Taylor, Brett McCully (2015) ***Environmental and fishery-induced effects on life histories and assemblages of parrotfishes.*** **PhD thesis, James Cook University.**

Environmental and fishery-induced effects on life histories and assemblages of parrotfishes

Thesis submitted by

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In January 2015

For the degree of Doctor of Philosophy

In the College of Marine and Environmental Sciences

James Cook University

Acknowledgments

Foremost, I thank my primary supervisor J. Howard Choat for facilitating this opportunity, providing perceptive insights and allowing me immeasurable freedom to explore my interests throughout the entire process. Working with him has been the highlight of this PhD. I also thank Garry Russ for his comments and continuous support throughout my candidature. This work was financially supported by the NOAA Pacific Islands Fisheries Science Center (PIFSC) and the Guam Coral Reef Initiative.

There are many people I am grateful to for their assistance during the development of this thesis. From my time at the University of Guam, I thank Ciemon Caballes, Joe Cummings, Carl De la Cruz, Angie Duenas, Andrew Halford, Steve Lindfield, Alyssa Marshell, Jenny McIlwain, Jason Miller, Nick Pioppi, Mark Priest and Anna Simeon for field or logistical assistance. From the PIFSC, I thank Bob Humphreys and Edward DeMartini. From across Micronesia, I thank the Yap Marine Resources Management Division, Yap Divers, the Conservation Society of Pohnpei, the Kosrae Conservation and Safety Organization, the Kosrae Village Resort, the SS Thorfinn, chiefs and residents of Ifalik, Satawal, and Lamotrek, Vanessa Fread, Scotty Malakai, Trace Lorrin, Taylor Paul, Peter Houk and Kevin Rhodes.

At James Cook University (or elsewhere in Australia), discussions with or assistance from Simon Brandl, Nick Graham, Rick Hamilton, Hugo Harrison, Andrew Hoey, Rhondda Jones, Phil Munday, Morgan Pratchett, Sue Reilly, Jairo Rivera, Liz Tynan and David Williamson were greatly appreciated.

Finally, I thank my parents for their perpetual encouragement in my career journey and my beautiful wife Kendra, who has been there beside me for the entire ride.

Statement on the Contribution of Others

This thesis was funded by research grants from the Guam Coral Reef Initiative and the NOAA Pacific Islands Fisheries Science Center. The contributions of colleagues during the collection of data are all acknowledged. Contributions from co-authors on those manuscripts that have been published from chapters herein are as follows: Prof. Howard Choat contributed conceptual and editorial input for chapters 2, 3 and 5; Prof. Garry Russ and Dr. Peter Houk contributed conceptual and editorial support for chapter 3; and Steven Lindfield assisted with data collection for chapter 5. I was supported by a Postgraduate Research Scholarship for the duration of my thesis. The work was conducted under JCU Animal Ethics permit number A1674 and University of Guam Institutional Animal Care and Use Committee permit number UOG1202.

General Abstract

Characteristics of fish communities that are important to fishery managers include the life histories of targeted species, the spatial variation in community dynamics (e.g., species' abundance and demographic variation), and the spatial scales at which communities are critically observed. At present, our understanding of life history and demographic variability for many exploited coral-reef fishes is poor, and this hinders our ability to interpret fishery dynamics and develop sound conservation policies. Across Indo-Pacific coral reefs, parrotfishes (Labridae: tribe Scarinae) in particular are a ubiquitous and diverse component of reef-fish assemblages that are increasingly prevalent in commercial and artisanal fisheries harvests. The objective of this thesis was to examine patterns of demographic variation among and within species across several spatial scales and relate observations to environmental and anthropogenic factors.

As anthropogenic and environmental factors interact across spatial scales, sampling programs designed to disentangle these are required by both ecologists and resource managers. Hence, I have combined a variety of methods and analyses to explore patterns of demographic and community-level variation in parrotfish assemblages from Micronesia. First, I used fishery-independent sampling coupled with standard ageing (using sagittal otoliths) and gonad histology techniques to determine growth patterns, life spans, mortality rates, and timing of maturation and sex change for twelve common parrotfishes representing five genera in Micronesia. Interspecific variation in key life-history traits was explored using multivariate analysis. I then applied these trait data to examine the effect of life histories on vulnerability to overexploitation across the twelve species. Vulnerability for each species was derived from independent measures associated with both temporal (20-year catch records) and spatial abundance datasets. Subsequent studies were based on parrotfish abundance, biomass and body length estimates derived from stereo-video surveys spanning eight islands across Micronesia. I first examined variation in timing of sex change for exploited parrotfishes using a novel method across a range of environmental, anthropogenic and geographic factors. Finally, parrotfish assemblage structure, size distribution and phylogenetic diversity were assessed in a multi-scale context against potential environmental, biogeographic and anthropogenic correlates.

Across all species examined, there was a high level of correlation among life-history traits. However, relationships between length-based and age-based traits were weakest, with a tenuous link between maximum body size and life span. Species were significantly grouped at two major levels based on multivariate analysis of similarities among life-history traits. The first grouping was driven by length-based parameters (lengths at maturity and sex change, maximum length) and separated the small- and large-bodied species. Within these, species were grouped by age-based parameters (age at maturity, mortality, life span). Groupings based on demographic and life-history features were independent of phylogenetic relationships at the given taxonomic level. Further, Most traits examined were significant predictors of vulnerability across species, but their relative utility differed considerably. Length-based traits (e.g., lengths at maturity and sex change, maximum length) were superior to age-based traits (e.g., life span), but one age-based trait, age at female maturation, emerged as the optimal overall. The results reiterate that body size is an important character differentiating species, but interspecific variation in age-based traits complicates its use as a life-history proxy. Easily-derived metrics such as maximum length can be effective management tools when applied to phylogenetically-related multispecies assemblages, but more holistic and comprehensive demographic data should be sought, especially in data-deficient and heavily impacted regions.

Results from the sex change analysis were highly dependent on spatial scale. Fishing pressure was the most influential factor determining length at sex change at the within-island scale where a wide range of anthropogenic pressure existed. Sex transition occurred at smaller sizes where fishing pressure was high. Among islands, however, differences were overwhelmingly predicted by reefal-scale structural features, a pattern evident for all species examined. For the most abundant species, *Chlorurus spilurus*, length at sex change increased at higher overall densities and greater female-to-male sex ratios at all islands except where targeted by fishermen; here the trend was reversed. This implies differing selective pressures on adult individuals can significantly alter sex change dynamics, highlighting the importance of social structure, demography and the selective forces structuring populations. For community assemblages, results indicated that correlates of assemblage structure are also scale-dependent; biogeographic distributions of species and island geomorphology hierarchically influenced community patterns across islands whereas biophysical features and anthropogenic pressure influenced community assemblage structure at the within-island scale. Species richness and phylogenetic diversity increased with greater broad-scale habitat diversity associated with different island geomorphologies. However, within-island patterns of abundance and biomass varied in response to biophysical factors and levels of human influence unique to particular islands. While the effect of fishing activities on community composition and phylogenetic diversity was obscured across island types, fishing pressure was the primary correlate of mean parrotfish length at all spatial scales.

In these analyses, considerable life-history and community-level responses to exploitation were observed, but results suggest potential fishing effects on demography and assemblage structure may be obscured by natural variation at biogeographic scales. Hence, despite widespread fishery-induced pressure on Pacific coral reefs, the structuring of parrotfish assemblages at broad spatial scales remains a story largely dependent on habitat; that is, the geomorphological features of islands that facilitate spatial heterogeneity in coral reef communities. Biological communities across islands will likely respond to exploitation differently, and therefore equations for biodiversity conservation and fisheries management should integrate inherent features of island geomorphology alongside human impact levels.

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Chapter 1: General Introduction

The demographic configuration of biotic communities is influenced by evolutionary and regional processes as well as biophysical features of the surrounding environment (Ricklefs 1987). Life-history traits are important components that broadly reflect the ecological diversification distinguishing species (Winemiller and Rose 1992). Among these traits, body size is the most easily identifiable and is physiologically linked to many life-history processes (Calder 1984). For marine fishes, interspecific trait variation has been extensively studied for decades because of its importance to fisheries management.

Nearly sixty years ago Beverton and Holt (1957) outlined the potential influence of life-history traits on marine fisheries harvests in their seminal book. The concepts proposed have been applied broadly to temperate commercial fisheries in the decades since (e.g., Adams 1980, Winemiller 2005), but have only trickled down to tropical fisheries science, often in a non-coherent way. The principal reason for this is that the systematic collection of age-based life-history information for tropical reef fishes has lagged tremendously behind that of temperate fisheries, a result of both logistical (lack of funding and scientific manpower in most tropical nations) and theoretical constraints (prior notion that tropical fishes do not deposit annual increments in sagittal otoliths due to the lack of climatic variation; Longhurst and Pauly 1987, Fowler 2009). Further, the initial accumulation of age-based data taught us that demographic dynamics of tropical fishes were much different than had been previously speculated, with considerable longevity in many reef fish families dispelling the idea that coral reefs are comprised of short-lived, high turnover species (Panella 1974, Sale 1980). At present, most assessments of fishery vulnerability have relied on inferred, rather than measured, life-history trait values for targeted species.

Ecological responses to environmental variability are dynamic and this is reflected in patterns from demographic processes of individual species all the way up to assemblage structure of biotic communities (Cowen 1990, Friedlander and Parrish 1998). Regarding reproductive processes specifically, Petersen and Warner (2002) highlighted that knowledge of natural geographic variation is central to resource management, but this information is virtually non-existent for all coral reef species. This remains true for most demographic and community-level processes on coral reefs. Rather, greater effort has been placed on measuring the identifiable effects of human extraction (i.e., fishing effects) across space and through time. However, the selective forces associated with fishing pressure and natural geographic variability are highly dissimilar (Bohnsack 1990), thus a critical issue is the need to disentangle the variation associated with both environmental and anthropogenic factors. Stemming from this is the concept of spatial scale, particularly at which scale(s) different factors emerge as recognizably important (Sale 1998).

A core issue against which this thesis is designed is that recent history has seen an increasing impact on coral-reef fisheries throughout the Indo-Pacific region and there is a general consensus that such disturbances may have flow-on effects regarding demographic and community-level responses. These include both direct (reductions in abundance and biomass of target species, phenotypic and genotypic changes to populations) and indirect (changes to habitat, trophic cascades, behaviour and function of individuals/species) effects on species and populations (DeMartini and Smith 2015). Addressing such questions related to the scales introduced above (from regional single-species population biology to community ecology across broad spatial scales) necessitates a community of study organisms possessing the requisite biological characteristics ideally suited for an array of sampling techniques. For this reason, I focus on parrotfishes (Labridae; Scarinae) throughout this thesis.

Across the Indo-Pacific, parrotfishes, or scarine labrids, are represented by a comparably large number of species that often co-occur in high abundance within the same habitat. Collectively, they encompass a broad range of body sizes and life spans (Choat and Robertson 2002), and are sexually dimorphic female-to-males sex changers (dimorphic both in body size and, for many species, colouration, the latter of which allows rapid and non-invasive sex determination *in situ*). Because of their often vibrant body colouration and foraging behaviour, parrotfishes are highly conspicuous members of the reef fauna, thus facilitating accurate surveys of abundance using standard visual survey techniques (Watson et al. 2010). Like other labrids, scarines show evidence of high plasticity in demographic traits across space (Gust 2004, Gust et al. 2002). Further, perhaps no group of marine fishes carries stronger implications than parrotfishes regarding their effect on benthic biota through feeding processes (Carpenter 1986, Choat 1991, Mumby et al. 2006). They are considered to be important elements of the global coral reef ecosystem as they have the capacity to modify the benthic biota of coral reefs either by scraping surfaces or excavating calcareous structure, thus contributing to bioerosion (Bellwood and Choat 1990). A final and key feature of parrotfishes is that they are harvested circumtropically in subsistence and commercial fisheries. Within the Indo-Pacific, parrotfishes consistently represent a substantial portion of the reef-associated harvest, whereby a majority of the catch is selectively targeted by spearfishers at night (Dalzell et al. 1996).

Assessment of the capacity of parrotfishes to respond to both anthropogenic disturbance and natural variation is no simple task. Despite their morphological similarity they are a phylogenetically complex group showing high levels of evolutionarily recent diversification (Robertson et al. 2006; Smith et al. 2008; Alfaro et al. 2009; Choat et al. 2012). There is also evidence of substantial clade-specific demographic variation (Choat and Robertson 2002). The two major groups of parrotfishes (Sparisomatinine and Scarinine) support a number of abundant and very widespread species, especially in the Indo-Pacific, that occupy a wide variety of shallow water habitats and reef systems. At present, a disproportionate amount of the demographic data on Indo-Pacific parrotfishes has been obtained from reefs associated with continental and high-island margins of the western Pacific (primarily the Great Barrier Reef [GBR]; Choat et al. 1996; Choat and Robertson 2002). It is unclear whether parrotfishes from the more isolated atolls and islands of the central Pacific have similar demographic profiles as evidence to date suggests that taxa from the GBR may show substantially greater life spans than conspecifics from isolated oceanic islands (Trip et al. 2008). Finally, although parrotfishes are harvested over most of their geographical range, the methods and intensity of fishing vary widely both within and between ocean basins.

Aims and thesis structure

This thesis represents a multi-scale mensurative experiment with a primary aim to investigate the role of environmental and anthropogenic drivers of variation in the demography and community ecology of parrotfishes. Specific topics range from regional population biology to broad-scale community patterns, providing a comprehensive and holistic examination of demographic patterns and processes for a common and highly exploited group of coral reef fishes. The studies herein take place in Micronesia where parrotfishes constitute a large portion of the reef associated fishery harvest (Houk et al. 2012). Micronesia (spanning from approximately 5° to 20°N latitude in the western Pacific Ocean) is comprised entirely of small oceanic islands in a generally oligotrophic region of the Indo-Pacific. Island types vary from small coral islands to atolls to complex barrier reef systems characterized by extensive lagoonal, back reef, and reef flat habitat between the landmass and outer reef. Further, this region supports a diverse assemblage of parrotfishes including representatives of the major phyletic groupings (Myers 1999).

In **Chapter 2**, I examine the inter-specific variation in life history traits among species comprising a parrotfish community. This chapter represents the most comprehensive synthesis of life-history variation within any phylogenetically-related group of coral reef fishes to date. Twelve species from five genera were collected using fishery-independent sampling at the islands of Guam and Pohnpei, Micronesia, and growth patterns, life span, mortality rates and timing of maturation and sex change were quantified. Species were then grouped using multivariate analysis based on trait values.

Chapter 3 extends directly from the previous chapter, where I combine both fishery-dependent and independent data to examine the predictive capacity of life-history traits (derived in Chapter 2) on the vulnerability to overexploitation in parrotfishes. Most previous studies qualify fishery vulnerability through inferred processes, whereby life histories of targeted species are inferred from body size and vulnerability is subsequently inferred from life history, with the assumption of an absolute relationship between life history and vulnerability. Ecological dynamics are much more complex than this. Hence, I quantify vulnerability to overexploitation for each of twelve species from Guam based on independent response variables from spatial (biomass patterns across a gradient of fishing pressure) and temporal (mean harvested length across twenty-year catch records) datasets. These values are then used to assess the capacity of length- and age-based life history traits to predict vulnerability to overexploitation across species.

In subsequent chapters, the focus switches from inter-specific variation in life history traits to intra-specific variation and assemblage structure across different spatial scales. In **Chapter 4**, I examine variation in timing of sex change for exploited parrotfishes using an innovative approach across a range of environmental, anthropogenic and geographical factors. High-resolution length estimates were derived using stereo-video technology to survey parrotfish assemblages spanning seven islands across Micronesia. Results demonstrated considerable life-history responses to exploitation, but a hierarchical influence of environment at broad spatial scales. Major patterns among parrotfish species were compared.

Finally, **Chapter 5** provides a multi-scale examination of assemblage-level patterns of abundance, biomass, mean length, species richness and phylogenetic diversity across eight islands of Micronesia. The primary aim was to determine the relative contribution and scale-dependence of environmental, anthropogenic and biogeographic factors in structuring parrotfish communities.

Chapter 2: Comparative demography of commercially important parrotfish species from Micronesia

Taylor, B. M., Choat, J. H. (2014) Comparative demography of commercially important parrotfish species from Micronesia. *Journal of Fish Biology* 84: 383-402 (doi: 10.1111/jfb.12294)

Introduction

Coral reef fisheries target a diverse assemblage of fishes with a wide range of biological and demographic features. Understanding or predicting the effects of exploitation on species assemblages has been hindered by a lack of information regarding the life histories of many heavily targeted species. Because many life-history variables have units of time (Charnov 1993), the demographic study of marine fishes has been contingent on estimates of age, primarily through analysis of sagittal otoliths, thereby facilitating species-specific estimates of growth, life span, mortality and reproductive variables. In recent decades, age-based studies have identified several demographic processes that are essential in the management of reef fishes (Choat and Robertson 2002, Grandcourt 2002, Heupel et al. 2010, Currey et al. 2013). Yet, there remain gaps in present knowledge, especially in oceanic regions of the Indo-Pacific Ocean where reef-associated fisheries represent a significant source of income and protein for island nations but where infrastructure and funding for such research are limited (Houk et al. 2012).

Parrotfishes (Labridae: tribe Scarinae) are of particular interest in this context as they are regarded as both ecologically and commercially important on coral reefs worldwide. They are among the most diverse and abundant groups found on coral reefs and have the capacity to modify the benthic biota either by scraping surfaces (grazing) or excavating calcareous structure (bioerosion; Bellwood and Choat 1990, Bellwood 1995a,b). Parrotfishes are also increasingly subject to artisanal, subsistence and commercial fisheries of the western Pacific Ocean. They are especially vulnerable to nocturnal fishing and recent data on fisheries suggest that they represent a significant portion of the reef-associated harvest (up to 40% in some localities; Rhodes et al. 2008, Houk et al. 2012). While large-bodied species are often heavily targeted because of their greater commercial value, both small- and large-bodied species can be numerically abundant in the overall harvest (Rhodes et al. 2008).

Parrotfishes have highly plastic growth (Gust et al. 2002) and complex sexual ontogenies (protogynous hermaphroditism; Choat and Robertson 1975) with dual sexual pathways (diandry and monandry; Robertson and Warner 1978), sexual dimorphism (Choat et al. 1996) and complex mating systems (Colin and Bell 1991, Kuwamura et al. 2009). As a group, they encompass a variety of body sizes and can range considerably in maximum lifespan among species (Choat and Robertson 2002). Otolith-based studies from unexploited populations have shown that life histories of conspecific parrotfishes can vary significantly between assemblages at multiple scales, patterns probably driven by biological or external environmental factors (Gust et al. 2002, Gust 2004). A disproportionate amount of the demographic data on Indo-Pacific species, however, has been obtained from unexploited reefs associated with continental margins of the western Pacific [primarily the Great Barrier Reef (GBR)]. Detailed life-history studies from exploited regions are scarce, and given the putative ecological and commercial importance of parrotfishes, it is critical to understand and parameterize basic population processes such as growth, mortality and reproduction.

Body size and lifespan are critical traits in fisheries (Berkeley et al. 2004, Birkeland and Dayton 2005). Larger fishes yield higher monetary value for fishers and are consequently more desirable, but large body size and long life span are traits presumed to predispose populations to increased vulnerability to overexploitation (Adams 1980). Therefore, there has been considerable interest in the relationship between body size and life span across species (Choat and Robertson 2002). Demographic studies on tropical marine fishes demonstrate variable phylogenetic patterns of length-age relationships, which are dependent on taxonomic level and biogeographic region. For example, maximum length and age were poorly correlated for tropical surgeonfishes (Acanthuridae) across five genera and two ocean basins whereas the relationship among parrotfishes (six genera) was strong (Choat and Robertson 2002). Body size and age alone, however, provide an abbreviated picture of life history. Jennings et al. (1998) determined that a suite of life history characteristics best predicted vulnerability across exploited species. In particular, age at maturity has emerged as an important trait for predicting fishery vulnerability (Jennings et al. 1998) and for monitoring responses to fishing over time (Trippel 1995, Jennings et al. 1999a). Hence, the paucity of age-based demographic information for many exploited taxa remains an impediment both to regional fisheries management and to life-history theory.

This study used fishery-independent sampling to determine life-history traits (growth, maturation, sex change, maximum length, life span and mortality) in 12 common and heavily targeted parrotfish species from Guam and Pohnpei, Micronesia. These species encompass a wide range of body sizes and are targeted primarily by spearfishers, including commercial night-time scuba spearfishing in Guam. They represent *c.* 98 and 63% of the parrotfish biomass on outer reefs of Guam and Pohnpei

(B. Taylor, unpublished data). These data are used to address two major objectives: (1) determine whether consistent relationships exist among life-history variables, particularly between maximum length and life span, across related species comprising five genera and (2) quantitatively establish species groups based on interspecific variation in life-history characteristics and determine the drivers of significant groupings. Finally, these data and species groupings facilitate the opportunity for future studies to empirically test the vulnerability of the species studied to overexploitation against historical fishery trends.

Methods

Collection of specimens

The 12 parrotfish species were collected at the islands of Guam (unincorporated U. S. territory; 13°27’N 144°46’E) and Pohnpei (Federated States of Micronesia; 6°53’N 158°13’E) in 2011 and 2012. These species include the stareye parrotfish *Calotomus carolinus* (Valenciennes 1840), bicolour parrotfish *Cetoscarus bicolor* (Rüppell 1829), tan-faced parrotfish *Chlorurus frontalis* (Valenciennes 1840), Pacific steephead parrotfish *Chlorurus microrhinos* (Bleeker 1854), bullethead parrotfish *Chlorurus spilurus* (Valenciennes 1840), Pacific longnose parrotfish *Hipposcarus longiceps* (Valenciennes 1840), filament-fin parrotfish *Scarus altipinnis* (Steindachner 1879), rainbow parrotfish *Scarus forsteni* (Bleeker 1861), blue-barred parrotfish *Scarus ghobban* Forsskål 1775, palenose parrotfish *Scarus psittacus* Forsskål 1775, redlip parrotfish *Scarus rubroviolaceus* Bleeker 1849 and yellowband parrotfish *Scarus schlegeli* (Bleeker 1861). All samples of *C. bicolor*, *H. longiceps*, and *S. ghobban* were obtained from Pohnpei while the remaining species were sampled from Guam. Collections were designed to obtain an adequate and representative sample of each species examined for derivation of life-history variables. Hence, sampling was done primarily (84% of samples) using spearguns and hand-spears while free-diving and individual fish were collected without preference for body size or colour phase. Additional samples were obtained using two methods. First, samples were purchased either directly from fisherman (4%) or from fish markets (11%). Second, specimens illegally poached from marine protected areas were donated by the Guam Division of Aquatic and Wildlife Resources (1%).

All fish were placed in ice and processed immediately upon returning to the laboratory. Fork length (*FL*; nearest mm) and mass (*M*; nearest g) were recorded for each specimen. Gonad mass was measured to the nearest 0.001 g and gonads were preserved in a buffered formalin solution (formaldehyde 4%, acetic acid 5%, and calcium chloride 1.3%). Sex and female maturity stages (immature, mature active and mature resting) were determined macroscopically as described by West (1990) and initial and terminal body colour phase was noted. Sagittal otoliths were removed, cleaned in ethanol and stored dry.

Age determination

Individual ages were estimated by counting opaque growth zones on transverse sections of sagittal otoliths (Fig. 2.1). Otolith processing procedures were performed as described by Taylor and McIlwain (2010). Blind reads of opaque growth zones were performed on three separate occasions for each specimen. Final age was determined when two or more counts agreed. If agreement was not achieved after three counts, the sample was excluded from the analysis. Final age was interpreted in whole years, as backcalculation of settlement dates based on annual spawning periods was not possible because most species spawn (and consequently recruit) throughout the year (B. Taylor, personal observation). For individuals <1 year, otolith sections were ground with lapping film, polished by hand with alumina powder and viewed through a compound microscope. Age was estimated by counting daily rings on three independent occasions as performed earlier, and final age was taken as the mean of three counts when counts were within 10% of the median. Samples with counts >10% of the median were excluded from the analysis.

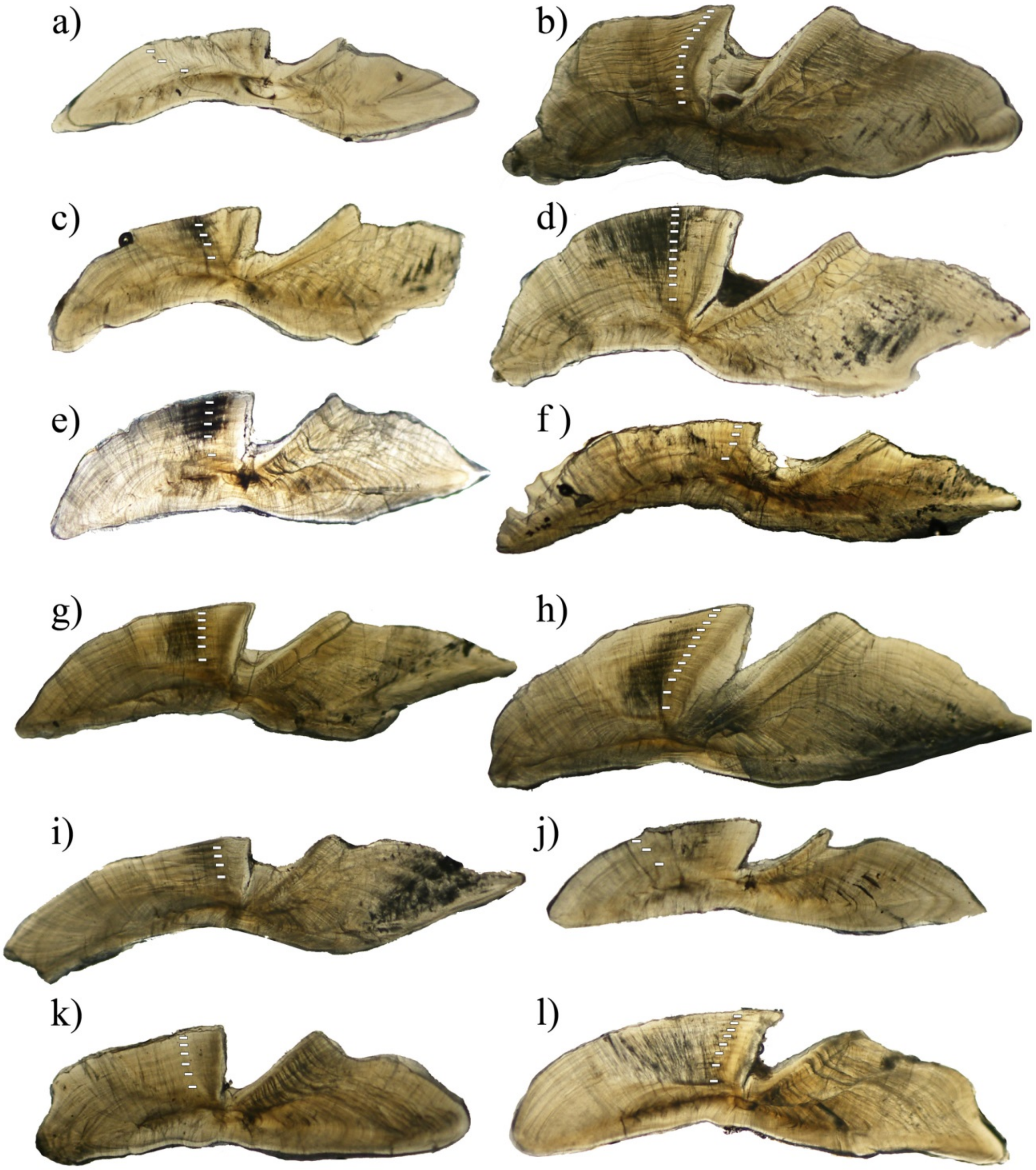

Figure 2.1. Transverse sections of sagittal otoliths displaying annual increments: (a) *Calotomus carolinus*, (b) *Cetoscarus bicolor*, (c) *Chlorurus frontalis*, (d) *Chlorurus microrhinos*, (e) *Chlorurus spilurus*, (f) *Hipposcarus longiceps*, (g) *Scarus altipinnis*, (h) *Scarus forsteni*, (i) *Scarus ghobban*, (j) *Scarus psittacus*, (k) *Scarus rubroviolaceus*, (l) *Scarus schlegeli*. Images are not to one scale.

Transverse sections of sagittal otoliths for all species consistently displayed alternating opaque and translucent zones and structural properties that strongly reflect those of validated samples from other localities at the family, genus or species level. Banding patterns and otolith structure were visibly similar among all species, with more pronounced similarities within each genus (*Scarus*, *Chlorurus*, *Calotomus* and *Cetoscarus*; *Hipposcarus* most resembles *Scarus*) (Fig. 2.1). Validation of the annual periodicity of deposited increments has been achieved previously for *C. spilurus* (as *C. sordidus*; Choat et al. 1996) and *S. schlegeli* (Lou 1992) on the GBR. Because of time and effort constraints, such validation was not performed in this study. In reviewing the necessity of this process, Choat et al. (2009) conceded that while incremental bands in tropical otoliths can be difficult to detect (Fowler 1995), virtually no evidence exists for increment formation that is not annual.

