BIOLOGY OF PARROTFISHES

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Biology of Parrotfishes

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Preface

Parrotfish are found on almost every coral reef in the world. It is this ubiquity, coupled with their brilliant colouration and fused 'beak-like' jaws, that have long attracted the attention of those looking and working on tropical reefs. Parrotfishes also have an incredibly diverse and complex array of reproductive and mating strategies that vary both among and within species. However, it is their unique feeding action that has stimulated much scientific endeavour. The morphological innovations of the oral jaws allow parrotfishes to bite through reef carbonates, while the pharyngeal jaws allow them to grind ingested carbonates into sand particles. These innovations not only enable parrotfishes to access nutritional resources that are largely unavailable to other fishes, but make them one of the most important groups of fishes within coral reef ecosystems. No other group of fishes is so inextricably linked to the structural dynamics of their ecosystem. Despite their importance to reef ecosystems, the threats to parrotfish are numerous and severe: from the global effects of ocean warming and acidification to the local effects of overfishing, pollution and habitat degradation.

The aim of this book is to synthesise what is currently known about the biology of parrotfishes, and to consider why are parrotfishes so important to the ecology of coral reefs? The book provides a series of reviews that are intended to provide a firm grounding in the understanding of the morphology, diet, demography, distribution, functional ecology, and current threats of this group. Importantly, it provides new insights into their diet and food processing ability, their life-histories, and the influence of habitat and environment on parrotfish populations, and also identifies emerging research topics and future directions. We hope this book will appeal to students, early-career and established researchers, alike, and will stimulate further investigation into this fascinating and unique group of fishes.

Lastly, we wish to thank to all of those who contributed to this book. We invited the international authorities on various aspects of the biology of parrotfishes to contribute to the book and were overwhelmed by their positive and enthusiastic responses. We would also like to thank David Bellwood for initiating our interest in parrotfishes, sharing his extensive knowledge, and guiding our scientific development. We sincerely thank the reviewers of each chapter of this book for their constructive and insightful comments. Finally, we are extremely grateful for the ongoing support from our families (especially Jess, Kiara, Caelen, and João) for their ongoing support that has enabled us to undertake important and interesting scientific pursuits.

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Contents

The Ecology of Parrotfishes in Marginal Reef Systems

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Introduction

Parrotfishes (Labridae, Scarinae) are a ubiquitous group of reef fishes that are primarily distributed across the world's tropical oceans (Fig. 1). Currently, 100 species of parrotfishes are recognized (Parenti and Randall 2011), with most occupying shallow (0–50 m) tropical marine habitats, primarily coral reefs, although the distribution of several species extends into subtropical and temperate latitudes (Bonaldo et al. 2014). Indeed, the first parrotfish to be described to science was the Mediterranean parrotfish *Sparisoma cretense* (Linnaeus, 1758) based on a specimen collected in Crete (35ºN). Given their distribution, it is perhaps not surprising that the majority of research on the ecology of parrotfishes has focused

on low latitude, or tropical, coral-dominated habitats (e.g., Ogden and Buckman 1973, Robertson et al. 1982, Bellwood and Choat 1990, Bruggemann et al. 1994, Hoey and Bellwood 2008, Bonaldo et al. 2011), with comparatively little research on the ecology of parrotfishes on marginal, or high-latitude, reefs. There is, however, growing interest in the ecology of marginal reefs, largely due to the poleward range expansions of organisms and the tropicalization of marginal reef communities (e.g., Greenstein and Pandolfi 2008, Yamano et al. 2011, Baird et al. 2012, Verges et al. 2014, 2016), and the potential of marginal reefs to act as refugia from climate change (e.g., Riegl and Piller 2003, Lybolt et al. 2011). So what conditions define a 'marginal' reef?

Kleypas et al. (1999) define marginal reefs as those reefs that occur near or beyond the 'normal' environmental limits or reef distribution. Through the analysis of environmental data for ca. 1,000 reef locations, Kleypas et al. (1999) conclude that reef distribution is limited by temperature (weekly sea surface temperature: 18.0–31.5ºC), salinity (monthly average 30–40 PSU), nutrients (nitrate: < 2 µmol litre^{-1}; phosphate: < 0.4 µmol litre^{-1}), aragonite saturation (Ω-arag > 3.5), and light penetration, such that any reefs that exist outside these limits are considered marginal. While the relative importance of each of these environmental conditions in limiting reef development remains unclear (e.g., temperature, aragonite saturation, and light penetration often covary), temperature has been suggested to be a useful proxy for the limits of reef development, in particular along latitudinal gradients (Jokiel and Coles 1977, Johannes et al. 1983, Kleypas et al. 1999). Indeed, the majority of reefs considered to be 'marginal' are those that occur at high latitudes and hence outside the normal temperature limits for reef development (e.g. Lord Howe Island, Arabian/Persian Gulf, mainland Japan, Gulf of California, southern Brazil, see Fig. 2). We acknowledge that marginal reefs exist outside of high latitude environments (e.g., low salinity and low light environments in the Gulf of Thailand or inshore Great Barrier Reef), however they fall outside of the scope of this chapter.

In this chapter, we provide an overview of what is currently known of the ecology of parrotfishes on marginal, high latitude reefs. We start by describing the general biotic and abiotic conditions that characterize high latitude reefs, and how these may influence various aspects of parrotfish ecology within these systems. We then use case studies from four marginal reef systems (the Arabian Peninsula, eastern Australia, southern Japan, and Brazil) to explore the ecology of parrotfishes in these unique environments in greater detail. For each of these reef systems, we describe how changes in benthic communities and topographic complexity along latitudinal gradients relate to the distribution, abundance, and species richness of parrotfishes. We also consider how environmental conditions influence the functional impact of parrotfishes within these systems, and how these vary among taxonomic groups. In doing so, we seek to identify any generalities in the response of parrotfishes to the biotic and abiotic conditions experienced within these marginal reef systems.

