

CHAPTER

4

Dynamic Demography: Investigations of Life-History Variation in the Parrotfishes

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Introduction

Over the last decade, a large number of publications have focused on the impacts of parrotfishes (Scarinae, Labridae) feeding on the sessile biota of coral reefs as well as the impacts of fishing on parrotfish assemblages, both regionally and globally. Despite this, over the same time period there have been relatively few studies on the demography and population dynamics of the group. An ever-increasing literature focusing on their functional and trophic ecology as scrapers and bioeroders of reef substrate emphasizes this disparity. However, the relatively few existing demographic studies establish how much more there is to learn about variation in age-based demography through both space and time. Life-history traits and their spatial and temporal dynamics have fundamental importance to both trophic ecology and fisheries management, the latter becoming increasingly important with the widespread exploitation of parrotfishes in commercial and artisanal fisheries.

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 within assemblages (Winemiller and Rose 1992). For parrotfishes, there exists a high level of ecological convergence whereby phylogenetically diverse species manifest similar sizes and foraging modes (Choat et al. 2012). As a result, we often observe a high number of species co-occurring in similar habitats. Despite this, parrotfish assemblages from various regions display considerable inter-specific demographic variability in terms of life-history traits, with maximum adult

body sizes ranging from approximately 15 cm to greater than 1 m and maximum life spans ranging from less than 3 yr to greater than 40 yr. The study of demographic pattern and process is critical to both ecologists and resource managers.

Parrotfish abundance has been found to be the most influential factor structuring some reef fish assemblages (i.e., they are comparatively speciose and abundant; Campbell and Pardede 2006) and perhaps no group of marine fishes exhibits more influence on the benthic biota through feeding processes (Carpenter 1986, Choat 1991, Mumby et al. 2006). They are considered to be ecologically 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, Bellwood 1995a, b). Evidence suggests that body size has a considerable effect on rates of grazing and bioerosion (Bellwood 1995b, Alwany et al. 2009, Hoey Chapter 6) and the functional performance of individual parrotfishes increases non-linearly with increasing body size (Lokrantz et al. 2008). Species abundance and composition are also key variables; for example, one species in particular, *Bolbometopon muricatum*, can account for approximately 85 percent of annual parrotfish bioerosion on unexploited outer shelf reefs of the Great Barrier Reef (GBR) and this discrepancy likely exists elsewhere (Bellwood et al. 2003, Hoey and Bellwood 2008). Additionally, parrotfishes have historically been subject to fisheries exploitation in most regions circumtropically, and evidence suggests their prevalence in reef-associated harvests is increasing in many areas where other reef fish families have declined from overexploitation (Dalzell et al. 1996, Houk et al. 2012). Hence, growth rate, maximum body size, age at maturation and life span are important characteristics of populations that relate directly to yield and sustainability (Beverton and Holt 1957). Presently, these data are scarce or non-existent for most regions where parrotfishes are harvested.

Parrotfishes have dynamic and distinctive life histories. In fact, many of their general traits and characteristics make them highly suitable study species for addressing research questions regarding population or assemblage dynamics. Parrotfishes exhibit complex sexual ontogenies whereby most species are protogynous hermaphrodites (female-to-male sex change; Reinboth 1968, Choat and Robertson 1975), representing at least two sexual pathways across species (diandry and monandry; Robertson and Warner 1978). Two phylogenetically distinct species (*B. muricatum* and *Leptoscarus vaigiensis*) are identified as functional gonochores, whereby for *B. muricatum* at least, males pass through an immature female phase (Robertson et al. 1982, Hamilton et al. 2008). Nearly all species display sexual dimorphism in body size, in which males on average are larger at a given age than females (Choat et al. 1996). Many species also phenotypically express sexual dichromatism through distinct color phases (Randall 1963), allowing rapid and non-invasive sex determination *in situ*. Further, because of their often vibrant body coloration and foraging behavior, parrotfishes are highly conspicuous members of the reef fauna, thus facilitating accurate surveys of abundance using standard underwater visual survey techniques (Watson et al. 2010). The study of parrotfish demography is enhanced by complementing these traits with length-at-age information for individuals.

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 (Sparisomatine 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 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 (Taylor and Choat 2014). In addition, although parrotfishes are harvested over most of their geographical range, the fishing methods and intensity vary widely both within and between ocean basins.

This chapter aims to facilitate future age-based research on the demography and life-history of parrotfishes. Herein, we outline procedures for the classification and analysis of demographic variation and review what has been learned to date. Over 40 years have passed since the first age-based work on this group, yet the current primary literature reflects an incipient understanding at best regarding the broad-scale patterns of demographic variation across space. Hence, this generates a series of proposed investigative problems with associated preliminary hypotheses for future research. Specifically, we address issues pertaining to phylogenetic diversity, biogeography, and habitat effects as well as their associated interactions. Finally, we discuss the importance of previous and future findings to fishery management and biodiversity conservation, given the probable increase in anthropogenic pressure in years to come.

Classifying and Analyzing Demographic Information

Deriving Age-based Information

The ability to age teleost species using calcareous structures (reviewed in Fowler 2009, Moltchanivskyj and Cappel 2009) underpins our knowledge of life-history theory in marine fishes and provides a unique advantage over many other taxa for which such information is not easily accessible. A variety of structures (e.g., otoliths, spines, scales, vertebrae, various other bones) chronologically records ontogenetic information for individuals throughout their life span. A review of fish biology literature from the last century overwhelmingly demonstrates that these techniques have predominantly been focused on temperate species, especially those constituting highly valued fisheries (Beamish 1992, Fowler 2009). Work on tropical species has lagged tremendously behind that of temperate species for a number of reasons resulting from both logistical (lack of funding and scientific manpower in most developing tropical nations) and theoretical constraints (prior notion that tropical fishes do not deposit annual increments in calcareous structures based on the comparative lack of climatic variation; Munro 1983, Longhurst and Pauly 1987, Fowler 2009). To date, most ageing work on tropical fishes has focused on valuable fishery species. However, the initial accumulation of age-based data has taught us that life histories of tropical fishes were collectively 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 (Pannella 1974, Sale 1980).

Sagittal otoliths (or 'ear bones') have become the primary medium for the estimation of annual ages in teleost fishes, given their superior reliability and interpretability for a wide range of taxa. Their use necessitates euthanizing individual fish, which is not an ethical issue where samples can be derived from fishery-caught specimens. However, fishery-independent sampling is an important endeavor, especially when specific research objectives (e.g., groundtruthing fishery-dependent data, comparisons across habitats or

regions, phenotypic responses of populations within and outside of marine reserves) are desired, and such studies can be designed with negligible impact to populations (Kritzer et al. 2001). In some cases, the use of non-lethal ageing techniques can be a valuable tool, particularly for overfished species and those of high conservation value (e.g. Hobbs et al. 2014).

The first study to estimate age-based traits in a parrotfish examined banding patterns, presumed to represent annual increments, in various bones (opercula, cleithra and hyomandibula) of *Scarus iseri* from the southern Caribbean (Warner and Downs 1977). More recent otolith-based work on the species suggests their age designations were likely accurate and their study provided the first insights into the age-based dynamics between sexes and between primary (males with female coloration that never changed sex) and terminal phase males (vibrantly colored males that underwent metamorphosis from female coloration). The first validation of age estimates from calcareous structures came from the GBR 15 years later for *Scarus schlegeli* (Lou 1992). Since then, there have been just over 20 studies detailing age-based information for parrotfishes based on calcareous structures. Fourteen of these appear in the primary peer-reviewed literature (Warner and Downs 1977, Lou 1992, Choat et al. 1996, Grandcourt 2002, Gust et al. 2002, Choat et al. 2003, Kume et al. 2009, Paddack et al. 2009, El-Sayed Ali et al. 2011, Taylor and Choat 2014, Ebisawa et al. 2016a, b, Lessa et al. 2016, Taylor and Pardee 2017), two in book chapters (Choat and Robertson 2002, Hamilton and Choat 2012) and several more in unpublished academic theses or grey literature. Most of this work has been carried out in the Indo-Pacific region. However, despite the sparse nature of demographic parrotfish studies, a considerable diversity of inter- and intra-specific dynamics has been uncovered, which we will highlight herein.

Throughout this chapter we primarily refer to age-based information derived from annual increment patterns (annuli) in sectioned sagittal otoliths. Parrotfishes, like many teleost fishes, deposit consistent opaque and translucent zones within the otolith structure that correspond to annual patterns of growth and can be best identified via thin transverse sections through the otolith primordium (i.e., core) using low power microscopy with either reflected or transmitted light (Fig. 1). Structural properties of otoliths, for whole otoliths and banding patterns across transverse sections, broadly reflect phylogenetic differences among species, with greatest similarity among closely related species (Taylor and Choat 2014). To date, annual periodicity in otolith increments has been validated in seven species of parrotfish (*B. muricatum*, *Chlorurus spilurus*, *Scarus frenatus*, *Sc. niger*, *Sc. schlegeli*, *Sc. rivulatus*, *Sparisoma viride*), all but one are from the GBR (Lou 1992, Choat et al. 1996, Choat et al. 2003, Andrews et al. 2015; all validations performed using tetracycline tagging with the exception of Andrews et al. [bomb radiocarbon dating]). There generally exists a gradient in optical clarity within species where ease of interpretability increases from low to high latitudes (Choat et al. 2009), but consistent annual incremental structures are present at all latitudes. Further, a strong and generally linear relationship exists between otolith weight and annual age within species (Choat et al. 1996). The predictive capacity of this relationship (Lou et al. 2005, Wakefield et al. 2014) is underutilized at present among tropical fishery managers.

Classifying Demographic Traits

An initial task is to develop the appropriate suite of metrics for quantifying demographic and life-history patterns. Here, we present comparative information using mean maximum length and age. We quantify these traits as the mean length and age of the largest and

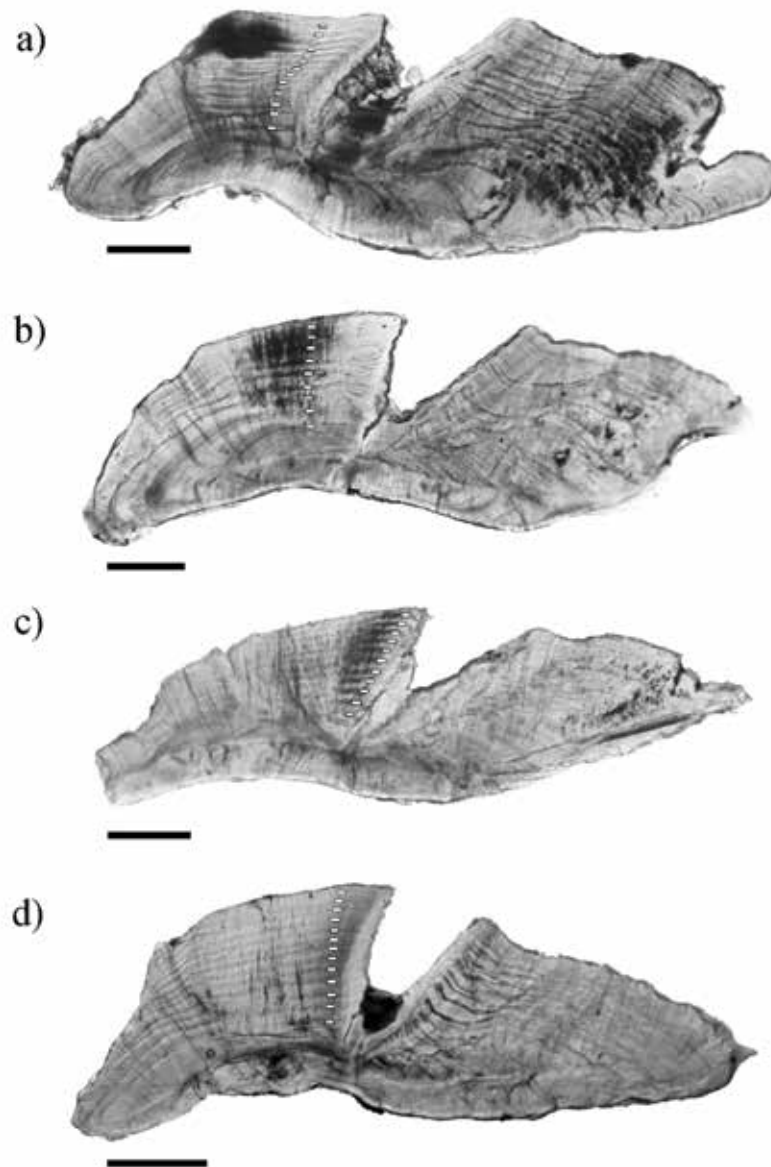


Fig. 1. Examples of transverse sections of sagittal parrotfish otoliths displaying annual increment patterns (denoted by white marks). Species are (a) *Cetoscarus bicolor* (Red Sea, Saudi Arabia), (b) *Chlorurus microrhinos* (Great Barrier Reef, Australia), (c) *Hipposcarus harid* (Red Sea, Saudi Arabia) and (d) *Scarus frenatus* (Yap, Micronesia). Scale bars are 500 μm .