Growth and mortality

Patterns of growth were modelled using the reparameterized von Bertalanffy growth function (rVBGF) (Francis 1988). The rVBGF contains three parameters, L_τ, L_ω and L_μ, that represent mean length at arbitrary ages τ, ω and μ. Trip et al. (2008) provided a compelling rationale for using rVBGF, especially for sex-specific, regional and interspecies comparisons of growth parameters, because τ, ω and μ can be set to biologically meaningful ages. The rVBGF is represented by $L_t = L_\tau + \left(L_\mu - L_\tau\right)[1 - r(2)(t - \tau)\left(\mu - \tau\right)^{-1}](1 - r^2)^{-1}$, where $r = (L_\mu - L_\omega)(L_\omega - L_\tau)^{-1}$. For 11 species, τ, ω and μ were represented by ages 1, 3 and 5 years, because the majority of growth (82 – 100%; mean = 96.3%) occurs by age 5 years. For *C. carolinus*, τ, ω and μ were represented by ages 1, 2 and 3 years because the maximum age for this species did not exceed 3 years. The model was fitted for each species (males, females and combined) by minimizing the negative log-likelihood under the assumption that length at age t (L_t) is normally distributed with a mean of L_t and standard deviation σ. Curves were fitted by constraining the y-intercept to a common length at settlement taken as L_0 = 15 mm *FL* (based on Bellwood and Choat 1989), to improve precision of parameter estimates (Kritzer et al. 2001).

Growth was also presented using the standard and more common VBGF. The VBGF and rVBGF equations describe the same curve but with different parameter values. The VBGF is represented by $L_t = L_\infty[1 - e^{-K(t - t_0)}]$, where L_t is the *FL* (mm) of a fish at age t (years), L_∞ is the mean asymptotic *FL*, K is a coefficient describing the curvature of growth towards L_∞ and t_0 is the hypothetical age when *FL* = 0.

Length-at-age data were subject to random resampling with replacement and analyzed to produce 1000 bootstrap estimates of growth parameters from the rVBGF and VBGF, and 95% confidence intervals for parameters were taken as the 2.5 and 97.5 percentiles of the predicted values (Haddon 2001). Differences in length-at-age among species were presented using 95% confidence ellipses surrounding estimates of parameters L_1 and L_5. Confidence ellipses were generated using the function *dataEllipse* of the *car* package in the R statistical computing language (Fox and Weisberg 2011).

Estimates of total mortality (*Z*) were obtained for 11 of the 12 species using age-based catch curves (Beverton and Holt 1957), where the natural logarithm of the frequency of samples per age class was plotted against age and *Z* equalled the absolute value of the slope from a curve fitted to the descending values. Species were considered fully recruited to the sampling regime at the modal (peak frequency) age and frequency values of zero were excluded from the analysis. For *C. carolinus*, the age range was not large enough to estimate mortality using catch curves (only two age classes fully recruited to the sampling). Maximum age was considered the age of the oldest individual sampled for each species. Because samples came from exploited populations, however, variable truncation of maximum ages among species may cause the perceived maximum age to be poorly suited for comparative life span estimates. Hence, mean maximum age ($T_{\max}$) and mean maximum length ($L_{\max}$) were calculated as the mean age and length of the oldest and largest 25% of the sample for each species following Choat and Robertson (2002). Comparisons of maximum age and length parameters were made graphically among species using bivariate 95% confidence ellipses surrounding bootstrapped estimates of $T_{\max}$ and $L_{\max}$ as earlier and the relationship between these parameters across species was tested using regression analysis.

Reproduction

A sub-sample of gonads for each species was selected to validate macroscopic staging through histology. Here, classification of ovary stages followed criteria from West (1990). Preference for selection was given to ovaries that were difficult to stage macroscopically (e.g. mature resting individuals can appear very similar to late-stage immature and *vice versa*; Burchard et al. 2013). Gonads were not sampled for all *S. ghobban*, and due to the low remaining sample size, maturation parameters were not estimated. Ultimately, individuals were classified as male, female, or transitional (when degenerative vitellogenic ovaries were present with proliferating testis); females were classified as immature, mature active or mature resting; and males were identified as primary or secondary based on body colour phase and histological features of the testes, as described in Sadovy and Shapiro (1987).

The *FL* at 50% female sexual maturity (L_{50}) for each species examined was estimated by plotting the proportional frequency of mature active and mature resting females in size class bins for all female samples. The proportional frequencies were fitted with a logistic curve as follows: $P = \{1 + \mathrm{e}^{[-\ln(19)(L - L_{50})(L_{95} - L_{50})^{-1}]}\}^{-1}$, where P is the estimated proportion of mature females at a given length (L) and L_{50} and L_{95} are the *FL* at 50 and 95% maturity, respectively. Curves for each species were fitted using logistic regression analysis and the corresponding 95% confidence limits for each parameter were derived by bootstrap resampling as mentioned earlier (1000 iterations). The same procedure and equation form were used to determine age at 50% female maturity (t_{50}) and the *FL* at 50% sex change (X_{50}) with their associated 95% confidence limits. For sex change analyses, initial phase primary males were excluded as these males had undergone no physical metamorphosis. Further, age at sex change is not presented because not all females change sex during their life. Female maturation and sex change were examined relative to maximum size and life span by dividing L_{50} and X_{50} estimates by the respective L_{max} for each species and t_{50} values by T_{max} estimates.

Life-history analysis

A matrix (12 species, seven traits) was constructed of the following life-history variables from all species: mean maximum length (L_{max}), mean maximum age (T_{max}), total mortality rate (Z), length at 50% female maturity (L_{50}), age at 50% female maturity (t_{50}), length at 50% sex change (X_{50}) and growth in length from age 1 to age 3 years [L_{1-3} (rVBGF)]. The variable L_{1-3} captures the majority of remaining lifetime growth after the initial year (when all species grow rapidly) and is used here in place of the VBGF growth coefficient K because of concerns regarding the statistical utility of the K coefficient (Cerrato 1991). The relationships among parameters across species were examined using Pearson correlation coefficients corrected for multiple comparisons. Clustering analysis was used to explore relationships among species based on life-history traits. This was performed on a Bray-Curtis similarity matrix, which measured associations between samples using standardized [100 (variable) (sum of variables)$^{-1}$] life-history variables. Missing variables (Z for *C. carolinus*, L_{50} and t_{50} for *S. ghobban*) were predicted from best-fit relationships using stepwise multiple linear regression prior to the analysis. A linkage tree analysis was conducted on the similarity matrix and the similarity profile routine was simultaneously used to identify significant groupings at the $P = 0.05$ level (Clarke et al. 2008). This analysis was performed using the LINKTREE and SIMPROF functions (9999 permutations) in the PRIMER *v.* 6 software (www.primer-e.com).

Results

Age and growth analysis

Table 2.1 summarizes the sample sizes as well as the length and age ranges for each species. Length-at-age plots revealed highly variable growth profiles among species and sex-specific growth patterns within species, with males consistently reaching a larger asymptotic length (Fig. 2.2). Values of the VBGF coefficient K (sexes combined) ranged from 0.34 year^{-1} in *C. microrhinos* to 1.41 year^{-1} in *S. ghobban* (Table 2.2). Values of L_∞ ranged from 207 mm FL in *S. psittacus* to 457 mm FL in *C. microrhinos* (Table 2.2). Four species (*C. carolinus, C. microrhinos, H. longiceps* and *S. rubroviolaceus*) appeared to display continuous growth without demonstrating a strong asymptote in length-at-age by the final age class. The remaining eight species showed mild to strong determinate growth profiles in which length-at-age plots reached an asymptote with increasing age. Decreased life span resulting from high fishing pressure, however, may have masked determinate growth patterns in species considered continuous.

Table 2.1. Summary of sex-specific sample size, length and age distribution and rVBGF parameters for 12 parrotfish species from Micronesia.

Species	Sex	n	Min-max FL (mm)	Min age – t_{max} (yrs)	L_1	L_3	L_5
	Females	15	140-222	1 - 3	170	213	-
Calotomus carolinus	*Males*	19	193-287	2 - 3	156	258	-
	Total	34	140-287	1 - 3	163	247	-
	Females	33	182-428	2 - 8	185	326	368
Cetoscarus bicolor	*Males*	14	320-433	2 - 12	227	368	398
	Total	47	182-433	2 - 12	187	336	382
	Females	46	162-417	1 - 11	196	317	342
Chlorurus frontalis	*Males*	37	209-465	1 - 9	190	341	387
	Total	83	162-465	1 - 11	196	329	362
	Females	64	148-436	1 - 11	151	294	351
Chlorurus microrhinos	*Males*	16	310-501	3 - 8	158	326	407
	Total	80	148-501	1 - 11	144	300	378
	Females	211	36-231	0 - 9	138	193	199
Chlorurus spilurus	*Males*	136	173-265	2 - 8	151	223	233
	Total	347	36-265	0 - 9	139	206	216
	Females	42	224-389	1 - 5	223	318	330
Hipposcarus longiceps	*Males*	22	256-430	1 - 6	184	338	389
	Total	64	224-430	1 - 6	204	331	358
	Females	33	105-397	0 - 14	176	282	304
Scarus altipinnis	*Males*	20	214-410	1 - 7	171	316	365
	Total	53	105-410	0 - 14	172	294	327
	Females	55	179-298	1 - 12	174	252	262
Scarus forsteni	*Males*	25	239-339	2 - 8	170	279	304
	Total	80	179-339	1 - 12	171	262	278
	Females	20	232-328	1 - 6	243	286	287
Scarus ghobban	*Males*	11	278-366	2 - 5	235	323	332
	Total	31	232-366	1 - 6	237	305	309
	Females	60	92-249	0 - 6	118	176	185
Scarus psittacus	*Males*	54	109-252	2 - 5	192	211	211
	Total	114	92-252	0 - 6	130	195	205
	Females	32	213-371	1 - 5	201	317	340
Scarus rubroviolaceus	*Males*	25	253-435	2 - 6	187	330	372
	Total	57	213-435	1 - 6	189	326	363
	Females	52	96-290	0 - 8	175	220	222
Scarus schlegeli	*Males*	64	166-315	1 - 6	154	248	269
	Total	116	96-315	0 - 8	167	242	251

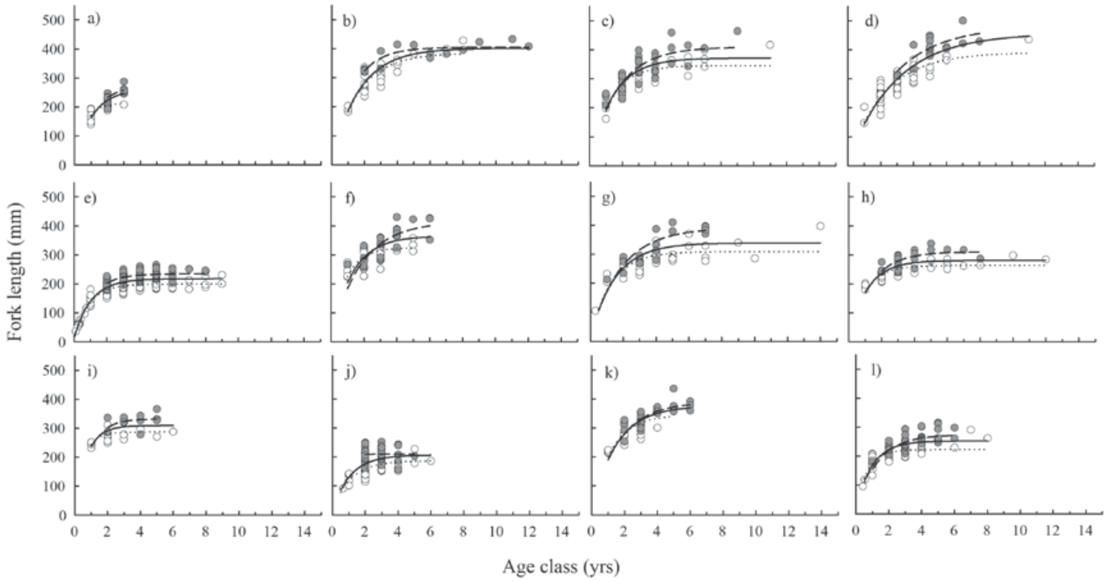

Figure 2.2. Fork length (FL)-at-age plots with best-fit reparameterized von Bertalanffy growth function (rVBGF) curves (○, females; ●, males; …., female growth curves; ---, male growth curves; ___, both sexes combined. All curves have been fitted through a common length at settlement (15 mm FL). (a) *Calotomus carolinus* (n = 34), (b) *Cetoscarus bicolor* (n = 47), (c) *Chlorurus frontalis* (n = 85), (d) *Chlorurus microrhinos* (n = 80), (e) *Chlorurus spilurus* (n = 347), (f) *Hipposcarus longiceps* (n = 65), (g) *Scarus altipinnis* (n = 53), (h) *Scarus forsteni* (n = 80), (i) *Scarus ghobban* (n = 31), (j) *Scarus psittacus* (n = 96), (k) *Scarus rubroviolaceus* (n = 55), (l) *Scarus schlegeli* (n = 116).

Table 2.2. Summary of life-history variables and their associated 95% confidence limits (below in parentheses, where appropriate) for 12 parrotfish species from Micronesia.

	Cc	*Cb*	*Cf*	*Cm*	*Cs*	*Hl*	*Sa*	*Sf*	*Sg*	*Sp*	*Sr*	*Ss*
L_∞ (mm *FL*)	263	402	372	457	218	366	339	281	310	207	376	252
	(238-302)	(376-431)	(350-397)	(419-504)	(214-223)	(337-401)	(314-370)	(269-294)	(292-329)	(190-232)	(351-407)	(240-267)
K (yr^{-1})	0.91	0.59	0.71	0.34	0.95	0.76	0.66	0.88	1.41	0.91	0.66	1.03
	(0.64-1.29)	(0.49-0.72)	(0.59-0.86)	(0.29-0.42)	(0.87-1.03)	(0.58-1.08)	(0.49-0.94)	(0.74-1.08)	(1.04-2.07)	(0.63-1.38)	(0.53-0.84)	(0.86-1.25)
t_0 (yr)	-0.065	-0.065	-0.058	-0.097	-0.075	-0.055	-0.069	-0.062	-0.035	-0.083	-0.062	-0.06
Z (yr^{-1})	-	0.27	0.38	0.43	0.59	0.71	0.25	0.34	0.50	1.03	0.63	0.81
		(0.18-0.36)	(0.31-0.46)	(0.31-0.55)	(0.48-0.70)	(0.50-0.91)	(0.12-0.39)	(0.21-0.48)	(0.27-0.73)	(0.83-1.23)	(0.54-0.72)	(0.67-0.96)
L_{50} (mm *FL*)	168	323	240	308	144	317	251	216	-	103	271	197
	(155-187)	(309-355)	(232-266)	(293-339)	(137-159)	(301-350)	(239-273)	(211-239)		(92-118)	(257-276)	(187-217)
t_{50} (yr)	1.14	3.05	1.55	3.70	1.30	3.12	2.89	1.79	-	1.36	1.91	1.99
	(1.03-1.27)	(2.79-3.51)	(1.40-1.76)	(3.32-4.44)	(1.18-1.46)	(2.86-3.40)	(2.67-3.03)	(1.70-2.08)		(1.22-1.51)	(1.76-2.00)	(1.79-2.19)
X_{50} (mm *FL*)	213	375	343	378	207	364	337	271	314	193	329	220
	(196-239)	(362-413)	(320-378)	(365-418)	(202-229)	(347-407)	(319-378)	(260-298)	(300-345)	(185-231)	(319-362)	(209-264)
T_{max} (yr)	3.0	7.3	5.9	5.9	5.4	4.6	7.8	6.5	4.8	3.8	4.8	4.6
	(2.5-3.2)	(4.8-9.7)	(4.7-7.1)	(4.7-6.8)	(4.9-5.8)	(3.9-5.2)	(5.7-9.5)	(5.0-7.8)	(3.7-5.6)	(3.3-4.2)	(4.0-5.5)	(3.9-5.2)

Plots of bivariate confidence ellipses surrounding the L_1 and L_5 estimates for each species demonstrate the diversity of growth profiles of Micronesian parrotfishes (Fig. 2.3a). A positive linear trend emerges across species ($r^2 = 0.279$, $F_{1,11} = 3.871$, $P = 0.078$) whereas *C. microrhinos* (slow initial growth but continues to a large size at year 5) and *S. ghobban* (rapid growth in first year but only moderate size by year 5) stand apart (Fig. 2.3a; $r^2 = 0.844$, $F_{1,9} = 43.160$, $P < 0.001$ with *C. microrhinos* and *S. ghobban* removed from the analysis). Values of L_{max} and T_{max} varied widely across species from 226 to 409 mm *FL* and 3 to 8 years, respectively (Fig. 2.3b). There was a positive, yet insignificant, relationship between these variables across species ($r^2 = 0.325$, $F_{1,10} = 4.817$, $P = 0.053$). Maximum ages ranged from 3 years in *C. carolinus* to 14 years in *S. altipinnis* (Table 2.1). Catch curves estimated values of Z ranging from 0.25 year^{-1} in *S. altipinnis* to 1.03 year^{-1} in *S. psittacus* (Fig. 2.4).

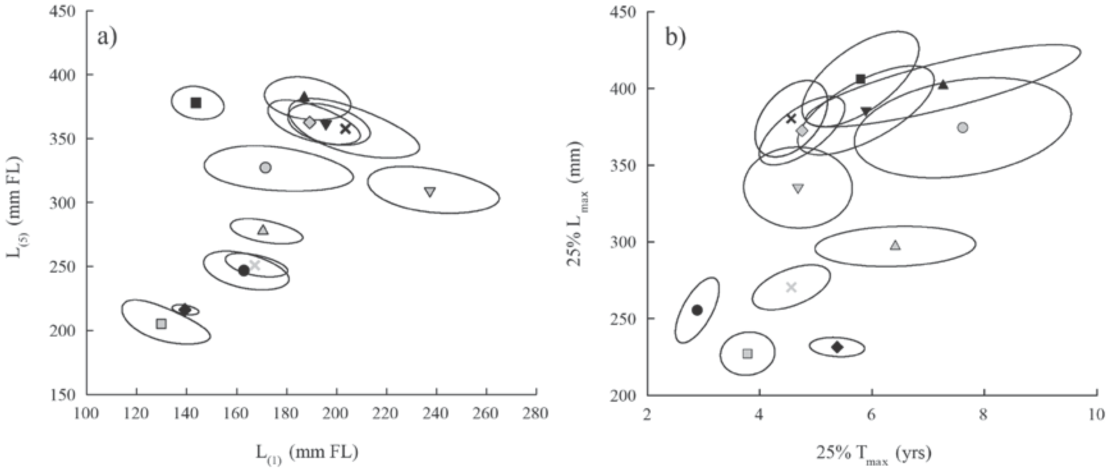

Figure 2.3. Graphical comparison of (a) reparameterized von Bertalanffy growth function (rVBGF) coefficients (based on fork length, FL) and (b) mean maximum length and mean maximum age coefficients for 12 parrotfish species using bivariate 95% confidence ellipses surrounding variable estimates. Because *Calotomus carolinus* maximum age was 3 years, L_3 was used in place of L_5 for this species. (a) *Calotomus carolinus* (●), (b) *Cetoscarus bicolor* (▲), (c) *Chlorurus frontalis* (▼), (d) *Chlorurus microrhinos* (■), (e) *Chlorurus spilurus* (♦), (f) *Hipposcarus longiceps* (×), (g) *Scarus altipinnis* (●), (h) *Scarus forsteni* (▲), (i) *Scarus ghobban* (▼), (j) *Scarus psittacus* (■), (k) *Scarus rubroviolaceus* (♦), (l) *Scarus schlegeli* (×).

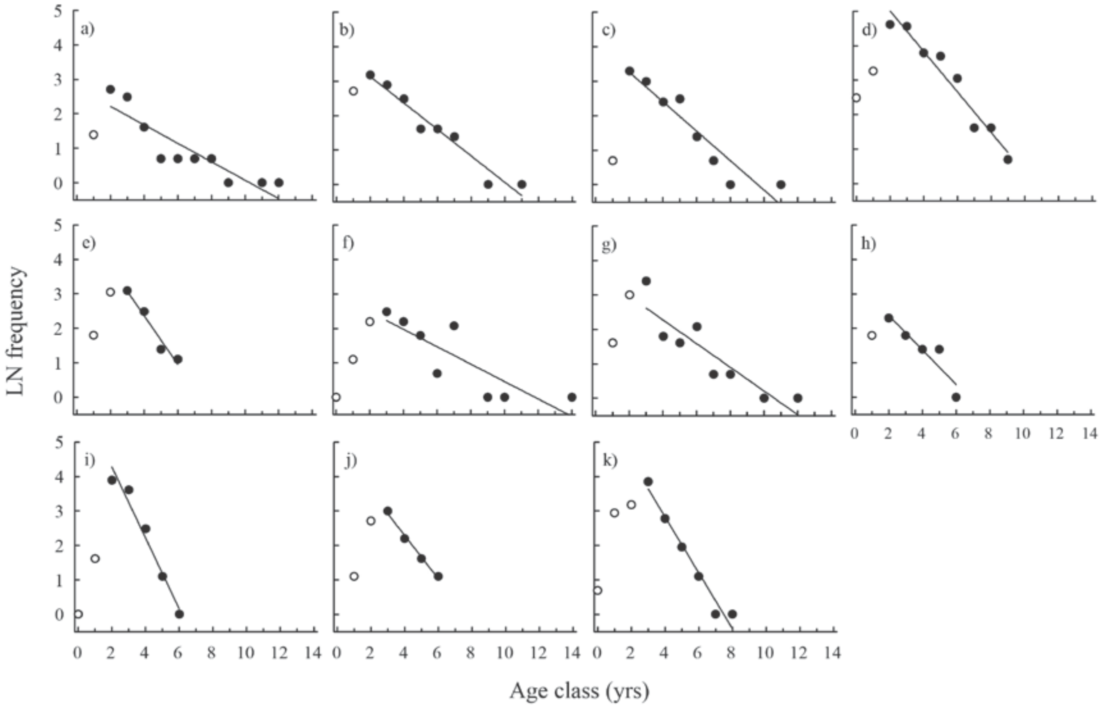

Figure 2.4. Age-based catch curves for eleven parrotfish species. Only filled points (those fully recruited to sampling gear) are included in regressions. a) *Cetoscarus bicolor* (*Z* = 0.27 yr^{-1}, r^2 = 0.81), b) *Chlorurus frontalis* (*Z* = 0.38 yr^{-1}, r^2 = 0.95), c) *Chlorurus microrhinos* (*Z* = 0.43 yr^{-1}, r^2 = 0.89), d) *Chlorurus spilurus* (*Z* = 0.59 yr^{-1}, r^2 = 0.95), e) *Hipposcarus longiceps* (*Z* = 0.71 yr^{-1}, r^2 = 0.96), f) *Scarus altipinnis* (*Z* = 0.25 yr^{-1}, r^2 = 0.70), g) *Scarus forsteni* (*Z* = 0.34 yr^{-1}, r^2 = 0.81), h) *Scarus ghobban* (*Z* = 0.50 yr^{-1}, r^2 = 0.86), i) *Scarus psittacus* (*Z* = 1.03 yr^{-1}, r^2 = 0.97), j) *Scarus rubroviolaceus* (*Z* = 0.63 yr^{-1}, r^2 = 0.99), k) *Scarus schlegeli* (*Z* = 0.81 yr^{-1}, r^2 = 0.97).

Reproductive biology

Female maturation schedules varied considerably (Fig. 2.5), with estimated L_{50} (FL) values ranging from 103 mm in *S. psittacus* to 323 mm in *C. bicolor* (Table 2.2). Age at maturity values (t_{50}) were equally variable and ranged from 1.1 years in *C. carolinus* to 3.7 years in *C. microrhinos* (Table 2.2). Overall, X_{50} estimates ranged from <200 mm in *S. psittacus* to nearly 400 mm FL in *C. microrhinos* and *C. bicolor* (Fig. 2.6, Table 2.2). These data indicate that Micronesian parrotfishes reach maturity from 62 to 83% of their L_{max}, with *S. psittacus* lying well outside the norm at 45% (overall mean = 69%), and from 24 to 43% of their T_{max}, with *C. microrhinos* and *H. longiceps* as outliers at 63 and 68% (overall mean = 41%). Sex change occurred from 82 to 95% of the L_{max} (mean = 89%).

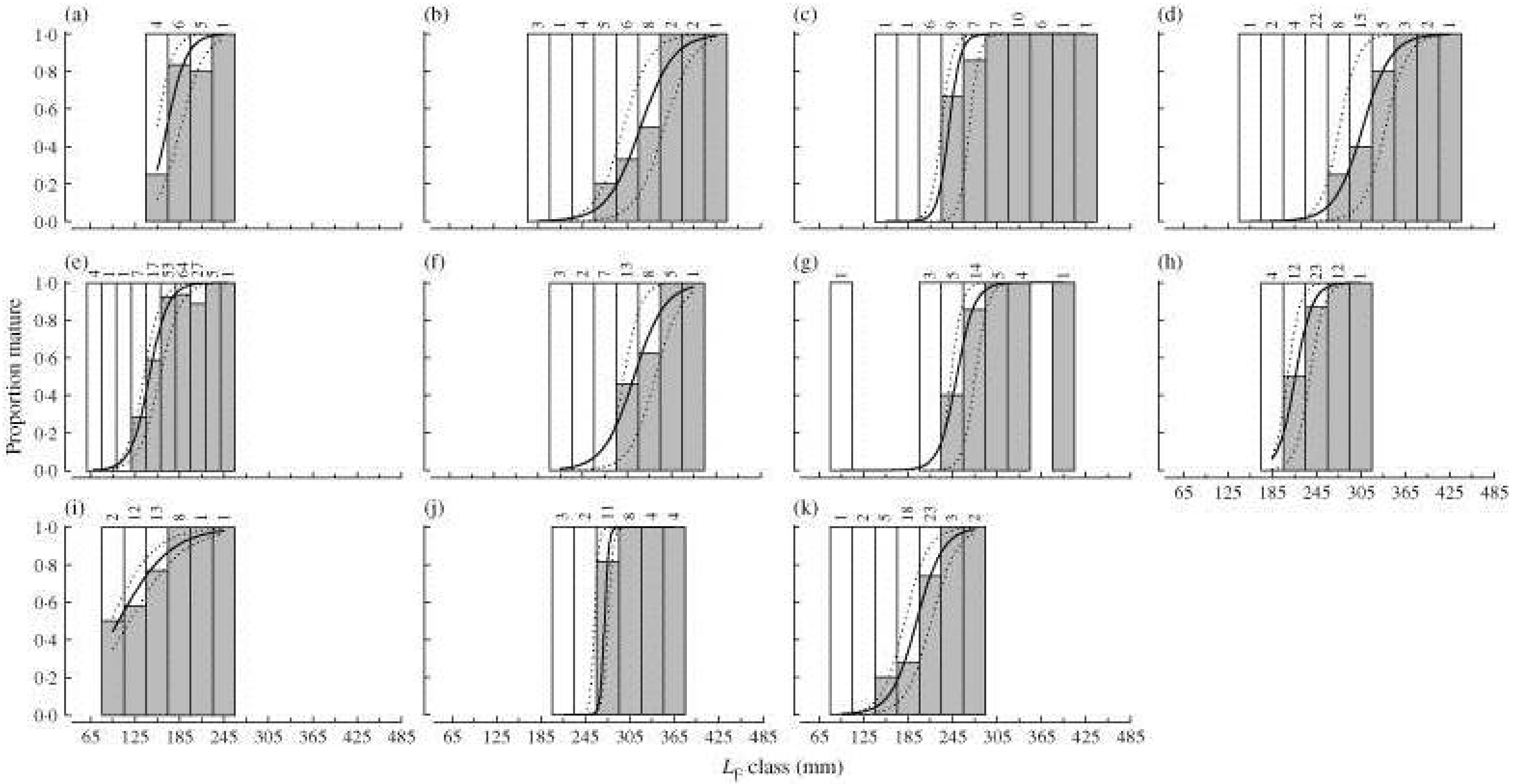

Figure 2.5. Proportional frequencies of immature (white bars) and mature (grey bars) females by size class for twelve parrotfish species. Logistic curves of estimated maturity schedules (solid lines) and associated 95% confidence limits (dotted lines) were derived from logistic regression analysis. a) *Calotomus carolinus*, b) *Cetoscarus bicolor*, c) *Chlorurus frontalis*, d) *Chlorurus microrhinos*, e) *Chlorurus spilurus*, f) *Hipposcarus longiceps*, g) *Scarus altipinnis*, h) *Scarus forsteni*, i) *Scarus psittacus*, j) *Scarus rubroviolaceus*, k) *Scarus schlegeli*.