Characteristics of Marginal Reefs

Marginal, or high latitude, reefs by definition occur beyond the normal environmental limits for coral reef development (see above), and as such one may expect marginal reefs to have lower coral cover than those of low latitude reefs. This is often, but not always the case. For example, the cover of live coral is relatively low in the Gulf of Oman (16 percent, Bento et al. 2016), Middleton Reef (19 percent, Hoey et al. 2014), Northwest Hawaiian Islands (10–20 percent, Vroom 2011), and southern Florida (< 6 percent, Moyer et al. 2003), whereas other marginal reefs have coral cover that is directly comparable or even greater
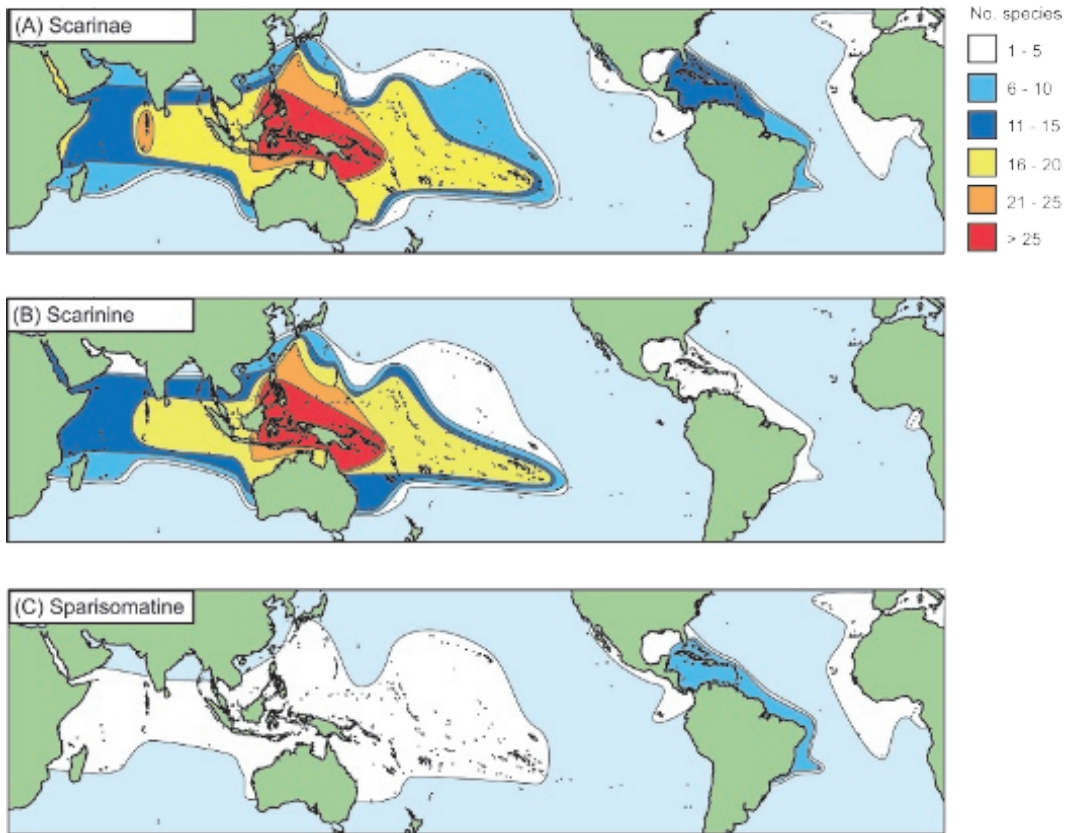
Fig. 1. Geographic distribution of species richness within the parrotfishes (A) Scarinae (all genera), and the two parrotfishes clades, (B) Scarinine (*Bolbometopon, Chlorurus, Cetoscarus, Hipposcarus,* and *Scarus*), and (C) Sparisomatine (*Calotomous, Cryptotomus, Leptoscarus, Nicholsina,* and *Sparisoma*). The distributions highlight the major biogeographic patterns with the Indo-Pacific supporting a higher diversity of scarinine species, while the Atlantic supports a higher diversity of sparisomatine species. Strong latitudinal gradients in species richness are evident in both the Indo-Pacific and Atlantic Oceans.

than that of low latitude reefs (e.g., southern Arabian Gulf: 56 percent, Bento et al. 2016; Sodwana Bay: 59 percent, Schleyer et al. 2008; Lord Howe Island: 37 percent, Hoey et al. 2011). These differences in coral cover likely reflect variation in the recent disturbance histories of each location (e.g., Bento et al. 2016), rather than suppressed rates of coral growth and/or recruitment due to lower water temperatures and geographic isolation. Moving further poleward from these reefs corals cease to produce enough calcium carbonate for reef accretion (Buddemeier and Smith 1999), but often exist, together with other organisms, as a thin veneer over rocky substrata.

Apart from potential differences in the cover of live corals, there are predictable differences in the taxonomic and morphological composition of corals between marginal and low latitude reefs. Several studies have shown that coral communities on high latitude reefs have fewer species, and are dominated by species with larger depth ranges, more robust morphologies, greater tolerance of turbid waters, and in some locations a greater proportion of species that brood larvae compared to those on lower latitude reefs (Coles 2003, Sommer et al. 2014, Keith et al. 2015, Mizerek et al. 2016). Species with robust
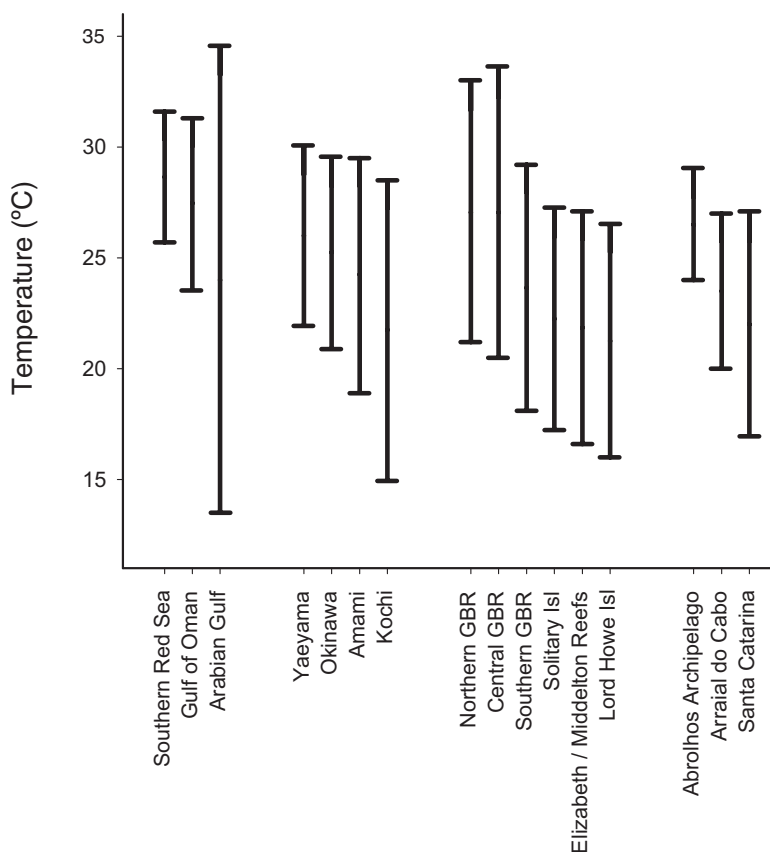
Fig. 2. Annual temperature ranges (minimum and maximum sea surface temperatures) experienced by several marginal reef systems around the Arabian peninsula, southern Japan, Australia's east coast, and Brazil. Temperature ranges for adjacent low latitude reefs are included for comparison.

morphologies (i.e., encrusting and massive growth forms), while less likely to be damaged or dislodged by oceanic swells, provide less complex physical structure than branching and tabular growth forms that are common on low latitude reefs. The physical structure of reef habitats is generally positively related to the abundance and/or diversity of associated reef fish assemblages (Graham and Nash 2013, Richardson et al. 2017), and as such any reductions in topographic complexity are likely to have adverse effects on fish assemblages, including parrotfishes (e.g. Heenan et al. 2016), and the delivery of their functional impact (Cvitanovic and Hoey 2010).