oldest quartile of a sampled population (Choat and Robertson 2002, Taylor and Choat 2014). They correlate strongly with absolute maximum length and age but vary less from random population samples when exposed to intense fishing pressure. Other important traits include the mean length at age at different ages across the life span, the mean length and age at female sexual maturation and the mean length at sex change. Age at sex change

in parrotfishes can be tenuous because sex change appears to be a highly length-influenced process and studies have found that not all females will change sex during their life span (Choat et al. 1996). Later in this chapter, we discuss the analytical tools that will be necessary to generate these demographic metrics and establish the patterns and processes underlying demographic variability in reef fishes.

Sexual Ontogeny and Dichromatism

Parrotfishes are frequently characterized as territorial species, displaying strong sexual dichromatism with protogyny as the dominant mode of male recruitment (Kazancıoğlu et al. 2009, Streebman et al. 2002). However these generalizations obscure a more complex picture especially with respect to male recruitment and sexual dichromatism. While the majority of species are either exclusively (monandric) or partially protogynous (diandric with some males recruiting prior to sex change), at least two appear to be either primary or secondary gonochorists. Robertson et al. (1982) classified *Leptoscarus vaigiensis* as a gonochorist based on size and color phase distributions and histological analysis. Hamilton et al. (2008) used histological analysis of several Solomon Islands populations to classify *B. muricatum* as a secondary gonochorist with all male recruitment occurring through pre-maturational sex change. Although pre-maturational sex change occurs in other species of parrotfish (Robertson and Warner 1978), no evidence of post-maturational sex change (a prerequisite of protogyny; Sadovy de Mitcheson and Liu 2008) was found in this species. However it is possible that protogyny occurs in other populations of this widespread species. Additional investigation based on histological analysis may reveal other examples of secondary gonochorism although this seems unlikely in dichromatic species. All species of tropical Atlantic Sparisomatinae are monandric whereas an Indo-Pacific Sparisomatine, *Calotomus spinidens*, possesses primary males (Robertson et al. 1982). It is unclear if the absence of diandry from tropical Atlantic species reflects trait differences derived through phylogenetic or biogeographic means.

The distribution of sexual dichromatism within parrotfishes is more complex. The majority of species are indeed dichromatic with clearly defined initial (IP) and terminal (TP) phases (*sensu* Warner and Robertson 1978). However, a conspicuous minority of species are monochromatic (Bellwood 2001). This includes large species with a schooling mode of foraging and includes some of the largest parrotfishes (*B. muricatum*, *Chlorurus enneacanthus* [Indo-Pacific]; *Sc. guacamaia*, *Sc. coelestinus*, *Sc. coeruleus* [tropical Atlantic]). Many of these species display specific markings, especially on the head region during spawning episodes but do not have defined IP and TP phases (Muñoz et al. 2014). The biogeography of color phase distribution is more complex. The large excavating clade parrotfishes comprising *Ch. microrhinos* (Pacific), *Ch. strongylocephalus* (Indian Ocean) and *Ch. gibbus* (Red Sea) have a predominantly red IP phase and a green TP phase. For *Ch. strongylocephalus* and *Ch. gibbus* the size distribution and relative abundance patterns conform to the usual monandric pattern with the red IP phase, which numerically dominates the female portions of the populations. For *Ch. microrhinos* the red IP phase represents less than three percent of the population with the majority of females displaying the green TP color phase (Choat unpublished data). *Ch. microrhinos* appears to be losing the IP color phase. A similar pattern is seen in *Sc. niger* in which the Red Sea and Indian Ocean populations have a distinct IP phase which is absent from the Pacific with all individuals displaying the TP color phase. Clearly the behavioral and evolutionary factors driving the development of dichromatism require further study.

Emerging Patterns in Parrotfish Demography

Spatial Heterogeneity within Ocean Basins: Geological History, Regional Habitat Structures and More

Spatial heterogeneity within and across ecosystems is a fundamentally important characteristic (Levin 2000), yet one that ecologists often attempt to control for in order to address other research questions. However, the value in studying this inherent variability is increasingly recognized (Hawkins 2012, Legendre and Legendre 2012). 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. Much of the research on coral reef fishes is conducted at very small spatial scales (Sale 1998). Regarding demographic variation across space, efforts have been focused on measuring the identifiable effects of human extraction (i.e., fishing effects). 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 (Wiens 1989).

Continental Margins versus Oceanic Reef Structures

Coral reefs occur in a number of geologically distinct environments. The most obvious distinction exists between continental margins and oceanic islands. Continental structures are typically characterized by broad, highly interconnected fringing and barrier reef systems. These are often comparatively eutrophic coral reef environments with considerable nutrient input from the adjacent mainland. Examples include the GBR in the western Pacific and the Mesoamerican Barrier Reef System in the western Caribbean. Conversely, oceanic coral reef systems are characterized by sparsely distributed small islands and submerged reef structures. Much of the Pacific Ocean is comprised of oceanic island systems that are characteristic of Micronesia, Melanesia and Polynesia. These reefs occur in oligotrophic regions with various levels of biotic larval interconnectivity facilitated through prevailing ocean currents. Regardless of geological history, coral-dominated environments are often made up of abundant and diverse parrotfish assemblages.

Evidence to date suggests that species associated with continental and high-island margins are larger-bodied and have longer life spans compared with conspecifics from oligotrophic oceanic reefs. Most of the examples stem from species comparisons between the GBR (continental margin) and Micronesia or the Line Islands (oceanic reef systems). Exceptions do exist, and the effects of latitude and variable fishing pressure complicate our ability to decipher the effect of geological history on demography. However, the pattern is quite consistent among conspecifics for which comparative data is available.

The most comprehensive data set for addressing this question exists for the parrotfishes, for which length-at-age data has been derived for a number of conspecifics from both the GBR and Micronesia; many of these were sampled at a similar latitude (~13-14°; Choat and Robertson 2002, Taylor and Choat 2014). Figure 2 compares length-at-age growth trajectories between regions for 10 species spanning four genera. The form of growth curves relative to region varies, but parrotfishes from the GBR consistently display larger size-at-age in the older age classes and in some cases considerably longer life spans. This

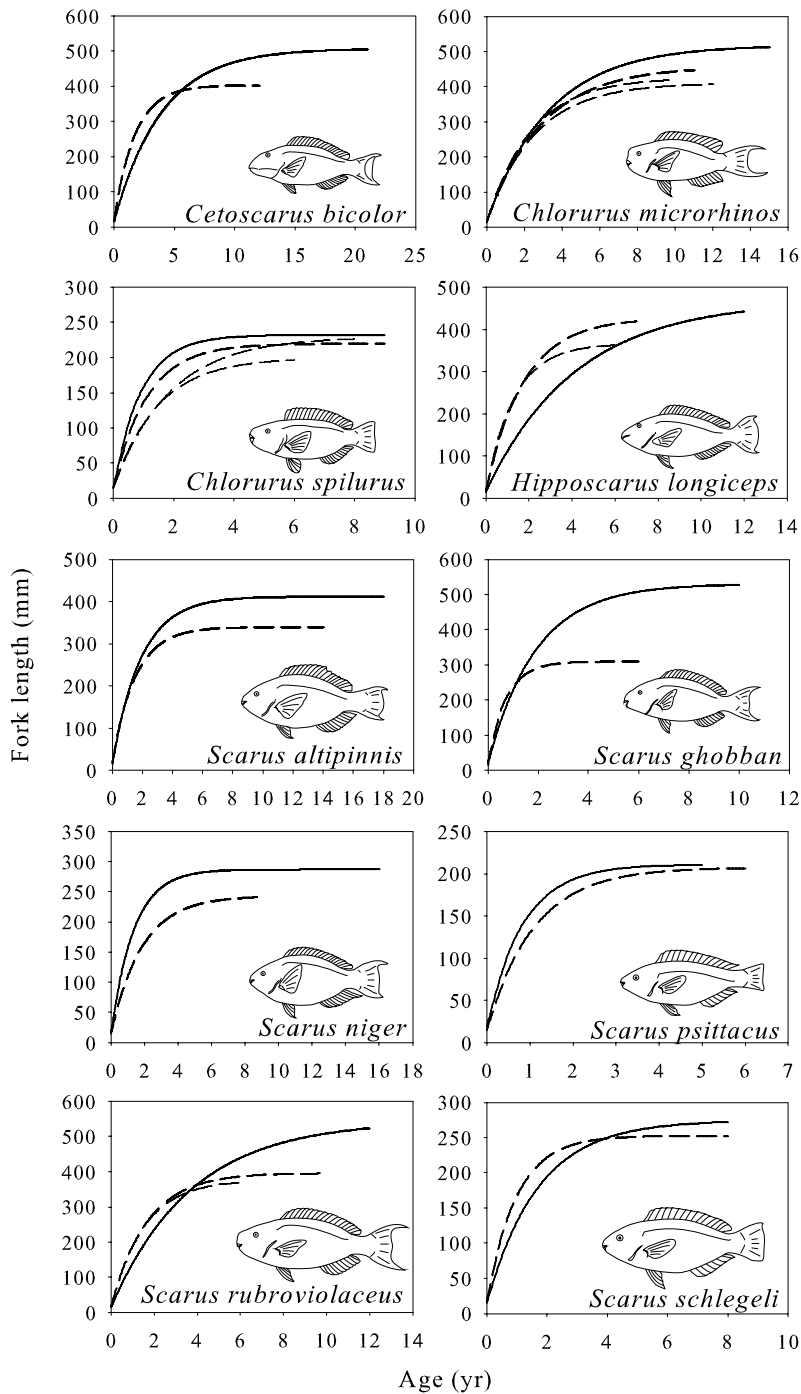


Fig. 2. Comparison of growth trajectories between conspecific parrotfish populations from the Great Barrier Reef (solid lines) and Micronesia (dashed lines). Multiple dashed lines for some species represent Micronesia islands of varying fishing intensity from lightly- to heavily-fished regions. Specimens were collected by fishery-independent sampling at each locality and age information was derived from sagittal otoliths. Von Bertalanffy growth functions were used to derive growth curves.