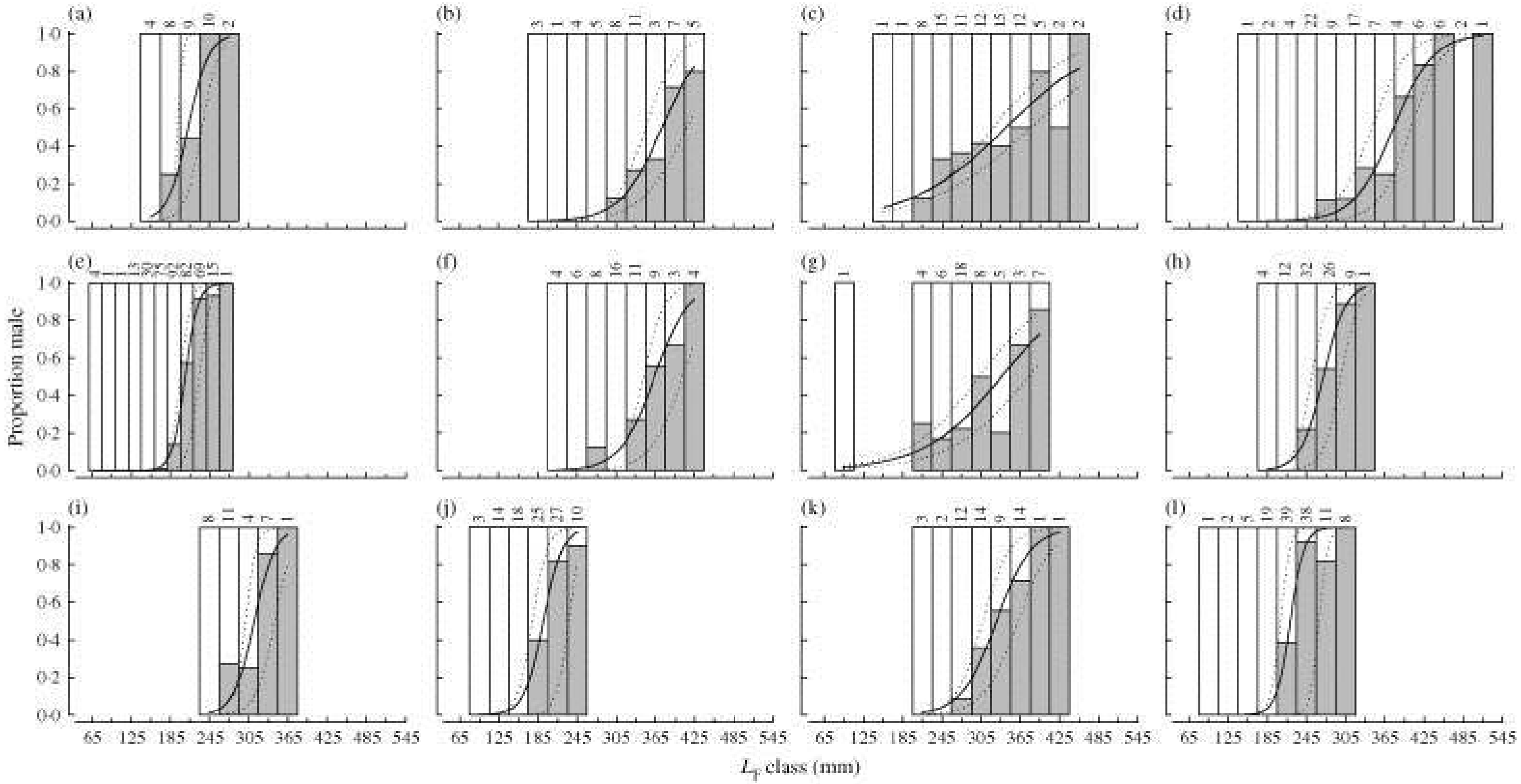

Figure 2.6. Proportional frequencies of females (white bars) and terminal males (grey bars) by size class for twelve parrotfish species. Logistic curves of estimated sex change schedules (solid lines) and associated 95% confidence limits (dotted lines) were derived from least squares regression analysis. a) *Calotomus carolinus*, b) *Cetoscarus bicolor*, c) *Chlorurus frontalis*, d) *Chlorurus microrhinos*, e) *Chlorurus spilurus*, f) *Hipposcarus longiceps*, g) *Scarus altipinnis*, h) *Scarus forsteni*, i) *Scarus ghobban*, j) *Scarus psittacus*, k) *Scarus rubroviolaceus*, l) *Scarus*

Life-history analysis

There was a high level of correlation among life-history traits across species (Table 2.3). Only two of the 21 correlations were not significant at the $P < 0.10$ level whereas 13 were significant at the $P < 0.05$ level (Table 2.3). In particular, $L_{\max}$ was highly correlated with the growth rate proxy $L_{1\text{-}3}$ and maturity and sex change parameters L_{50} and X_{50}. Age-based variables $T_{\max}$ and total mortality (Z) were also highly correlated, as were length-based parameters L_{50} and X_{50}. Conversely, $T_{\max}$ was poorly correlated with all maturity, sex change and maximum size variables.

The cluster analysis and similarity profile routine identified three significant species groupings at two major hierarchical levels based on similarity of life-history traits (Fig. 2.7). The first split was driven by length-based variables ($L_{\max}$, L_{50}, X_{50}; $\pi = 4.1$, $P < 0.001$) as smaller-bodied species *C. carolinus*, *C. spilurus*, *S. psittacus* and *S. schlegeli* separated from the remaining species. At the lower hierarchical level, groupings were driven by differences in age-based variables. Higher $T_{\max}$ and lower Z values for *S. schlegeli* and *C. spilurus* versus *C. carolinus* and *S. psittacus* (Table 2.2) drove the significant grouping among smaller-bodied species ($\pi = 1.1$, $P = 0.022$). Among the larger-bodied species, a significant split ($\pi = 1.7$, $P < 0.001$) was driven by one variable, age at maturity (t_{50}), in which *C. bicolor*, *C. microrhinos*, *H. longiceps* and *S. altipinnis* ranged from 2.9 to 3.7 years versus 1.4 to 1.9 years for *C. frontalis*, *S. forsteni*, *S. ghobban* and *S. rubroviolaceus*.

Table 2.3. Pearson correlation coefficients between life-history traits for Micronesian parrotfishes. Significance levels α = 0.10*, α = 0.05**. Non-significant relationships presented in grey.

	L_{50}	t_{50}	X_{50}	Z	*Longevity*	L_{max}	L_3 - L_1
L_{50}	-	0.84**	0.95**	0.57*	0.52	0.94**	0.92**
t_{50}		-	0.81**	0.41	0.53*	0.78**	0.75**
X_{50}			-	0.64**	0.58*	0.99**	0.88**
Z				-	0.91**	0.63**	0.54*
Longevity					-	0.57*	0.52*
L_{max}						-	0.91**
L_3 - L_1							-

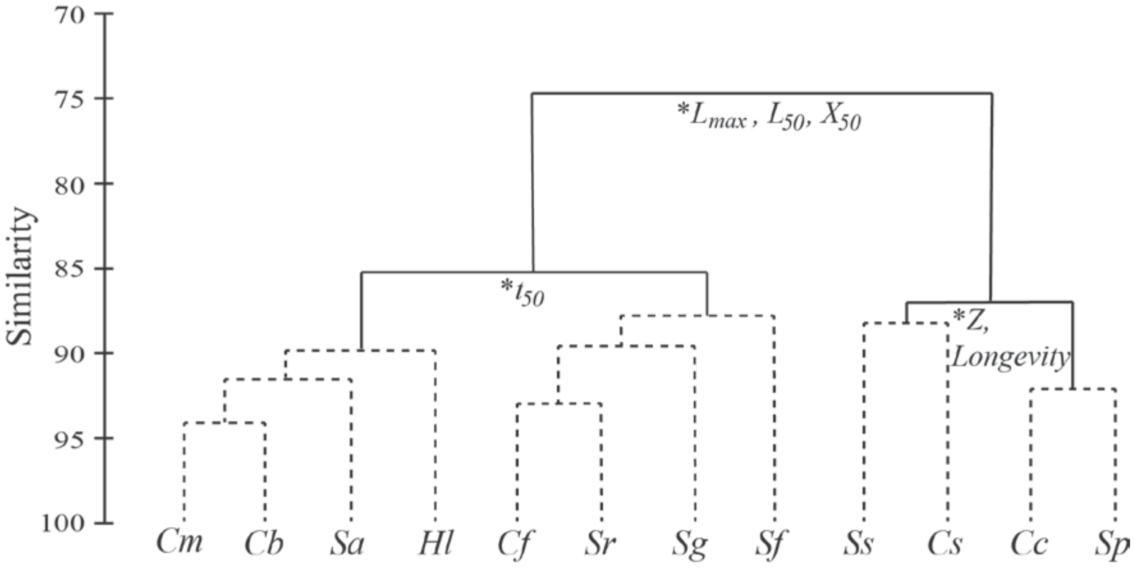

Figure 2.7. Dendrogram illustrating the similarity levels of 12 species of parrotfish from Micronesia based on seven life-history parameters. Variables were standardized prior to calculation of Bray-Curtis similarities. Species are denoted by genus and species initials. Significant groupings ($P < 0.05$* and $P < 0.001$***) were determined using similarity profile analysis and main drivers of groupings are indicated. Remaining non-significant groupings are indicated (----).

Discussion

Results from this demographic analysis identify several key features of Micronesian parrotfishes. First, they encompass a range of life histories, including considerable variation in body size, growth rate, age distribution, mortality and reproductive dynamics. A species not included in this analysis but native to Micronesia, the humphead parrotfish *Bolbometopon muricatum* (Valenciennes, 1840), would have extended this range immensely, as maximum length and life span estimates from elsewhere greatly exceed those of all species in the present study (Choat and Robertson 2002, Hamilton and Choat 2012). Second, given their growth profiles and life span, parrotfishes have life-history strategies that may be highly responsive to environmental change or anthropogenic stressors. In general, scarines grow relatively fast compared with other heavily targeted families on coral reefs, and they mature and change sex within 1-5 years of life. Parameterization of these major life-history processes is an invaluable first step before further investigations of assemblage dynamics or fishing effects can be conducted.

Relationships among life-history variables

Results demonstrated a high level of correlation among life-history traits, a pattern well-documented in marine fishes (Adams 1980, Hoenig 1983, Roff, 1984). The strongest relationships existed among length-based and among age-based variables, but not between the two, indicating a decoupling of life span and body size across species. A strong relationship between body size and life span has been demonstrated for many taxa (Speakman 2005), including parrotfishes from the GBR (Choat and Robertson 2002). Hence, the present negative result may reflect both locality-specific and fishing effects on traits. Intense fishing can directly decrease population mean maximum size and life span while increasing mortality through the selective removal of larger and older individuals (Beverton and Holt 1957). Thus, relationships between length- and age-based parameters may be strengthened in the absence of fishing. Also, the inclusion of *B. muricatum* would probably improve this relationship given that it would extend the range of most parameters.

Interspecific variation in life history

Body size is clearly an important characteristic differentiating species (LaBarbera 1989) and is physiologically linked with various life-history traits (Calder 1984). Therefore, a considerable amount of demographic variation among species is explained by this characteristic. Here, differences in length-based metrics (L_{max}, L_{50} and X_{50}) were most important in driving species groupings and separated the ‘large-’ and ‘small-bodied’ parrotfish species. These variables were highly correlated with each other and are thus nearly indistinguishable with regard to their relative importance in driving this pattern. Once separated, however, species were further sorted by differences in age-based variables. Winemiller and Rose (1992), in a more comprehensive analysis of North American fishes, also demonstrated the hierarchical importance of size in the multivariate structuring of species’ life histories. This concept, as well as the predictive power of body size, extends to many vertebrate taxa (Blueweiss et al. 1978, Stearns 1983).

While body size performs well as a life-history proxy for comparison among species, the present results demonstrate that such application should be done cautiously. Comparisons among closely related species of similar maximum length (e.g. *C. frontalis* and *C. microrhinos*; *S. altipinnis* and *S. rubroviolaceus*) reveal considerable variation in age-based parameters of importance to fisheries management. For example,

t_{50} was an important variable separating four species (*C. bicolor, C. microrhinos, H. longiceps* and *S. altipinnis*) from all others. Age at maturation is recognised as a critical life-history trait and the late onset of maturity is widely considered to predispose species to overexploitation (Jennings et al. 1998, Reynolds et al. 2005). Unfortunately, these data are scarce for many exploited coral-reef fishes, as exhaustive collections are required to obtain t_{50} estimates.

Interestingly, shared evolutionary histories appeared to have little effect on species groupings in the present study. Strong phylogenetic effects on life-history traits have been demonstrated elsewhere for marine fishes (Winemiller and Rose 1992, Choat and Robertson 2002), but given the low taxonomic level included in the present analysis (comparison of species within closely related genera), the result may not be surprising. Any given genus would comprise species which span a certain spectrum of life-history values, given the need for morphologically similar species to occupy different niches, and it is likely that spectra of closely related genera would overlap considerably (shown here for *Chlorurus* and *Scarus* especially). Hence, it is expected that the importance of phylogeny on life-history metrics would emerge with the inclusion of species at higher taxonomic levels (Stearns 1983).

One consideration is that Guam and Pohnpei differ in both island geomorphology and relative fishing pressure. Other studies (Taylor 2014; Taylor et al. in press) have demonstrated that both factors can have considerable effects on life-history trait values in parrotfishes. Hence, the sampling of species across islands likely affected the interspecific relationships to some degree. However, the magnitude of the effects of fishing pressure on traits is subordinate to that of island geomorphology (Taylor 2014), and intraspecific (within species) differences in traits are subordinate to that of interspecific (among species) differences. Therefore, the sampling across islands likely affected the observed patterns among species, but only to a minor degree. This can be demonstrated in canonical space (similar to Fig. 3.3) where conspecifics from different island types cluster near each other relative to other species.

Implications for future research

These and other data (Choat et al. 1996, Choat and Robertson 2002, Choat et al. 2003) also demonstrate the majority of parrotfishes globally are relatively short-lived compared with other reef-fish taxa. This, coupled with high flexibility in life-history traits, suggests they may be reasonably resilient or adaptable to exploitation. Few studies have focused heavily on vulnerability of parrotfishes to overexploitation but several studies suggest that they display a ‘weak’ response to fishing pressure (Russ and Alcala 1998, Jennings et al. 1999b). Fishery-induced changes in assemblage structure (Hawkins and Roberts 2003, Clua and Legendre 2008) and responses to protection (McClanahan et al. 2007, Stockwell et al. 2009), however, imply strong species-specific reactions to exploitation. Maximum body size has been used as a life-history proxy to assess parrotfish vulnerabilities (Jennings et al. 1999b), but variable growth rates and maturation schedules make this assumption tenuous. This study provides improved resolution by quantitatively grouping species based on a suite of life-history variables. It is presumed that species in the largest-bodied, latest-maturing group (*C. bicolor*, *C. microrhinos*, *H. longiceps* and *S. altipinnis*) would respond most negatively to intense fishing pressure whereas small-bodied species (*C. carolinus*, *C. spilurus*, *S. psittacus* and *S. schlegeli*) would be most resilient. Responses of the remaining species with more ‘intermediate’ life histories (*C. frontalis*, *S. forsteni*, *S. ghobban* and *S. rubroviolaceus*) may be clarified by further factors affecting vulnerability to capture such as schooling behaviour, depth and habitat distribution, and natural abundance. Empirical evaluations addressing these presumptions represent a logical next step for application of these data.

A final issue arising from the results is that Micronesian parrotfishes were considerably shorter-lived and smaller-bodied than conspecific parrotfishes in other regions. Using identical curve-fitting procedures, asymptotic sizes of Micronesian species were on average 15% smaller than those for GBR conspecific fishes across eight species (Choat et al. 1996, Choat and Robertson 2002). Only *S. psittacus* had comparable maximum sizes. Considerable differences in maximum age were evident for *C. bicolor*, *C. microrhinos, H. longiceps, S. rubroviolaceus* and *S. ghobban* compared with various regions (Choat and Robertson 2002, Grandcourt 2002). Review of the published literature concerning age-based demography of scarines suggests that life histories can be highly flexible and can vary significantly across space (Gust et al. 2002, Choat et al. 2003), but may also leave the impression that the biology of parrotfishes across the Indo-Pacific Ocean reflects that of the GBR, as this is where the vast majority of work has been performed. Hence, for such a critically important group, there may be a skewed interpretation of their biology on oceanic coral reefs. Such demographic variation may reflect environmental (Gust et al. 2001, 2002), geographic (Robertson et al. 2005, Ruttenberg et al. 2005) or fishing effects, but age and growth comparisons are not adequate to tease apart causation. Addressing this will require collection and analysis of life-history data throughout species’ ranges and across a range of environmental and anthropogenic variables to construct a more comprehensive picture of demography across ocean basins.

This study provides the most comprehensive synthesis of parrotfish life history to date from a region where they are heavily exploited. Scarines represent an increasingly prevalent component of multispecies fisheries throughout the Indo-Pacific

Ocean. Hence, these data should be accompanied by routine monitoring of fished populations in Micronesia over time as well as detailed empirical assessments of vulnerability based on life-history traits (Pinsky et al. 2011, Bender et al. 2013). Further, regional differences in traits of conspecifics highlight the importance of assessing life histories at a biogeographic scale.

Chapter 3: Life histories predict vulnerability to overexploitation in parrotfishes

Taylor, B. M., Houk, P., Choat, J. H., Russ, G. R. (2014) Life histories predict vulnerability to overexploitation in parrotfishes. *Coral Reefs* 33: 869-878. (doi:10.1007/s00338-014-1187-5)

Introduction

A pervasive and global trend in fisheries harvests has been the ongoing shift to taxa of lower trophic levels (Pauly et al. 1998). Whether or not this pattern reflects the magnitude of changes in actual fish communities is debated (Branch et al. 2010), but it does highlight that harvested species differ in their capacity to respond to exploitation (Jennings and Kaiser 1998). While documentation of this effect is greatest for commercial fisheries in temperate regions (Baum and Worm 2009), both historical and recent evidence suggests that coral reef fisheries mirror this pattern (Cheung et al. 2007, Hardt 2009, Mumby et al. 2012). Yet, the high species diversity associated with coral reef fisheries has resulted in a limited suite of life-history data available for assessing exploitation status and vulnerability across many species.

Vulnerability of a population to overexploitation is the product of intrinsic sensitivity (the response of the population to a defined mortality rate) and the degree of exposure to fishery exploitation. The sensitivity of a species is heavily influenced by life-history traits, especially those that dictate the rate of population turnover (Adams 1980). Exploitation in coral-reef fisheries is often highly selective compared with commercialized fisheries of industrialized nations, thus improved knowledge of life-history traits for harvested populations can be used to inform management decision making by identifying species most sensitive to a given rate of fishing mortality (King and McFarlane 2003). Currently, coral reef fisheries remain highly data-deficient, especially in many heavily impacted regions and for many targeted reef-fish families (Sadovy de Mitcheson et al. 2013).

On most coral reefs, parrotfishes (Labridae: tribe Scarinae) are a ubiquitous and species-rich group. Through processes of grazing and bioerosion, they have considerable influence on the benthic biota and are therefore considered ecologically important to structural processes on reefs (Bellwood and Choat 1990, Mumby et al. 2006). Parrotfishes have been historically harvested in many regions, but the increase in human populations, the advent of modern underwater fishing gear (SCUBA and underwater torch lights in particular), and the overexploitation of larger-bodied and highly preferred families has drastically increased the pressure on parrotfishes and boosted their prevalence in coral reef harvests of recent decades (Dalzell et al. 1996, Houk et al. 2012).

Despite their increasing prevalence in coral reef fisheries worldwide, comprehensive vulnerability assessments of parrotfishes are sparse compared with studies of their functional ecology (e.g., Bellwood and Choat 1990, Bellwood 1995a,b, Hoey and Bellwood 2008). Evidence suggests that, as a group, they have historically been exposed to lower fishery exploitation compared with more heavily targeted families including epinephelids, lutjanids, lethrinids, and carangids (Russ and Alcala 1998, Jennings et al. 1999b) and that the vast majority of species are designated as having a small likelihood of local extinction (Comeros-Raynal et al. 2012). However, recent studies increasingly demonstrate strong species-specific reactions to both exploitation and protection, potentially causing considerable changes to assemblage structure as well as ecological function (Hawkins and Roberts 2003, Clua and Legendre

2008, Bellwood et al. 2012, Houk and Musberger 2013, Mumby et al. 2013, Edwards et al. 2014). In support, parrotfishes may be highly susceptible to harvest for several reasons: they are very conspicuous, have shallow depth distributions and small home ranges, and are easily targeted at night. Hence, concerns are escalating as fishing effort increases on this group in many regions worldwide (Comeros-Raynal et al. 2012).

Here, we utilize both fishery-dependent and -independent data to examine the vulnerability of parrotfishes in response to fishing pressure and key covariates known to influence parrotfish assemblages. Our approach integrates extensive datasets from stereo-video surveys, historical fishery landings spanning two decades and life-history data from 12 species that comprised over 90% of the reported parrotfish catch biomass in Guam. We first establish gradients of change in species biomass with respect to exploitation and subsequently test the extent to which life-history traits predict responses to exploitation and might be used as proxies to species sensitivity for coral reef fisheries. Seven life-history traits were assessed against three independent vulnerability metrics derived within. The combined results provide an assessment of parrotfish vulnerability to overexploitation, but also extend to predict which life-history traits are most sensitive and best suited for fisheries management and conservation planning.

Methods

Study area and species

This study was conducted on Guam, Micronesia, where parrotfishes are harvested for commercial, recreational, and subsistence use. A large proportion of the commercial harvest comes from night spearfishing with SCUBA (Houk et al. 2012). High human population density, differences in coastline access and the placement of marine reserves yield a range of fishing intensities across sites. I focused on twelve species in five genera representing a range of demographic characteristics (Taylor and Choat 2014 [Chapter 2]). These species were the stareye parrotfish *Calotomus carolinus*, bicolour parrotfish *Cetoscarus bicolor*, tan-faced parrotfish *Chlorurus frontalis*, steephead parrotfish *Chlorurus microrhinos*, bullethead parrotfish *Chlorurus spilurus* (formerly *C. sordidus*), longnose parrotfish *Hipposcarus longiceps*, filament-fin parrotfish *Scarus altipinnis*, rainbow parrotfish *Scarus forsteni*, blue-barred parrotfish *Scarus ghobban*, palenose parrotfish *Scarus psittacus*, redlip parrotfish *Scarus rubroviolaceus*, and yellowband parrotfish *Scarus schlegeli*.

Life-history trait data

Seven life-history variables for the twelve species examined were quantified through research-associated sampling from a variety of heavily and lightly fished sites on Guam (samples for three species were derived from Pohnpei; detailed in Taylor and Choat 2014[Chapter 2]). These variables were mean length at female maturity (L_{50}), mean length at sex change (X_{50}), mean maximum length (L_{max}; mean length of largest quartile of the sampled population), a growth rate proxy (L_{1-3}; growth in mm from age 1 to 3 years), mean age at female maturity (t_{50}), mean maximum age (T_{max}; mean age of oldest quartile of sampled population), and the instantaneous total mortality rate (Z; Table 3.1). In order to summarize the variation among life-history traits, I performed a principal components analysis (PCA) with the seven life-history parameters as variables. All variables were standardized by their sum prior to analysis to provide equal weighting across variables. I considered the scores on the first principal component (PC1) to be a representative summary of the distribution of species along a life-history gradient.

Table 3.1. Life-history trait values for twelve parrotfish species from Micronesia.

Species	L_{50} (mm)	X_{50} (mm)	L_{max} (mm)	$L_{1\text{-}3}$ (mm)	t_{50} (year)	T_{max} (year)	Z (year^{-1})
Calotomus carolinus	168	213	257	84	1.1	3.0	1.04
Cetoscarus bicolor	323	375	405	149	3.1	7.3	0.27
Chlorurus frontalis	240	343	387	133	1.6	5.9	0.38
Chlorurus microrhinos	308	378	409	156	3.7	5.9	0.43
Chlorurus spilurus	144	207	230	67	1.3	5.4	0.59
Hipposcarus longiceps	317	364	382	127	3.1	4.6	0.71
Scarus altipinnis	251	337	377	122	2.9	7.8	0.25
Scarus forsteni	216	271	297	91	1.8	6.5	0.34
Scarus ghobban	244	314	337	68	1.4	4.8	0.50
Scarus psittacus	103	193	226	65	1.4	3.8	1.03
Scarus rubroviolaceus	271	329	373	137	1.9	4.8	0.63
Scarus schlegeli	197	220	270	75	2.0	4.6	0.81

[a] Values were derived from biological samples in Taylor and Choat (2014).

[b] L_{50}: mean length at female maturity; X_{50}: mean length at sex change; L_{max}: mean maximum length; $L_{1\text{-}3}$: growth in mm from age 1 to 3 years; t_{50}: mean age at female maturity; T_{max}: mean maximum age; Z: total mortality rate.

Parrotfish species biomass patterns

I used diver-operated stereo-video (Harvey and Shortis 1996) to survey parrotfish assemblages at 17 sites (Fig. 3.1) across a range of environmental variables and anthropogenic influences. At each site, 16 replicate timed swims (3-min long by 5 m across, averaging 322 m^2) were stratified at two depths (8 at 18-22 m, 8 at 6-10 m). The distance of each transect was measured by a towed GPS unit at the surface. I used the program EventMeasure (www.seagis.com.au) to measure individual fish lengths (mm fork length) and these lengths were converted to biomass estimates (kg) by applying length-weight relationships obtained from sampled individuals (Taylor and Choat 2014[Appendix A]). I used the spatial distribution of fishing effort from creel survey data to derive a site-specific index of fishing pressure for parrotfishes. The index summed the total fishing trips targeting parrotfishes by survey sector, while combining both shore-based and boat-based fisheries through a scaling factor (0.68, to account for different magnitudes of shore-based and boat-based catches in the fishery). Site values were divided by adjacent reef areas (km^2) and natural log-transformed. Additional environmental variables for each site included wave exposure (following Ekebom et al. 2003), reef slope (0 - 90°; mean of three measurements per transect), coral cover and rugosity (1 - 5 scale; mean of five estimates per transect), distance to reef pass or nearest major channel (km), adjacent reef type (lagoon, reef flat, fringing landmass), latitude, and longitude.

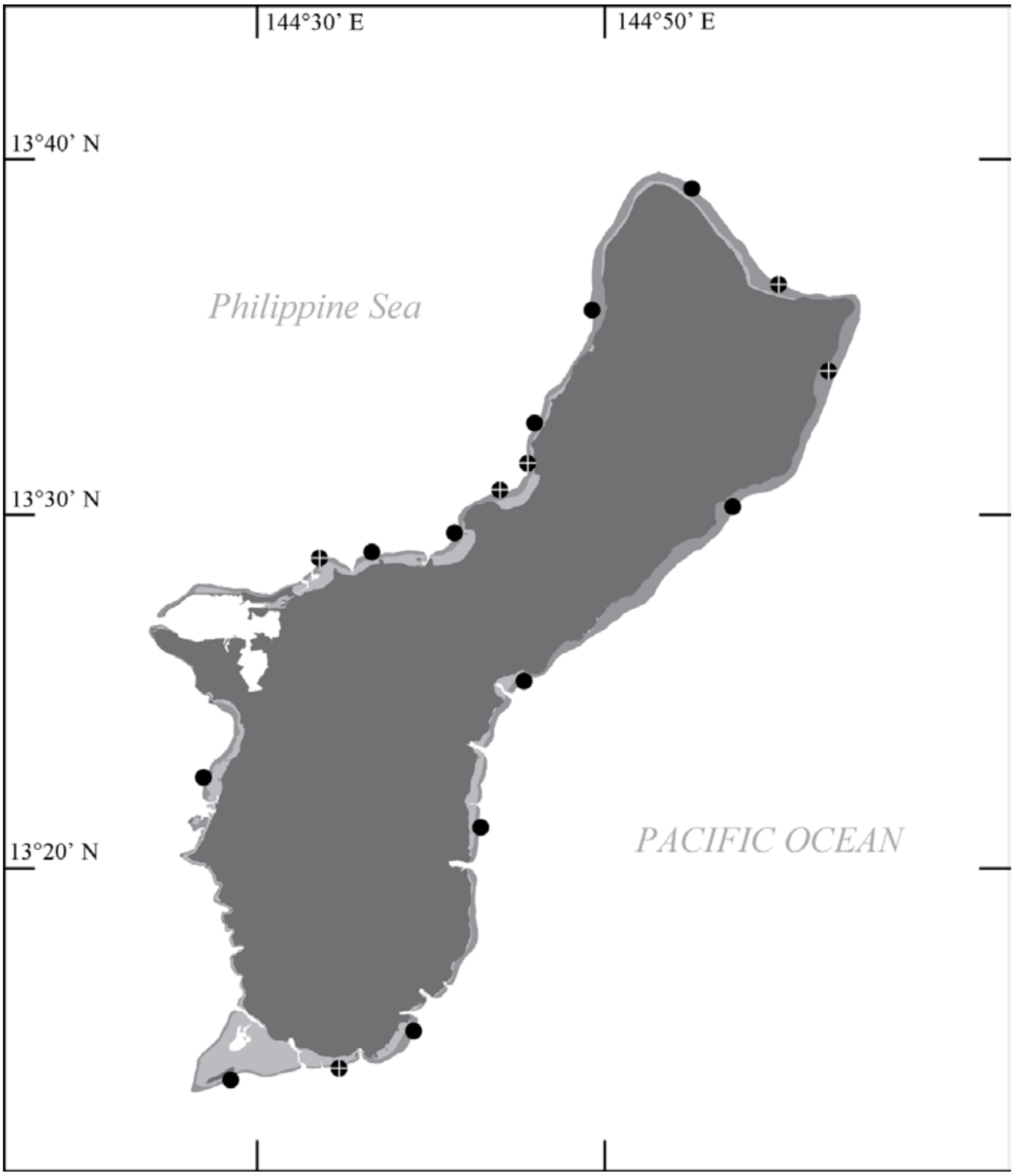

Figure 3.1. Map of Guam indicating study sites where stereo-video surveys of parrotfishes were conducted (black circles). White plus symbols indicate sites within marine reserves. Dark grey represents land, light grey represents reef flat or shallow lagoon, intermediate grey represents outer reef slopes.