Macroalgae, although often viewed as a sign of degradation on low latitude reefs, is typically abundant on marginal, high latitude reefs, including those in isolated locations (e.g., Hoey et al. 2011, Vroom 2011, Dalton and Roff 2013). This elevated abundance and biomass of macroalgae has several implications for the parrotfishes, and is covered in detail elsewhere in this volume (Fox Chapter 13). Briefly, the abundance and/or biomass of parrotfishes on tropical reefs has been shown to be negatively related to macroalgal cover (e.g. Williams and Polunin 2001, Fox and Bellwood 2007, Wismer et al. 2009, Rasher et al. 2013), with this relationship often viewed as evidence for the top-down control of algal communities. Conversely, macroalgae may influence parrotfish populations through the provision of dietary resources or physical structure (i.e., bottom-up processes).

There has been some uncertainty regarding the nutritional targets of parrotfishes, however, recent evidence demonstrates scarinine parrotfishes target protein-rich epilithic, endolithic and epiphytic microscopic phototrophs, primarily cyanobacteria (Clements et al. 2017, Clements and Choat Chapter 3). Given these nutritional targets it is not surprising that scarinine parrotfishes are rarely observed feeding on fleshy macroalgae (e.g., Hoey and Bellwood 2009, Loffler et al. 2015, Plass-Johnson et al. 2015). The few exceptions include records of some species feeding on calcified algae, such as *Halimeda* and *Amphiroa* (Mantyka and Bellwood 2007, Rasher et al. 2013), however it is possible they are targeting small epiphytic phototrophs on the surface of the algae rather than the alga itself. Similarly, although sparisomatine parrotfishes are widely regarded as browsers of macroalgae (Streelman et al. 2002, Bonaldo et al. 2014), it has been hypothesized that the majority of species are targeting protein rich epiphytes on the surfaces of macroalgae and seagrass (Clements and Choat Chapter 3). An exception to this may be the Indo-Pacific sparisomatine *Leptoscarus vaigiensis* that appears to predominantly feed on macroalgae and seagrass (Ohta and Tachihara 2004, Gullström et al. 2011).

The structure provided by stands of tall fleshy macroalgae has been shown to suppress feeding by scarinine parrotfishes on an inshore reef on the Great Barrier Reef, and it was suggested that the avoidance of dense stands was related to inability of these fishes to visually detect potential predators (Hoey and Bellwood 2011). Yet macroalgal beds appear to be an important juvenile habitat for several species of coral reef fish, including parrotfishes (Wilson et al. 2010, Hoey et al. 2013, Evans et al. 2014), as well as an important adult habitat for *L. vaigiensis* (Lim et al. 2016, Tano et al. 2017).

Together with these changes in benthic composition and topographic complexity, the environmental conditions of marginal reefs (e.g., colder and more variable water temperatures, higher wave energy, higher productivity and reduced light penetration) may pose physiological challenges for tropical parrotfishes inhabiting these areas. Fishes are ectotherms and as such their metabolism and energy requirements are largely governed by environmental temperature (Pörtner and Farrell 2008). Any changes in environmental temperature will, therefore, change the rates of biochemical and cellular processes required for homeostasis, and the energetic cost of growth, activity, and reproduction. These changes in metabolic demands may be met through increased intake of energy, reduced energy expenditure, or a combination of both. To date, the majority of research investigating the effects of temperature on the physiological performance of reef fish has focused on small, site-attached species, primarily pomacentrids and apogonids. This body of work has shown that increasing water temperature generally increases the oxygen consumption of fishes at rest, decreases their aerobic scope (a proxy for surplus energy available for physiological or ecological activities), and has variable effects on activity (reviewed in Hoey et al. 2016a). Similar responses have been recorded for larger-bodied species, such as the coral trout *Plectropomus leopardus*, with increasing temperature leading to a reduction in activity, and an increase in food consumption and oxygen consumption (Johansen et al. 2014, 2015, Clark et al. 2017). We are unaware of any studies that have examined the physiological responses of parrotfishes to changing temperature, however it would seem reasonable to expect that they would respond in a similar manner.

Marginal Reefs of the Arabian Region

The marine region of the north-western Indian Ocean, comprising the Red Sea, Arabian Sea, and Arabian/Persian Gulf, is characterized by a high level of endemism (DiBattista et al. 2016) and forms a biogeographic unit that is distinct from the rest of the western

Indian Ocean (Keith et al. 2013, Kulbicki et al. 2013). Large spatial and temporal variation in environmental conditions makes this one of the world's most variable tropical marine environments (Bauman et al. 2013). The Red Sea has relatively stable environmental conditions and is isolated from the Indian Ocean by the narrow and relatively shallow (140 m) Strait of Bab al Mandab. The area outside the Red Sea (i.e., Arabian Sea and Gulf of Oman) is characterized by monsoonal-driven upwelling events that cause major fluctuations in nutrients and water temperature (Fig. 2), resulting in limited coral reef development (i.e. rocky reefs with sparse coral cover) (McIlwain et al. 2011). The Arabian (or Persian) Gulf is possible one of the most extreme and variable environments in which extant coral reefs occur. Its shallow depth, restricted water exchange through the Strait of Hormuz, and high latitude location contribute to extreme variation in salinity and temperature (ca. 12–36°C, Fig. 2), high levels of turbidity and sedimentation (Riegl 1999) and low nutrient levels (Bauman et al. 2013). As a consequence of these extreme and variable conditions, coral reefs within the southern Arabian Gulf are largely two-dimensional structures with little vertical relief, and dominated by massive and submassive corals (Burt et al. 2011, Bauman et al. 2013).

