of juvenile and adult reef habitat, and had experienced different levels of historical fishing pressure. Survey data clearly demonstrated that *P. areolatus* abundances were highest at sites that supported inter connected juvenile and adult habitats. Sites with the highest adult *P. areolatus* abundances were adjacent to extensive complex lagoonal systems which provide prime recruitment habitat for *P. areolatus* (Almany et al. 2013). At these sites reef passes connect lagoonal habitats to fringing reef and barrier reefs, which are the typical habitat for adult *P. areolatus* (Rhodes 2012b). In the Westerns Solomon Islands these passes are also important for reproduction, with spawning aggregations of *P. areolatus* often forming at seaward facing mouths of passes (Johannes et al. 1999, Hamilton & Kama 2004).

The analysis of abundance patterns over these reef systems demonstrated that although fishing pressure was associated with significant reductions in abundance, the greatest differences emerged when reef systems with distinct habitat structures were compared. The fishing effects (Ghizo vs Parara) were small compared with the influences generated by habitat structure (Ghizo and Parara vs Tetepare). This finding should not be taken to imply that fishing does not have an impact of *P. areolatus*. As this work has shown, abundances where lower at the heavily fished site of Gizo relative to Parama, with *P. areolatus* at Gizo also having a younger age at maturity, a classical response to heavy fishing pressure (Rochet 2009). Moreover, as one would expect, age-based studies showed that mortality rates were much higher at the heavily fished sites of Marovo and Ghizo compared to the lightly fished sites at Roviana and Parara. This highlights that any attempts to investigate the impacts of fishing on abundance patterns of *Plectropomus* must take into account differences in habitat structure. While assessments at biogeographical or global scales may provide an interesting picture of the macroscale ecology of the species they offer little in the way of implementing effective management schemes.

6.3 Reproductive pathway

An important outcome of the reproductive component of this study is that despite *P. areolatus* gonads containing morphological features typically observed in protogynous species, there was no conclusive evidence of a protogynous reproductive pathway. No transitional individuals we found, conferring with other reproductive studies on this species from different geographical regions (Williams et al. 2008, Rhodes et al. 2013). Furthermore, *P. areolatus* in western Solomon Islands had an extended inactive bisexual (no prior spawning) phase. The fact that inactive bisexual individuals were present before the size of female maturity and overlapped with adult sizes suggests that males are likely to recruit directly from an inactive bisexual phase. All available information suggests that *P. areolatus* functions as a gonochoristic species in western Solomon Islands. This is similar to what Hamilton et al. (2008) discovered for the Bumphead parrotfish (*Bolbometopon muricatum*) in Solomon Islands. While many authors have suggested that protogynous species may be more vulnerable to fishing pressure (references within Blaylock & Shepard 2016), recent research by Robinson et al. (2017) suggests that protogynous species may in fact have more flexibility to adapt to fishing than gonochoristic species. Gonochorism may in fact increase the intrinsic vulnerability of *P. areolatus*, and is a life history characteristic that should be considered when developing management measures for this species.

6.4 Spawning aggregations of *P. areolatus*

The patterns of spawning aggregation formation displayed by *P. areolatus* at the Ghizo aggregation site showed some similarities to what has been reported in other parts of Solomon Islands. This study conferred with earlier local knowledge and in-water surveys in Marovo and Roviana Lagoon in the Western Solomon’s which have shown that *P. areolatus* spawning aggregations peak in abundances several days prior to the new moon (Johannes, 1988, Hamilton et al. 2012). While the lunar periodicity of spawning in *P. areolatus* seems constant across Melanesia, the annual seasonality of aggregations has been shown to vary from location to location on small spatial scales (Hamilton et al. 2005). Results from this study confirm that this is indeed the case in the Western Solomons. The peak aggregations at the Ghizo FSA aggregation occurred between March – June over multiple years, with smaller aggregations also forming outside of the peak season. This was in contrast to another well studied *P. areolatus* spawning aggregation located approximately 50 km away at Roviana Lagoon, where peak densities occurred between the months of December-April over multiple years, with smaller aggregations forming in other months (Hamilton et al. 2012). At the Ghizo FSA studied here the peak *P. areolatus* aggregation coincide with the months of the year when spawning aggregations of *Epinephelus fuscoguttatus* and *E. polyphekadion* also occur, a pattern that has also been seen at multi-species spawning sites in various other locations in Papua New Guinea and Solomon Islands (Hamilton & Manuai 2006, Hamilton et al. 2011, 2012). Predictable lunar periodicity of aggregation formation yet highly variable annual seasonality has management implications which are discussed below.

6.5 Management measures for *P. areolatus*

The fact that *P. areolatus* aggregate in large numbers at highly predicable times and places for the purpose of spawning makes this species highly vulnerable to overexploitation. These aggregations form in shallow water and occur ever month of the year, with each monthly aggregation period lasting between 7-14 days in duration (Hamilton et al. 2012). Night-time spearfishing has caused marked declines in *P. areolautus* spawning aggregations at other parts of western Solomon Islands (Hamilton et al. 2012) and elsewhere in the region (Hamilton et al. 2011), and is a common practice on Ghizo reefs. Indeed, it was noted in this study that the *P. areolatus* aggregation size at Ghizo decreased over the 5-year period the monitoring was conducted. While this could simply reflect natural variation in environmental conditions, it is more likely to be reflective of fishing pressure. Clearly, the management of FSA should be a top management priority.

The wide spread archipelagic nature of Solomon Islands and the fact that the authorities in charge of coastal fisheries are under-resourced presents a challenge for implementation of fisheries management measures. Nevertheless, as a result of the information collected during the course of this study, a revision of the Western Province Fisheries Ordinance now includes regulations aimed at the protection *P. areolatus*. *E. fuscoguttatus* and *E. polyphekadion* during their breeding seasons. Under the draft Ordinance there will be a complete ban on the fishing and sale of these three groupers during the 7-day period before new moon, day of new moon and 2 days after new moon i.e. a total of 10 days each month of the year. If adequately enforced, this year-round monthly lunar ban would cater for location-specific variation in the timing of spawning seasons in groupers. Another important aspect is that effectively enforced lunar bans would protect FSAs that are not currently known to regulators. Recently, information obtained in this research was also used to help formulate management recommendations for groupers across the Solomon Islands. The Ministry of Fisheries and Marine Resources is currently developing regulations under the 2016 Fisheries Act, and in a submission made to MFMR this year it was proposed that a precautionary approach that utilises a ten-day year-round lunar ban on the fishing or sale of groupers, as proposed for Western Province, be enforced across Solomon Islands.

Finally, it is acknowledged that due to weak national governance in Solomon Islands and a rapidly growing human population, policy changes alone are unlikely to be sufficient for adequately managing aggregating species. As well as implementing lunar bans, communities that hold customary tenure over their nearshore reefs should be encouraged to manage their grouper spawning aggregation sites through the establishment of networks of MPAs. Indeed, the limited larval dispersal patterns and tighter than expected stock-recruitment relationships in *P. areolatus* (Almany et al. 2013) strongly suggests that local management of FSAs will provide localized benefits. Recently, it has been shown that in Melanesia *P. areolatus* stocks can be effectively managed at spatial scales that make sense from ecological, cultural and political perspectives (Almany et al. 2015).

7 Reference

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