Historical fishery data

I used historical Guam creel survey data (protocols following Malvestuto et al. 1978) to explore fishery trends for each species. First, the length of harvested individuals by year was examined for the period of 1990-2009. Linear regression models on log-transformed values were used to test for significant declines in mean harvested length. A threshold of ≥10% overall change was applied to account for statistical significance resulting from the high sample sizes that existed. A second analysis focused on species-specific proportions of the parrotfish fishery through time (1990-2009). Annual proportional compositions (by total biomass) were square-root transformed and linear regression models were applied to identify significant declines over time for each species.

Statistical analysis

I applied multivariate regression trees (MRT; De'ath 2002) to examine parrotfish species biomass patterns and to identify the hierarchy of factors predicting variation in parrotfish assemblage structure. Canonical correspondence analysis (CCA; ter Braak 1986) was used to relate species distributions to explanatory variables. Dependent variables for both analyses were relative species abundances (i.e., biomass per unit area of parrotfish species standardized by site), while explanatory variables were fishing pressure and the environmental factors described above. Biomass data (kg hectare^{-1}) were square root-transformed prior to analysis to normalize the residual error structure in the pooled multivariate response (i.e., reduce the bimodal distribution of the residuals), and the MRT was pruned iteratively by cross validating the relative errors. Canonical correspondence analysis served to describe the relationship between species biomass patterns and environmental variables. I used species biomass data to create a

Bray-Curtis similarity matrix that quantified the degree of separation between each pair of species. Relationships were then visualized through an ordination procedure that hierarchically accounted for the greatest amount of variation in the multivariate dataset (i.e., created eigenvectors that maximized the amount of variance explained). Finally, explanatory factors were overlaid on the ordination based upon their association with each CCA axis. Axes were tested for significance using permutation tests.

Spatial biomass patterns were analyzed independently for each species with linear models to determine the combination of environmental and anthropogenic factors that best predicted species-specific patterns. Here, biomass estimates were ln[x + 1] transformed to address skewness in individual species biomass datasets. I used variance inflation factors (Zuur et al. 2009) to test for collinearity among explanatory variables and variables with values >5 were either removed from the analysis or combined through PCA. Coral cover and rugosity (highly collinear factors) were combined through values of the first principal component (explaining 94% of the variance among them) from PCA. Model selection was carried out by minimization of corrected Akaike's Information Criterion (AICc) through the *dredge* function in the *MuMIn* package, and models with the least number of explanatory variables within 2 AICc of the lowest were selected. For species that did not include fishing pressure in the optimal model, I regressed this variable against the residuals of the optimal model to derive the partial coefficient, given that the response to fishing pressure (whether significantly negative or not after controlling for effects of other environmental variables) forms the basis of my vulnerability assessment. These models are sufficiently robust to provide an estimation of responses to exploitation, provided that parrotfishes have been demonstrated to be habitat generalists whose abundance is strongly influenced by wave exposure (Gust 2002). However, disentangling the relative effects of fishing pressure and biophysical factors is a challenging task that requires additional information on larval supply, resource availability, proximity to nursery habitat, benthic composition, and predator abundance, all factors that will both affect parrotfish abundances and be affected by fishing pressure.

Vulnerability

I used two approaches based upon species responses to fishing pressure and historical catch datasets to define and quantify vulnerability to overexploitation. The first approach defined vulnerability as the incidence of three demographic responses (i.e., binary responses, yes or no) for each species: 1) Was there a significant negative correlation between biomass and fishing pressure? 2) Was there a significant negative change in mean harvested length? 3) Was there a significant decline of the species in the proportion of the fishery? Zero negative responses implied lowest vulnerability and three negative responses implied highest vulnerability, with the incidence vulnerability metric ranging between 0 and 1, corresponding to the proportion of individual questions satisfied. The second approach quantified vulnerability as the magnitude of response across spatial and historical metrics. Slopes or partial correlation coefficients of each relationship were standardized for equal scale, and vulnerability equalled the sum of responses for the two measures.

I lastly examined the extent to which life-history characteristics may have influenced vulnerability to overexploitation. These examinations used the suite of life-history traits as independent variables to predict both metrics of vulnerability. For incidence of negative responses, I used generalized linear models (GLM) with binomial errors and a logit link, because response variables were proportional data. For magnitude of response, I used linear regression models. Species scores on PC1 of the life-history PCA were used as explanatory variables to capture the holistic nature of differing life histories among species. Analyses between vulnerability and life-history traits were performed independently to determine which species and traits were greatest contributors to the findings, on the basis of AICc and r^2 values. In particular, I was interested in length-based versus age-based traits, given that correlations between the two are weakest (Taylor and Choat 2014 [Chapter 2]). I also examined any potential biases in the analyses that may be an artefact of phylogenetic relationships among species by fitting linear regressions (forced through the origin) to phylogenetically independent contrasts (PICs) of responses to exploitation and life-history traits. The reduced phylogeny was derived from Choat et al. (2012) with inclusion of the sparisomatine *Calotomus carolinus.* All analyses were performed in R version 2.15.3 (R Core Team 2013).

Results

Spatial patterns of fish biomass

The twelve species considered here represented 98% of the total parrotfish biomass on outer-reef slopes of Guam. Hierarchical variation in parrotfish assemblage structure among sites was described by MRT. A tree with three terminal nodes was optimal, explaining 41% of the variation, with splits driven by two explanatory variables: fishing pressure and distance to reef pass (Fig. 3.2a). Fishing pressure explained 27% of the MRT variation, as sites with higher fishing pressure had a greater proportion of smaller, early maturing species, as determined using the life-history spectrum from PCA that explained 74% of life-history variation along the first axis (Fig. 3.2a; Fig. 3.3). Sites associated with lower fishing pressure were further separated by the distance to reef passes. Distance to reef pass was not related to fishing pressure but rather corresponded with wave exposed areas fringing against the landmass. Sites far from reef passes were characterized by high abundances of *Chlorurus frontalis* and *S. rubroviolaceus* and low abundance of *S. schlegeli*. Results from CCA supported these findings, as the first axis accounted for 27% of the variation in species biomass patterns (P = 0.005), with fishing pressure, distance to reef pass, and exposure having strongest affinities with the first CCA axis (Fig. 3.2b). The remaining variables were less influential to the multivariate data structure, and had greatest affinities with the second axis of the CCA, which described only 9% of the variation (P = 0.042).

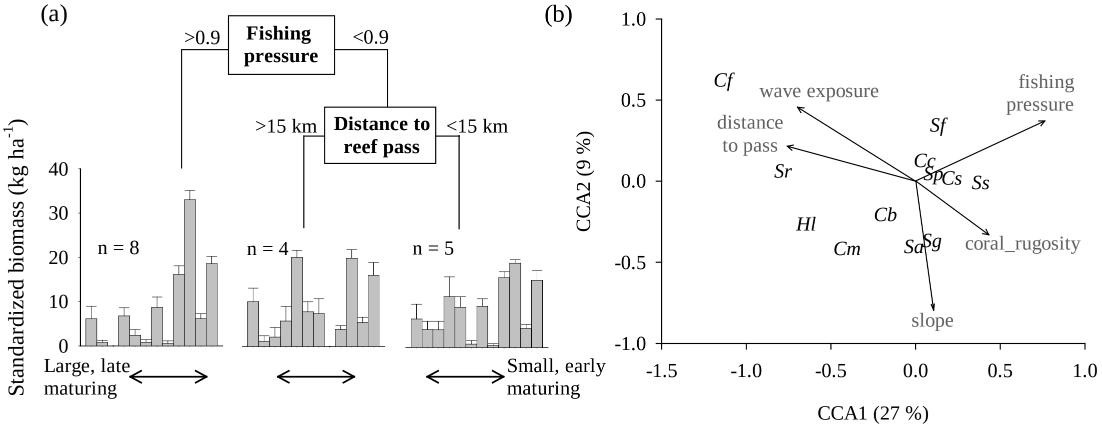

Figure 3.2. (a) Regression tree analysis demonstrating hierarchical drivers of parrotfish assemblage structure on Guam based on standardized biomass of twelve species. The order of species from left to right in plots at terminal nodes follows increasing values of the first principal component in Fig. 3.3, representing a summarized life-history spectrum across species. (b) Canonical correspondence analysis relating species distributions to explanatory variables across sites. Both axes are statistically significant. Species positions are denoted by genus and species initials (*Calotomus carolinus* = *Cc*, *Cetoscarus bicolor = Cb, Chlorurus frontalis = Cf, Chlorurus microrhinos = Cm, Chlorurus spilurus = Cs*, *Hipposcarus longiceps = Hl, Scarus altipinnis = Sa*, *Scarus forsteni = Sf, Scarus ghobban = Sg, Scarus psittacus = Sp*, *Scarus rubroviolaceus = Sr, Scarus schlegeli = Ss*).

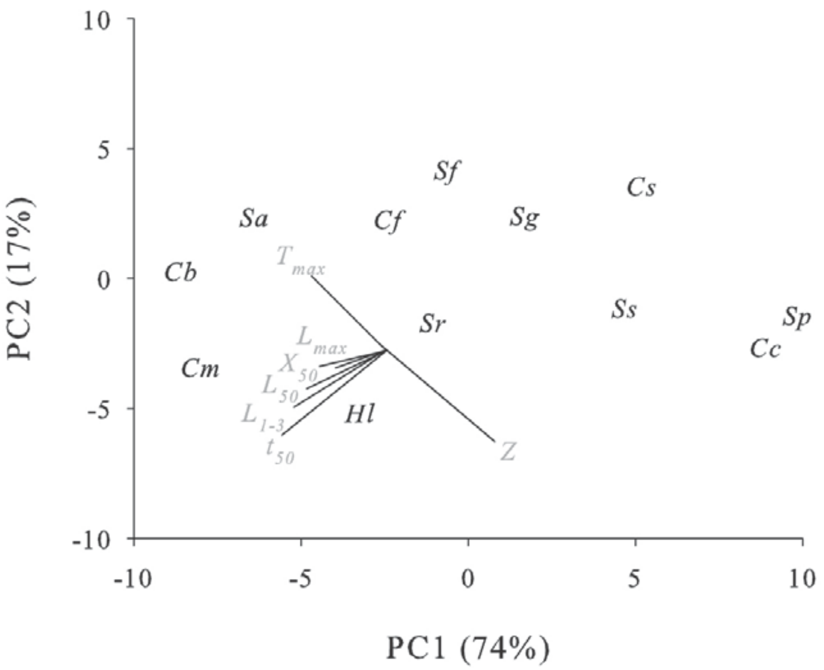

Figure 3.3. Principal components analysis of life-history traits of twelve parrotfish species. The first principal component explains 74% of the variation among species and therefore summarizes the life history spectrum across species. L_{50} = length at 50% female maturity; X_{50} = length at 50% sex change; L_{max} = mean length of largest quarter of sampled population (mean maximum length); L_{1-3} = growth in millimetres from age 1 to 3 years (growth rate proxy); t_{50} = age at 50% female maturity; T_{max} = mean age of oldest quarter of sampled population (mean maximum age); Z = instantaneous total mortality rate.

Overall, significant negative effects (decreased biomass) of fishing pressure were identified for five species (*Cetoscarus bicolor*, *Chlorurus microrhinos*, *Hipposcarus longiceps*, *Scarus altipinnis* and *S. rubroviolaceus*; Table 3.2). In addition, wave exposure, coral-rugosity, and adjacent habitat type appeared to be important environmental factors driving biomass patterns, but their relative influence varied among species.

Table 3.2. Structure of optimal linear models describing patterns of biomass (natural log-transformed) across sites for each of twelve parrotfish species on Guam. Partial coefficients and significance values for the factor *fishing pressure* are presented for each species. Values in grey indicate they were derived by fitting a linear model to the residuals of the optimal model, given *fishing pressure* was not included in the optimal model. *coral.rugosity* represents the first principal component summarizing variation between highly collinear factors *coral cover* and *rugosity*.

Species	**Optimal model structure**	**r^2**	**p-value**	**fishing pressure**	
				coefficient	**p-value**
Calotomus carolinus	exposure	0.05	0.383	-0.070	0.845
Cetoscarus bicolor	reef flat + fishing pressure	0.55	0.004	-3.612	0.014
Chlorurus frontalis	dist_pass + exposure	0.53	0.005	-0.056	0.964
Chlorurus microrhinos	lagoon + fishing pressure	0.39	0.031	-2.904	0.039
Chlorurus spilurus	coral.rugosity	0.32	0.018	0.159	0.428
Hipposcarus longiceps	fishing pressure + fringe	0.43	0.019	-4.164	0.010
Scarus altipinnis	exposure * fishing pressure	0.46	0.040	-5.471	0.030
Scarus forsteni	coral.rugosity + fringe	0.45	0.014	0.609	0.567
Scarus ghobban	coral.rugosity + slope	0.34	0.057	0.223	0.780
Scarus psittacus	exposure + coral.rugosity	0.34	0.052	-0.084	0.672
Scarus rubroviolaceus	fishing pressure + exposure	0.61	0.001	-4.054	0.011
Scarus schlegeli	fringe + dist_pass	0.71	<0.001	0.059	0.875

Historical patterns

Historical fishery data revealed considerable changes in both mean harvested fish length and proportions of particular species in the fishery, but these trends varied by species. Mean harvested fish length decreased significantly by at least 10% over 20 yrs for seven species (*Cetoscarus bicolor, Chlorurus microrhinos, H. longiceps, S. altipinnis*, *S. psittacus, S. rubroviolaceus* and *S. schlegeli*) from 1990-2009 (Table 3.3a). The greatest reduction in mean harvested length, as predicted by the linear model, was by 32% in *C. bicolor*. I also observed shifts in the composition of parrotfish catches over the two decades. Four species decreased significantly in fishery proportion (*C. microrhinos, H. longiceps*, *S. altipinnis* and *S. forsteni*) whereas three species (*C. spilurus, S. psittacus* and *S. schlegeli*) showed significant increases (Table 3.3b).

Table 3.3. Results of linear regression models for mean harvested length and fishery proportion from 1990 to 2009 for each of twelve parrotfish species on Guam.

a) species	**intercept**	**coefficient**	**± % ΔFL**	**residual df**	**p-value**	**r^2**
Calotomus carolinus	10.134	-2.33E-03	-4	105	0.587	0.003
Cetoscarus bicolor	52.353	-2.32E-02	-32	61	6.76E-04	0.174
Chlorurus frontalis	17.629	-6.00E-03	-4	290	0.107	0.009
Chlorurus microrhinos	27.511	-1.09E-02	-17	428	5.06E-05	0.038
Chlorurus spilurus	13.165	-3.88E-03	-6	993	0.002	0.009
Hipposcarus longiceps	40.494	-1.73E-02	-28	605	1.55E-10	0.066
Scarus altipinnis	30.350	-1.23E-02	-19	456	1.11E-06	0.051
Scarus forsteni	17.689	-6.02E-03	-9	181	0.040	0.023
Scarus ghobban	-0.982	3.28E-03	+1	151	0.545	0.002
Scarus psittacus	20.315	-7.47E-03	-12	541	4.74E-05	0.030
Scarus rubroviolaceus	43.710	-1.89E-02	-25	209	8.99E-07	0.109
Scarus schlegeli	24.770	-9.65E-03	-16	889	3.93E-06	0.024
b) species	**intercept**	**coefficient**	**± Δ %**	**residual df**	**p-value**	**r^2**
Calotomus carolinus	2.161	-0.001	0	18	0.528	0.023
Cetoscarus bicolor	-3.334	0.002	+1	18	0.600	0.016
Chlorurus frontalis	-4.609	0.002	+5	18	0.559	0.019
Chlorurus microrhinos	18.755	-0.009	-12	18	0.004	0.385
Chlorurus spilurus	-21.913	0.011	+18	18	0.004	0.372
Hipposcarus longiceps	33.039	-0.016	-21	18	5.82E-04	0.491
Scarus altipinnis	17.359	-0.009	-7	18	0.028	0.240
Scarus forsteni	11.942	-0.006	-3	18	0.033	0.229
Scarus ghobban	-3.060	0.002	0	18	0.713	0.008
Scarus psittacus	-13.851	0.007	+6	18	0.002	0.431
Scarus rubroviolaceus	8.920	-0.004	0	18	0.391	0.041
Scarus schlegeli	-11.634	0.006	+8	18	0.040	0.215

Assessment of vulnerability to overexploitation

Vulnerability scores from the incidence and magnitude metrics were similar in terms of species rankings, with *C. bicolor*, *C. microrhinos, H. longiceps, S. altipinnis,* and *S. rubroviolaceus* being most sensitive. The life-history trait spectrum (PC1) was a significant predictor of vulnerability to overexploitation, explaining 53% of the variation across species for both the incidence ($P = 0.0042$, Fig. 3.4a) and magnitude ($P = 0.0070$, Fig. 3.5a, Table 3.4) metrics. In addition, most life-history traits significantly predicted vulnerability to overexploitation, but their predictive capacities varied considerably, explaining between 10 to 84% of the variation for incidence (Fig. 3.4b-h) and 12 to 67% of the variation for magnitude (Fig. 3.5b-h; Table 3.4). Overall, length-based parameters (L_{50}, X_{50}, L_{max}, and L_{1-3}) were generally better predictors than the age-based parameters T_{max} and Z. However, age at maturity (t_{50}) was the best predictor for both vulnerability metrics. These results were consistent for analyses applying PICs (Fig. 3.6), suggesting that relationships were not confounded by underlying shared evolutionary histories among species.

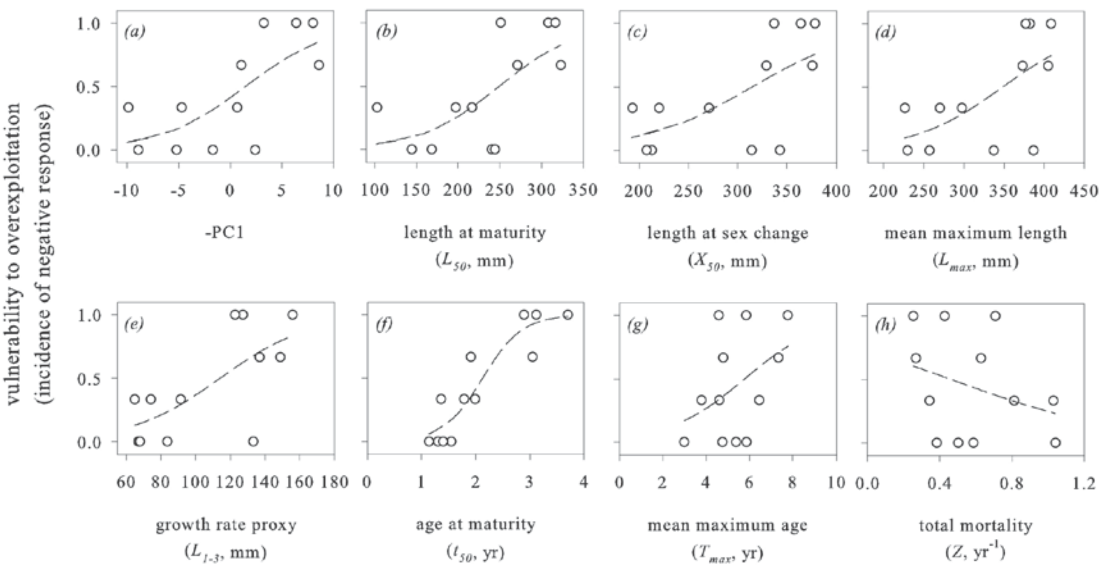

Figure 3.4. Vulnerability to overexploitation as incidence of negative response across twelve parrotfish species related to individual life-history traits. Dashed lines represent the best fit from a generalized linear model.

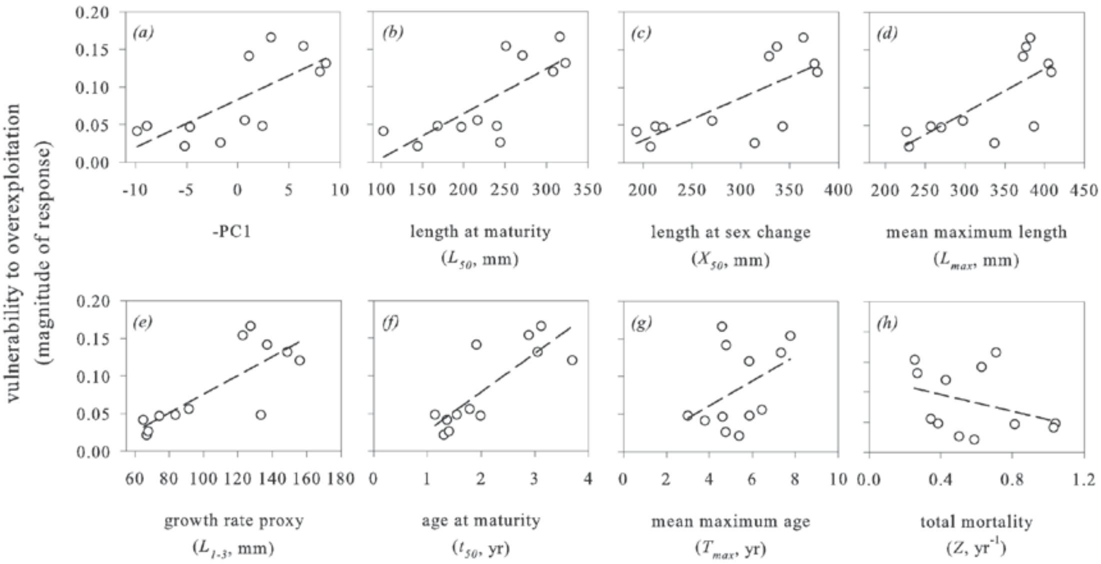

Figure 3.5. Vulnerability to overexploitation as magnitude of response across twelve parrotfish species related to individual life-history traits. Dashed lines represent the best fit from a linear regression model.

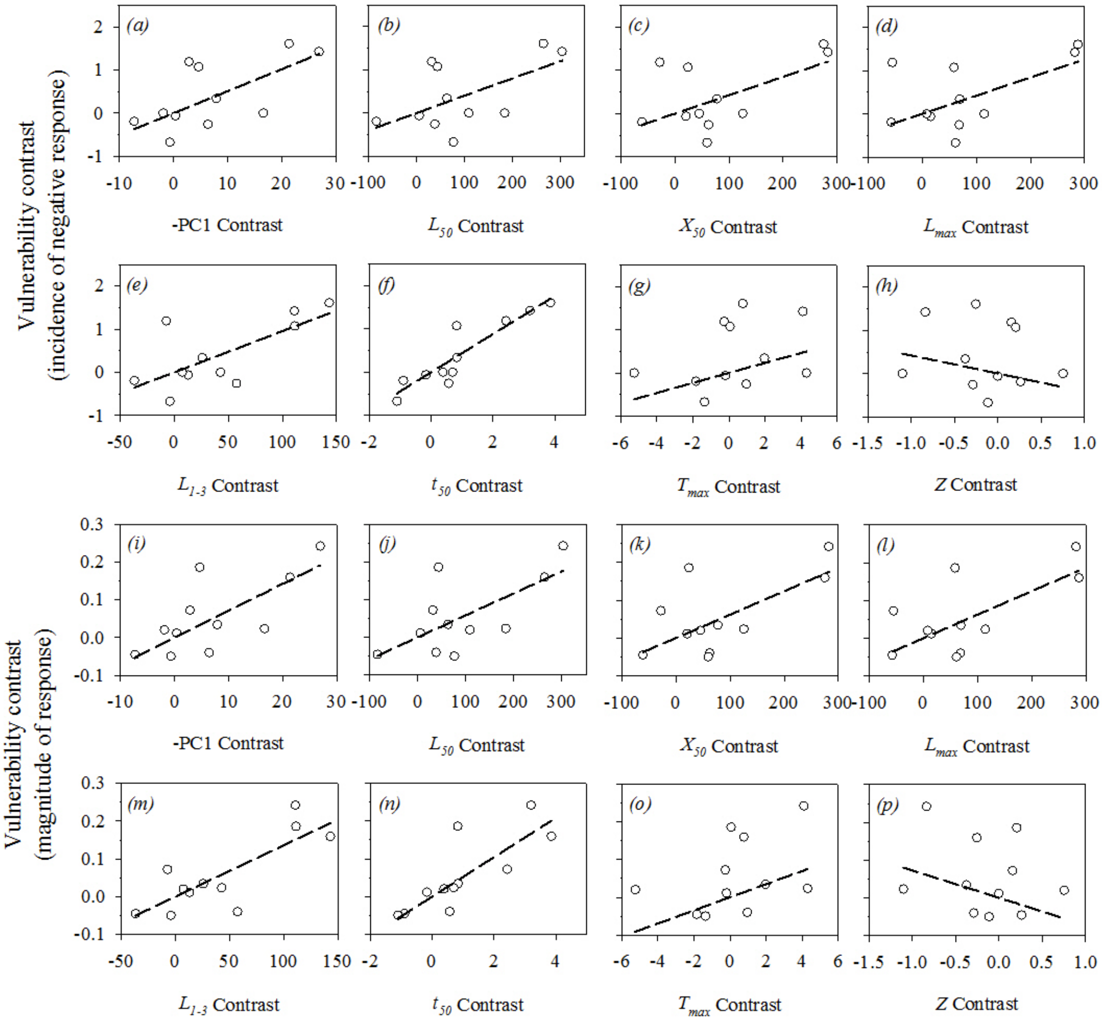

Figure 3.6. Plots of linear regressions performed on phylogenetically independent contrasts of the responses to exploitation (incidence of negative response [a-h] and magnitude of response [i-p]) and life-history traits across twelve parrotfish species.