Ecology of Parrotfishes on Marginal Reefs of the Arabian Region

Twenty species of parrotfish (18 scarinine, 2 sparisomatine) have been reported from the Arabian region, with the vast majority (17 species) occurring within the Red Sea. Many of these species are regional or local endemics. For example, *Scarus arabicus* and *Scarus zufar* are only known from the Arabian Sea and southern coast of Oman, respectively, while *Scarus persicus* is restricted to the Arabian Gulf and coast of Oman (Choat et al. 2012). Consequently, there is a strong subregional structure in the taxonomic composition of parrotfishes between the Arabian Gulf, Arabian Sea, and Red Sea (Hoey et al. 2016b). Reefs in the Arabian Gulf are characterized by two species (*Sc. persicus, Scarus ghobban*), in the Arabian Sea by the same two species and *Scarus fuscopurpureus* in the north, and *Sc. arabicus* and *Sc. zufar* in the south, and the Red Sea by a diversity of scraping and excavating species (Hoey et al. 2016b). Although variation in the abundance and/or biomass of parrotfishes among habitats in the Red Sea (e.g. Bonaldo et al. 2014, Khalil et al. 2017) resembles that of other regions (Burkepile et al. Chapter 7), the lack of reef development and hence clearly defined reef zones precludes among-habitat comparisons for the Arabian Sea or Arabian Gulf.

The species richness of parrotfish and the abundance of excavating parrotfishes on shallow reef slopes (ca. 6m depth) decline from the Red Sea to the Arabian Sea and Arabian Gulf (Fig. 3). The decrease in species richness may be expected given the biogeography of the region (e.g., DiBattista et al. 2016), however the near-complete absence of excavating parrotfishes in the Arabian Sea is striking. Two species of excavating parrotfishes (*Chlorurus sordidus* and *Chlorurus strongylocephalus*) have been recorded along the coast of Oman, but they appear to be extremely rare. The lack of excavating parrotfishes on reefs in the Arabian Sea is in stark contrast to the relatively high abundance of scraping parrotfishes in this region (Fig. 3), and suggests that some aspect of their feeding or nutritional ecology may be contributing to these differences. Scraping and excavating parrotfishes typically feed from similar surfaces (dead coral or carbonates covered by epilithic algal matrix, EAM) but differ in the depth of their bite. Scraping parrotfishes typical take shallow (< 1 mm) bites, while excavating parrotfishes take deeper bites and remove greater quantities of the underlying substrata with each bite (Hoey and Bellwood 2008). This difference in feeding mode and the hard underlying substrata (i.e. rocky reef) in this area may have contributed
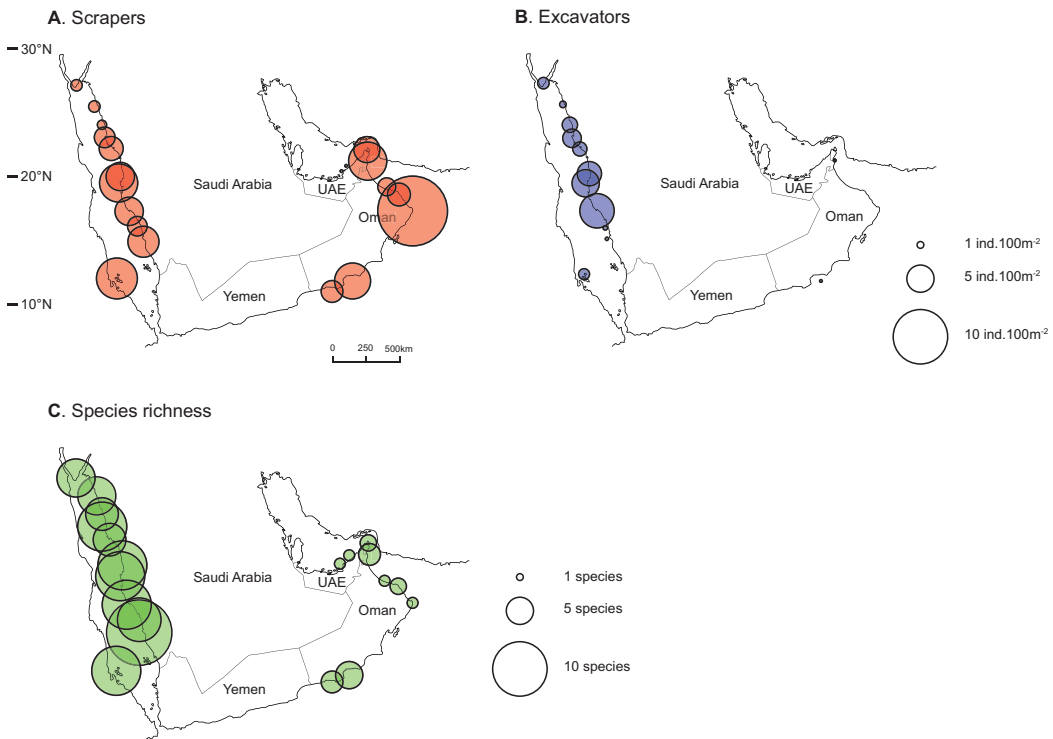
Fig. 3. Spatial variation in the abundance and species richness of scarinine parrotfishes on shallow reef slopes in the Arabian Peninsula. (A) Abundance of scraping parrotfishes (*Scarus, Hipposcarus*), (B) abundance of excavating parrotfishes (*Bolbometopon, Cetoscarus, Chlorurus*) and (C) species richness of parrotfishes. Circles are proportional to mean abundances or total number of species recorded in each location. Data are from Alwany et al. 2009, Afeworki et al. 2013, Hoey et al. 2016b. Note, no data for the abundance or species richness of parrotfishes were available for the coast of Yemen.

to the lack of excavating parrotfishes. Feeding on hard surfaces has been reported to cause dentition damage in large-bodied Atlantic parrotfishes (Bonaldo et al. 2007).

Five species of parrotfish have been reported from the Arabian Gulf, however all appear to be rare, with only two species (*Sc. persicus* and *Sc. ghobban*) recorded during extensive surveys of reefs in the southern Arabian Gulf, with densities of less than one individual per 1000 m² for both species combined (Feary et al. 2010, Hoey et al. 2016b). Other herbivorous fishes (i.e., Siganidae, Acanthuridae) are equally rare on these reefs (Feary et al. 2010, Burt et al. 2011), suggesting the low densities may be a consequence of the extreme temperatures on the physiology of these fishes, reductions in the quantity and/ or quality of dietary resources, or fishing. Although fishing has led to marked declines in parrotfish populations in many locations (e.g., Bellwood et al. 2012, Taylor et al. 2014), they are not primary targets of fishers within the Arabian Gulf (Grandcourt 2012).