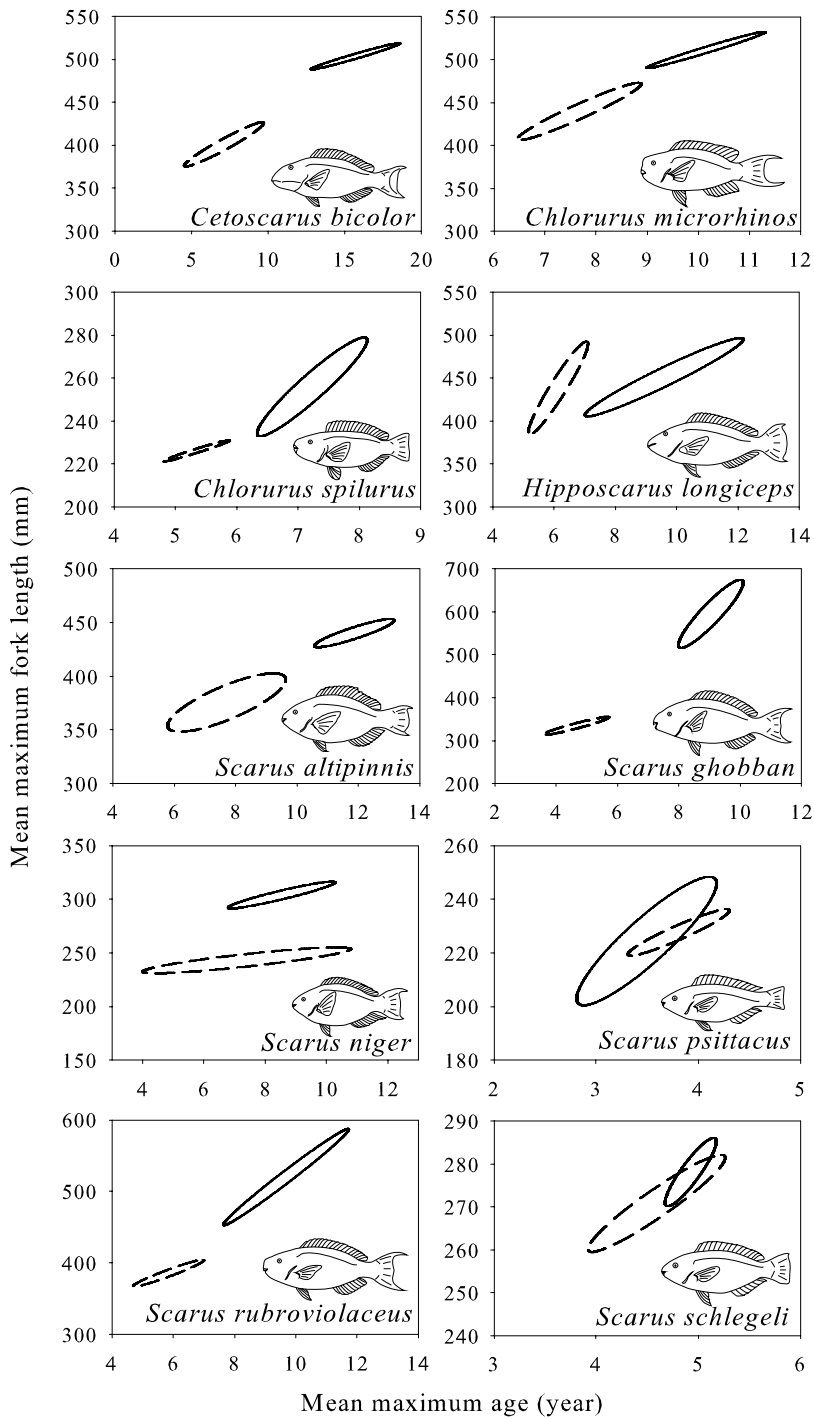


Fig. 3. Comparisons of 95% confidence ellipses surrounding estimates of mean maximum length and mean maximum age (parameters defined within text) for conspecific parrotfish populations from the Great Barrier Reef (black lines) and Micronesia (dashed lines). Specimens were collected by fishery-independent sampling at each locality and age information was derived from sagittal otoliths.

is reflected in patterns of mean maximum length and age (Fig. 3). However, the effects of fishing are potentially a major confounding factor between these data sets; parrotfishes represent a major fishery target in Micronesia whereas they are not harvested on the GBR. Could the observed differences potentially reflect truncated life spans and selection (driven by fishing pressure) for smaller-bodied fishes at Micronesian localities? This is certainly a legitimate concern and this effect has likely occurred at least to some degree. However, Micronesian samples collected across lightly and heavily exploited outer reefs of different islands displayed growth profiles more similar to each other than to the GBR and, in some cases, lightly exploited areas had shorter life spans (e.g., *Ch. microrhinos*, *Ch. spilurus*, *Sc. rubroviolaceus*; Fig. 2). At a smaller spatial scale, the same was true for species systematically sampled from marine reserves (by special permit) on Guam compared with heavily fished sites (*Ch. spilurus*, *Sc. psittacus*; Barba 2010). Further, this data is complemented with high-resolution *in situ* length estimates from stereo-video surveys spanning uninhabited to heavily exploited reefs of Micronesia and protected reefs of the northern GBR, where parrotfishes are not harvested. Using *Ch. microrhinos* as an example (a widespread, relatively abundant and highly targeted species throughout the Indo-Pacific), mean length decreased with increasing human density in Micronesia (Taylor et al. 2015). However, the largest length classes at all Micronesian islands (including uninhabited areas) were similar to each other and yet much smaller than those from the northern GBR, where maximum recorded lengths were nearly 20 percent greater. This suggests that the observed differences in length-at-age are indeed unique to each region. Unfortunately, this sampling represents only two distinct areas and much more sophisticated analyses and sampling programs are necessary to clarify within-region patterns. Limited information on exploited fish populations from the high-latitude, isolated oceanic islands of Hawaii has revealed even greater longevity than on the GBR, not only for parrotfishes (Howard 2008), but also for acanthurids (Claisse et al. 2009, Andrews et al. 2016).

Regional Habitat Structures and Fishing Pressure

Most work on the demography of parrotfishes has been carried out at intermediate spatial scales (10's-100's km) and highlights the influence of regional habitat, density dependence, predation and human exploitation on demographic traits. The magnitude of intra-specific variability in parrotfish life-history traits was first demonstrated by Gust et al. (2002) among mid- and outer-shelf reef systems of the GBR. Consistent differences were found for three parrotfish species (and one acanthurid) whereby considerably smaller length-at-age and shorter life spans corresponded with higher natural mortality rates on outer shelf reefs. Observed differences were attributed to density-dependence given that parrotfish densities at the outer shelf reefs were on average four times greater than those of mid shelf reefs. Early maturation and sex change at small body sizes as well as high proportions of initial phase primary males were also characteristic of the high-density outer shelf populations (Gust 2004), and suggest that considerable variability in reproductive dynamics can occur over relatively small spatial scales (~20 km).

In contrast, age-based analysis of the Caribbean stoplight parrotfish *Sp. viride* suggested limited variability in life-history traits over a broad spatial scale (Choat et al. 2003). However, latitude (proxy for water temperature) and human population density (proxy for fishing pressure) had identifiable influences on the mean maximum sizes and mortality rates of populations, but not on maximum ages. No relationship existed among

fishing pressure, abundance or growth rate. At smaller spatial scales (< 10 km), life span doubled from inshore to offshore reefs (Paddock et al. 2009).

As previously mentioned, sexual dimorphism in color phases for many parrotfish species facilitates rapid and non-invasive sex determination from visual surveys. The presence of initial phase primary males is a confounding factor, as functional males displaying initial phase coloration will be classified as females. For the estimation of sex change schedules, however, this appears to be a negligible issue. Histological examination of gonads was performed on sexually dimorphic species from Micronesia, and a comparison of estimates of lengths at 50 percent sex change across species and geographic locations using histology (initial phase primary males excluded) and color-phase ratios by length class (initial phase primary males scored as females) from biological specimens demonstrates that even when the proportion of primary males is high (> 20 percent of IP individuals, > 60 percent of functional males), estimates using color phases only differ by less than six percent (Fig. 4). This is because the mean length of initial phase primary males is consistently much smaller than the length at sex change; hence, the presence of primary males has only a small influence on estimates of the length at 50 percent sex change, even when they are in high proportions.

Several studies have used this technique to examine variability in life-history traits across environmental gradients from visual survey data. Among remote atolls of the NW Hawaiian Islands and the northern Line Islands, DeMartini et al. (2005, 2008) documented shifts in the length at sex change for several parrotfish species along a gradient of predator biomass. In both locations, parrotfish length at sex change consistently decreased with increasing biomass of apex predators, implying that higher rates of mortality associated with increased predation yields a compensatory shift in life-history processes whereby sex change occurs earlier. Across seven islands of Micronesia, Taylor (2014) identified strong scale-dependence in covariates of length at sex change for *Ch. spilurus*. Fishing pressure influenced this trait considerably at the within-island scale, with higher fishing pressure yielding smaller lengths at sex change. Across islands, however, broad-scale features of island geomorphology overwhelmingly predicted patterns of length at sex change. This was consistent for all dichromatic parrotfish species for which resolution was adequate from survey data ($n = 4$). The proximal mechanism driving this pattern is unknown, but likely relates to inherent differences in assemblage structure and the influence of reef geomorphology on reproductive behavior (i.e., how reef morphology affects population size, travel distance to spawning sites and reproductive mode). Collectively, these studies demonstrate high adaptive flexibility in demographic traits of parrotfishes and contradict the model of invariant length at sex change within species (Allsop and West 2003). Further, they demonstrate that demographic variability can be driven by a range of external biotic and abiotic factors and therefore patterns will depend on both the measurable influence (i.e., value range) of factors and the spatial scale of observation.

To this point we have dealt primarily with habitat structure and the configuration of reef systems within an ocean basin and the interaction between the structure of reef ecosystems and fishing. This reveals the critical nature of a spatial and habitat context when evaluating demographic patterns in reef fishes. Without this consideration, there is a high probability of confounding the influence of habitat structure and fishing pressure on parrotfish abundances and demographic patterns.

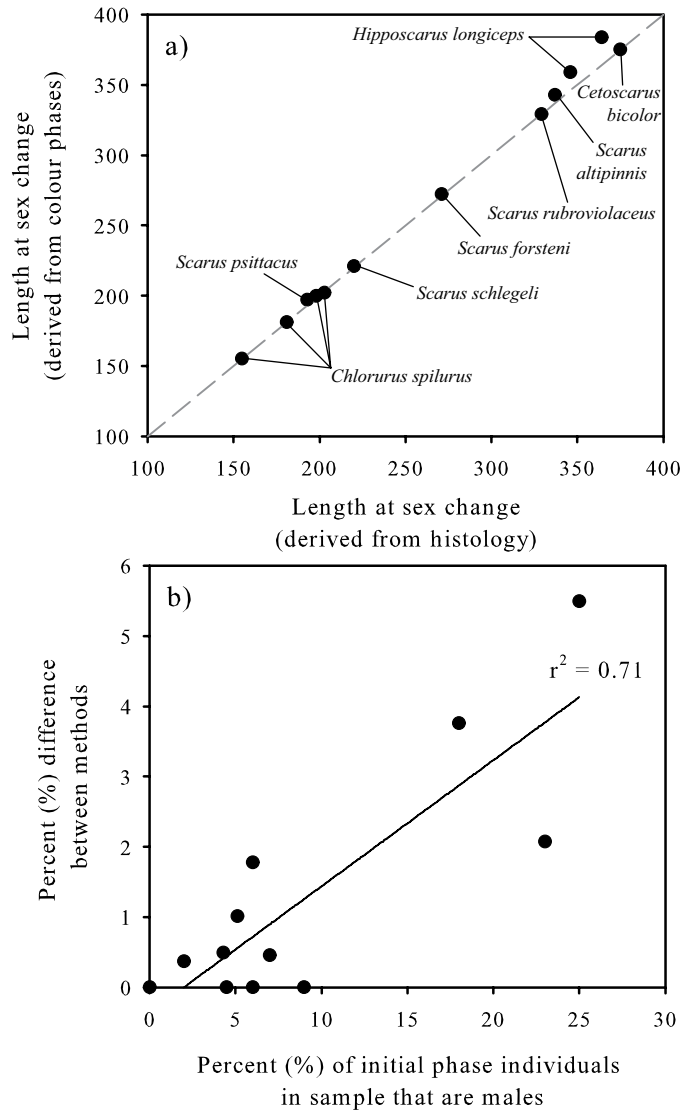


Fig. 4. (a) Relationships between estimates of length at sex change based on histological examination of gonad stages (initial phase primary males excluded; x -axis) and color-phase ratios (initial phase primary males scored as females; y -axis) by length class from biological specimens across parrotfish species and different populations within species in Micronesia. A dashed line represents a one-to-one ratio. (b) Relationship between the percent of initial phase males represented in the male portion of each population and the difference in length-at-sex-change estimates between the two above methods.