Table 3.4. Model results predicting the vulnerability to overexploitation based on (a) incidence of negative response (generalized linear models) and (b) magnitude of response (linear regression models) across twelve parrotfish species based on various life history traits. PC1 = relative values along a life-history spectrum, L_{50} = length at 50% female maturity; X_{50} = length at 50% sex change; L_{max} = mean length of largest quarter of sampled population (mean maximum length); $L_{1\text{-}3}$ = growth in millimetres from age 1 to 3 years (growth rate proxy); t_{50} = age at 50% female maturity; T_{max} = mean age of oldest quarter of sampled population (mean maximum age); Z = total mortality rate. Traits are ordered by decreasing r^2 values.

a) trait	**intercept**	**coefficient**	**residual deviance**	**p-value**	**AICc**	**r^2**
t_{50}	-5.851	2.748	8.11	0.0013	21.5	0.84
PC1	-0.357	0.243	18.11	0.0042	31.6	0.53
L_{50}	-5.218	0.021	19.15	0.0061	32.6	0.50
$L_{1\text{-}3}$	-4.431	0.039	18.93	0.0029	32.4	0.47
X_{50}	-5.636	0.018	20.52	0.0064	34.0	0.42
L_{max}	-6.302	0.018	20.71	0.0067	34.2	0.41
T_{max}	-3.288	0.569	25.93	0.0502	39.4	0.18
Z	0.955	-2.062	28.03	0.1420	41.5	0.10

b) trait	**intercept**	**coefficient**	**$F_{1,10}$**	**p-value**	**r^2**
t_{50}	-0.025	5.15E-2	20.24	0.0011	0.67
$L_{1\text{-}3}$	-0.049	1.24E-3	17.01	0.0021	0.63
L_{50}	-0.055	5.95E-4	13.92	0.0039	0.58
L_{max}	-0.108	5.80E-4	12.07	0.0060	0.55
X_{50}	-0.083	5.63E-4	11.62	0.0067	0.54
PC1	0.083	6.37E-3	11.41	0.0070	0.53
T_{max}	-0.005	1.65E-2	2.17	0.1712	0.18
Z	0.124	-6.96E-2	1.38	0.2660	0.12

Discussion

The results demonstrate a high capacity for predicting responses to exploitation in parrotfishes on the basis of life-history traits. The predictive power of length-based traits, particularly maximum length, is encouraging for management efforts given that maximum length can be readily attained from basic field surveys or fishery data. However, age at female maturity, a trait seldom estimated for tropical fish, emerged as the best predictor of vulnerability to overexploitation. For many species, inferring this parameter from maximum length estimates may be tenuous because of considerable interspecific variation in the body size-maturity relationship (Taylor and Choat 2014 [Chapter 2]). The remaining age-based traits (mean maximum age and mortality) had low capacities for predicting the response to exploitation as compared with length-based traits and age at maturity. Nevertheless, signatures of vulnerability to overexploitation in the parrotfish assemblage were significantly related to many life-history traits, suggesting that effective fisheries and conservation management can be straightforward, provided adequate biological data is available for species of interest.

The capacity for predicting the response to exploitation varied among length-based and age-based traits. While age-based mortality and lifespan were consistently poor predictors, age at maturity was considerably better than all other traits. The timing of sexual maturation has a profound effect on the turnover time and intrinsic rate of increase of populations (Cole 1954). Hence, I expect the intrinsic sensitivity of late-maturing species to exploitation to be high. Late maturation and large body size, two traits that are often related, have been found to be the best predictors of vulnerability in the long-term across various harvested stocks and species (Reynolds et al. 2005). Sharks and rays, for example, have considerably delayed maturation schedules compared with other harvested taxa and the ubiquitous decline of elasmobranch populations globally has largely been attributed to this trait (Smith et al. 1998, Stevens et al. 2000). However, both within and across taxonomic groups, large body size draws increased targeting pressure from fishermen because of higher economic gains from larger fish. Clearly, selective harvesting pressure and life-history traits interact to drive species assemblage responses to exploitation, but studies that control for differential mortality rates across species have demonstrated that the pattern of response is consistent (Jennings et al. 1998, Hutchings 2001, Denney et al. 2002).

Analyses applying PICs demonstrated that vulnerability tests did not simply reflect differences derived from shared evolutionary histories. Because life-history strategies and ecological traits differ among taxa through patterns of ancestry, taking phylogenetic relationships into consideration is important in vulnerability assessments (Felsenstein 1985, Harvey 1996). Jennings et al. (1999b) conducted independent assessments of three commonly harvested families (including parrotfishes) and used maximum length as a proxy for summarized life histories while controlling for phylogenetic differences within each family. They concluded that cross-species analysis may be inappropriate because of lack of statistical independence in life-history traits among species. In the present study, correcting for phylogeny appeared to be unnecessary (see Ricklefs and Starck 1996) because life-history spectra are broadly overlapping among genera (Taylor and Choat 2014 [Chapter 2]) and therefore do not reflect phylogenetic relationships. This result reflects the high degree of ecological convergence in parrotfishes whereby species from diverse phylogenetic backgrounds manifest similar sizes and foraging modes (Choat et al. 2012). However, I expect that both life history and ecology will have a much stronger phylogenetic signature at higher taxonomic levels (i.e., inclusion of other fish families), thus requiring statistical consideration.

The present study relied upon a general definition of vulnerability when assessing species responses to exploitation. However, an important distinction exists between vulnerability to capture and vulnerability to overexploitation. While interrelated, the former represents how likely a species or population is to be targeted by fishermen and the latter represents the biological response to exploitation at the population level. A population may be subject to high fishing mortality yet does not show signs of overexploitation because of a resilient life-history strategy. Factors influencing the vulnerability to capture include ecological and behavioral traits not fully considered in my assessment such as schooling behavior, depth, and habitat distribution, natural abundance, reproductive behavior, and nocturnal resting sites in shallow water. The degree to which these traits may have affected the overexploitation metrics was not assessed. However, the addition of schooling behaviour (scored as present or absent) in the vulnerability models provides no insight into vulnerability to overexploitation ($P = 0.39$ [incidence] and $P = 0.47$ [magnitude]). This result is somewhat surprising given that parrotfishes are most vulnerable to capture at night while resting and schooling behavior facilitates the harvest of a greater proportion of nearby individuals with little effort. In support of this, ecological and behavioral traits have emerged as subordinate to life-history traits in prior vulnerability assessments (Reynolds et al. 2005) and these results corroborate this trend given that life-history traits heavily dictated responses to exploitation. Further, many behavioral traits appear to overlap considerably within the scarine Labridae (Colin and Bell 1991, Bellwood 1994). Nevertheless, the influences of ecology and behavior on species' vulnerabilities will likely differ among taxa and therefore represent an important conservation and management issue.

On Guam, parrotfishes represent one quarter of the total reef-associated biomass of fish catch (Houk et al. 2012). With a large number of avid spearfishers as well as a commercial SCUBA-spear fishery, fishing pressure here is comparatively high, yet fishing effort is spatially variable because of limited coastline access in several areas, the existence of marine reserves, and high wave energy during the winter trade wind season. This gradient is reflected in the MRT analysis where fishing pressure was the most important variable explaining the reduction of large-bodied, late-maturing species (Fig. 3.2). Not only was this trend clear based upon current parrotfish biomass patterns, but a decline in mean body length of large-bodied, late-maturing species in the catch biomass was detected over the past twenty years. A good contrast to the present study is that of Jennings et al. (1999b), who reported weak responses of parrotfishes to fishing pressure in Fiji, as catches of grouper (Epinephelidae) and snapper (Lutjanidae) exceeded those of parrotfishes by factors of two to four, respectively. On Guam, these trends are virtually reversed, as parrotfishes are the dominant catch alongside surgeonfishes (Houk et al. 2012). Among the five species determined to be most vulnerable to overexploitation, only a few sites with the lowest fishing pressure constituted the majority of the observed biomass (5 of 17 sites [<30%] constitute 68% of the biomass of these five species).

Because of the deficiency of age-based life-history data for many coral reef fishes, assessments of vulnerability often have had to rely upon length-based inferences of life-history parameters (Thorson et al. 2014). While useful, the present analysis highlights the importance of accurate parameterization and also of interspecific variation in trait relationships. For instance, the one species which caused the most variation in vulnerability models was *Chlorurus frontalis*. This heavily-targeted species was among the largest-bodied and longest-lived parrotfishes on Guam, but had a surprisingly early age at maturity facilitated by fast growth early in the life span (Taylor and Choat 2014 [Chapter 2]). Showing strong affinities with wave exposure and distance to reef passes and little response to fishing pressure, *Chlorurus frontalis* had comparatively high residuals within all life-history vulnerability models, with the exception of age at maturity. These findings suggested that predicting vulnerability from length-based characteristics may not always be appropriate, highlighting the importance of expanding bio-sampling programs in data-deficient coral reef fisheries to better understand the magnitude of such exceptions (Comeros-Raynal et al. 2012, Sadovy de Mitcheson et al. 2013).

This detailed assessment has demonstrated that vulnerability to fishing in parrotfishes is strongly linked to species' life-history traits and that certain species can be highly susceptible to overexploitation. Fishing 'down' coral-reef food webs can focus pressure upon herbivore and detritivore families, and this shift has strongest implications for the slow-growing and large-bodied species. Furthermore, this conclusion comes even without the inclusion of the bumphead parrotfish *Bolbometopon muricatum* (native to Guam and elsewhere in Micronesia) which has undergone range-wide declines from overfishing (Dulvy and Polunin 2004, Bellwood et al. 2012) and is undoubtedly more vulnerable to overexploitation than any species examined here. Clearly, there is increasing concern for the future sustainability of fisheries on coral reefs, especially as fisheries shift their focus to lower trophic levels (Mumby et al. 2012).

I conclude that the diversity of demographic characteristics coupled with our poor understanding of the basic biology of many coral reef fishes hinder our ability to manage these complex fisheries. The mostly straightforward responses of parrotfishes to exploitation on the basis of life-history traits were encouraging, and likely result from the strong relationship between body size and age (Choat and Robertson 2002). However, this pattern may not emerge for other families, particularly the Acanthuridae, which differ substantially in their demographic features (Choat and Robertson 2002). I therefore encourage future efforts to derive accurate age-based life-history information for multispecies assemblages in data-deficient and increasingly impacted regions.

Chapter 4: Drivers of protogynous sex change differ across spatial scales

Taylor, B. M. (2014) Drivers of protogynous sex change differ across spatial scales. *Proceedings of the Royal Society B: Biological Sciences* 281: 20132423. (doi: 10.1098/rspb.2013.2423)

Introduction

The increasing rate of fisheries exploitation, both commercial and artisanal, on coral reef populations is a matter of concern on a global basis (Jennings and Polunin 1996). Largely restricted to shallow water environments, coral reef fishes are considered to be especially vulnerable to expanded fishing activities. In addition, many targeted species are protogynous hermaphrodites (female to male sex transition), which is widely considered a defining feature of the vulnerability of reef fishes to size-selective exploitation (Hawkins and Roberts 2003). However, the demographic consequences of exploitation on protogynous populations and the extent to which anthropogenic influences on sex change schedules may be obscured by natural variation has yet to be clarified (Petersen and Warner 2002).

The mechanisms involved in protogynous sex change dynamics have been studied extensively for decades (Warner et al. 1975, Robertson and Warner 1978). Much of this work demonstrated the importance of social systems in determining when and why to change sex and this is largely dependent on or facilitated by local demography, mortality schedules of populations, or even habitat effects on various spatial scales (Warner and Hoffman 1980, Warner 1982, 1988a). Ultimately, what dictates the timing of sex change is the goal of maximising the reproductive value of individuals, and thereby the reproductive output of populations (Munday et al. 2006).

Protogynous hermaphroditism often results in the restriction of males to the larger size classes of a population. Hence, the impact of size-selective fishing on protogynous species is considered especially detrimental as selective removal of large individuals may deplete males to the extent that reproductive outputs of fished populations are compromised (Bannerot et al. 1987, Coleman et al. 2000). This argument generally assumes the length and age of sexual transition is fixed with the corollary that gonochoristic species have a greater capacity to respond to fishing pressure than protogynous species (Huntsman and Schaaf 1994, Alonzo and Mangel 2004). However, both experimental and observational studies have demonstrated a high adaptive capacity, especially in the labrids, to alter the timing of sex change in response to selective removal of individuals (Warner 1982, Warner and Swearer 1991, Hamilton et al. 2007). Although, this response may differ across species (Munday et al. 2006) and its utility as a compensatory mechanism when faced with heavy fishing pressure will be dependent on the intensity and extent of extraction on the population.

Another factor influencing the timing of sex change is the surrounding environment. Environmental effects on sex change and sexual demography in reef fishes have received little attention (Warner 1988b, Petersen and Warner 2002), despite substantial evidence for considerable intraspecific natural variation (Warner and Hoffman 1980, Cowen 1990, Gust 2004, DeMartini et al. 2005). Many environmental factors affect life-history traits either directly or indirectly by processes occurring across various spatial scales such as differences in temperature (e.g., latitudinal), quantity and distribution of habitats or resources, and density-dependent processes. However, much of this work has focused on smaller spatial scales (among habitats) whereas potential regional or larger patterns in widely-distributed species are necessary information for fisheries management (Pinca et al. 2012).

In this study I address three major questions: i) What is the hierarchical nature of drivers structuring length at sex change at different spatial scales? ii) How does selective pressure (e.g., fishery selection) influence sex change dynamics? and iii) Are general patterns from the above questions consistent across related species or are responses species-specific? This was done using high-resolution length estimates obtained from stereo-video surveys of parrotfishes at two spatial scales across oceanic islands. Islands ranged considerably both in reef habitat configuration as well as anthropogenic pressure. Responses to factors at differing scales will importantly influence the ability to predict or assess future changes, especially in data-poor tropical regions.

Methods

Study species and location

This study was conducted across seven islands in the biogeographic region of Micronesia. These included two high fringing island systems (Guam and Kosrae) with limited lagoon or backreef habitat, two high island barrier reef systems (Pohnpei and Yap) with extensive lagoon, reef flat, mangrove and backreef habitat and three atoll island systems (Sorol, Ifalik and Lamotrek; Fig. 4.1). The bullethead parrotfish *Chlorurus spilurus* is the most numerically common parrotfish species throughout Micronesia and many regions of the Indo-Pacific. It has two colour phases: females and primary males exhibit a brown initial-phase (IP) colouration that is highly distinct from that of large terminal-phase (TP) males which are bright blue-green to yellow. Most TP individuals are secondary males (have previously functioned as mature females) and all have undergone physical metamorphosis from IP colouration (Choat and Robertson, 1975). The confounding factor of IP primary males represents only a small proportion of IP individuals across Micronesian populations and does not affect estimates of sex change schedules (Fig. 4.2). Bullethead parrotfish are heavily targeted by fishermen on Guam where they comprise ~15% of the parrotfish landings in the recent decade (Guam Department of Agriculture, unpublished data). However, they are unfished or lightly harvested at the other islands (Rhodes et al. 2008, Houk et al. 2012).

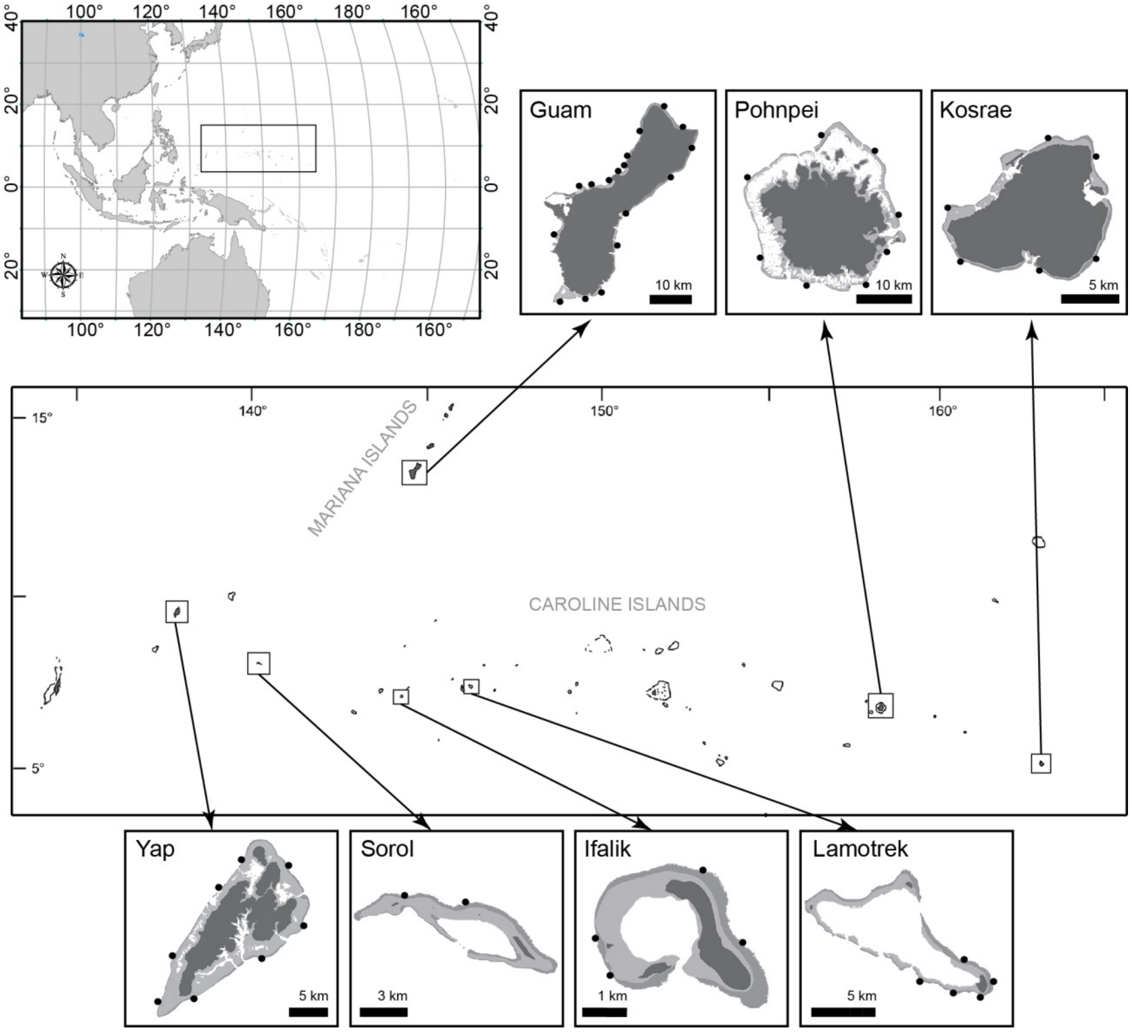

Figure 4.1. Spatial distribution of surveyed islands in Micronesia and maps of survey sites. All coordinates refer to the North (latitude) and East (longitude) hemispheres. Shading at each island refers to land (dark grey), reef flat and shallow lagoon (light grey) and outer reef habitats (intermediate grey).

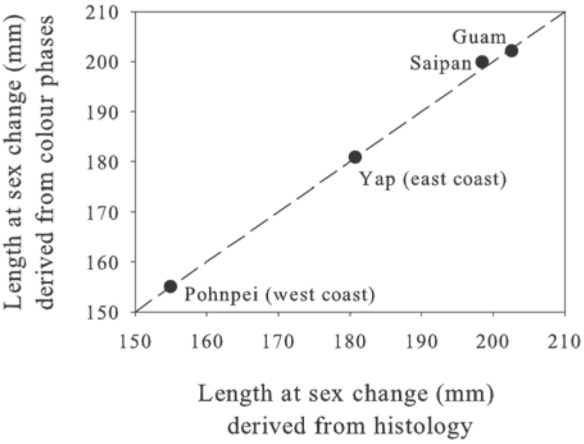

Figure 4.2. Relationship between estimates of length at sex change based on histological examination of gonads (initial phase [IP] primary males excluded; x-axis) and colour phase ratios by length class (IP primary males scored as females; y-axis) from biological specimens at four islands in Micronesia: Guam (4.3% of all IP are primary males; total n = 347), Saipan (5.1% IP primary males; Saipan is north of Guam in the Mariana islands but not included in the study; n = 48), Yap (4.5% IP primary males; n = 50), and Pohnpei (9.0% IP primary males; n = 50). Dashed line represents 1-to-1 ratio. Specimens were collected by spear on outer reef slopes at each island, stored in ice and processed immediately upon returning to the laboratory. Length at sex change was estimated by fitting a logistic curve to the proportion of secondary male (histological examination) or terminal phase (colour phase ratios) individuals by length class.

Population surveys

Bullethead parrotfish populations were surveyed at 50 sites on the outer reef slopes across the seven islands (Fig. 4.1). At each site, individuals were surveyed using diver-operated stereo video (Harvey and Shortis 1996) along 16 replicate transects (5 m wide by 3 minutes long, averaging 315 m^2) stratified at two depths (6-10 m and 18-22 m). Individuals were quantified, measured (mm fork length) and categorized by colour phase using the EventMeasure software (www.seagis.com.au). These surveys also provided estimates of operational density and sex ratio (density and sex ratio of individuals above mean length at female maturity; hereinafter ‘density’ and ‘sex ratio’). Length at 50% sex change (X_{50}) was estimated at each site by pooling the individual observations across transects and depths and fitting a logistic curve to the proportion of TP individuals in 10 mm length classes (average precision for length measurements was <10 mm). DeMartini et al. (2005) discussed the use of colour phases from visual surveys with centimetre-scale accuracy to estimate X_{50}. Stereo-video technology improves the resolution of length estimates by an order of magnitude compared with standard visual surveys (precision in millimetres versus centimetres).

For Guam, a site-specific fishing pressure index for parrotfishes was derived from historical creel survey data (survey protocols follow Malvestuto et al. 1978) collected since Jan 2001, when marine reserves were enforced, because the spatial distribution of fishing effort changed with the enforcement of five marine reserves. The index summed the total number of fishing trips targeting parrotfishes by sector, combining the shore-based (Hensley and Sherwood 1993) with the boat-based (Myers 1993) surveys, with shore-based values multiplied by a scaling factor (0.68) to account for differences in relative catch efficiency between the two fisheries. Site-specific values were divided by respective reef areas (km^2) and natural log-transformed.

Additional explanatory variables for each site included wave exposure (following Ekebom et al. 2003), reef slope (0 - 90°; mean of 3 measurements per transect), coral cover and rugosity (1 - 5 scale; mean of 5 estimates per transect), distance to reef pass (km), predator biomass, latitude and longitude. Predator biomass represented the mean biomass density of all species known or highly suspected to prey upon adults of smaller-bodied parrotfish species based on an exhaustive literature search regarding diets and length-weight ratios of all piscivores recorded during surveys.

Analysis

Two complementary statistical techniques (Hawkins 2012) were employed to model the response of length at sex change across sites. First, univariate regression trees (Breiman et al. 1984) were used to analyse the hierarchical structuring of variation in the response variable (X_{50}; square root-transformed) relative to the explanatory variables. This was done at the within-Guam level and the Micronesia level (among sites across islands). Fishing pressure was excluded from explanatory variables in the Micronesia-scale analysis because Guam is the only island where *C. spilurus* is heavily targeted, whereas island type (fringing, barrier or atoll reef system) was included as a factor. Cross validation of relative error (CVRE) was used to prune the trees.

I also fitted models to determine the combination of factors that best predicts X_{50} patterns for *C. spilurus* at the two scales. Across sites at Guam, where human extraction from fishing may have a strong effect on demographic processes, I fitted generalised linear models (GLM) with Gaussian errors and an identity link (Dobson 2002). Explanatory variables included the fishing pressure index and all environmental variables described above. At the Micronesia-scale, the nested structure called for linear mixed effects model (LME) analysis, where island (random factor) was nested within island type (fringing, atoll or lagoon reef system; fixed factor) and all environmental variables were included as fixed factors. Fishing pressure was again dropped from the explanatory variables at this scale, but special consideration regarding its effects is included in the interpretation of the results. Prior to fitting models, explanatory variables were tested for collinearity using variance inflation factors (Zuur et al. 2009) and variables with values over 3 were removed from the analysis. Coral cover and rugosity (highly collinear factors) were combined using values of the first principal component (explaining 94 and 89% of variance among them at the Guam and Micronesia scales, respectively) from a principal components analysis on the covariance matrix. The mixed model was fitted using the *lme* function of the *nlme* package in the R statistical computing language (Pinheiro et al. 2013). Model selection for the LME was done via multi-model averaging (Burnham and Anderson 2002) based on minimisation of corrected Akaike's Information Criterion (AICc) using the *dredge* function in the *MuMIn* package in R. The ten LME models with the lowest AICc values were refitted with restricted maximum likelihood estimation and model validation was carried out by plotting standardized residuals against fitted values to identify violation of homogeneity. Residuals were also plotted against explanatory variables to check for potential trends.

Finally, to determine whether potential trends across island types were specific to *C. spilurus* or were common among related species, I pooled observations of three other sexually dimorphic parrotfish species for which there was great enough resolution (*Scarus forsteni, S. schlegeli,* and *S. rubroviolaceus*) from video surveys at the island type scale and compared trends in X_{50} using boxplots based on 50 bootstrapped re-estimates from the sampled distributions. I also present X_{50} estimates for fringing (Guam) and barrier reef systems (Yap and Pohnpei pooled) from biological samples based on histological examination of gonads for a fourth species, *Chlorurus microrhinos*, which does not show strong phenotypic evidence of sexual transition.

Results

On Guam, X_{50} ranged considerably across sites from 185 to 244 mm fork length. The regression tree model indicates fishing pressure was the most important variable explaining this variation ($r^2 = 0.42$; Fig. 4.3a). Sites with higher fishing pressure had significantly smaller X_{50} values, suggesting that selective removal of TP males prompts sex change in smaller individuals. Results from the GLM differed slightly in that density was the best predictor of X_{50} across sites ($P = 0.0017$), whereas fishing pressure was next ($P = 0.0229$), followed by the coral-rugosity metric ($P = 0.0529$; Table 4.1). However, density and fishing pressure were considerably correlated ($r^2 = 0.32$) on Guam despite variance inflation factors indicating low collinearity.

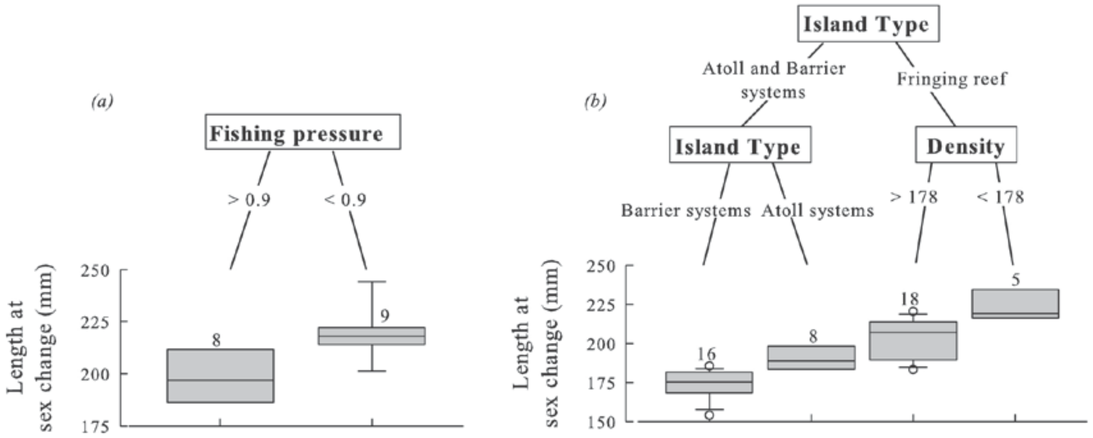

Figure 4.3. Regression tree analysis describing variation in length at sex change for *Chlorurus spilurus* a) among sites on Guam and b) among sites across seven islands in Micronesia. Density refers to density of reproductive individuals per hectare and Fishing pressure refers to values of the fishing pressure index (ranging from 0.08 to 1.93). Numbers above plots refer to sample sizes of sites for each terminal node.

Table 4.1. Parameters for generalized linear models predicting the length at sex change for *Chlorurus spilurus* across 17 sites on Guam. (See text for parameter descriptions.)

Model	Variable	Intercept	Coefficient	Std	DF	Z	P	AICc
GLM1	Density	15.1	-0.0015	0.0004	16	-3.81	0.0017	22.7
GLM2	Fishing Pressure	14.7	-0.0008	0.0003	16	-2.53	0.0229	28.2
GLM3	Coral-Rugosity	14.5	-0.2431	0.1157	16	-2.10	0.0529	29.8

Among islands, X_{50} values ranged from 154 to 244 mm fork length (Fig. 4.4a). Three sites at Lamotrek contained *C. spilurus* abundances too low to estimate X_{50}. At this scale, island configuration appeared to be driving most of the variation in the response variable (Fig. 4.4b), and a nested analysis of variance demonstrated significant differences in X_{50} among island types ($F_{2,40} = 36.27$, $P < 0.0001$) but not among islands nested within island types ($F_{4,40} = 1.96$, $P = 0.119$). Regression tree analysis confirms the hierarchical structuring of variation based on island type (Fig. 4.3b), in which the optimal model based on CVRE was the split between fringing reef systems and atoll and barrier reef systems. I display additional splits, which further separated the data by island type (atolls versus barrier reef systems) and by density within fringing reef systems.