Tropical organisms, including reef fishes, have evolved in relatively stable thermal environments and typically have a narrower thermal tolerance than temperate species, and are therefore potentially more sensitive to changes in temperature (Tewksbury et al. 2008). The extreme temperature variation within the Arabian Gulf (annual temperature range ≥ 20°C) may preclude many tropical species from inhabiting this region. Indeed, the reef fish fauna of the Arabian Gulf is depauperate (Burt et al. 2011). Further, although

the favored feeding surfaces of parrotfishes (i.e. EAM covered surfaces) are abundant within the southern Arabian Gulf (Bauman et al. 2013, Bento et al. 2016), the high rates of sedimentation (Riegl 1999) reduce their nutritional value to herbivorous fishes (e.g., Bellwood and Fulton 2008, Gordon et al. 2016).

Irrespective of the underlying mechanism(s), these changes in the abundance and composition of parrotfishes has important implications for the spatial distribution of their functional impact. Using bite rates for each species and the area or volume of bite scars of closely related species, Hoey et al. (2016a) estimated that the area of reef surface grazed by parrotfishes decreased from an average of 210 and 150 percent year^{-1} in the Red Sea and Arabian Sea, respectively, to only 4 percent year^{-1} in the Arabian Gulf. Similarly, estimated erosion rates decreased from an average of 1.57 kg m^{-2}year^{-1} in the Red Sea to 0.43 and 0.01 kg m^{-2}year^{-1} in the Arabian Sea and Arabian Gulf, respectively. Importantly, rates of grazing and erosion within the Arabian Gulf, and to a lesser extent the Arabian Sea, may be even lower than these estimates due to the suppression of feeding during the colder months. Preliminary data for *Sc. persicus* from the northern Arabian Sea indicate that a 6°C decrease in water temperature (from 29°C to 23°C) led to a 50–60 percent decrease in bite rate (Hoey unpublished data). While changes in the nutritional quality of food items cannot be discounted, the reduction in feeding is consistent with predicted temperature-induced changes in metabolic demands.

Marginal Reefs of Eastern Australia

There is extensive coral reef formation along Australia's east coast, from the Great Barrier Reef and reefs of the Coral Sea in the north, to the high latitude oceanic reefs of Lord Howe Island, Elizabeth and Middleton Reefs, and several non-accreting coral communities along the New South Wales coast (Harriott et al. 1999, Mizerek et al. 2016). Lord Howe Island (31°33′S), approximately 630 km east of mainland Australia, is the world's southernmost coral reef, and Elizabeth (30°S) and Middleton (29°30′S) reefs, approximately 200–260 km to the north, are considered the world's southernmost platform reefs. These isolated reef systems receive warm tropical waters from the East Australian Current (EAC) that originates between 17–19°S in the Coral Sea and tracks largely southward along the east Australian coast until 30–32°S where it bifurcates, with one part flowing eastward across the Tasman Sea delivering warm water to these southern offshore reefs, and the other part continuing largely along the coast (Ridgway and Dunn 2003).

Over 100 coral species have been recorded from the offshore reefs of Lord Howe Island, and Elizabeth and Middleton Reefs, however there is little consensus as to which species are present (see Baird et al. 2017 for discussion). This is considerably lower than the > 300 coral species recorded on the GBR, and markedly higher than most reefs between 28°S and 31°S on the east Australian coast, the only exception being the Solitary Islands where as many as 90 coral species have been reported (Harriott et al. 1999, Harriott and Banks 2002). Warming of global sea surface temperatures and the strengthening of the EAC is leading to poleward expansions of both corals (e.g. Baird et al. 2012) and fish (e.g., Feary et al. 2014) down Australia's east coast. Such tropicalization of marine organisms is leading to novel interactions as tropical species are exposed to temperate and subtropical species for the first time, and can have a dramatic and lasting impact of marine ecosystems (Verges et al. 2016).

Together with these differences in species richness there are considerable differences in the cover of live coral and macroalgae, and the composition of coral communities

both among and within these marginal reefs (e.g., Dalton and Roff 2013). Coral cover is relatively high on Lord Howe Island (mean: 37 percent; range: 2–57 percent), moderate on Elizabeth Reef (mean: 29 percent; range: 15–37 percent), and low on Middleton Reef (mean: 19 percent; range: 8–26 percent) (Hoey et al. 2011, 2014). Coral cover tends to be lower on the subtropical coastal reefs of eastern Australia (< 1–25 percent, Harriott et al. 1999, Harriott and Banks 2002) and dominated by encrusting and submassive corals attached to the underlying rocky substratum (Harriott and Banks 2002, Dalton and Roff 2013). One unifying feature of most of the high latitude reefs in the region, both coastal and offshore, is the relatively high cover (ca. 20–30 percent) of fleshy macroalgae (Hoey et al. 2011, 2014, Dalton and Roff 2013).

Ecology of Parrotfishes on Marginal Reefs of Eastern Australia

The offshore high latitude reefs of Lord Howe Island, Elizabeth and Middleton Reef have a distinctive marine fauna, with several species of endemic fishes (Francis 1993). However, the parrotfish fauna of these reefs are primarily a subset of the 27 species that occur on GBR, with 14 species reported from Lord Howe Island, and 22 from Elizabeth and Middleton reefs (Hoey et al. 2014). Interestingly, the excavating species *Chlorurus frontalis* is one of the most common parrotfish species on Elizabeth and Middleton reefs, but is rare on the GBR. Relatively few parrotfish species (2–3 species) are present on the coastal high latitude reefs in the region, although large individuals of *Sc. ghobban* and *Scarus altipinnis* (>30 cm total length) have been observed as far south as Sydney (A. Hoey pers. obs.).

Comparisons of the abundances and species richness of parrotfishes along Australia's east coast reveal clear spatial variation (Fig. 4). The abundances of scraping parrotfishes were broadly comparable between mid-shelf reef crests of the GBR and Elizabeth and Middleton Reefs (ca. 10 ind 100m^{-2}), but decreased markedly at Lord Howe Island (2.2 ind 100m^{-2}), and were almost completely absent on the coastal reefs of the Solitary Islands (< 0.1 ind 100m^{-2}; Fig. 4). Similar spatial variation was apparent in the abundances of excavating parrotfishes, ranging from 0 ind 100m^{-2} in the Solitary Islands to 4.1 ind 100m^{-2} on the GBR. The decline in the abundances of both groups of scarinine parrotfishes from Elizabeth and Middleton reefs to Lord Howe Island is difficult to resolve as they are both isolated offshore reefs, with similar temperature ranges (Fig. 2), are separated by only 200–260 km, have low human population densities (Elizabeth and Middleton reefs are unpopulated, Lord Howe Island's population is less than 800), and parrotfishes are not targeted by fishers. The differences in parrotfish populations may be related to reef structure. A recent study investigating the drivers of parrotfish biomass in the central and western Pacific showed that low islands and atolls (such as those of Elizabeth and Middleton reefs) support higher biomass of excavating parrotfishes than reefs surrounding high islands (such as Lord Howe Island) (Heenan et al. 2016). Similarly, island geomorphology was an important predictor of parrotfish assemblages across Micronesia, and was suggested to be due to the broad-scale habitat diversity associated with different geomorphologies (Taylor et al. 2015).