Biogeographic and Phylogenetic Signatures in Demographic Traits

Parrotfishes have undergone a relatively recent evolutionary diversification with expansion into the tropical ocean basins of the world. These basins have highly dissimilar geological

and climatic histories. For instance, total area, coral reef habitat area and the number of island habitats increases by three, one and three orders of magnitude, respectively. This occurs from the Red Sea to the Caribbean and tropical Atlantic, to the Indian Ocean and to the Pacific Ocean (Table 1). Concordantly, the mean range size of parrotfish species increases by an order of magnitude across these ocean basins (Table 1). Given the level of variation, we must evaluate whether growth rates, life spans and associated turnover times of species respond to environmental disturbance on ecological and evolutionary time scales and if this is reflected among ocean basins. To assess this we consider three sources of demographic variation: (i) Environmental factors, especially changes in temperature occurring over latitudinal gradients, indicative of demographic variation at ecological time scales; (ii) biogeographic factors which reflect the differing geological histories of ocean basins and have a largely evolutionary signature (biogeographic factors are appropriately sampled over longitudinal geographic gradients that cover different ocean systems); and (iii) the influence of phylogeny and evolutionary relationships amongst the different clades of parrotfishes based on a comprehensive phylogenetic reconstruction of the taxa in question. To help put this into perspective we firstly review the main features of parrotfish phylogeny and evolutionary history.

Table 1. Broad-scale habitat and parrotfish range size metrics from major ocean basins containing coral reef habitat

	<i>Red Sea</i>	<i>Caribbean</i>	<i>Indian</i>	<i>Pacific</i>
Area (10 ⁶ km ²)	0.4	2.7	67.4	152.6
Habitat area (10 ⁶ km ²)	0.017	0.026	0.032	0.201
Island habitats	24	1,242	7,561	29,959
Mean parrotfish species range area (10 ⁶ km ²)	0.34	2.1	2	7.5
Pliocene/Pleistocene disturbance regime	Regionally severe, locally high	Regionally high, locally high	Regionally moderate, locally moderate	Regionally moderate, locally high

Phylogenies confirm the placement of parrotfishes as a tribe nested within the family Labridae (Westneat and Alfaro 2005). The major divergences in parrotfish evolution have been relatively recent. Phylogenies identify two major clades, the Sparisomatines (sometimes identified as the 'seagrass clade') and the Scarinines (the 'reef clade'), although this is open to question. Although both clades appear to have undergone an initial divergence within the Tethyan region, the geography of subsequent diversification is different. Fossil evidence places the initial diversification of Sparisomatines within the Tethys Sea with most of the subsequent diversification and reef colonization occurring within the Atlantic Ocean now dominated by the genus *Sparisoma* with 15 extant species mainly in the western Atlantic. Diversification in *Sparisoma* occurred primarily during the Pliocene and Pleistocene. A less-diverse clade comprising six species characterised by the genera *Calotomus* and *Leptoscarus* colonized the Indo-Pacific.

The Scarinines (a more-diverse clade) also appear to have originated in the Tethyan region but with the main episodes of reef colonization and diversification tending eastwards which established this clade throughout the Indo-Pacific dominated by two genera, *Scarus* (currently 52 species) and *Chlorurus* (18 species). Diversification in both

genera was mainly a Pliocene/Pleistocene event with *Chlorurus* being more recent than *Scarus*. While *Chlorurus* distributions extend from the Red Sea to the central Pacific, *Scarus* is more cosmopolitan with distributions extending from the Red Sea to the east Pacific. The genus is also present in the tropical Atlantic with the possibility that colonization of this ocean was via southern Africa. More recently, a single Lessepsian migrant (*Sc. ghobban*) has colonized the eastern Mediterranean. Three additional Scarinine genera *Bolbometopon*, *Cetoscarus* and *Hipposcarus* form distinct clades with their origination preceding *Scarus* and *Chlorurus*. These genera are confined to the Indo-Pacific.

A number of trends emerge when length distributions of parrotfishes are mapped onto a complete phylogeny. Firstly, there are clear phylogenetic differences in size structure with the mean size of the older clades (the Sparisomatine parrotfishes) being significantly lower than that of the more recent clade (the Scarinines). Sizes within the Scarinines are variable with the differences being driven by a few very large species ranging from 65 to 130 cm maximum fork length. There are also geographic correlations with body size. The Atlantic parrotfishes have marginally smaller mean lengths than those of the Indo-Pacific but length distribution is complex. Overall differences among ocean basins largely reflect the domination of the Atlantic fauna by Sparisomatine parrotfishes.

Demographic Variation over Geographic Gradients

Variation in demographic processes, primarily growth rates and longevity reflect the three factors (environmental, biogeographic, and phylogenetic) identified at the start of this section. The following analyses are designed to distinguish between these sources of variation, especially the alternatives of common geological and oceanic histories (historical biogeography) versus common evolutionary relationships (phylogeny).

The geography of demographic processes is approached hierarchically, first by analysing trends along latitudinal gradients and secondly along a longitudinal axis that incorporates different ocean basins, each with its unique geological and oceanographic history. Sampling latitudinal gradients provides a means of estimating the influence of systematic changes in environmental variables, primarily temperature, on growth rates and longevity often over small spatial scales. Previous work shows that ectotherms respond predictably in terms of growth rates and size structure to changes in temperature in accordance with the temperature-size rule (Atkinson 1994, Trip et al. 2008). As ectotherms, we expect parrotfish body size to be inversely related to water temperature; i.e., maximum body size will increase with increasing latitude as mean water temperature decreases (Atkinson 1994, Atkinson and Sibly 1997). Evidence from other reef fish families suggests maximum age will also conform to this pattern (Robertson et al. 2005, Trip et al. 2008). Sampling over longitudinal gradients across ocean basins may reflect changes that have occurred over evolutionary time scales including differences in life span (Trip et al. 2008).

Latitudinal Gradients: The Impact of Temperature

The predictable nature of latitudinal variation is illustrated by the following data set that incorporates estimates of mean maximum length and mean maximum age of nine populations of the widespread parrotfish *Ch. spilurus* over a gradient of 22° of latitude. Mean maximum length and age estimates were highly correlated. Individuals at low latitude sites were smaller than those at high latitudes and, on the average, had relatively short life spans (Fig. 5). The largest and longest-lived individuals occurred in the colder and more

productive waters in higher latitudes which is similar to the latitudinal distribution of life span seen in acanthurids (Robertson et al. 2005, Trip et al. 2008) and other species (e.g., Cappo et al. 2013). Estimates for the different populations show a great deal of variation within the central-southern part of the sampling gradient. This reflects the complexity of reef habitats in this region and the fact that the sampled populations are drawn from both the western Pacific and the eastern Indian Oceans. This indicates that longitudinal variation in reef habitats and the surrounding ocean environment may reflect the influence of long-term historical factors and should be incorporated into future sampling designs.

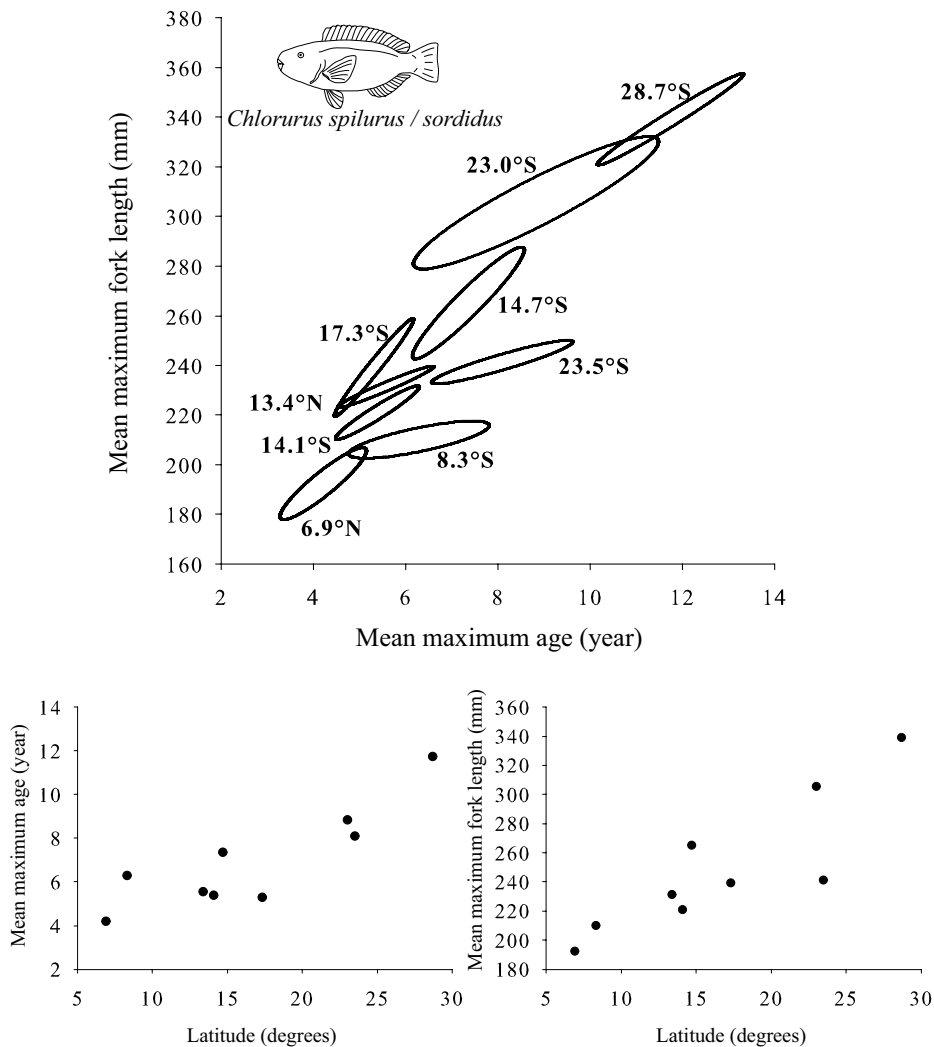


Fig. 5. Relationships between mean maximum age, mean maximum length (parameters defined in text) and latitude for the *Chlorurus spilurus / sordidus* clade. Ellipses represent 95% confidence regions. Sample sites are as follows: 6.9°N: Pohnpei, Micronesia; 8.3°S: Solomon Islands; 13.4°N: Guam, Micronesia; 14.1°S: Scott Reef, Western Australia; 14.7°S: Lizard Island, Great Barrier Reef; 17.3°S: Rowley Shoals, Western Australia; 23.0°S: Ningaloo, Western Australia; 23.5°S: One Tree, Great Barrier Reef; 28.7°S: Abrolhos, Western Australia.

Longitudinal Gradients and Life Span

Previous studies of longitudinal variation of the acanthurid *Ctenochaetus striatus* (Trip et al. 2008) identified a trend in longevity, with maximum ages achieved by western Pacific populations being significantly greater than those from localities within the Indian Ocean. Differences in growth rate emerged at more localized scales. To determine if the trend in longevity occurred in other groups, we obtained age and size estimates of five species or clades of parrotfishes by sampling over a gradient of 105° of longitude extending from the central Red Sea to the western Pacific Ocean. This gradient encompassed three ocean basins of varying size, habitat availability and the extent and severity of disturbances over the Pliocene to Pleistocene epochs. These range from the western Pacific contiguous with the Pacific Ocean proper characterized by a variety of reef habitats covering a wide area of the coastal and oceanic ecosystem to the Red Sea, relatively limited in geographic extent and the amount of reef habitat available. Moreover, the impacts of major environmental disturbances will be regionally moderate in larger ocean basins and severe in smaller systems with limited reef habitats as in the Red Sea (Table 1).