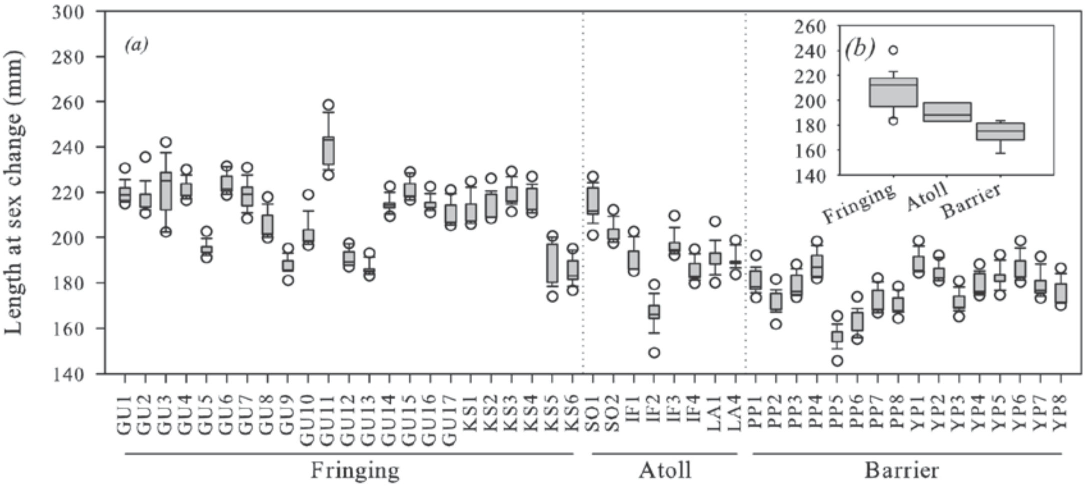

Figure 4.4. (a) Distribution of length at sex change values for *Chlorurus spilurus* across sites. Boxplots based on 50 bootstrapped re-estimates of samples from each site. (b) Boxplots summarizing length at sex change values at different island types. Open circles indicate 5th and 95th percentiles throughout. Atoll, barrier and fringing refer to island type classifications associated with each site.

Of the ten optimal LME models, four were eliminated based on outliers or low homogeneity in residual plots. The remaining six models shared a common feature in that density, island type and the interaction between these were always included (Table 4.2). Island type was significant in every case, indicating that the response of X_{50} is dependent on island configuration (Table 4.3). While density was never significant, the interaction between density and island type always was, suggesting that the relationship between X_{50} and density varies by island type, thus necessitating further examination (Table 4.3). Other factors emerging in models included coral-rugosity, reef slope, and wave exposure (Table 4.2). These factors were important at the within-island scale and varied in importance among islands.

Table 4.2. Model structure for the six optimal linear mixed-effects (LME) models predicting length at sex change for *Chlorurus spilurus* across 47 sites on seven islands in Micronesia. Parameter significance values are provided in Table 4.3.

Model	Structure	Log-likelihood	AICc
LME1	Density*Isl_Type + Coral-Rugosity + Slope	-17.76	61.6
LME2	Density*Isl_Type + Slope	-19.45	61.8
LME3	Density*Isl_Type + Coral-Rugosity	-19.74	62.3
LME4	Density*Isl_Type	-21.57	62.9
LME5	Density*Isl_Type + Wave exposure	-20.25	63.4
LME6	Density*Isl_Type + Coral-Rugosity + Wave exposure	-18.82	63.8

Table 4.3. Parameters and significance values for the six optimal linear mixed effects (LME) models predicting the length at sex change for *Chlorurus spilurus* across sites and islands in Micronesia.. P-values in **bold** are significant at the 0.05 level.

a) LME1	Variable	numDF	denDF	F	P	
	Intercept	1	35	15006.86	**<0.0001**	Log-
	Density	1	35	0.68	0.4165	likelihood = -17.76
	Island type	2	4	10.88	**0.0241**	AICc = 61.6
	Coral-Rugosity	1	35	3.05	0.0897	
	Slope	1	35	11.08	**0.0021**	
	Density*Isl_type	2	35	4.11	**0.0249**	
b) LME2	Variable	numDF	denDF	F	P	
	Intercept	1	36	17194.21	**<0.0001**	Log-
	Density	1	36	1.22	0.2760	likelihood = -19.45
	Island type	2	4	11.89	**0.0207**	AICc = 61.8
	Slope	1	36	10.44	**0.0026**	
	Density*Isl_type	2	36	4.33	**0.0206**	
c) LME3	Variable	numDF	denDF	F	P	
	Intercept	1	36	14482.05	**<0.0001**	Log-
	Density	1	36	1.55	0.2212	likelihood = -19.74
	Island type	2	4	9.83	**0.0286**	AICc = 62.3
	Coral-Rugosity	1	36	3.20	0.0820	
	Density*Isl_type	2	36	7.26	**0.0022**	
d) LME4	Variable	numDF	denDF	F	P	
	Intercept	1	37	13937.13	**<0.0001**	Log-
	Density	1	37	1.54	0.2232	likelihood = -21.57
	Island type	2	4	9.45	**0.0305**	AICc = 62.9
	Density*Isl_type	2	37	7.60	**0.0017**	
e) LME5	Variable	numDF	denDF	F	P	
	Intercept	1	36	14926.15	**<0.0001**	Log-
	Density	1	36	1.49	0.2305	likelihood = -20.25
	Island type	2	4	10.17	**0.0270**	AICc = 63.4
	Wave exposure	1	36	11.03	**0.0021**	
	Density*Isl_type	2	36	3.42	**0.0437**	
	Variable	numDF	denDF	F	P	
f) LME6	Intercept	1	35	15306.01	**<0.0001**	Log-
	Density	1	35	1.49	0.2297	likelihood = -18.82
	Island type	2	4	10.44	**0.0259**	AICc = 63.8
	Coral-Rugosity	1	35	3.24	0.0807	
	Wave exposure	1	35	9.76	**0.0036**	
	Density*Isl_type	2	35	3.44	**0.0434**	

There was an overall positive relationship between density and sex ratio across sites and this strengthened within island types (Fig. 4.5a), where fringing reef systems (particularly Guam sites) stood apart from atoll and barrier reef systems. Plots of X_{50} by density reiterate that the response of X_{50} is dependent on island type, but also highlight the interaction between density and island type (Fig. 4.5b). The relationship (expressed by the slope) between density and X_{50} is positive for atoll and barrier reef systems as well as for Kosrae (fringing reef system, although variation among the six Kosrae sites is too high for definitive conclusion), whereas on Guam, where *C. spilurus* is heavily targeted, this relationship was reversed. The same patterns were observed for relationships between sex ratio and X_{50}, where Guam not only stands apart in terms of a negative correlation, but also has a much higher range of sex ratios indicating greater proportions of IP individuals.

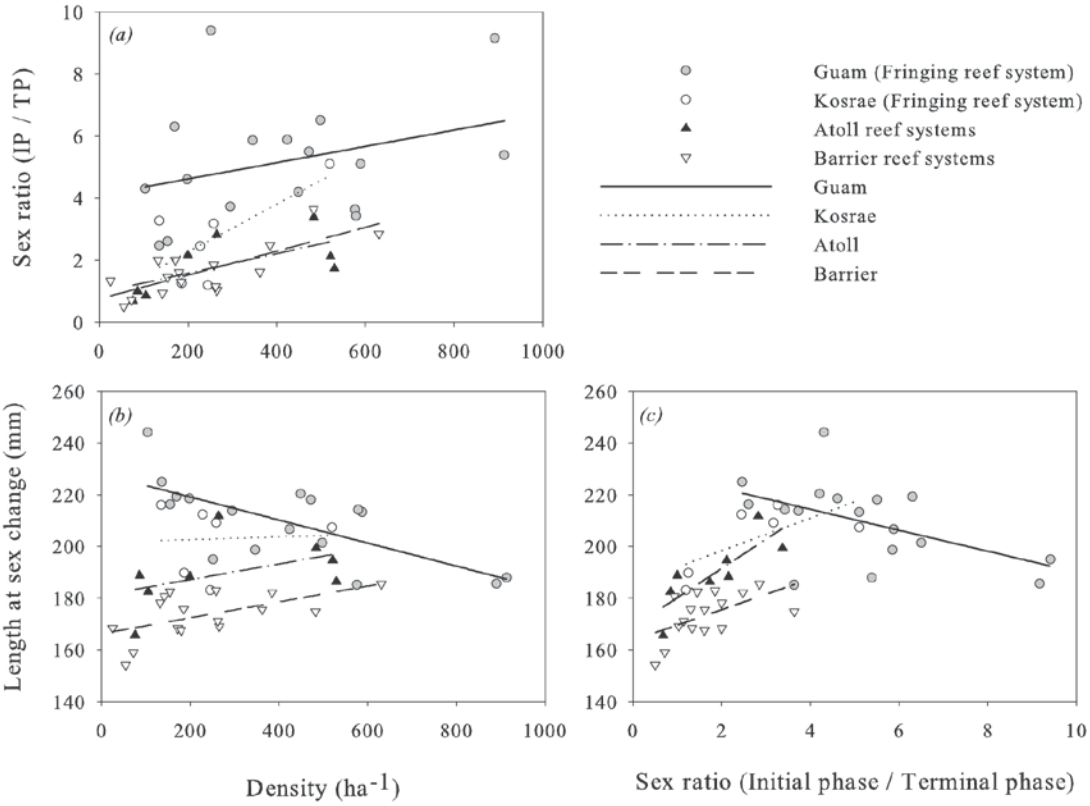

Figure 4.5. Relationships between (a) density and sex ratio, (b) density and length at sex change and (c) sex ratio and length at sex change for *Chlorurus spilurus* at different island types in Micronesia. Fringing reef systems Guam and Kosrae are separated to highlight the different selective pressures between them.

Data for other species pooled at the island type scale demonstrates that the major pattern observed for *C. spilurus* (X_{50} at Fringing reef systems >> X_{50} at atoll reef systems > X_{50} at barrier reef systems) is consistent across related species (Fig. 4.6). One minor exception was *S. forsteni*, for which X_{50} was greater at barrier than at atoll reef systems. Overall, the response of X_{50} appears to be dependent on island configuration in a very similar manner across all parrotfishes evaluated.

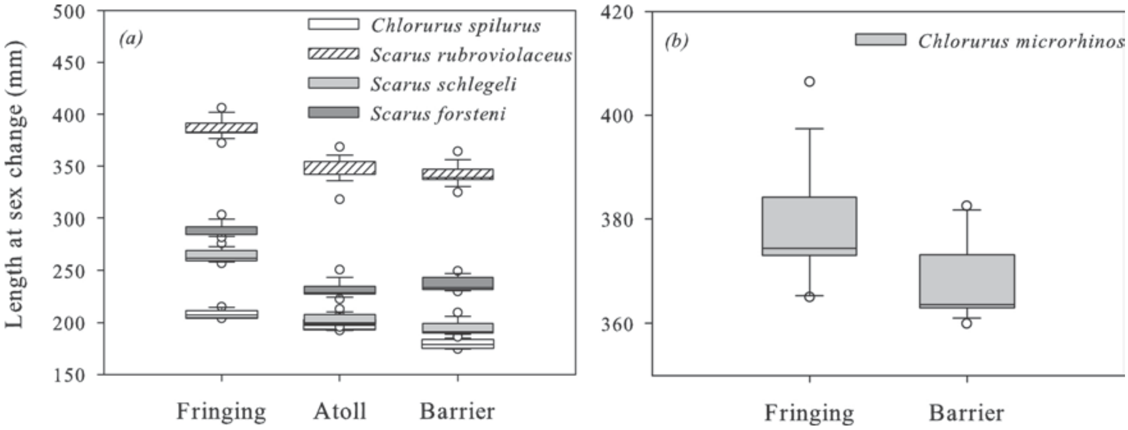

Figure 4.6. Length at sex change of (a) *Chlorurus spilurus, Scarus rubroviolaceus*, *Scarus schlegeli* and *Scarus forsteni* based on stereo-video length measurements and (b) *Chlorurus microrhinos* based on histological assessment of gonads from biological samples. Data are pooled across sites and islands within island types. Boxplots based on 50 bootstrapped re-estimates from population samples and open circles indicate 5th and 95th percentiles.

Discussion

A substantial number of studies have demonstrated latitudinal and temperature effects on patterns of life-history variation (Atkinson 1994, Robertson et al. 2005, Trip et al. 2008). On smaller spatial scales, sexual demography and the timing of sex change have been shown to vary in coral reef fishes across different reef configurations and reef sizes (Warner et al. 1975, Warner and Hoffman 1980, Gust 2004). Here, results demonstrate a clear effect of reef configuration among oceanic islands on the timing of sex change in parrotfishes over broad spatial scales (1000s kms) that overrides the effects of latitude, fishing pressure and local-scale environmental factors. This highlights the inherent intraspecific plasticity in life-history traits and challenges the overlooked assumption that these traits are equivalent across oceanic islands within a biogeographic region. There are strong implications for assessments of fishing effects, given that potential impacts of fishing on demographic processes are obscured by the strong effect of island type, leaving limited potential for inference across islands. Thus, comparisons of traits among populations with respect to potential fishing effects are precluded unless these differences in reef structure and configuration are adequately controlled by survey design (DeMartini et al. 2008) or statistical analysis.

The magnitude of the perceived island-effect on the timing of sex change was unexpected. Given the distribution of islands surveyed, the observed patterns reflect locality-specific adaptive responses to local environments and differential selective pressures unique to each island type. However, the proximal mechanism driving the observed differences will be difficult to isolate. The island types considered here can be qualitatively defined by their diversity and relative proportions of various habitats present. The presence, scale and proximity of particular habitats have a strong influence on the diversity and carrying capacity of reef fish assemblages (Williams 1991, Mumby et al. 2004) and analysis of fish communities on oceanic islands throughout the Pacific reveals predictable structuring of trophic groups based on the island types described here (Pinca et al. 2012). In particular, Pinca et al. (2012) found that, after partialling out the effects of fishing, parrotfish density and biomass was positively related to barrier reef systems with lagoons and negatively related to atolls and low complexity fringing reef systems, whereas fringing reefs supported greater mean body sizes. Specific habitats prevalent in wave-protected environments like lagoons provide major nursery habitat for many parrotfishes, including *C. spilurus* (Adam et al. 2011, DeMartini et al. 2013), and therefore may boost abundance potential for adults. Interspecific density-dependent processes such as competition and predation have considerable effects on population demography and likely influence the social mating systems distinctively at each island type (Gust 2004). Further, the high correlation between length at sex change and other length-based life-history metrics in Micronesian parrotfishes (Taylor and Choat, 2014 [Chapter 2]) suggests that similar patterns would be observed for other variables including length at maturity and mean maximum length.

While potential demographic responses to heavy fishing were subordinate to island-effects, responses to fishing pressure were clearly evident at the within-island scale. On Guam, where *C. spilurus* has been increasingly targeted over the past decade, there was a significant decline in length at sex change at sites of heavy fishing pressure, indicating a compensatory response to the disproportionate targeting of larger TP males (Warner and Swearer 1991). The level of the response suggests a high adaptive capacity to fishery extraction at this scale, although the differences remain less pronounced than those among island types. The timing of sex change is heavily influenced by the relative size of individuals, the sex ratio of social groups and local density (Munday et al. 2006), and the plots in Fig. 4.5 illustrate several interesting effects of fishery extraction on these relationships. The fringing reef systems Guam and Kosrae stand apart with the highest values of X_{50}, but Guam differs from all islands with respect to range of sex ratios and the relationships between X_{50}, density and sex ratio, which implies that differing selective pressures (i.e., fishery selection versus natural selection) can significantly alter the dynamics of sex change and possibly those of other life history traits. Hence, the significant interaction identified in LME models was driven by differences in selection pressures among island types, where Guam dominated the response in fringing reef systems.

The high abundance and almost ubiquitous distribution of *C. spilurus* across sites facilitated high-resolution analysis of sex change parameters at two very different spatial scales. Obviously, this is difficult to achieve for less abundant species without greatly increasing the sampling effort within each site (surveys already covered over

5000 m^2 of reef area on average). However, pooled data for other parrotfish species strongly suggests that the patterns identified among island types are consistent across related species, especially in that length at sex change is greatest at fringing reef systems where adult densities in part may be relatively low because of reduced replenishment resulting from less local nursery habitat. These species have a range of life histories (Taylor and Choat 2014 [Chapter 2]) and, across all the islands, are subject to variable exploitation levels from light (*C. spilurus* and *S. schlegeli*) to intense (*S. rubroviolaceus* and *C. microrhinos*) fishing pressures. As sexually dimorphic protogynes there is a consistent fisher targeting of large males. For the most heavily targeted species *C. microrhinos*, the length distribution from the heavily fished Guam population was severely truncated compared with Yap and Pohnpei, whereas a greater length at sex change was still observed on Guam (Fig. 4.7). This again highlights that observed island-effects override potential fishing effects but further analysis of the plasticity among species is warranted. Peterson and Warner (2002) stressed that our knowledge of flexibility in sex change stems mainly from higher-density small reef fishes whereas the capacity for adaptation in life history traits is of prime importance in larger fishery species. Experimental work on small reef fishes (Warner 1982, Warner and Swearer 1991) and within-island demographic data from the present study demonstrate a high capacity for altering the timing of sex change following selective male removal, but examples from aggregating groupers (Bannerot et al. 1987, McGovern et al. 1998) suggest that the capacity for sex ratio compensation after heavy fishing may be low. A plausible explanation is that potential flexibility in traits is dependent on the life history of the species considered. Longer-lived, later maturing species like many groupers have a lower turnover rate and will therefore respond to changes in population structure at a slower pace. However, responses will always be dependent on the scale, intensity and selectivity of the fishery extraction on a given population, which may hinder generalizations from the limited existing examples.

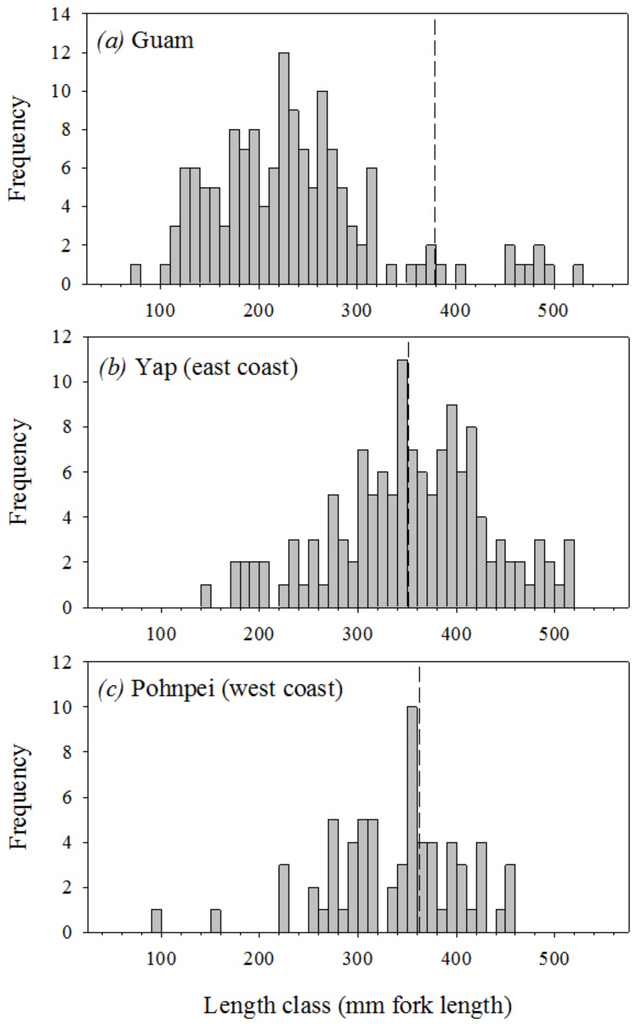

Fig. 4.7. Length-frequency distributions of *Chlorurus microrhinos* from (a) Guam, (b) Yap and (c) Pohnpei from diver-operated stereo-video surveys. Dashed lines represent the mean length at sex change for each population, derived from histological analysis of (a) 80, (b) 48 and (c) 75 specimens across the maturation and sex transition length range. Specimens were collected by fishery-independent sampling on outer reef slopes at each island. Length at sex change was estimated by fitting a logistic curve to the proportion of secondary male individuals by length class (primary males were excluded).

The LME models identified several other factors influencing variation in X_{50} including coral-rugosity, reef slope and wave exposure. The effects of these factors were apparent at the within-island scale and were not consistent across islands or island types, but rather varied among them. For example, exposure and slope had a strong correlative relationship with X_{50} on Pohnpei, whereas that with the coral-rugosity metric was weak. On Yap, these relationships were reversed. On Guam, potential effects of environmental variables were obscured by fishing effects. Interestingly, predator biomass did not emerge as an important predictor as seen in other studies (DeMartini et al. 2005, 2008), although the estimated range of predator biomass values in those studies were 1-2 orders of magnitude greater than observed here, suggesting top-down influence on demography of prey may be weak across many sites in the present study. Sample replication was not high enough on other islands to make similar conclusions but the results at this scale demonstrate that environmental factors can have variable effects on population demography among islands, and this likely reflects inherent differences in habitat structure (specifically, the value range of each factor) at each island.

Understanding the variation in demographic traits across multiple spatial scales is recognized as a management priority (Choat et al. 2003). This study demonstrates that while selective fishing can have a profound effect on traits, inherent differences based on reefal-scale environmental properties may obscure these effects at broader spatial scales. However, this represents only a piece of a much larger puzzle which extends beyond oligotrophic oceanic island systems to include continental reef systems as well as intra-island habitat effects and an underlying effect of historical biogeography that influences the distribution, ecology and demography of coral reef fishes. Studies of both environmental and fishery-induced effects on populations understandably avoid large spatial-scale surveys because of logistical concerns and low statistical power (Jennings and Kaiser 1998). But multi-scale processes in coral reef ecology remain an important gap in our knowledge base that has been acknowledged for over a decade (Sale 1998, Petersen and Warner 2002, Munday et al. 2006).

Chapter 5: Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities

Taylor, B. M., Lindfield, S., Choat, J. H. (in press) Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. *Ecography* (doi:10.1111/ecog.01093)

Introduction

The structuring of biological communities varies at different spatial scales (Wiens 1989). Within biogeographic regions, the hierarchical influence of physical, biological and anthropogenic factors yield community-level responses distributed in patches across the landscape. The resultant heterogeneity is an important feature in the maintenance of biodiversity (Levin 2000) and ecological flexibility (Bellwood and Hughes 2001). Hence, multiscale processes and their influence on species distribution and abundance patterns are of major importance to ecologists (Legendre 1993).

A key objective in spatial ecology is to understand the relative influence of ecosystem drivers and their hierarchy. While species complexes have evolved under and are continuously subject to the constraints of their physical and biotic environment, these processes are subject to major influences through the ongoing expansion of human populations (Vitousek et al. 1997). In particular, human extraction in the marine environment has influenced biological communities for thousands of years, yet our quantitative understanding of marine biota has only developed in the last century (Jackson et al. 2001). This has included the intensive study of effects of fishing over recent decades (reviewed in Jennings and Kaiser 1998, Jackson et al. 2001, Pauly et al. 2005). In this context, long-term data sets provide the most acute insights to potential fishing effects on species assemblages, but such data sets are scarce and often cover small areas, thus limiting inference to the perceivable effects over broader spatial scales. Instead, the partitioning of variance components across spatially structured communities has provided promising insights to the relative influences of fishing and environment (Borcard et al. 1992).

Coral reefs across small oceanic islands are a prime, if not extreme example of spatial heterogeneity in biological systems (Sale 1998). These ecosystems represent isolated patches of highly diverse biotic communities structured by the presence or absence of various habitat types (Friedlander and Parrish 1998) and interconnected by larval dispersal at various levels depending on biological processes and ocean conditions. On coral reefs worldwide, parrotfishes (Labridae; tribe Scarinae) are a ubiquitous component and are ideal subjects for addressing questions of community ecology for several reasons, including their relatively high diversity, conspicuous nature and their considerable abundance of many species within similar habitats. Previous studies have found parrotfishes to be habitat generalists, in that assemblage structure and biomass are poorly correlated with differences in substrata, but better predicted by wave exposure and shelf position (Gust et al. 2001, Gust 2002). At broader spatial scales (among oceanic islands), demographic processes are driven by island geomorphology, whereas the effects of fishing materialize within islands (Taylor 2014 [Chapter 4]). In recent decades, parrotfishes have emerged as a major fisheries resource throughout the tropics, escalating concerns for their sustainability and their functional role as grazers and bioeroders of reef substrate (Bellwood et al. 2012, D’agata et al. 2014). Parrotfishes typically demonstrate a weak response to fishing in areas where higher trophic-level species dominate the fishery

(Russ and Alcala 1998, Jennings et al. 1999b), but strong species-level responses to fishing pressure (Clua and Legendre 2008) driven by differing life histories among species suggest a high capacity for fishing-induced changes in parrotfish assemblages (Taylor et al. 2014 [Chapter 3]). The magnitude of this effect at different spatial scales is poorly known.

This study presents a multi-scale examination of patterns in parrotfish assemblage structure and size distribution across eight oceanic islands of Micronesia. A primary objective was to determine the amount of spatial variation in species composition that is related to environmental, anthropogenic, or geographic factors. In addition, given that Taylor (2014 [Chapter 4]) identified strong differences in demographic rates at broad scales driven by island geomorphology, I modelled variation in fish length estimates, species richness and phylogenetic diversity across the same scale to determine the relative influence of fishing as these metrics have been demonstrated to change more rapidly under intense fishery extraction compared to life-history traits (Jennings and Kaiser 1998). I hypothesize that assemblage structure, mean fish size, species richness and diversity will be hierarchically structured across space, with the influence of fishing pressure emerging significantly only at small spatial scales (within islands or distinct island types).

Methods

Study area

I surveyed parrotfish assemblages at eight islands across Micronesia spanning 8° latitude and 25° longitude. These included seven islands in the Caroline island chain (Federated States of Micronesia) and one island from the Mariana archipelago (Fig. 5.1). Island types were classified based on geological features producing unique diversities and relative proportions of finer-scale habitats. These included two high fringing island systems (Guam [Mariana] and Kosrae) with limited lagoon or backreef habitat; two high-island barrier reef systems (Yap and Pohnpei) with extensive lagoon, reef flat, mangrove and backreef habitat; three atoll island systems (Sorol, Ifalik [historically Ifaluk] and Lamotrek) and one low coral island with a small fringing reef (Satawal). Human population densities ranged from 0 (Sorol, uninhabited) to over 1000 people per km^2 of reef area (Guam; Table 5.1).

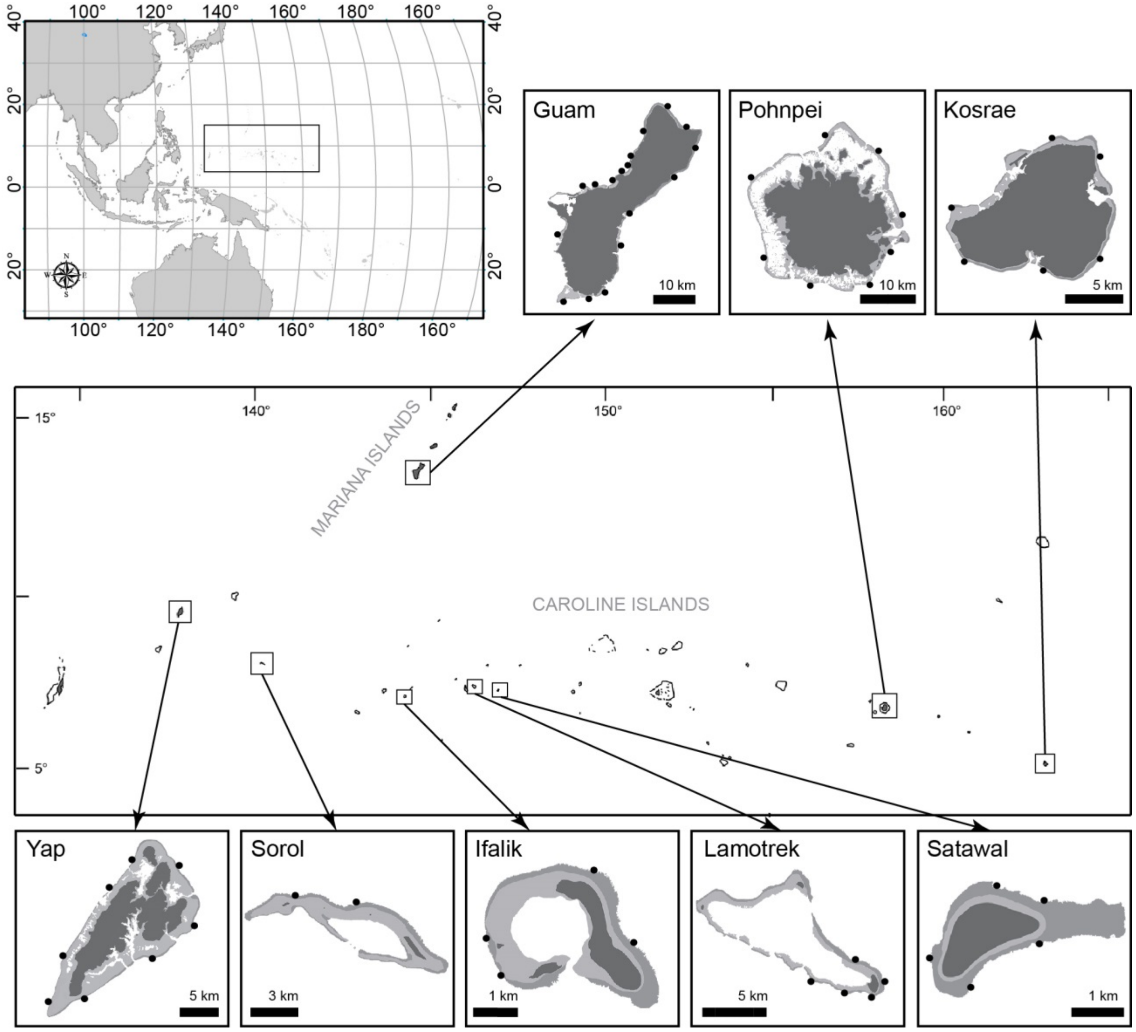

Figure 5.1. Locations of 55 sites across eight islands in Micronesia where surveys for parrotfishes were conducted.