Perhaps the most striking pattern is the almost complete absence of parrotfishes within the Solitary Islands, despite similar latitude and temperature ranges as the offshore reefs, and moderate coral cover. Only five individual parrotfishes (two *Sc. altipinnis* and three *Sc. ghobban*) were recorded in surveys that covered over 10 hectares of shallow reef, with all individuals being observed on reefs surrounding the northernmost island, North Solitary Island (Hoey unpublished). It is likely that the lack of parrotfishes within the Solitary Islands is related, at least in part, to the lack of accreting reef in this area, and hence the

A. Scrapers

B. Excavators
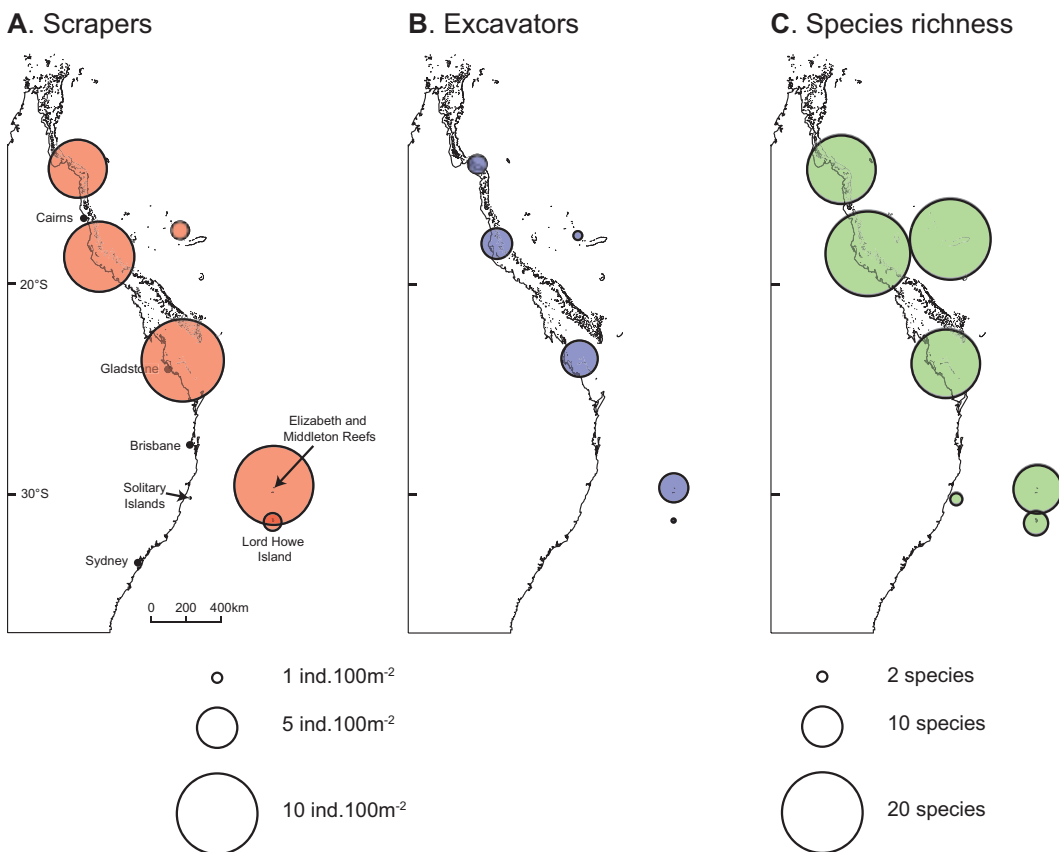
C. Species richness

Fig. 4. Spatial variation in the abundance and species richness of scarinine parrotfishes on low and high latitude reefs of eastern Australia. (A) Abundance of scraping parrotfishes (*Scarus, Hipposcarus*), (B) abundance of excavating parrotfishes (*Bolbometopon, Cetoscarus, Chlorurus*) and (C) species richness of parrotfishes. Circles are proportional to mean abundances or total number of species recorded in each location. Data are based on replicate 50 × 5 m belt transects on shallow reef crests in each location (GBR: Trapon et al. 2013; Coral Sea: Ceccarelli et al. 2008; Lord Howe Island: Hoey et al. 2011; Elizabeth and Middleton reefs: Hoey et al. 2014; Solitary Islands: Hoey unpublished data – March 2013).

impact of the hard underlying substratum (i.e., rock) on their feeding (as discussed above for the Arabian Sea).