For all five species groups there was a consistent trend of a reduction in life span from the western Pacific to the Red Sea. Populations from Indian Ocean localities had lower longevities than those of the Pacific and generally were higher than those of the Red Sea (Fig. 6). Trends in size were less consistent. Red Sea populations displayed smaller mean maximum sizes than those of the western Pacific. However, for populations of *Ch. sordidus/spilurus*, *Sc. niger* and *Sc. frenatus*, the maximum sizes were greatest in the central and western Indian Ocean while the mean ages were relatively low, especially in the Seychelles. This confirms that growth patterns are likely to be sensitive to conditions prevailing at particular reef sites while longevities appear to be consistent over whole ocean basins.

Separating Phylogenetic vs Geographic Effects

At a global scale parrotfishes show phylogenetic partitioning. The Indo-Pacific region is dominated by a high diversity of Scarinine parrotfishes with relatively fewer Sparisomatines (five species of the genus *Calotomus* and one *Leptoscarus*). Only three Indo-Pacific Sparisomatines are widespread (*L. vaigiensis*, *Ca. carolinus* and *Ca. spinidens*). In contrast, the tropical Atlantic supports only nine Scarinines of which six species occur within the greater Caribbean (Robertson and Cramer 2014). Sparisomatine parrotfishes display a greater diversity within the tropical Atlantic (15 species) with one species, *Sparisoma cretense*, colonizing temperate reef environments. The 15 currently recognized species of *Sparisoma* are widely distributed over the tropical Atlantic with seven in the Greater Caribbean (*sensu* Robertson and Cramer 2014), five endemic to Brazil and its offshore islands and three endemic to the central and eastern Atlantic.

Comparative demographic analysis of the Sparisomatine versus the Scarinine parrotfishes sampled from the Greater Caribbean and western Pacific Ocean regions reveals that the former manifests smaller mean sizes and reduced life spans (Choat and Robertson 2002). In general, Sparisomatine parrotfishes comprised populations of relatively small fast growing species with potentially high turnover rates. Specifically, the tropical Atlantic and Indo-Pacific species display very short life spans (< five years), rapid growth and relatively small sizes. Only one tropical Atlantic species, *Sp. viride*, achieved a mean maximum age in excess of five years and the maximum sizes achieved were less than 40 cm fork length. For Scarinines the greatest mean maximum ages occurred in Pacific species. The three oldest species (*B. muricatum*, *Ce. bicolor* and *Sc. frenatus*) achieved mean

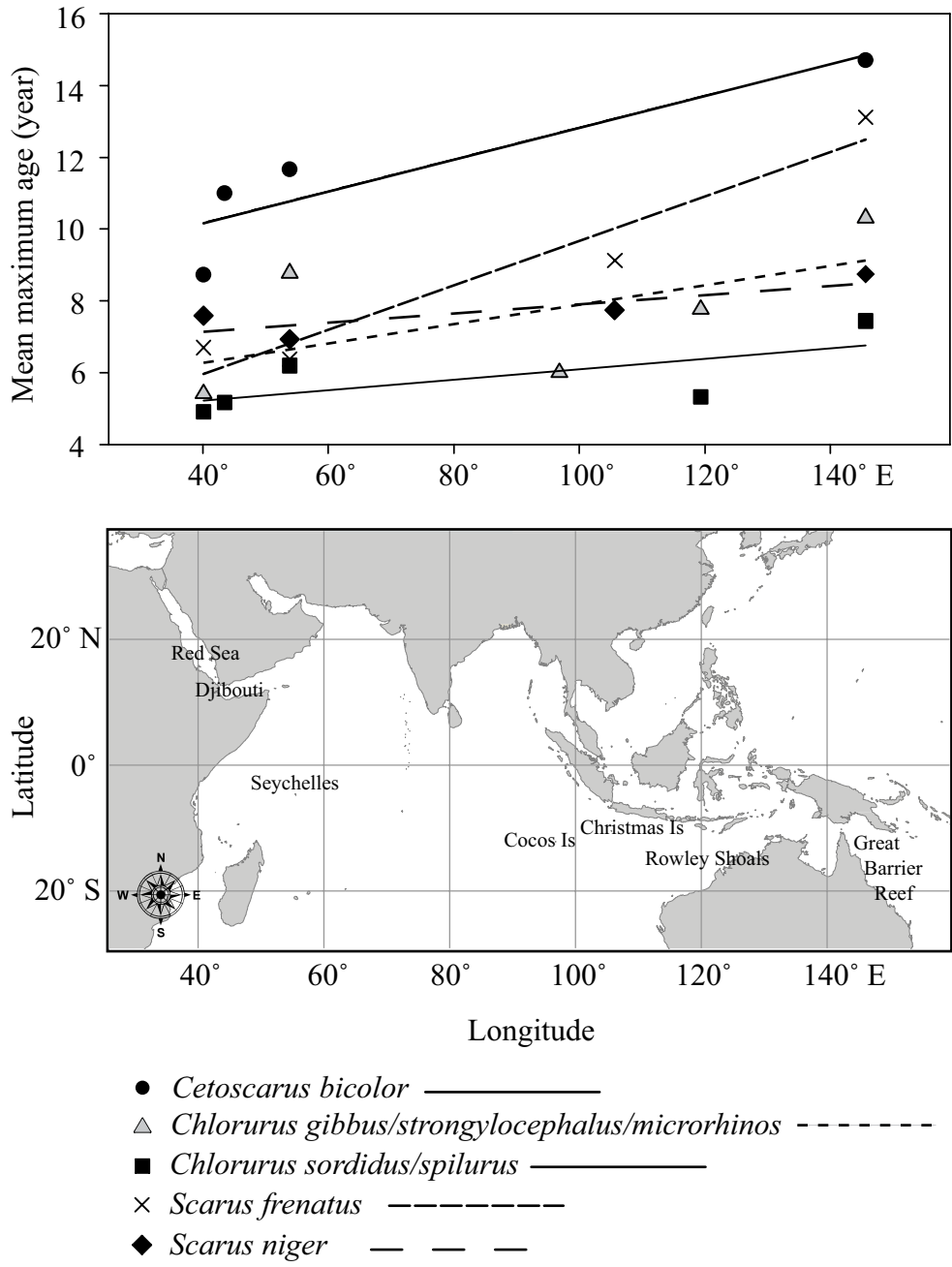


Fig. 6. Consistent patterns of increase in mean maximum age (defined in text) for species or species clades along a longitudinal gradient reflecting an increase in ocean basin size from the Red Sea to the western Pacific Ocean.

maximum ages in excess of 15 yr. The three oldest tropical Atlantic species *Sc. guacamaia*, *Sc. coelestinus* and *Sc. coeruleus* achieved mean maximum ages of 12.3, 12.8 and 10.2 yr, respectively, despite the fact that *Sc. guacamaia* is the second largest parrotfish species recorded anywhere (Fig. 7). For Scarinines, the tropical Atlantic species have shorter life

spans and grow rapidly compared to Pacific species. A further distinguishing feature of the Pacific species were the variable growth patterns, most notably asymptotic growth with extended life spans in the relatively small species *Ch. spilurus*, *Sc. frenatus* and *Sc. niger*.

In summary, Sparisomatine species have small sizes and short life spans regardless of their oceanic and biogeographic history suggesting that phylogeny was the dominant influence on demography. Scarinines generally have larger mean sizes and greater life spans than Sparisomatines regardless of their biogeographic history and present location. However, there are also between-ocean differences, with species in the tropical Atlantic being shorter lived at a given length than those of the Pacific despite the presence of some very large species endemic to the Atlantic (Fig. 7). Given the combined demographic data set it appears there may be some feature of the tropical Atlantic that selects for relatively fast growth, short life spans and higher population turnover in parrotfishes relative to the Pacific. The underlying reasons for these differences are unclear. However, the reduced life span of Red Sea and Caribbean species compared to those of the Indo-Pacific suggests that Ocean basin size and the frequency and magnitude of disturbance to the reef habitat would be appropriate starting points.

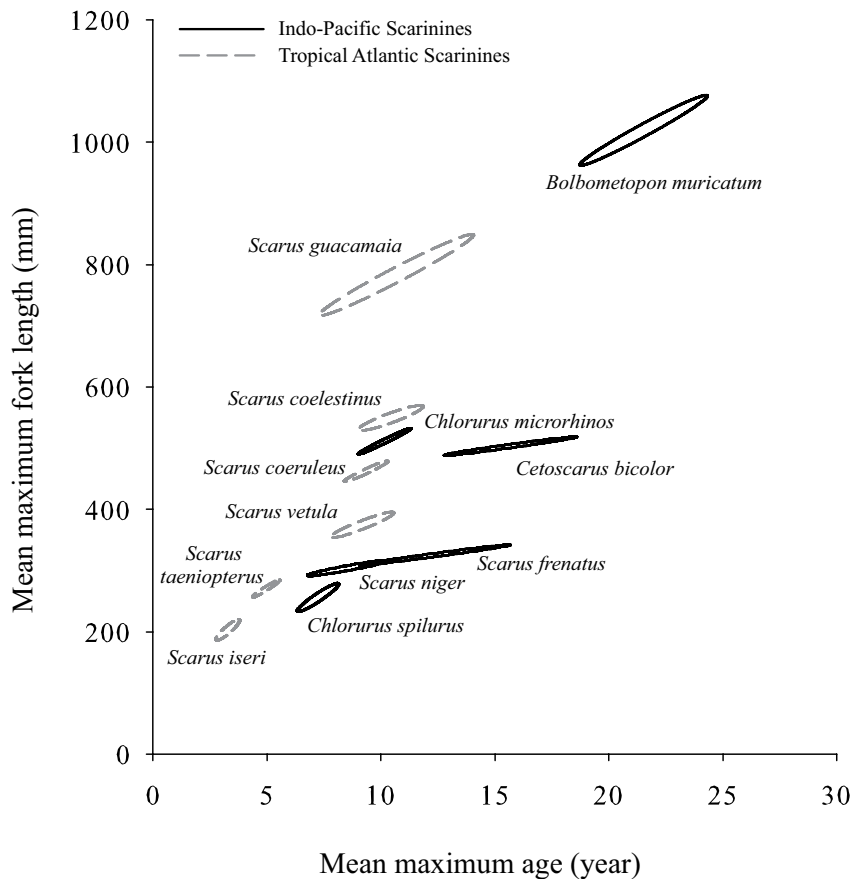


Fig. 7. Relationship between mean maximum age and mean maximum length (parameters defined in text) across Indo-Pacific (black lines in 95% confidence ellipses) and tropical Atlantic (grey dashed lines) Scarinine parrotfishes. Species from the Indo-Pacific tend to have longer life spans for a given maximum body size.

What are the Main Questions Raised by these Preliminary Analyses and How Might they be Resolved?

We identify four issues that have emerged from recent ecological studies on parrotfishes: (1) the importance of carrying out demographic analyses at multiple spatial scales; (2) identifying ecological and evolutionary processes in the response of populations to environmental variation; (3) the impact of demographic studies on the management of fisheries; and (4) the need for more comprehensive demographic analyses.

The Importance of Spatial Scale in Demographic Analysis

Both the abundance and demographic traits of parrotfishes may be modified by environmental disturbances, either anthropogenic or natural. The critical questions facing reef scientists and especially managers concern the spatial extent of these effects. Do they constitute a footprint that extends over whole ocean basins or are they restricted to specific reef systems? Previously, these questions have been answered through integrative analyses that tested for the effects of environmental disturbance on the demographic traits in question. In the case of anthropogenic factors, the spatial boundaries of the effect are not often defined and in many cases it is assumed that they were regional or even global in extent (Legendre and Legendre 2012). In many instances, spatial structuring in data sets is either controlled for or the possibility ignored with the consequence that anthropogenic effects emerged as significant factors in species abundance and distributions. However, it is now clear that the influence of environmental disturbance and variation on ecological traits may be highly scale-dependent, especially with specific regards to parrotfish assemblages (Taylor 2014, Taylor et al. 2015).