Table 5.1. Summary of human and broad scale geomorphologic metrics for each of eight Micronesian islands surveyed.

Island	**Population (2010)**	**Coral reef area (km2)**	**Geomorphology**	**Land area (km^2)**	**Range of fishing pressure values (people km^{-2})**
Guam	159358	137	High island, fringing reef system	540	19-1383
Ifalik	578	5	Atoll reef system	1.4	70-105
Kosrae	6616	21	High island, fringing reef system	110	166-305
Lamotrek	329	17	Atoll reef system	0.9	27-40
Pohnpei	34574	150	High island, barrier reef system	345	0-382
Satawal	501	2	Low coral island reef system	1.2	147-221
Sorol	0	14	Atoll reef system	0.9	0-0
Yap	7370	106	High island, barrier reef system	118	0-76

Surveys

Demographic surveys of parrotfishes were conducted at 55 sites across the eight islands (Fig. 5.1) to quantify abundance and biomass using diver-operated stereo-video (Harvey et al. 2010). At each site, 16 replicate timed-swim transects (5 m wide by 3 min long, averaging 315 m^2) were stratified at two depths (6-10 m and 18-22 m). Within any video frame, fish within 8 m in front and 2.5 m either side of the camera trajectory were included in the transect. Individual parrotfishes within transects were identified to species, categorized by colour phase, and measured to the nearest millimetre (fork length) using the EventMeasure software (www.seagis.com.au). Predatory fish species were also quantified and these included all species known or highly suspected to prey upon adults of smaller-bodied parrotfish species based on an exhaustive literature search regarding diets and length-weight ratios of all piscivores recorded during surveys.

Individual fish lengths were converted to biomass (kg) using species-specific length-weight relationships derived primarily from biological samples (Taylor and Choat 2014 [Chapter 2]) or from the FishBase database (Froese and Pauly 2011). Environmental variables were also quantified from video transect frames. These included reef slope (0-90°; mean of three measurements per transect), live coral cover and substrate rugosity (1-5 scale; mean of five estimates per transect), and predator biomass. Replicates of reef slope were measured to the degree using a protractor on randomly selected video frames. Live coral cover and substrate rugosity were estimated from a visual appraisal of the survey area following the procedure described by Wilson et al. (2007). This approach correlates well with line-intercept transects for benthic composition and chain-measured rugosity, reef height and number of holes in the reef substrate (Wilson et al. 2007). Predator biomass represented the mean biomass density (kg $hectare^{-1}$) of all predator species. Other site-specific explanatory variables included wave exposure (following

Ekebom et al. 2003), geographical position (latitude and longitude), island type (n = 4; described above), fishery market type (no fishery, subsistence, commercial or commercial export), and fishing pressure (described below).

For the Caroline Islands, site-specific fishing pressure values were calculated as the human population of adjacent municipalities divided by the associated reef area (km^2). Values were adjusted (reduced by one-third), based on discussions with fishermen and island chiefs, at windward sites with high wave exposure to account for the reduced fishing pressure where conditions are more dangerous for approximately half of the calendar year. Kronen et al. (2010) found population density to be the optimal predictor of fishing pressure for Pacific island communities that had a high dependence on marine resources. Within the Caroline islands, reef fishing activities are considerably localized, particularly for Yap and the three atoll systems which maintain a traditional tenure system where fishing rights for a reef belong to the adjacent municipality (Kronen and Tafileichig 2008). At Pohnpei and Kosrae, marine resources are accessible to fishers from other villages, however the mean distance fishers travel is within the scale of municipality boundaries at these islands (Rhodes et al. 2011). Because of the expanded use of engine-powered boats and multiple launching facilities on Guam, the distribution of fishing effort is not related to adjacent population density. Hence, fishing pressure values for Guam sites were derived from historical creel survey data collected by the Guam Department of Aquatic and Wildlife Resources between 2001 and 2010 (survey protocols following Malvestutuo et al. 1978). The index summed the total number of fishing trips targeting parrotfishes by sector, combining the shore-based (Hensley and Sherwood 1993) with the boat-based (Myers 1993) surveys. Shore-based values were multiplied by a scaling factor to account for differences in relative catch efficiency between the two fisheries. Site-specific fishing pressure values were divided by the associated reef area (km^2). Guam values were incorporated with the other islands by scaling them based on island population densities (people km^{-2} reef area) as well as per capita consumption rates of reef fishes, the latter of which is considerably lower in Guam compared with other islands (Rhodes et al. 2011). Some inherent bias is likely from the combination of these metrics; however, estimates were based on high-resolution socio-economic data (Rhodes et al. 2011; 2010 government population census) and weekly creel survey data spanning a decade.

Analysis

Assemblage structure

I tested the spatial structuring in parrotfish assemblages across Micronesia by evaluating the normalized Mantel statistic r_M for detrended abundance and biomass datasets. This was performed across six distance classes spanning the distribution of study sites using a multivariate Mantel correlogram (Oden and Sokal 1986). Correlations at each distance class were tested for significance using 999 permutations.

Patterns of assemblage structure in parrotfish communities and driving factors were assessed and related using redundancy analysis (RDA; van den Wollonberg 1977). Abundance and biomass densities of species per hectare were hellinger-transformed to account for zero values in assemblage composition data. Numeric explanatory variables were transformed accordingly to promote normality (natural log transformation: reef slope, predator biomass; natural log(x + 10): fishing pressure) and variables were centred and standardized prior to multivariate analysis. Four subsets of explanatory variables were delineated for partitioning of variance: 1) biophysical environment (wave exposure, reef slope, coral cover, rugosity and predator biomass), 2) island geomorphology (island type), 3) geography (latitude and longitude), and 4) fishing impact (fishery market and site-specific fishing pressure index). Collinearity among explanatory variables was checked using variance inflation factors (Neter et al. 1996). Coral cover and rugosity (highly collinear factors) were combined by using values of the first principal component (explaining 90% of the variance among them) from a principal components analysis on the covariance matrix (hereinafter coral.rugosity).

I suspected from prior knowledge that species distributions across the region (specifically between the Mariana and Caroline island groups) may cause spatial structuring. Hence, RDA analysis was followed by partial RDA (pRDA) to reassess correlations among parrotfish assemblage structure and environmental factors while controlling for the influence of structuring across geographic space. I further measured the relative importance of the four subsets of explanatory variables through variance partitioning to extract the shared and independent variance portions explained by each subset (Borcard et al. 1992). Permutation tests were used to determine the significance level of each portion.

Parsimonious reduction of explanatory variables was performed on the model using forward, backward and stepwise selection methods. When resulting models differed, the optimal was selected based on the lowest Akaike’s information criterion (AIC) value. This was performed not to improve the original model, but rather to assess which variables within subsets were most or least important at the among-island scale. RDA analyses were repeated at the within-island scale (among sites within islands) and within-geomorphology scale to re-evaluate the influence of factors at smaller scales and the consistency of patterns. To avoid low samples sizes, this was only performed among sites on Guam, and among sites at atoll reef systems. On Guam, an additional categorical variable was included (Adjacent habitat: lagoon, reef flat, fringing landmass) as Guam was the only island to contain a considerable variety of habitats adjacent to reef slopes.

Mean length, phylogenetic diversity and species richness

I fitted models to determine the factors that best predict mean fish length, phylogenetic diversity and species richness of Micronesian parrotfish assemblages at biogeographic scales. Linear mixed effects (LME) models, with island (random factor) nested within island type (fixed factor) and all other explanatory variables as fixed factors, were used to account for non-independence given the hierarchical structure of data from surveys of oceanic islands (Qian et al. 2010). Response variables were mean parrotfish lengths for each site pooled across species (both including and excluding *Bolbometopon muricatum*, whose minimum length from surveys exceeded the largest parrotfish recorded from all other species), phylogenetic diversity (biomass- and abundance-weighted), and species richness (number of species by site). Phylogenetic diversity for each site was computed using the phylogenetic entropy index (Allen et al. 2009) and was based on the parrotfish phylogeny presented in Choat et al. (2012; Fig. 5.2). The mixed models were fitted with all explanatory variables and subsequent model selection was done via multi-model averaging (Burnham and Anderson 2002). Relative performance of the resultant model combinations was assessed using the corrected AIC (AICc) and models within 2 AICc of the optimum were evaluated. The mean length analysis was repeated at the species level for five widespread and abundant species (*Chlorurus microrhinos*, *Chlorurus spilurus* [formerly *sordidus*], *Scarus forsteni*, *Scarus rubroviolaceus* and *Scarus schlegeli*) to explore both inter- and intra-specific patterns.

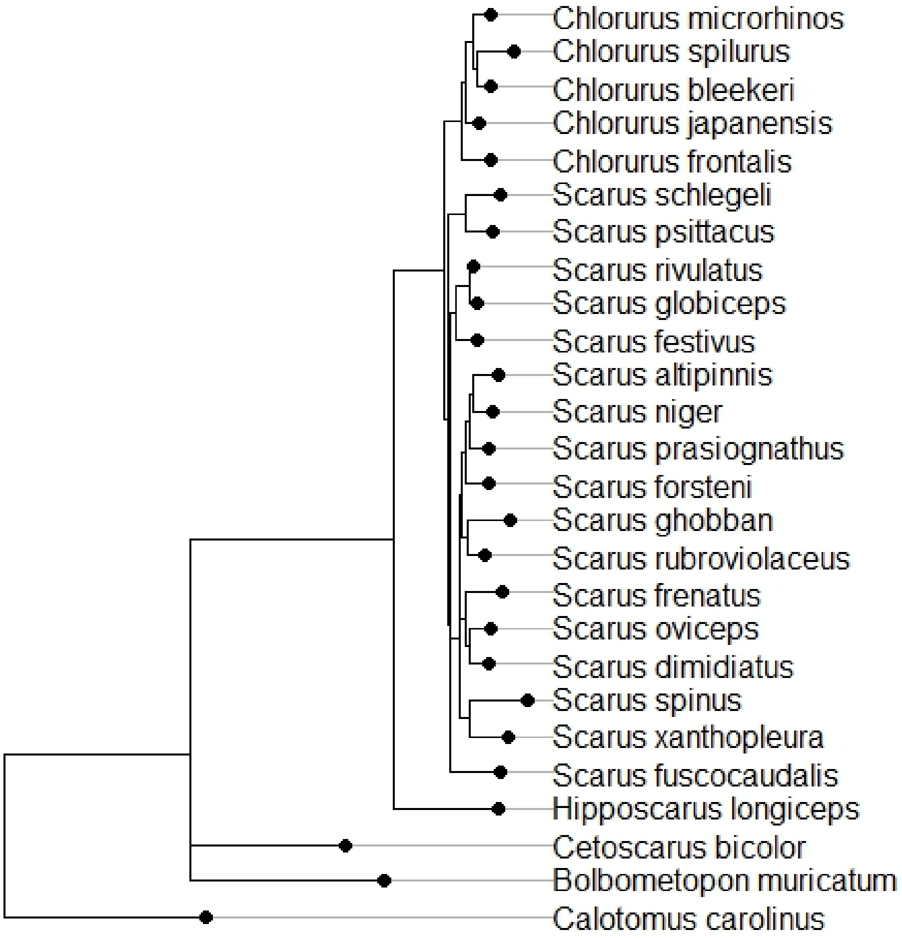

Figure 5.2. Phylogenetic tree of 26 parrotfish species surveyed in Micronesia. This reduced tree was derived from Choat et al. (2012) and was used in calculations of phylogenetic diversity.

Results

Assemblage structure

A total of 26 species of scarine labrids representing six genera were recorded in surveys (Fig. 5.2). Results from the Mantel correlogram indicate significant positive correlation in the first distance class (among sites within islands; $P = 0.001$), significant negative correlation in the second distance class (mean distance between nearest neighbouring islands; $P = 0.023$), and significant negative correlation in the fifth distance class (mean distance between Mariana and Caroline island chains; $P = 0.005$). RDA analysis of assemblages based on species abundance patterns returned five significant axes explaining 58% of the total variation (adjusted r^2). The first two axes accounted for, respectively, 32 and 18% of the total explained variation. Sites from islands Guam (fringing reef system) and Satawal (low coral island) were independently separated from remaining sites (Fig. 5.3a). Guam’s separation correlated with latitude (as a proxy for disjunct species distributions among the Mariana and Caroline islands) and site scores correlated negatively with abundance of *Scarus niger* (a species very common in the Carolines but virtually nonexistent in the Mariana Islands) along the RDA 1 axis whereas Satawal’s separation was driven by its unique island type along the second axis (Fig. 5.3a). Further separation existed between atoll and barrier reef systems while Kosrae (high fringing reef system) clustered with barrier systems Yap and Pohnpei. Relationships among sites were more perceptible when spatial effects (latitude and longitude variables) were partialled out (Fig. 5.3b). Once geographic trends were accounted for, the structuring of assemblages relative to island geomorphology was highly apparent along both axes. The low coral island Satawal remained separated, now along the first axis, and its separation was driven by unusually low abundances of *C. spilurus* and a greater proportion of *S. rubroviolaceus* at these sites. Guam no longer stood apart, however, but rather clustered with the other high fringing reef system Kosrae along the second RDA axis which delineated atoll, fringing and barrier reef systems (Fig. 5.3b). Differences within these systems were driven largely by reef substrate (coral.rugosity) along RDA 1. Fishing pressure, predator biomass, wave exposure and reef slope had only marginal effects on parrotfish assemblage structure at this scale.

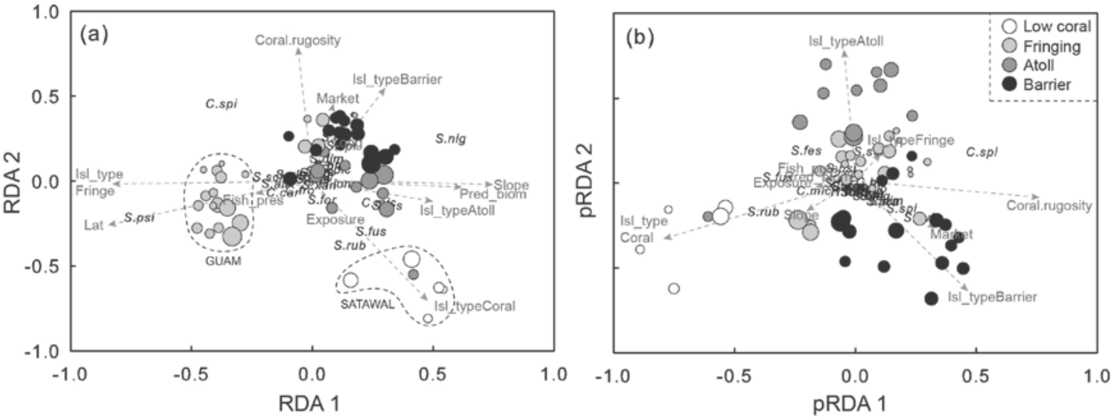

Figure 5.3. Redundancy analyses (RDA) explaining patterns of abundance-weighted parrotfish assemblage structure across 55 sites at eight Micronesian islands based on relationships with biophysical, geographic, geomorphologic and anthropogenic factors. All explanatory variables were explicitly included in (a) whereas the effect of geography was partialled out in (b). Sites are visually scaled (bubble sizes) by the abundance-weighted phylogenetic diversity score at each site.

Results were similar when these analyses were applied to species biomass data, although larger-bodied species such as *Cetoscarus bicolor, C. microrhinos* and *B. muricatum* had greater influence on patterns because they contributed more to assemblage biomass than abundance. The model explained 48% of the total variation (adjusted r^2) and the first two axes accounted for 25 and 14% respectively. Guam and Satawal sites again stood apart when all explanatory variables were explicitly considered (Fig. 5.4a). Biomass RDA results differed from those of abundance in that the high fringing reef system Kosrae was separate from barrier reef systems and there was little distinction between atoll and barrier reef systems (Fig. 5.4a). The partial RDA controlling for latitude and longitude demonstrated clear separation of low coral island sites along the first axis and barrier reef systems along the second axis (Fig. 5.4b). The large bumphead parrotfish *B. muricatum* was only recorded at barrier reef systems (Yap and Pohnpei). Fringing and atoll reef systems clustered together and all systems were spread considerably across the first axis, which was strongly associated with the reef substrate metric coral.rugosity.

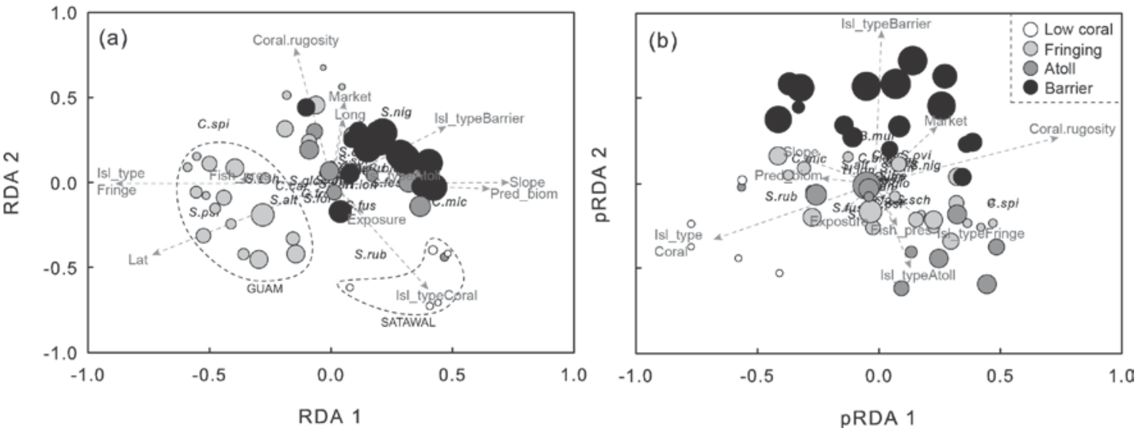

Figure 5.4. Redundancy analyses (RDA) explaining patterns of biomass-weighted parrotfish assemblage structure across 55 sites at eight Micronesian islands based on relationships with biophysical, geographic, geomorphologic and anthropogenic factors. All explanatory variables were explicitly included in (a) whereas the effect of geography was partialled out in (b). Sites are visually scaled (bubble sizes) by the biomass-weighted phylogenetic diversity score at each site.

For RDA analyses based on abundance and biomass data respectively, island geomorphology explained the most variance (38.3 and 30.4%) followed by biophysical environment (32.1 and 25.5%), geography (31.0 and 24.0%) and fishing impact (8.4 and 9.2%). All of these variance portions were statistically significant (Table 2). Much of the explained variation, however, was shared among the variable subsets: 21.1% (abundance) and 15.3% (biomass) was shared between island geomorphology and physical/biological environment, 15.0% (abundance) and 11.8% (biomass) between island geomorphology and geography, 18.8% (abundance) and 14.4% (biomass) between biophysical environment and geography, whereas fishing impact shared all of its explained variation with the other subsets for abundance data and 8.5% (of a total 9.2%) for biomass (Fig. 5.5). Remaining variance portions explained independently by each variable subset were statistically significant for all but fishing impact (Table 5.2).

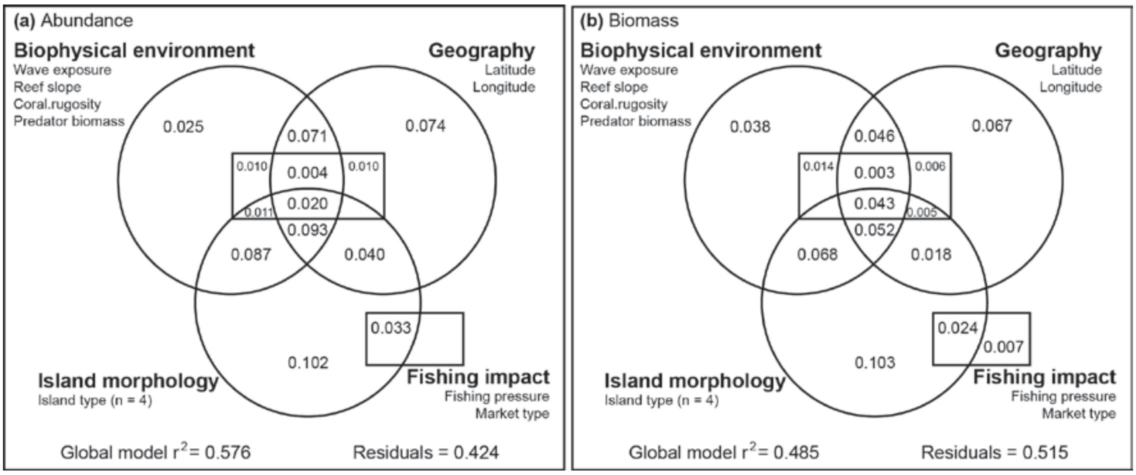

Figure 5.5. Venn diagrams describing the partitioning of variance among explanatory subsets for (a) abundance and (b) biomass trends of parrotfish assemblages across eight islands in Micronesia. Variance portions less than zero are not displayed.

Table 5.2. Summary of variance partitioning among explanatory variable subsets for (a) abundance- and (b) biomass-weighted parrotfish assemblage structure across 55 sites at eight Micronesian islands using redundancy analysis. Significance levels are indicated (*** < 0.001, ** < 0.01, * < 0.05, NS > 0.05).

(a) Abundance

Model or subset		**Variance explained (%)**	**df**	**F**	**Significance level**
Global model		57.6	11,43	7.7	<0.001
Biophysical environment	(total)	32.1	4,50	7.4	<0.001
	(independent)	2.5	4,43	1.7	0.004
Geography	(total)	31.0	2,52	13.1	<0.001
	(independent)	7.4	2,43	4.9	<0.001
Island geomorphology	(total)	38.3	3,51	12.2	<0.001
	(independent)	10.2	3,43	4.7	<0.001
Fishing impact	(total)	8.4	2,52	3.5	0.002
	(independent)	< 0.0	2,43	0.9	0.554

(a) Biomass

Model or subset		**Variance explained (%)**	**df**	**F**	**Significance level**
Global model		48.5	11,43	5.6	<0.001
Biophysical environment	(total)	25.5	4,50	5.6	<0.001
	(independent)	3.8	4,43	1.9	0.002
Geography	(total)	24.0	2,52	9.5	<0.001
	(independent)	6.7	2,43	3.9	<0.001
Island geomorphology	(total)	30.4	3,51	8.9	<0.001
	(independent)	10.3	3,43	4.1	<0.001
Fishing impact	(total)	9.2	2,52	3.7	<0.001
	(independent)	0.7	2,43	1.3	0.151

Parsimonious variable reduction was performed for models containing all explanatory variables explicitly as well as for each variable subset. For the explicit model, island type and latitude were the most significant variables explaining parrotfish assemblage patterns for both abundance and biomass data. For abundance data, the explanatory variables fishing pressure, market type, predator biomass and wave exposure were excluded given they did not contribute significantly to the final model. Parsimonious variable exclusions were the same for biomass data with the exception that fishing pressure was included in the optimal model. At the subset level, all variables were retained with the exception of predator biomass within the biophysical environment subset for both abundance and biomass data. Repeating the variance partitioning analysis for biomass data indicated that the variance independently explained by the fishing impact subset (1.4%) became marginally significant ($P = 0.039$) when predator biomass was excluded from the analysis.

Results of the within-island and within-geomorphology RDA analyses are summarized in Table 5.3. At this scale, spatial effects (latitude and longitude) were unimportant, whereas the correlative significance of biophysical variables such as wave exposure, coral.rugosity, adjacent habitat and predator biomass emerged in optimal models. Fishing pressure was also an important variable structuring parrotfish assemblages on Guam, but not across atoll reef systems, and had a stronger influence when the response variable was biomass. On Guam, where a wide range of fishing pressure exists across sites, this variable accounted for 57% and 28% of the explained variance in biomass-weighted and abundance-weighted assemblage structure, respectively, and was the primary explanatory variable describing patterns of biomass. Across atoll reef systems, where population densities ranged from 0 to over 100 people km^{-2} of reef area, assemblage structure based on both biomass and abundance of parrotfishes was correlated with coral.rugosity. The relationship with predator biomass was positive (i.e., parrotfish abundance was greater at sites with higher predator biomass).

Table 5.3. Parsimoniously selected optimal redundancy analysis models for Guam and atoll reef systems based on patterns of parrotfish biomass and abundance. Significance levels based on permutation tests are indicated for individual explanatory variables and for models.

System	**Optimal model components**	**Variance explained (%)**	**P-value**
Guam (biomass)	Fishing pressure	16.9	0.004
	Wave exposure	9.6	0.028
	Adjacent habitat	6.0	0.063
	Total variance explained	**29.4**	**0.005**
Guam (abundance)	Coral.rugosity	12.6	0.001
	Wave exposure	9.4	0.017
	Fishing pressure	8.8	0.015
	Adjacent habitat	7.4	0.087
	Total variance explained	**31.8**	**0.005**
Atolls (biomass)	Coral.rugosity	13.5	0.041
	Total variance explained	**13.5**	**0.041**
Atolls (abundance)	Coral.rugosity	13.7	0.015
	Predator biomass	3.9	0.058
	Total variance explained	**23.4**	0.008

Mean length

Multi-model averaging returned seven LME models describing patterns of mean length across space for Micronesian parrotfishes within 2 AICc values of the optimum. The common feature among these models was the consistent inclusion of fishing pressure, which had a strong negative relationship with mean length, and island type (Table 5.4). Fishing pressure was consistently the most significant factor, suggesting that even though island type has a considerable structuring effect, the influence of fishing pressure can override this effect across biogeographic scales. Repeating this analysis for five widespread and relatively abundant species suggests that this pattern manifests through both the reduction in mean length of individual species (Fig. 5.6) as well as the proportional change in species composition with increasing fishing pressure. Fishing pressure was included as a factor in optimal models for three of the five species examined (*C. microrhinos*, *C. spilurus* and *S. rubroviolaceus*) and had negative correlation coefficients with each (Fig. 5.6).

Table 5.4. Analysis of variance table for the optimal linear mixed effects models (based on AICc) for mean length across eight islands in Micronesia for (a) all parrotfishes combined and widespread species (b) *Chlorurus microrhinos*, (c) *Chlorurus spilurus*, (d) *Scarus forsteni*, (e) *Scarus rubroviolaceus* and (f) *Scarus schlegeli*.