The decreased abundance and altered taxonomic composition of parrotfishes on these high latitude reefs will lead to decreased rates of grazing and erosion. This may be further accentuated by any reductions in metabolic rates, and hence feeding rates at higher latitudes. Comparisons of feeding rates of adult individuals of three species of scarinine parrotfishes (*Sc. ghobban, Scarus psittacus, Scarus schlegeli*) show declines of 39 to 71 percent between the GBR (Lizard Island 14°30'S; Heron Island 23°30'S) and Lord Howe Island (Fig. 5). It should be noted that these data are based on limited sample sizes, did not account for potential changes in the nutritional quality of dietary resources or the quantity consumed per bite, however the consistency of the declines in feeding rate suggest they may be a consequence of lower water temperatures on Lord Howe Island. If this is the case, then
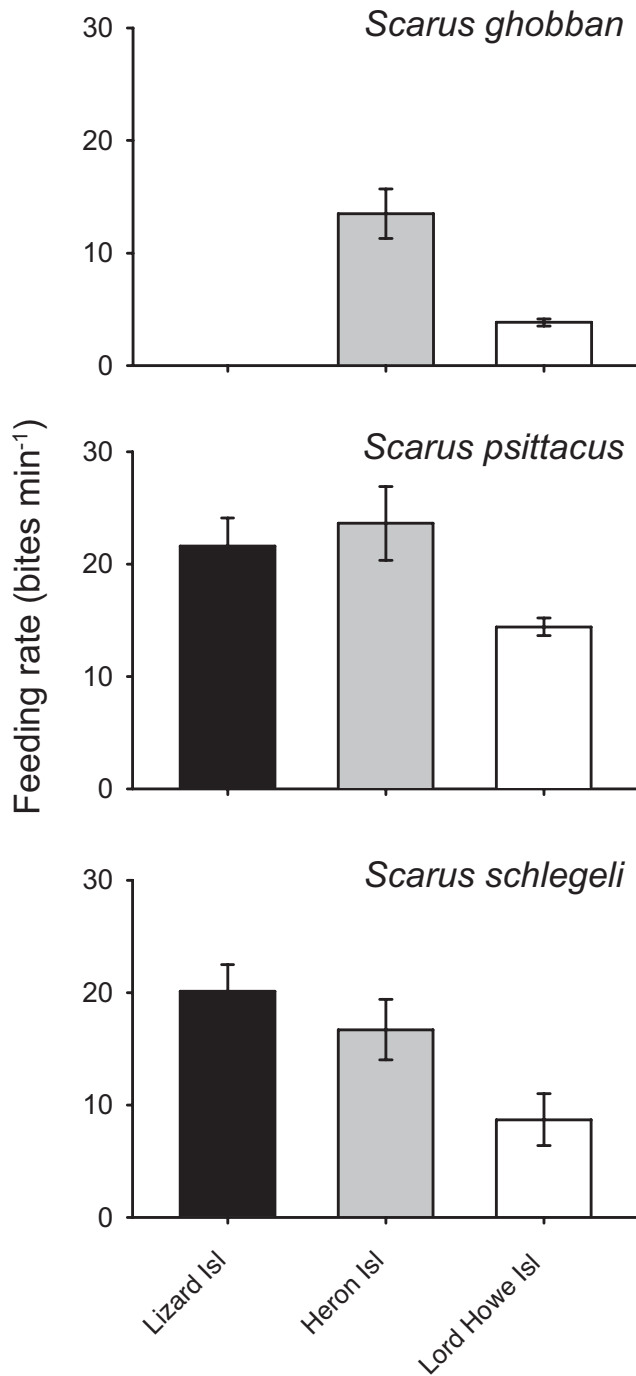
Fig. 5. Variation in the feeding rate of (A) *Scarus ghobban,* (B) *Scarus psittacus,* and (C) *Scarus schlegeli* among three locations spanning 17° of latitude on Australia's east coast (Lizard Island: 14°30'S, Heron Island: 23°30'S, Lord Howe Island: 31°30'S). Feeding rates for Heron Island and Lizard Island are from Bellwood and Choat 1990. Feeding rates for Lord Howe Island are based on replicate 3-minute focal individual observations.

such reductions in feeding rate of parrotfishes may be widespread across high latitude reefs, and together with decreases in the abundance of parrotfishes will reduce the amount of material they ingest, the volume of carbonates they erode and sediments they rework. Further, increases in other herbivorous taxa, such as subtropical acanthurids (i.e., *Prionurus* spp) and urchins on both coastal and offshore high latitude reefs (e.g., Hoey et al. 2011, Verges et al. 2016) compared to low latitude reefs (e.g., Cheal et al. 2012) may indicate a reduced importance of parrotfishes in the functioning of these reefs.

Marginal Reefs of Southern Japan

Japanese coral reefs extend from the southern Ryukyu Islands (24°N) to Tanegashima Island (31°N), and in the Ogasawara (Bonin) Islands south of 27°N (Ministry of Environment and Japanese Coral Reef Society, 2004). Reef formation transitions from continuous fringing reefs with extensive reef flats (up to 1 km wide) in the southern Ryukyu Islands (south of 27°N), to patchily distributed fringing reefs with narrow reef flats in the northern Ryukyu Islands (27–31°N), and non-accreting coral communities on rocky substrates in the area north of 31°N to the central mainland of Japan.

Approximately 415 scleractinian species belonging to 78 genera have been recorded from Japanese reefs, with the vast majority of species occurring in the Ryukyu Islands (Ministry of Environment and Japanese Coral Reef Society, 2004). This species-rich coral fauna is due, at least in part, to the northward flowing Kuroshio Current, which brings warm tropical waters from the Philippines along the Ryukyu Islands to the Pacific coast of the Japanese mainland. Declines in sea surface temperature (SST) associated with the Kuroshio Current have been related to the latitudinal gradient in coral species richness. The greatest number of coral species occur in the southern Ryukyu Islands (ca. 380 species: Yaeyama region, 24°N) and decrease with increasing latitude (340 species: Okinawa region, 26°N; 220 species: Amami region, 28°N; 200 species: western and central Japanese mainland 32°N; 50 species: eastern Japanese mainland, 34–35°N). Over the last few decades, however, rising SSTs and a strengthening of the Kuroshio Current has contributed to the range expansion of several tropical coral and fish species onto the temperate Japanese coasts (Yamano et al. 2011, Verges et al. 2014).

Ecology of Parrotfishes on Marginal Reefs of Southern Japan

Up to 36 parrotfish species belonging to seven genera have been reported from Japanese waters (Nakabo 2013), although several of these on marginal reefs appear to be tropical vagrants and the number of species with established populations is likely to be considerable lower. Of these 36 species, the vast majority (35 spp.) have been recorded in the Ryukyu Islands, the only exception being *Scarus obishime*, which is endemic to the Ogasawara Islands. Parrotfishes tend to display clear among-habitat distributions on reefs within the Ryukyu Islands, as have been reported in many other locations (Burkepile et al. Chapter 7). Among scraping and excavating (i.e., scarinine) parrotfishes, species such as *Chlorurus bowersi*, *Scarus niger*, *Scarus festivus*, and *Scarus forsteni* occur primarily on the outer reef slopes, whereas *Chlorurus spilurus*, *Scarus rivulatus*, and *Scarus schlegeli* occur in both the inner reef flats and the outer reef slopes (Shibuno et al. 2008). Among the browsing (i.e., sparisomatine) species, *Calotomus carolinus* occurs in coral reef habitats, whereas *Leptoscarus vaigiensis* and *Calotomus spinidens* are restricted to seagrass and macroalgal beds (Sano 2001, Shibuno et al. 2008).

Species richness and abundance of parrotfishes within the Ryukyu Islands decrease with increasing latitude and is largely driven by changes in the abundance of scraping and excavating (i.e., scarinine) parrotfishes (Fig. 6). In particular, significant decreases in the abundance of parrotfishes are evident between subtropical (Ryukyu Islands) and temperate (Japan mainland) regions, and are likely related to the lack of coral reef habitat as well as the low winter water temperatures (<18°C) in temperate regions. Contrary to the latitudinal distribution patterns of most parrotfish species, *Calotomus japonicus* and *Scarus ovifrons* are primarily distributed from the northern Ryukyu Islands to the central Japanese mainland (Nakabo 2013), and as such are regarded as subtropical species. *Calotomus japonicus* occur in rocky habitats and/or seaweed beds where they have been observed to feed on both red and brown macroalgae, including *Sargassum* (Terazono et al. 2012). The feeding activity of *Ca. japonicus* is positively related with seawater temperature, and increasing coastal SST during autumn and winter over the last 30 years have extended their period of intensive feeding. The increase in the feeding of *Ca. japonicus*, as well as other herbivorous fishes, has been implicated in the loss kelp forests in southern Japan (Serizawa et al. 2004, Verges et al. 2014). *Scarus ovifrons* is a large-bodied species (up to 80 cm total length, TL) that occurs in rocky and coral-dominated reefs, however its feeding ecology and life history characteristics are poorly understood.