The dominant message arising is that both the scale of observation and the spatial pattern of reef configuration and habitat structure are critical in interpreting parrotfish life-history information and their response to fishing pressure (Taylor et al. 2015). Hierarchical sampling designs that integrate measures of oceanographic history, reef configuration and habitat structure with estimates of fishing mortality are a priority. In these circumstances, multi-scale sampling of demographic and life-history traits, independent of anthropogenic factors becomes valuable, especially age-based reproductive data. Reproductive data such as age at maturity is important to fisheries management and related generation times are also critical in estimating evolutionary responses to natural or anthropogenic disturbances.

Ecological vs Evolutionary Demographic Responses

Demographic traits in ectotherms, especially fishes, are highly sensitive to environmental variation. Short-term responses represent phenotypic plasticity and involve rapid shifts in physiological and demographic traits, especially growth rates. This enables individuals to cope with environmental variation and is particularly important in marine fish where dispersive larvae may lead to marked habitat changes between generations (Warner 1997). For reef fishes, marked differences in growth rates can be observed among populations occupying different habitats separated by small linear distances (Gust et al. 2002), suggesting that this variation is best interpreted as phenotypic plasticity (Dudgeon et al. 2000). In multi-scale demographic studies, differences in growth rates often emerge at localized scales (Robertson et al. 2005, Trip et al. 2008, Paddock et al. 2009).

In contrast, consistent differences in life span were observed above at regional scales and reflected differences between ocean basins. This was interpreted as a longer-term

evolutionary response to historical patterns in ocean environments seen at geographic scales. However, Gust et al. (2002) and Gust (2004) identified significant variation in growth rates and life span in parrotfish populations at very local scales. The study sites did not manifest the levels of temperature change associated with variation over latitudinal gradients. Demographic variation was interpreted as a consequence of density-dependent processes as recruitment strength varied significantly among the sites tested. Moreover, reductions in life span were associated with the larger number of piscivores at some sites. It is clear that both phenotypic plasticity and adaptation to prevailing oceanic regimes moulded by the environmental history of an area can result in scale-associated demographic variation, especially for life span. Research priorities in this area include investigation of trade-offs between initial growth rates and life span at local and geographic scales and the plasticity of development, growth and maturation with respect to temperature and feeding regime. To date, the common-garden experiments necessary to resolve these issues have been restricted to particular taxa, primarily pomacentrids. However, advances in reef fish culture including groups such as labrids coupled with advances in genomics now establish the possibility of resolution through common-garden experiments and genomic analysis in a number of species.

Demographic Studies and Their Impact on Management and Conservation

Parrotfishes are increasingly important fishery resources throughout the majority of their geographic range. Hence, the impact of human exploitation on parrotfish communities has emerged as a critical management and conservation issue (Jackson et al. 2014). 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 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. 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, 2014). 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). 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). 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, age at female maturation has been found to be the optimal predictor of vulnerability to overexploitation among parrotfish species (Taylor et al. 2014), thus encouraging the collection of age-based information for harvested species. The spatial

variability in life-history traits demonstrated in this chapter 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.

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 community 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 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 we have presented 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. Simple monitoring programs can alleviate many of these gaps, but such programs require sustained funding, resources and capacity. Questel and Russ (Chapter 14) provide a review of the responses of parrotfish communities to sustained protection in marine reserves.

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 maturation and sex change (Law 2000, Hamilton et al. 2007, Hamilton and Caselle 2015), 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 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.

Demographic Analysis

Length-at-age data is incorporated into demographic analyses primarily through growth models. A majority of demographic studies involving reef fishes have used the von Bertalanffy Growth Function (VBGF) to model the relationship between length and age, generate estimates of rates and compare growth performance across populations. For parrotfishes, this has provided information of spatial patterns in their demographic characteristics (e.g. Gust et al. 2002). However a number of authors have questioned the biological interpretation of the VBGF parameters, especially K (Knight 1968, Roff 1980, Craig 1999, Lester et al. 2004, Trip et al. 2008, Trip et al. 2014a).

A misconception is that K is a measure of growth rate, even though K is a reciprocal of time with units of time^{-1} (not $\text{length} \cdot \text{time}^{-1}$ as would be expected for a growth rate). Rather, K varies with the age at which the growth trajectory reaches (or would reach) asymptotic length L_{∞} , and is a measure of the curvature of a growth trajectory. Asymptotic growth curves generate high K values, whereas indeterminate curves generate lower values. While this may be correlated with differences in growth rate, this interpretation requires the following caveats. First, growth rate varies with age over the length of the life span and is thus a dynamic demographic trait that would best be represented using growth rate-at-age as opposed to a single value such as parameter K . Second, parameter K does not adequately reflect differences in growth rate between groups of fishes (e.g. between sexes). To illustrate this point: we use the following examples, the bumphead parrotfish *B. muricatum* (Hamilton and Choat 2012) and the humphead wrasse *Cheilinus undulatus* (Choat et al. 2006). In both species, males and females grow at a similar rate until sexual maturity is achieved. In *B. muricatum*, males continue to grow at similar rates whereas female growth decelerates considerably (Hamilton and Choat 2012). The differences are even more striking in *C. undulatus* where male growth rate accelerates and becomes linear. If K was a measure of growth rate, then we would expect to find K values that either (a) are similar between males and females reflecting the absence of sex-specific growth over the first years of life, or (b) are greater in males reflecting faster growth in males following sexual maturity. Yet, fitting VBGF growth trajectories to male and female *B. muricatum* generates a greater K value in females (0.15) than males (0.10). This is because females reach asymptotic size earlier. If, however, K values were used to establish the patterns of differences in growth rate between the sexes in this species, the conclusions would lead to a diagnosis of faster growth in females.

Alternative solutions to the traditional VBGF exist and are being increasingly used in demographic studies of reef fishes, including in parrotfishes (e.g. Trip et al. 2008, Claisse et al. 2009, Ruttenberg et al. 2011, Donovan et al. 2013, Taylor and Choat 2014). A model that has received increasing attention in the recent years is the re-parameterised VBGF (rVBGF, Francis 1988). This model describes the relationship between length and age in the same way as the traditional VBGF (they are two equations of the same function), but generates model parameters that differ significantly from the traditional VBGF parameters. The rVBGF produces parameter estimates of mean length at three ages across the life span, which is inherently biologically relevant and interpretable and allows the comparison of

mean length at a given age (i.e. growth rate up to that age) across populations (or sexes). Trip et al. (2014a) demonstrated two other benefits in using the rVBGF parameters (over the traditional VBGF parameters). First, the rVBGF parameters are significantly more stable than the VBGF ones, indicating that they are better suited for comparative purposes. And second, the rVBGF parameters produce estimates of mean length at age in the ascending part of the growth trajectory (e.g. parameter of mean length at age one, L_1) that are closer to the most likely 'true' value (the value found when modelling growth using large numbers of new recruits) than VBGF parameter K . We propose that the rVBGF be used and presented alongside the VBGF, especially when estimating growth rate (mean length at age) and comparing growth among populations.

Female maturation has proven to be a reliable predictor of vulnerability to exploitation among parrotfishes, and thus represents a valuable demographic metric (Taylor et al. 2014). However, collecting and analysing reproductive data is usually costly and time-consuming. An alternative analytical tool was proposed by Scott and Heikkinen (2012), who use a Broken-Stick (BS) model to estimate age at sexual maturation from length-at-age information. The BS models length-at-age data using two linear regressions that describe, respectively, the ascending and asymptotic (or would-be asymptotic) arms of the growth trajectory, and that smoothly join at the point where growth slows down or reaches the asymptote (the change-point). Scott and Heikkinen (2012) successfully demonstrated that the change-point may be used as a proxy for age at sexual maturation in north Atlantic plaice. While the BS model represents a potentially powerful tool for the estimation of age at sexual maturation in future demographic studies, it requires field-testing and calibration in reef species manifesting a variety of growth curves.

Discussion

The necessity of a more comprehensive database on parrotfish population dynamics is underlined by two factors. First, with the serial depletion of many groups of reef fishes by fishing, those groups lower in the trophic pyramid, primarily parrotfishes, are now targeted at higher rates by reef fisheries on a global scale (Pauly et al. 1998). Secondly, predictions of environmental change in tropical ocean environments including temperature cover a range within which significant demographic changes would be expected (Munday et al. 2008). This review confirms the findings of previous studies on the demography of parrotfishes: age-based demographic traits are highly variable in their expression, both intra- and inter-specifically. Difficulties in determining the factors responsible for demographic variation reflect the fact that diversity in growth rates, the timing of maturation and sex change and longevity interact to provide a variety of solutions to the problems posed by environmental variation and anthropogenic disturbance. Clarification of the underlying processes requires that the investigation of demographic traits must incorporate spatial analyses that identify the scales at which the main effects emerge. This mandates a hierarchical sampling design incorporating spatial scale from the level of individual reef systems to biogeographic regions covering whole ocean basins. Such investigations are likely to be complex.

Systematic sampling over latitudinal and longitudinal gradients confirms established patterns of demographic variation as a consequence of environmental variation and also retrieves novel results that reflect the influence of ocean basin history. Demographic trends over a comprehensive latitudinal gradient confirm the temperature-size rule with mean size and age positively correlated with latitude as seen in temperate water labrids (Trip et al. 2014b). Longitudinal trends appear to reflect the evolutionary history of reef systems

in terms of tectonic processes. Within the Indo-Pacific, ocean basin size and the diversity and extent of reef habitat appears to be associated with extended life spans. At the western margins of the Indian Ocean, the Gulf of Aden and the Red Sea, life spans of equivalent clades are approximately half of those of the western Pacific. More importantly, life spans of parrotfishes in the tropical Atlantic are also reduced compared with those of the Pacific Ocean but with the added complication of a strong phylogenetic signal that reflects the evolutionarily-distinct nature of the faunas in each ocean. The combination of latitudinal and longitudinal sampling also identifies the need to distinguish between demographic changes that occur on ecological time scales including variation in growth rates and those that appear to reflect evolutionary processes such as biogeographic trends in life span.

The use of demographic proxy values derived from related species or by extrapolating results from a single locality to other localities may be seen as a solution to the complexity and species diversity of coral reef fisheries. The emerging picture of species and locality-specific variation in parrotfishes and also in many other groups suggests that caution is needed in developing such proxies to compensate for the data-poor status of many tropical fisheries. While there is no substitute for species and locality-specific sampling, the continued development of new analytical methods including estimation of age- and size-specific maturity from growth curves is worth pursuing. This reflects the importance of this parameter in fisheries science and the demanding nature of sampling additional reproductive data for coral reef fishes.

Conclusion

The historical harvest of parrotfishes and variable harvest rates through both space and time complicate our ability to uncover natural demographic trends. Without historical baselines, ecologists must retrospectively interpret present patterns amid a geographic matrix muddled by a range of human influences. Disentangling the effects and identifying the scales and magnitudes of natural and human-induced variability is a management priority. The proposed spatial scale of many of the hypotheses presented demands enhanced coordination among fish biologists from various geographic regions. Regional 'age and growth' life-history assessments of common species are a necessary initial step and have great utility to fisheries management in the respective regions. Yet, simple comparisons of length-at-age and maturation or sex change schedules among regions do not facilitate an understanding of the pattern-driving processes or the implications for fishery and conservation management at broader scales. Rather, future assessments should employ spatially-explicit, mixed-effects modeling over several spatial scales and comprehensive age-based data sets to tease apart interactive effects influencing demographic processes.