(a) All parrotfishes combined

Variable	numDF	denDF	F	P	Coefficient response
Intercept	1	45	2988	<0.0001	
Fishing pressure	1	45	7.7	0.0082	-
Island type	3	4	10.4	0.0234	(categorical variable)

(b) *Chlorurus microrhinos*

Variable	numDF	denDF	F	P	Coefficient response
Intercept	1	39	577.1	<0.0001	
Fishing pressure	1	39	6.0	0.0188	-
Exposure	1	39	3.7	0.0611	+

(c) *Chlorurus spilurus*

Variable	numDF	denDF	F	P	Coefficient response
Intercept	1	41	4320.2	<0.0001	
Fishing pressure	1	41	8.9	0.0048	-
Island type	3	4	6.8	0.048	(categorical variable)

(d) *Scarus forsteni*

Variable	numDF	denDF	F	P	Coefficient response
Intercept	1	38	1148.9	<0.0001	
Island type	3	4	3.0	0.1548	(categorical variable)
Exposure	1	38	3.0	0.0898	+

(e) *Scarus rubroviolaceus*

Variable	numDF	denDF	F	P	Coefficient response
Intercept	1	31	1098.5	<0.0001	
Fishing pressure	1	31	3.0	0.0919	-
Slope	1	31	10.2	0.0033	+

(f) *Scarus schlegeli*

Variable	numDF	denDF	F	P	Coefficient response
Intercept	1	35	3381.4	<0.0001	
Island type	3	4	10.6	0.0225	(categorical variable)
Latitude	1	35	4.5	0.0416	-
Longitude	1	35	10.8	0.0024	-

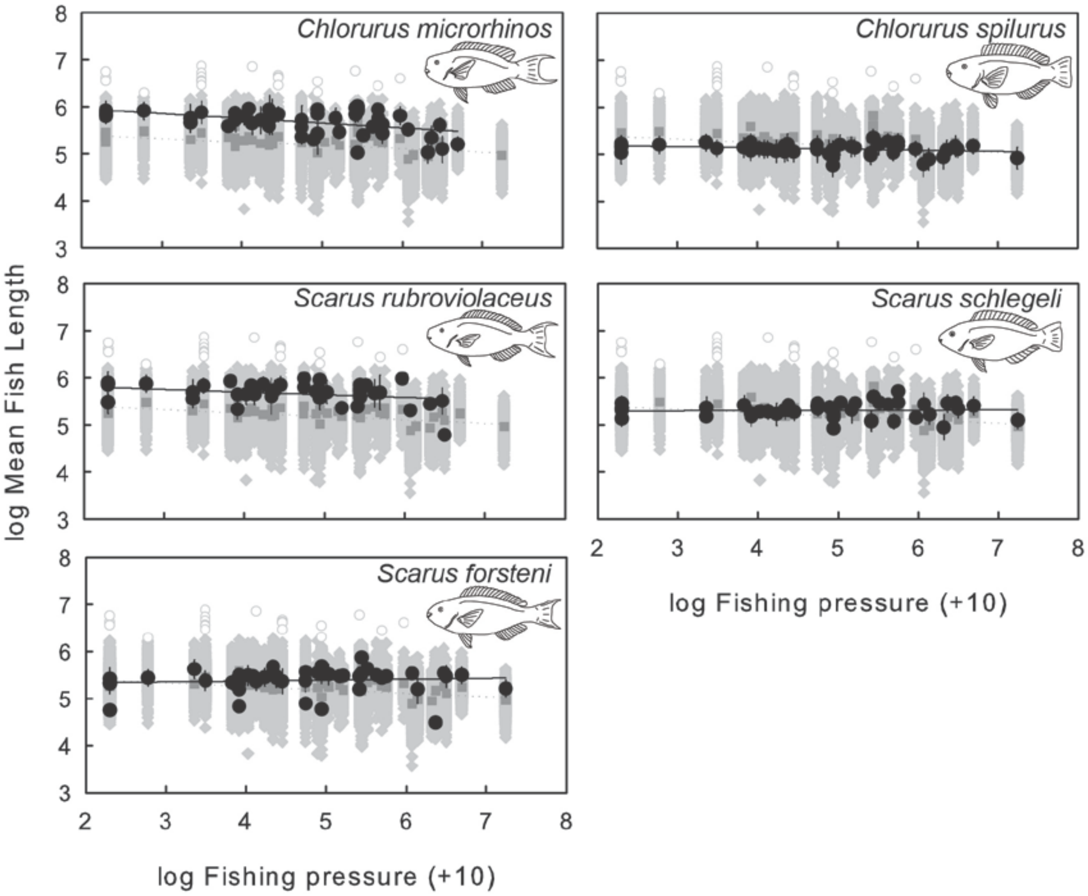

Figure 5.6. Patterns of mean length (±S.E.; black circles, solid line) versus fishing pressure indices across 55 sites at eight Micronesian islands for five common and widespread species of parrotfishes. Lengths of all parrotfish individuals are shown in light grey, overall mean lengths in intermediate grey (associated linear trend: dotted line). Lengths for the exceptionally large-bodied *Bolbometopon muricatum* are indicated by white circles.

Species richness and phylogenetic diversity

A summary of optimal LME model outputs explaining patterns of species richness and phylogenetic diversity are provided in Table 5.5. Island type, slope and coral.rugosity were consistently the most important factors driving patterns of parrotfish species richness across Micronesia. Richness increased with increasing habitat diversity at the island geomorphology scale (low coral systems had the lowest richness values whereas barrier reef systems had the highest; Fig. 5.7a). Richness also increased at greater values of coral.rugosity and decreased at steeper reef slopes. For biomass-weighted phylogenetic diversity, island geomorphology was the only significant factor. Similar to species richness, biomass-weighted diversity was lowest at low coral systems (Satawal), and increased from fringing to atoll to barrier reef systems (Fig. 5.7b). These results differed substantially with abundance-weighted phylogenetic diversity (Fig. 5.7c), for which coral.rugosity and fishing pressure were the primary explanatory factors. Nested analysis of variance identified highly significant differences among island types for species richness ($F_{3,47}$ = 13.4, $P < 0.001$) and biomass-weighted phylogenetic diversity ($F_{3,47}$ = 18.3, $P < 0.001$), but not for abundance-weighted diversity ($F_{3,47}$ = 2.6, $P = 0.060$). Differences existed among islands nested within island types for richness ($F_{4,47}$ = 3.3, $P < 0.05$), but not for biomass-weighted diversity ($F_{4,47}$ = 1.2, $P = 0.324$).

Table 5.5. Analysis of variance table for the optimal linear mixed effects models (based on AICc) for (a) species richness, (b) biomass-weighted phylogenetic diversity and (c) abundance-weighted phylogenetic diversity of parrotfish assemblages across eight islands in Micronesia. Directions of responses (positive or negative) to each explanatory variable are indicated.

(a) Species richness

Variable	numDF	denDF	F	P	Coefficient response
Intercept	1	45	1112.9	<0.0001	
Island type	3	4	13.2	0.0153	(see Fig. 5.7a)
Coral.rugosity	1	45	4.9	0.0315	+
Slope	1	45	5.4	0.0249	-

(b) Biomass-weighted phylogenetic diversity

Variable	numDF	denDF	F	P	Coefficient response
Intercept	1	47	617.0	<0.0001	
Island type	3	4	18.0	0.0087	(see Fig. 5.7b)

(c) Abundance-weighted phylogenetic diversity

Variable	numDF	denDF	F	P	Coefficient response
Intercept	1	45	617.0	<0.0001	
Coral.rugosity	1	45	7.56	0.0086	-
Fishing pressure	1	45	3.77	0.0585	-

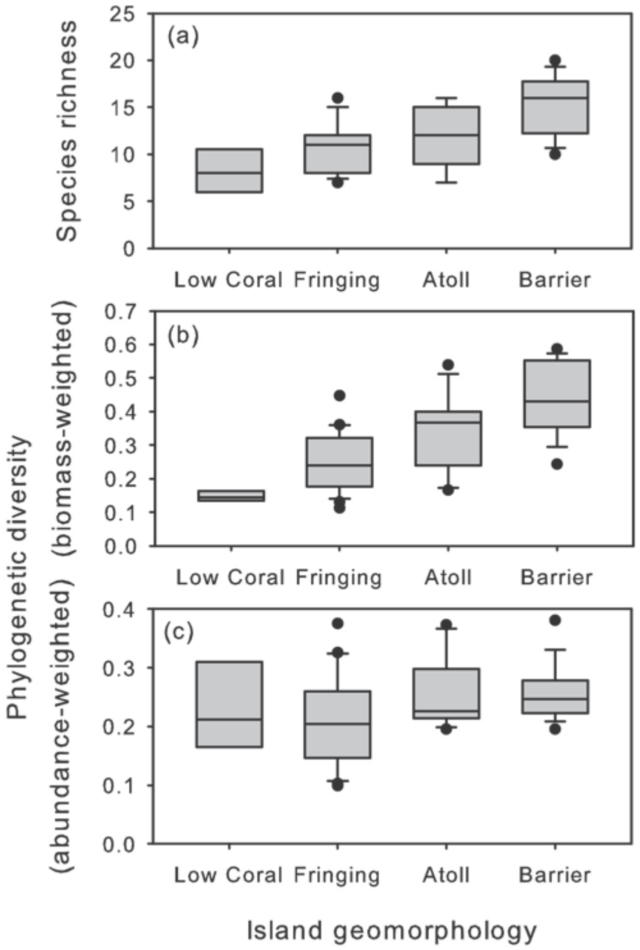

Figure 5.7. Distribution of parrotfish species richness, biomass- and abundance-weighted phylogenetic diversity across four distinct island geomorphologies.

Discussion

An increased focus on the identifiable effects of fishing on parrotfish communities has emerged recently and studies have spanned several spatial scales, from within islands to across entire ocean basins as well as circumtropical meta-analyses (Hawkins and Roberts 2003, Clua and Legendre 2008, Stockwell et al. 2009, Bellwood et al. 2012, Comeros-Raynal et al. 2012, Pinca et al. 2012, D'agata et al. 2014, Edwards et al. 2014, Lindfield et al. 2014, Taylor 2014 [Chapter 4], Valles and Oxenford 2014, Taylor et al. 2014 [Chapter 3]). Many of these studies either ignore or statistically control for environmental variability and biogeographic species distributions in order to isolate the effects of fishing, and have reported a variety of influence levels of human extraction on assemblage structure, diversity and ecological function. In the present study, I identified substantial scale-dependence in the observable effects of human exploitation on parrotfish assemblages. At biogeographic scales (i.e., across Micronesian islands) island geomorphology and species distribution patterns had an overriding predictive effect on assemblage structure, species richness and phylogenetic diversity (biomass-weighted) whereas biophysical features of the reef environment and fishing pressure from human populations exerted the greatest influence within islands or across similar island types. This necessitates that studies account for scale-dependent habitat effects when comparing fish assemblages across island types.

The island types considered in the present study are representative of the diversity of oceanic islands comprising Micronesia and other regions of the central and western Pacific Ocean. I observed strong increases in parrotfish species richness and biomass-weighted phylogenetic diversity with an increase in broad-scale habitat diversity associated with the different island geomorphologies. The hierarchical importance of island type was also reflected in patterns of assemblage structure. Given the substantial literature regarding the effects of habitat on reef fish diversity and assemblage structure (e.g., Friedlander and Parrish 1998, Friedlander et al. 2010, Messmer et al. 2011), the results should not be surprising. However, most studies addressing this relationship have focused at relatively small spatial scales whereas assessments across biogeographic regions considering variability in island geomorphology are rare, likely because of the increased time and cost required for such study designs as well as the potential decrease in statistical power (Jennings and Kaiser 1998). Further, as mentioned before, many of the broad-scale studies focus specifically on human impacts while controlling for habitat effects. Unfortunately, such an approach has often come before an adequate understanding of the underlying and hierarchically-structured influences of habitat and biogeography on fish assemblages.

Of particular interest is the scale of influence that coral.rugosity has on parrotfish assemblage structure. These factors had the greatest influence among site-specific habitat variables at broad spatial scales and influenced the majority of the fish assemblage variation within distinct island types. Coral cover and rugosity are the two major components contributing to structural complexity in coral reef ecosystems, and the influence of structural complexity on fish abundance and biomass is well documented (Graham and Nash 2013). In the present analysis, these factors are clearly critical in structuring fish assemblages and their influence is evident at multiple spatial scales.

Biological communities across islands will likely respond to exploitation differently, and I posit that equations for biodiversity conservation and fisheries management must integrate inherent features of island geomorphology alongside human impact levels. Ultimately, these and similar results find their optimal use among resource managers, working at the scale of islands or sections of reef systems within islands. Scale-dependence in fishing effects on demography (Taylor 2014 [Chapter 4], present study) suggests that conservation goals should maintain a regional focus but with more explicit management objectives at the local scale. For example, if conservation of functional roles (reviewed in Bonaldo et al. 2014) is the objective, then habitat affinities for key species at several spatial scales must be clearly identified and applied to protected-area management. Too often I encounter comparisons of reef fish resources, commonly focused on iconic species such as *B. muricatum*, among islands of Micronesia and elsewhere without regard for inherent environmental differences that influence fish assemblages and biomass. Such comparisons carry an underlying assumption that fishery resources among islands were equivalent in the absence of fishing pressure. Regional and biogeographic data demonstrate this is highly unlikely. Geomorphological factors such as reef size and habitat diversity have profound effects on the abundance and diversity of targeted taxa with smaller reefs lacking lagoonal systems being particularly vulnerable to overfishing. While broad-scale generalizations of the relationships between human density and reef fish communities provide credible reference points, their utility to resource managers is limited. An important concept, however, is how to interpret this information with regard to individual islands; for this, the consideration of island geomorphology is imperative.

Regarding the scale-dependence of factors structuring parrotfish communities, finer-scaled features such as benthic substrate condition, wave exposure and reef slope have a very important effect on assemblage structure across sites, but often differ in their recognizable influence among islands (Friedlander et al. 2003). This probably reflects the distinct value ranges of factors at each island. At biogeographic scales, the effects of fishing on assemblage structure appear to fall among these finer-scale factors. However, this conclusion is conditional not only on the spatial scale of observation, but also on the taxonomic scale. Given the observed effect of island geomorphology and species distributions on parrotfish assemblage structures, we would not expect fishing pressure to explain much variation in terms of abundance, and only slightly more in biomass, despite there being a considerable range of vulnerabilities to overexploitation among species. In the context of multivariate assemblage data, observing significant fishing effects across space would likely require localized extinctions or at least severe depletions of species at a magnitude that would override differences related to island geomorphology and habitat features. The inclusion of higher taxonomic levels representing a range of trophic levels would provide greater potential for identifying a strong response to fishing pressure across island types (Jennings and Kaiser 1998), and this has been demonstrated across island nations throughout the Pacific basin (Pinca et al. 2012). However, the increase is only marginal, with fishing pressure explaining between four and eleven percent of the variation in reef fish community structure independently for abundance and biomass patterns across various trophic groups. Despite the considerable range of human pressure and the observed effects of fishing at this scale, Pinca et al. (2012) found that biological communities are still predominantly predicted by underlying habitat features such as island type and substrate condition as well as species distributions.

While fishing pressure may explain a subordinate amount of variation in parrotfish assemblages across broad spatial scales, D’agata et al. (2014) demonstrated that biomass-weighted phylogenetic and functional diversity declines substantially with increasing human population density. This result was not replicated in the present study for phylogenetic diversity (with the caveat of different spatial distribution of sites among studies). Phylogenetic and functional diversity are important features of biological communities that shape ecosystem processes and organization (Chapin et al. 1997). The estimation of such metrics can be heavily influenced by large-bodied species that are phylogenetically distinct; among parrotfishes, the bumphead parrotfish *B. muricatum* has the strongest influence on biomass-weighted values due to its comparatively large size, evolutionary history (Choat et al. 2012), and ecological peculiarity as a coral predator (Bellwood et al. 2003). There is no doubt that among scarines *B. muricatum* is the most vulnerable species to overexploitation (Donaldson and Dulvy 2004, Dulvy and Polunin 2004, Hamilton and Choat 2012) and it has been shown to drive patterns of phylogenetic and functional diversity among parrotfishes across a variety of spatial scales (Bellwood et al. 2003, Bellwood et al. 2012, D’agata et al. 2014). However, this species has specific and differing habitat requirements at the recruit/juvenile and adult portions of its life history (Aswani and Hamilton 2004) and biogeographic patterns of demography for the species likely reflect not only human exploitation patterns, but also habitat factors limiting its abundance and distribution (Kobayashi et al. 2011). In the present study, *B. muricatum* presence at broad spatial scales was not related to fishing pressure, but rather corresponded strongly with barrier reef systems (Yap and Pohnpei, both have active commercial fisheries for the species), and therefore with the presence of complex back reef ecosystems. Within these islands, the strongest predictor of *B. muricatum* abundance and biomass was fishing pressure across sites. No bumphead parrotfishes were recorded on outer reef slopes at the other islands sampled, including the uninhabited atoll Sorol. This iconic species has received considerable attention regarding fishing effects for logical reasons. However, I propose that a better understanding of habitat requirements at several spatial scales and throughout its life history will be required for effective conservation.

Because of the nature of collecting replicated samples among oceanic islands, pseudoreplication was an inherent issue in the multivariate analysis, though this was remedied for univariate response variables (richness, diversity and length) using mixed effects models (Millar and Anderson 2004). Although resultant sample sizes at the island geomorphology level ranged from one to three, the strong clustering among sites of morphologically similar yet spatially distinct islands suggested the influence of island type was compelling. Furthermore, the clear divergence of the lone low coral island (Satawal) from other islands in Figs. 5.3 and 5.4 reflects a consistent feature of small oceanic islands deficient of habitat diversity throughout the Indo-Pacific region. Satawal’s divergence was driven by very low abundance and biomass of what is elsewhere the predominant species, *C. spilurus*, as well as comparatively high prevalence of *S. rubroviolaceus*, a common but less abundant species that demonstrates affinity for low-complexity fringing reef habitat on several spatial scales (Mumby et al. 2013). In support, across uninhabited islands of the Phoenix Islands group (Kiribati), *C. spilurus* are virtually non-existent where lagoons are absent, whereas the species is among the most abundant scarine at islands containing lagoons that connect to the outer reef (M. Priest, personal communication). Ultimately, the influence of island geomorphology on fish assemblages deserves expanded consideration. A logical first step would be to provide improved quantification of features describing islands. Geomorphology and reef area appear to be somewhat correlated, and broad-scale habitat diversity varies inherently across island types. Hence, development of island geomorphology as a continuous, rather than categorical variable may potentially explain even more variance in patterns of assemblage structure and biodiversity.

These results suggest the response variable that is most sensitive to increased human extraction is mean length. Unlike assemblage structure, species richness or diversity, mean length was most highly correlated with fishing pressure at all spatial scales, where higher fishing pressure corresponded with smaller body sizes. This was observed when all species were grouped together (with or without the exceptionally large-bodied *B. muricatum*) as well as for various individual species, including species determined to have comparatively high (*C. microrhinos*) and low (*C. spilurus*) vulnerability to overexploitation. Mean length has consistently proven to be a reliable and robust indicator of exploitation level across a variety of exploited fishes through time (Shin et al. 2005, Methratta and Link 2006), across space (Hawkins and Roberts 2003, Valles and Oxenford 2014) and in fishery population models (Ault et al. 2005). Fishery-induced declines in mean length of parrotfish communities are the result of declines within populations of species, where larger-bodied species typically display a greater magnitude of decline (Valles and Oxenford 2014), as well as changes in assemblages, where even slight reductions in the proportion of larger-bodied species can have a considerable effect on overall mean length. Within populations, the associated trait selectivity from exploitation leads to evolutionary downsizing which may have unexpected consequences for ecological and genetic diversity (Alós et al. 2014). Small-scale fisheries, which dominate oceanic island nations, are historically data-poor in terms of harvest trends and life-history information regarding targeted species (Dalzell et al. 1996). However, these results highlight the importance of collecting temporal data on the composition and lengths of harvested species, monitoring practices that require considerable funding and effort but provide substantial insights to fishery-induced changes and relevant management procedures. Further, historical data should be considered wherever possible to recognize the magnitude of change that may have previously taken place within a system.

To conclude, widespread and historical human exploitation of the marine environment has had a considerable effect on marine communities (Jackson et al. 2001, Pinca et al. 2012). However, these results demonstrate that fishing pressure is not the default hypothesis explaining community-level patterns of reef fish distribution across broad spatial scales, a notion that is prevalent in the primary literature. The identifiable effects on assemblages are dependent on both the spatial and taxonomic scale of observation as well as the range of human impacts across the study area. For parrotfishes and likely all tropical reef fishes on oceanic islands, patterns largely reflect spatial heterogeneity in environmental features at several scales, and retroactively disentangling the influence of fishing and environment remains a challenge. I encourage future studies to test hypotheses regarding fish assemblage structure and diversity across islands of differing geomorphology.

Chapter 6: General Discussion

In this thesis, I have used an array of methods and analyses to resolve patterns and identify ecological drivers of inter- and intraspecific parrotfish demography and assemblage structure across Micronesia. This yielded an understanding of life-history variation among and within species, responses to ecological correlates at the species and assemblage levels, and the importance of spatial-scale and hierarchical scale-dependence to our ability to identify significant environmental and anthropogenic correlates. In Chapter 2, I quantified life-history traits of twelve parrotfish species and measured the association among traits across species. Chapter 3 applied these data as well as spatial and temporal fisheries trends to assess the relationship between life history and vulnerability to overexploitation. Chapters 4 and 5 evaluated patterns of demography and assemblage structure across several spatial scales in Micronesia. With a passive glance, one may interpret contradictory messages from Chapter 3 versus Chapters 4 and 5. On the contrary, Chapter 3 purports a high capacity for structural changes to exploited parrotfish communities and, likewise, Chapters 4 and 5 demonstrate that demographic and assemblage-level responses to exploitation are strong within or among homogenous study regions (e.g. within islands). However, our ability to detect these responses from spatial data is diminished at biogeographic scales, depending on the influence of island geomorphology or various bottom-up processes driving demographic patterns. Hence, this thesis represents a comprehensive assessment of the associations between life history, environmental factors, human exploitation and their hierarchy across different spatial scales.

Implications for conservation and management

Parrotfishes are increasingly important fishery resources throughout the majority of their geographic range (McClanahan 1994, Aswani and Hamilton 2004, Rhodes et al. 2008, Houk et al. 2012). Hence, the impact of human exploitation on parrotfish communities has emerged as a critical management and conservation issue (Bellwood et al. 2012). Knowledge of life-history traits is the cornerstone to understanding and predicting population dynamics and this information underpins historical fishery management (Thorson et al. 2014). However, traditional species-level management is almost entirely impractical in coral reef fisheries where several hundreds of species are harvested at various rates from the same reef system. Rather, ecosystem-based management approaches are advocated for tropical coastal environments (Olsson et al. 2008). Ecosystem-based management of parrotfish fisheries is highly regarded because of the ecological role of parrotfishes and their influence on benthic biota through processes of grazing and bioerosion (Mumby 2006, in press). But age-based demographic information remains an imperative component contributing to our ability to successfully manage and conserve parrotfishes as both fishery resources and functional grazers of reef substrate.

Vulnerability of a species to overexploitation is largely dependent on the inherent sensitivity (the biological response to increased mortality) of a population to harvest. Sensitivity, in turn, is primarily driven by life-history traits, especially those influencing population growth rate and turnover time. Parrotfish fisheries target a large number of species (Rhodes et al. 2008), yet the magnitude of demographic responses to fishing pressure are often highly species-specific (Dulvy and Polunin 2004, Clua and Legendre 2008, Bellwood et al. 2012, Valles and Oxenford 2014, Taylor et al. 2014

[Chapter 3]). As expected, these responses are predicted by inter-specific variability in life-history trait values, whereby large-bodied and late-maturing species are most sensitive (Taylor et al. 2014 [Chapter 3]). Length-based traits such as mean maximum length are reliable predictors (Clua and Legendre 2008), and maximum length metrics are easily derived from fishery surveys or underwater visual census. However, I found that the age at female maturation was the optimal predictor of vulnerability to overexploitation among species, thus encouraging the collection of age-based information for harvested species. The spatial variability in life-history traits demonstrated here suggests that trait values cannot be extrapolated across space for any given species. This creates a problem for tropical fisheries science given the dearth of age-based information for most species. However, the relationships among species (i.e., species' trait values relative to those of others) will likely remain consistent across space, and thus established relationships provide a foundation for predicting responses elsewhere. This is an important concept and should be considered broadly among resource managers. While intraspecific trait variability hinders broad-scale adoption of simple management efforts (for example, minimum size limits), the intrinsic vulnerability of any species relative to that of other species will likely remain constant, and this provides a powerful basis for assessing assemblages once these relationships are established.

Human exploitation has had a profound effect on parrotfish communities, both directly (through harvesting of parrotfishes; Hawkins and Roberts 2003, Bellwood et al. 2012) and indirectly (through removal of predators; DeMartini et al. 2005, 2008). However, given the small- and broad-scale variability in demographic trends of parrotfishes, a key message that emerges is that fishing pressure should not be the default hypothesis for explaining observed differences in parrotfish life history, abundance or assemblage structure. Although fishing has clearly demonstrable impacts, these emerge at relatively local scales and are highly context dependent. Therefore, fisheries and biodiversity management should be crafted to particular localities and reef systems. It would be unwise, for example, to extrapolate findings from the western tropical Atlantic or the east coast of Africa as guides for management of central Indo-Pacific reefs other than in very general terms. What is clear, however, is that latitude (temperature), predation pressure and geomorphological factors such as reef size and habitat diversity may have profound effects on the demography and diversity of target taxa in the absence of fishing. Parrotfishes appear to be a model group for understanding some of these effects across broad spatial scales, but more research is required.

The information presented in this thesis is largely biased towards observations across space. Temporal observations, however, are of greater importance to regional fisheries management and have a higher capacity to elucidate fishery-induced demographic responses. The data-poor condition of most coral reef associated fisheries means that temporal data on length structure, composition and age-based demography of harvested parrotfishes are rare (Johannes 1998). Simple monitoring programs can alleviate many of these gaps, but such programs require sustained funding, resources and capacity.

From a life-history perspective, a potential concern is the long-term ‘Darwinian’ effects of fishing on parrotfish traits (Conover 2000, Law 2007). Selective mortality is amplified in many parrotfish fisheries because of the consistent sexual dimorphism within species. As a result, males are often targeted at much higher rates. As protogynous hermaphrodites for which sexual transition is driven by social structure (Muñoz and Warner 2003), alterations of size-based sex ratios have notable effects on the reproductive dynamics of populations. This can include changes in population fecundity (Ratner and Lande 2001), mean length and age at sex change and maturation (Law 2000, Hamilton et al. 2007), proportional prevalence of primary males (Munday et al. 2006), and mating strategies (Rowe and Hutchings 2003). Such phenotypic responses have been observed in many taxa but the magnitude and consequences of evolutionary changes are poorly understood. Because of the low level of heritability of life-history traits, Law (2007) suggested that evolutionary changes caused by sustained fishery selection would occur on decadal time scales. Archaeological evidence from the Hawaiian Islands demonstrates that body size distributions of harvested species were similar for hundreds of years until modern times (Longenecker et al. 2014). Present-day body size distributions have decreased substantially amid concurrent increases in fishing pressure. Continuous management of important life-history traits, such as mean age at maturity, has been advocated for incorporating fishery-induced evolution into future management of fish stocks (Kuparinen and Merila 2007). This necessitates the systematic collection of age-based life-history information from locations over time. Few research or management programs focused on coral reef fisheries exercise the requisite foresight, but this approach would provide valuable insights to fishery-induced changes over the long-term, especially in areas where parrotfish fisheries are expanding.

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Appendix A: Length-weight regression parameters of twelve parrotfish species from Chapters 2 and 3

Species	n	A	B	r^2
Cetoscarus bicolor	43	1.875E-05	3.006	0.98
Calotomus carolinus	33	1.049E-05	3.146	0.99
Chlorurus frontalis	88	9.130E-06	3.157	0.98
Chlorurus microrhinos	77	2.006E-05	3.019	0.99
Chlorurus spilurus	369	1.281E-05	3.113	0.97
Hipposcarus longiceps	69	2.184E-05	2.970	0.97
Scarus altipinnis	53	1.262E-05	3.086	0.98
Scarus forsteni	84	3.365E-05	2.918	0.94
Scarus ghobban	31	8.899E-06	3.126	0.96
Scarus psittacus	108	2.010E-05	3.007	0.97
Scarus rubroviolaceus	57	1.899E-05	3.021	0.99
Scarus schlegeli	125	5.001E-05	2.843	0.95

Appendix B: Publications arising from this thesis

1. Taylor, B. M. (2014) Drivers of protogynous sex change differ across spatial scales. *Proceedings of the Royal Society B: Biological Sciences* 281: 20132423. (doi: 10.1098/rspb.2013.2423)
2. Taylor, B. M., Choat, J. H. (2014) Comparative demography of commercially important parrotfish species from Micronesia. *Journal of Fish Biology* 84: 383-402 (doi: 10.1111/jfb.12294)
3. Taylor, B. M., Houk, P., Choat, J. H., Russ, G. R. (2014) Life histories predict vulnerability to overexploitation in parrotfishes. *Coral Reefs* 33: 869-878 (doi:10.1007/s00338-014-1187-5)
4. Taylor, B. M., Lindfield, S.J., Choat, J. H. (in press) Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. *Ecography* (doi:10.1111/ecog.01093)
5. Taylor, B. M., Trip, E. D. L., Choat, J. H. (in press) Dynamic Demography: Investigations of Life-History Variation in the Parrotfishes. In (Hoey A. S., Bonaldo, R., Bellwood, D. R., eds) The Biology and Ecology of Parrotfishes. Taylor and Francis.

Appendix C: Publications during candidature not arising from this thesis

1. Taylor B.M., McIlwain J.L., Kerr A.M. (2012) Marine reserves and reproductive biomass: a case study of a heavily targeted reef fish. *PLoS ONE* 7 (6): e39599. (doi:10.1371/journal.pone.0039599)
2. Rhodes K.L., Taylor B.M., Wichilmel C.B., Joseph E., Hamilton R.J., Almany G.R. (2013) Reproductive biology of squaretail coralgrouper *Plectropomus areolatus* using age-based techniques. *Journal of Fish Biology* 82: 133-1350. (doi:10.1111/jfb.12076)
3. Taylor B.M., Mills J.S. (2013) Movement and spawning migration patterns suggest small marine reserves can offer adequate protection for exploited emperorfishes. *Coral Reefs* 32: 1077-1087. (doi:10.1007/s00338-013-1065-6)
4. Taylor B.M., Rhodes K.L., Marshell A., McIlwain J.L. (2014) Age-based demographic and reproductive assessment of orangespine, *Naso lituratus*, and bluespine, *Naso unicornis*, unicornifishes. *Journal of Fish Biology* 85: 901-916. (doi:10.1111/jfb.12479)