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References Cited

- Alfaro, M.E., C.D. Brock, B.L. Banbury and P.C. Wainwright. 2009. Does evolutionary innovation in pharyngeal jaws lead to rapid lineage diversification in labrid fishes? *BMC Evol Biol* 9: 255.
- Allsop, D.J. and S.A. West. 2003. Life history: changing sex at the same relative body size. *Nature* 425: 783–784.
- Alwany, M.A., E. Thaler and M. Stachowitsch. 2009. Parrotfish bioerosion on Egyptian Red Sea reefs. *J. Exp. Mar. Biol. Ecol.* 371: 170–176.
- Andrews, A.H., J.H. Choat, R. Hamilton and E.E. DeMartini. 2015. Refined bomb radiocarbon dating of two iconic fishes of the Great Barrier Reef. *Mar. Freshwater Res.* 66: 305–316.
- Andrews, A.H., E.E. DeMartini, J.A. Eble, B.M. Taylor, D.C. Lou and R.L. Humphreys. 2016. Age and growth of bluespine unicornfish (*Naso unicornis*): a half-century life-span for a keystone browser, with a novel approach to bomb radiocarbon dating in the Hawaiian Islands. *Can. J. Fish. Aquat. Sci.* 73: 1575–1586.
- Atkinson, D. 1994. Temperature and organism size—a biological law for ectotherms? *Adv. Ecol. Res.* 25: 1–58.
- Atkinson, D. and R.M. Sibly. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends. Ecol. Evol.* 12: 235–239.
- Barba, J. 2010. Demography of parrotfish: age, size and reproductive variables. M.S. Thesis, James Cook University, Townsville, Queensland.
- Beamish, R.J. 1992. The importance of accurate ages in fisheries science. pp. 8–22. *In*: D.A. Hancock (ed.). Proceedings of the Australian Society for Fish Biology workshop on the Measurement of Age and Growth in Fish and Shellfish. Bureau of Rural Resources, Australian Government Publishing Service, Canberra, Australia.
- Bellwood, D.R. 2001. Scaridae. Parrotfishes. pp: 3468–3492. *In*: K.E. Carpenter and V. Niem (eds.). The Living Marine Resources of the Western Central Pacific. Bony Fishes Part 4 (Labridae to Latmeridae), Estuarine Crocodiles, Sea Turtles, Sea Snakes, and Marine Mammals. FAO.
- Bellwood, D.R. 1995a. Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef, Australia. *Mar. Biol.* 121: 419–429.
- Bellwood, D.R. 1995b. Carbonate transport and within-reef patterns of bioerosion and sediment release by parrotfishes (family Scaridae) on the Great Barrier Reef. *Mar. Ecol.-Prog. Ser.* 117: 127–136.
- Bellwood, D.R. and J.H. Choat. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ. Biol. Fish.* 28: 189–214.
- Bellwood, D.R., A.S. Hoey and J.H. Choat. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecol. Lett.* 6: 281–285.
- Bellwood, D.R., A.S. Hoey and T.P. Hughes. 2012. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *P. Roy. Soc. Lond. B. Bio.* 279: 1621–1629.
- Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. UK Ministry of Agriculture and Fisheries, London.
- Bohnsack, J.A. 1990. The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. NOAA Technical Report NMFS-SEFC 261, 40 pp.
- Campbell, S.J. and S.T. Pardede. 2006. Reef fish structure and cascading effects in response to artisanal fishing pressure. *Fish. Res.* 79: 75–83.

- Cappo, M., R.J. Marriott and S.J. Newman. 2013. James's rule and causes and consequences of a latitudinal cline in the demography of John's Snapper (*Lutjanus johnii*) in coastal waters of Australia. *Fish. B-NOAA*. 111: 309–324.
- Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecol. Monogr.* 56: 345–364.
- Choat, J.H. 1991. The biology of herbivorous fishes on coral reefs. pp. 120–155. *In*: P.F. Sale (ed.). *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego.
- Choat, J.H. and D.R. Robertson. 1975. Protogynous hermaphroditism in fishes of the family Scaridae. pp: 263–283. *In*: R. Reinboth (ed.). *Intersexuality in the animal kingdom*. Springer-Verlag, Heidelberg.
- Choat, J.H. and D.R. Robertson. 2002. Age-based studies. pp: 57–80. *In*: P.F. Sale (ed.). *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press, San Diego.
- Choat, J.H., L.M. Axe and D.C. Lou. 1996. Growth and longevity in fishes of the family Scaridae. *Mar. Ecol-Prog. Ser.* 145: 33–41.
- Choat, J.H., D.R. Robertson, J.L. Ackerman and J.M. Posada. 2003. An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. *Mar. Ecol-Prog. Ser.* 246: 265–277.
- Choat, J.H., C.R. Davies, J.L. Ackerman and B.D. Mapstone. 2006. Age structure and growth in a large teleost, *Cheilinus undulatus*, with a review of size distribution in labrid fishes. *Mar. Ecol-Prog. Ser.* 318: 237–246.
- Choat, J.H., J.P. Kritzer and J.L. Ackerman. 2009. Ageing in coral reef fishes: do we need to validate the periodicity of increment formation for every species of fish for which we collect age-based demographic data. pp. 23–54. *In*: B.S. Green, B.D. Mapstone, G. Carlos and G.A. Begg (eds.). *Tropical Fish Otoliths: Information for Assessment, Management and Ecology*. Springer, Netherlands.
- Choat, J.H., O.S. Klanten, L. Van Herwerden, D.R. Robertson and K.D. Clements. 2012. Patterns and processes in the evolutionary history of parrotfishes (Family Labridae). *Biol. J. Linn. Soc.* 107: 529–557.
- Claissie, J.T., M. Kienzle, M.E. Bushnell, D.J. Shafer and J.D. Parrish. 2009. Habitat- and sex-specific life history patterns of yellow tang *Zebrasoma flavescens* in Hawaii, USA. *Mar. Ecol-Prog. Ser.* 389: 245–255.
- Clua, E. and P. Legendre. 2008. Shifting dominance among Scarid species on reefs representing a gradient of fishing pressure. *Aquat. Living. Resour.* 21: 339–348.
- Conover, D.O. 2000. Darwinian fishery science. *Mar. Ecol-Prog. Ser.* 208: 303–307.
- Craig, P.C. 1999. The von Bertalanffy growth curve: when a good fit is not enough. *Naga* 22: 28–29.
- Dalzell, P., T.J.H. Adams and N.V.C. Polunin. 1996. Coastal fisheries in the Pacific islands. *Oceanog. Mar. Biol.* 34: 395–531.
- DeMartini, E.E., A.M. Friedlander and S.R. Holzwarth. 2005. Size at sex change in protogynous labroids, prey body size distributions, and apex predator densities at NW Hawaiian atolls. *Mar. Ecol-Prog. Ser.* 297: 259–271.
- DeMartini, E.E., A.M. Friedlander, S.A. Sandin and E. Sala. 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Mar. Ecol-Prog. Ser.* 365: 199–215.
- Donovan, M.K., A.M. Friedlander, E.E. DeMartini, M.J. Donahue and I.D. Williams. 2013. Demographic patterns in the peacock grouper (*Cephalopholis argus*), an introduced Hawaiian reef fish. *Environ. Biol. Fish.* 96: 981–994.
- Dudgeon, C.L., N. Gust and D. Blair. 2000. No apparent genetic basis to demographic differences in scarid fishes across continental shelf of the Great Barrier Reef. *Mar. Biol.* 137: 1059–1066.
- Dulvy, N.K. and N.V.C. Polunin. 2004. Using informal knowledge to infer human-induced rarity of a conspicuous reef fish. *Anim. Conserv.* 7: 365–374.
- Ebisawa, A., K. Kanashiro, I. Ohta, M. Uehara and H. Nakamura. 2016a. Changes of group construction accompanying with growth and maturity in blue-barred parrotfish (*Scarus ghobban*), and influences of the fishing targeting the immature group to the stock. *Reg. Stud. Mar. Sci.* 7: 32–42.

- Ebisawa, A., I. Ohta, M. Uehara, H. Nakamura and K. Kanashiro. 2016b. Life history variables, annual change in sex ratios with age, and total mortality observed on commercial catch on Pacific steephead parrotfish, *Chlorurus microrhinos* in waters off the Okinawa Island, southwestern Japan. *Reg. Stud. Mar. Sci.* 8: 65–76.
- El-Sayed Ali, T., A.M. Osman, S.H. Abdel-Aziz and F.A. Bawazeer. 2011. Growth and longevity of the protogynous parrotfish, *Hipposcarus harid*, *Scarus ferrugineus* and *Chlorurus sordidus* (Teleostei, Scaridae), off the eastern coast of the Red Sea. *J. Appl. Ichthyol.* 27: 840–846.
- Fowler, A.J. 2009. Age in years from otoliths of adult tropical fish. pp: 55–92. *In: B.S. Green, B.D. Mapstone, G. Carlos and G.A. Begg (eds.). Tropical Fish Otoliths: Information for Assessment, Management and Ecology.* Springer, Netherlands.
- Francis, R.I.C.C. 1988. Are growth parameters estimated from tagging and age-length data comparable? *Can. J. Fish. Aquat. Sci.* 45: 936–942.
- Grandcourt, E.M. 2002. Demographic characteristics of a selection of exploited reef fish from the Seychelles: preliminary study. *Mar. Freshwater. Res.* 53: 122–130.
- Gust, N. 2004. Variation in the population biology of protogynous coral reef fishes over tens of kilometers. *Can. J. Fish. Aquat. Sci.* 61: 205–218.
- Gust, N., J.H. Choat and J.L. Ackerman. 2002. Demographic plasticity in tropical reef fishes. *Mar. Biol.* 140: 1039–1051.
- Hamilton, S.L., J.E. Caselle, J.D. Standish, D.M. Schroeder, M.S. Love, J.A. Rosales-Casian, and O. Sosa-Nishizaki. 2007. Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecol. Appl.* 17: 2268–2280.
- Hamilton, R.J., S. Adams and J.H. Choat. 2008. Sexual development and reproductive demography of the green humphead parrotfish (*Bolbometopon muricatum*) in the Solomon Islands. *Coral Reefs* 27: 153–163.
- Hamilton, R.J. and J.H. Choat. 2012. Bumphead Parrotfish – *Bolbometopon muricatum*. pp. 490–496. *In: Y. Sadovy de Mitcheson and P.L. Colin (eds.). Reef Fish Spawning Aggregations: Biology, Research and Management.* Springer, Dordrecht.
- Hamilton, S.L. and J.E. Caselle. 2015. Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *P. Roy. Soc. Lond. B. Bio* 282: 20141817.
- Hawkins, B.A. 2012. Eight (and a half) deadly sins of spatial analysis. *J. Biogeogr.* 39: 1–9.
- Hawkins, J.P. and C.M. Roberts. 2003. Effects of fishing on sex-changing Caribbean parrotfishes. *Biol. Conserv.* 115: 213–226.
- Hobbs, J.-P.A., A.J. Frisch, S. Mutz and B.M. Ford. 2014. Evaluating the effectiveness of teeth and dorsal fin spines for non-lethal age estimation of a tropical reef fish, coral trout *Plectropomus leopardus*. *J. Fish. Biol.* 84: 328–338.
- Hoey, A.S. and D.R. Bellwood. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27: 37–47.
- Houk, P., K. Rhodes, J. Cuetos-Bueno, S. Lindfield, V. Fread and J.L. McIlwain. 2012. Commercial coral-reef fisheries across Micronesia: a need for improving management. *Coral Reefs* 31: 13–26.
- Howard, K.G. 2008. Community structure, life history, and movement patterns of parrotfishes: large protogynous fishery species. PhD Thesis. University of Hawaii, Honolulu.
- Jackson, J.B.C., M.K. Donovan, K.L. Cramer and V.V. Lam. 2014. Status and trends of Caribbean coral reefs: 1970–2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.
- Kazancioglu, E., T.J. Near, R. Hanel and P.C. Wainwright. 2009. Influence of sexual selection and feeding functional morphology on diversification rate of parrotfishes (Scaridae). *Proc. R. Soc. Lond. B. Bio.* 276: 3439–3446.
- Knight, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. *J. Fish. Res. Board. Can.* 25: 1303–1307.
- Kritzer, J.P., C.R. Davies and B.D. Mapstone. 2001. Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates. *Can. J. Fish. Aquat. Sci.* 58: 1557–1568.
- Kume, G., Y. Kubo, T. Yoshimura, T. Kiriya and A. Yamaguchi. 2009. Life history characteristics of the protogynous parrotfish *Calotomus japonicus* from northwest Kyushu, Japan. *Ichthyol. Res.* 57: 113–120.

- Kuparinen, A. and J. Merila. 2007. Detecting and managing fisheries-induced evolution. ?? 22: 652–659.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES. J. Mar. Sci. 57: 659–668.
- Law, R. 2007. Fisheries-induced evolution: present status and future directions. Mar. Ecol. Prog. Ser. 335: 271–277.
- Legendre, P. and L. Legendre. 2012. Numerical ecology, 3 edn. Elsevier, Amsterdam.
- Lessa, R., C.R. Da Silva, J.F. Dias and F.M. Santana. 2016. Demography of the Agassiz's parrotfish *Sparisoma frondosum* (Agassiz, 1831) in north-eastern Brazil. J. Mar. Biol. Assoc. UK. 96: 1157–1166.
- Lester, N.P., B.J. Shuter and P.A. Abrams. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proc. R. Soc. Lond. B. Bio. 271: 1625–1631.
- Levin, S.A. 2000. Multiple scales and the maintenance of biodiversity. Ecosystems 3: 498–506.
- Lokrantz, J., M. Nystrom, M. Thyresson and C. Johansson. 2008. The non-linear relationship between body size and function in parrotfishes. Coral Reefs 27: 967–974.
- Longenecker, K.E.N., Y.L. Chan, R.J. Toonen, D.B. Carlon, T.L. Hunt, A.M. Friedlander and E.E. Demartini. 2014. Archaeological evidence of validity of fish populations on unexploited reefs as proxy targets for modern populations. Conserv. Biol. 28: 1322–1330.
- Longhurst, A. and D. Pauly. 1987. Ecology of tropical oceans. Academic Press, San Diego.
- Lou, D.C. 1992. Validation of annual growth bands in the otolith of tropical parrotfishes (*Scarus schlegelii* Bleeker). J. Fish. Biol. 41: 775–790.
- Lou, D.C., B.D. Mapstone, G.R. Russ, C.R. Davies and G.A. Begg. 2005. Using otolith weight-age relationships to predict age-based metrics of coral reef fish populations at different spatial scales. Fish. Res. 71: 279–294.
- Moltschaniwshyj, N. and M. Cappo. 2009. Alternatives to sectioned otoliths: the use of other structures and chemical techniques to estimate age and growth for marine vertebrates and invertebrates. pp. 133–173. In: B.S. Green, B.D. Mapstone, G. Carlos and G.A. Begg (eds.). Tropical Fish Otoliths: Information for Assessment, Management and Ecology, Springer, Netherlands.
- Mumby, P.J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecol. Appl. 16: 747–769.
- Mumby, P.J. 2014. Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs. Fish. Fish. 17: 266–278.
- Mumby, P.J., C.P. Dahlgren, A.R. Harborne, C.V. Kappel, F. Micheli, D.R. Brumbaugh, K.E. Holmes, J.M. Mendes, K. Broad and J.N. Sanchirico. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science. 311: 98–101.
- Munday, P.L., J.W. White and R.R. Warner. 2006. A social basis for the development of primary males in a sex-changing fish. Proc. R. Soc. Lond. B. Bio. 273: 2845–2851.
- Munday, P.L., G.P. Jones, M.S. Pratchett and A.J. Williams. 2008. Climate change and the future for coral reef fishes. Fish. Fish. 9: 261–285.
- Muñoz, R.C. and R.R. Warner. 2003. Alternative contexts of sex change with social control in the bucktooth parrotfish, *Sparisoma radians*. Environ. Biol. Fish. 68: 307–319.
- Muñoz, R.C., B.J. Zgliczynski, B.Z. Teer and L.J. Laughlin. 2014. Spawning aggregation behavior and reproductive ecology of the giant bumphead parrotfish, *Bolbometopon muricatum*, in a remote marine reserve. Peer J 2, e681.
- Munro, J.L. 1983. Caribbean coral reef fishery resources. ICLARM, Manila.
- Paddack, M.J., S. Sponaugle and R.K. Cowen. 2009. Small-scale demographic variation in the stoplight parrotfish *Sparisoma viride*. J. Fish. Biol. 75: 2509–2526.
- Pannella, G. 1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. pp. 28–39. In: T.B. Bagenal (ed.). The Ageing of Fish. Unwin Brothers Unlimited, Surrey, England.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese and F. Torres Jr. 1998. Fishing down marine food webs. Science 279: 860–863.
- Petersen, C.W. and R.R. Warner. 2002. The ecological context of reproductive behavior. pp. 103–118. In: P.F. Sale (ed.). Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. Academic Press, San Deigo, CA.

- Randall, J.E. 1963. Notes on the systematics of parrotfishes (Scaridae), with emphasis on sexual dichromatism. *Copeia* 1963: 225–237.
- Ratner, S. and R. Lande. 2001. Demographic and evolutionary responses to selective harvesting in populations with discrete generations. *Ecology* 82: 3093–3014. ??
- Reinboth, R. 1968. Protogynie bei Papageifischen (Scaridae). *Z. Naturforsch.* 23: 852–855.
- Rhodes, K.L., M.H. Tupper and C.B. Wichimel. 2008. Characterization and management of the commercial sector of the Pohnpei coral reef fishery, Micronesia. *Coral Reefs* 27: 443–454.
- Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235: 167–171.
- Robertson, D.R. and R.R. Warner. 1978. Sexual patterns in the labroid fishes of the western Caribbean. II: the parrotfishes (Scaridae). *Smithsonian Contributions to Zoology* 255: 1–26.
- Robertson, D.R. and K.L. Cramer. 2014. Defining and dividing the greater Caribbean: insights from the biogeography of shorefishes. *PLoS One* 9, e102918.
- Robertson, D.R., R. Reinboth and R.W. Bruce. 1982. Gonochorism, protogynous sex-change and spawning in three Sparisomatine parrotfishes from the western Indian Ocean. *Bull. Mar. Sci.* 32: 868–879.
- Robertson, D.R., J.L. Ackerman, J.H. Choat, J.L. Posada and J. Pitt. 2005. Ocean surgeonfish *Acanthurus bahianus*. I. The geography of demography. *Mar. Ecol. Prog. Ser.* 295: 229–244.
- Robertson, D.R., F. Karg, R. Leao de Moura, B.C. Victor and G. Bernardi. 2006. Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. *Mol. Phylogenet. Evol.* 40: 795–807.
- Roff, D.A. 1980. A motion for the retirement of the von Bertalanffy function. *Can. J. Fish. Aquat. Sci.* 37: 127–129.
- Rowe, S. and J.A. Hutchings. 2003. Mating systems and the conservation of commercially exploited marine fish. *Trends. Ecol. Evol.* 18: 567–572.
- Ruttenberg, B.I., S.L. Hamilton, S.M. Walsh, M.K. Donovan, A. Friedlander, E. DeMartini, E. Sala and S.A. Sandin. 2011. Predator-induced demographic shifts in coral reef fish assemblages. *PLoS ONE* 6, e21062.
- Sadovy de Mitcheson, Y. and M. Liu. 2008. Functional hermaphroditism in teleosts. *Fish. Fish.* 9: 1–43.
- Sale, P.F. 1980. The ecology of fishes on coral reefs. *Oceanog. Mar. Biol.* 18: 367–421.
- Sale, P.F. 1998. Appropriate spatial scales for studies of reef-fish ecology. *Aust. J. Ecol.* 23: 202–208.
- Scott, R.D. and J. Heikkinen. 2012. Estimating age at first maturity from change-points in growth rate. *Mar. Ecol. Prog. Ser.* 450: 147–157.
- Smith, L.L., J.L. Fessler, M.E. Alfaro, J.T. Streebman and M.W. Westneat. 2008. Phylogenetic relationships and the evolution of regulatory gene sequences in the parrotfishes. *Mol. Phylogenet. Evol.* 49: 136–152.
- Streebman, J.T., M. Alfaro, M.W. Westneat, D.R. Bellwood and S.A. Karl. 2002. Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. *Evolution* 56: 961–971.
- Taylor, B.M. 2014. Drivers of protogynous sex change differ across spatial scales. *Proc. R. Soc. Lond. B. Bio.* 281: 2013–2423.
- Taylor, B.M. and J.H. Choat. 2014. Comparative demography of commercially important parrotfish species from Micronesia. *J. Fish. Biol.* 84: 383–402.
- Taylor, B.M. and C. Pardee. 2017. Growth and maturation of the redlip parrotfish *Scarus rubroviolaceus*. *J. Fish. Biol.* (in press).
- Taylor, B.M., P. Houk, G.R. Russ and J.H. Choat. 2014. Life histories predict vulnerability to overexploitation in parrotfishes. *Coral Reefs* 33: 869–878.
- Taylor, B.M., S.J. Lindfield and J.H. Choat. 2015. Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. *Ecography* 38: 520–530.
- Thorson, J.T., J.M. Cope and W.S. Patrick. 2014. Assessing the quality of life history information in publicly available databases. *Ecol. Appl.* 24: 217–226.
- Trip, E.L., J.H. Choat, D.T. Wilson and D.R. Robertson. 2008. Inter-oceanic analysis of demographic variation in a widely distributed Indo-Pacific coral reef fish. *Mar. Ecol. Prog. Ser.* 373: 97–109.

- Trip, E.D.L., P. Craig, A. Green and J.H. Choat. 2014a. Recruitment dynamics and first year growth of the coral reef surgeonfish *Ctenochaetus striatus*, with implications for acanthurid growth models. *Coral Reefs* 33: 879–889.
- Trip, E.D.L., K.D. Clements, D. Raubenheimer and J.H. Choat. 2014b. Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. *J. Anim. Ecol.* 83: 866–875.
- Vallès, H. and H.A. Oxenford. 2014. Parrotfish size: a simple yet useful alternative indicator of fishing effects on Caribbean reefs. *PLoS ONE* 9, e86291.
- Wakefield, C.B., A.J. Williams, S.J. Newman, M. Bunel, C.E. Dowling, C.A. Armstrong and T.J. Langlois. 2014. Rapid and reliable multivariate discrimination for two cryptic *Eteline* snappers using otolith morphometry. *Fish. Res.* 151: 100–106.
- Warner, R.R. 1997. Evolutionary ecology: how to reconcile pelagic dispersal with local adaptation. *Coral Reefs* 16: S115–S120.
- Warner, R.R. and I.F. Downs. 1977. Comparative life histories: growth vs. reproduction in normal males and sex-changing hermaphrodites of the striped parrotfish, *Scarus croicensis*. pp. 275–282. *In: Third International Coral Reef Symposium, Miami*. Rosential School of Marine and Atmospheric Science, Miami, Florida.
- Warner, R.R. and D.R. Robertson. 1978. Sexual patterns in the labroid fishes of the western Caribbean. I: The wrasses (Labridae). *Smithsonian Contributions to Zoology* 254: 1–27.
- Watson, D.L., E.S. Harvey, B.M. Fitzpatrick, T.J. Langlois and G. Shedrawi. 2010. Assessing reef fish assemblage structure: how do different stereo-video techniques compare? *Mar. Biol.* 157: 1237–1250.
- Westneat, M.W. and M.E. Alfaro. 2005. Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Mol. Phylogenet. Evol.* 36: 370–390.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3: 385–397.
- Winemiller, K.O. and K.A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci.* 49: 2196–2218.