Species richness and abundance of tropical parrotfish species in temperate Japanese waters are approximately two and five times greater, respectively, in coral-rich than rocky reef habitats, and seasonal changes in these numbers closely match those of SST (Nakamura et al. 2013). The majority of parrotfishes on these temperate reefs are juveniles (< 10 cm TL);
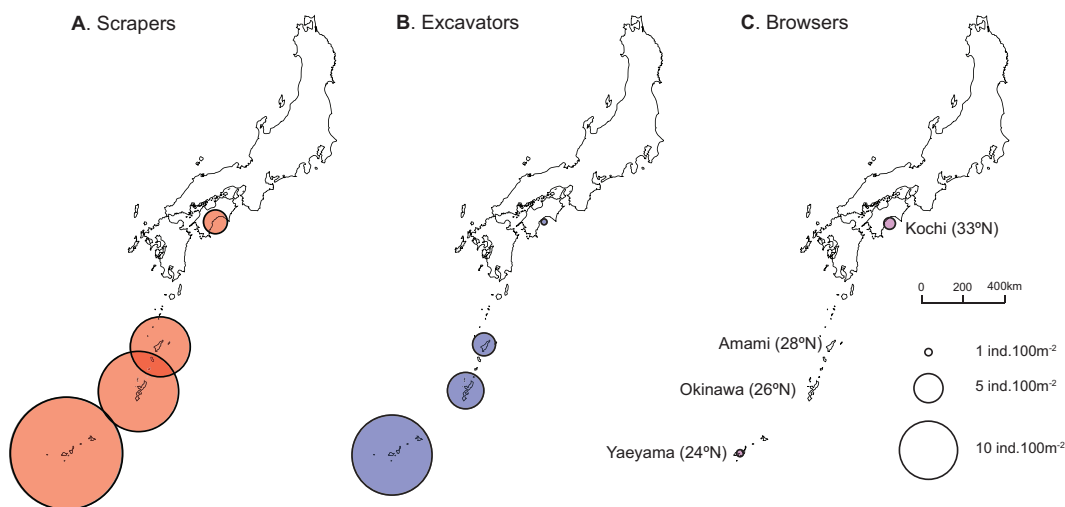
Fig. 6. Spatial variation in the abundance of parrotfishes in southern Japan. (A) Abundance of scarinine scraping parrotfishes (*Scarus, Hipposcarus*), (B) abundance of scarinine excavating parrotfishes (*Cetoscarus, Chlorurus*), and (C) abundance of sparisomatine 'browsing' parrotfishes. Circles are proportional to mean abundances or total number of species recorded in each location. Data are from 56–60 replicate 20 m² transects along inner reef flats (within 1–3 m depth) and shallow reef slopes (2–10 m) in the Ryukyu Islands, and coral-rich habitats (2–10 m) in Kochi (*n* = 56 for each region in the Ryukyu Islands and *n* = 60 for Kochi). Data were collected during spring (April–May), summer (August), and late autumn (November–December) in each region in 2004–2005 for the Ryukyu Islands and in 2009–2010 for Kochi.

the lack of larger-bodied individuals suggests they may not be surviving the colder water temperatures during winter. The only exception to this is *Sc. ghobban* which comprises approximately 75 percent of the total abundance of tropical parrotfishes at Kochi (33°N), southern Japan, with individuals ranging in size from 4 to 30 cm TL. The higher abundance coupled with the presence of larger individuals suggest *Sc. ghobban* may have established populations on the temperate Japanese reefs (Nakamura et al. 2013).

The mechanism/s that have allowed *Sc. ghobban* to establish on these temperate reefs, while other parrotfish species appear unable to overwinter, remains unclear but may be related to differences in thermal tolerances or feeding habitats among species. Interestingly, small-bodied (< 10 cm TL) *Sc. ghobban* have been observed to feed almost exclusively from the surfaces of dead corals, while larger individuals (10–30 cm TL) tend to feed equally from the surfaces of dead coral, boulders, and rocky reefs (Nakamura unpublished). The feeding rates of *Sc. ghobban* (> 10 cm TL) on these temperate Japanese reefs during summer (ca. 15 bites min^{-1}) are directly comparable to those reported from other tropical reefs (GBR: 13.9 bites min^{-1}; Red Sea 10.9 bites min^{-1}; Bonaldo et al. 2014), but in late autumn and winter the feeding rates decrease substantially (ca. 1–5 bites min^{-1}). Nevertheless, the expansion of coral habitat coupled with increasing winter SSTs on Japanese temperate reefs may lead to an increase in suitable feeding substrates for tropical scraping and excavating parrotfish species.

Marginal Reefs of Brazil

The Brazilian coast and oceanic islands encompass unique reef formations and marine life, with high rates of endemism for a number of groups of reef organisms (Maida and Ferreira 1997, Floeter et al. 2001, Rocha 2003). The region hosts a large number of endemic species, and consequently represents a biogeographic province in the Western Atlantic (Gilbert 1972, Briggs 1974, Floeter and Gasparini 2000), separated from the Caribbean by the mouths of the Amazon and Orinoco rivers, and by the sediment-rich coastline of the Guyanas. Larval exchange between the Brazilian and the Caribbean provinces is limited, as connectivity between these areas has been discontinuously maintained along geological time by eustatic processes that weaken the Amazon influence (Floeter et al. 2001, Rocha 2003).

The Brazilian province congregates a number of geological landscape features that constrain the establishment of coral reef ecosystems, such as the high rainfall and massive riverine input, convergence of subtropical currents, and the relatively narrow continental platform (Maida and Ferreira 1997, Leão et al. 2003). Growth of biogenic reefs, including coral reefs, is limited to north-eastern Brazil, an area characterized by seasonal inputs of freshwater and sediments, and the resuspension of sediments by strong winds and currents (Maida and Ferreira 1997). Eighteen species of scleractinian corals have been recorded from the Brazilian province, and not surprisingly all have a massive or encrusting morphology that are resistant to sedimentation and high turbidity (Maida and Ferreira 1997). There is a complete absence of branching scleractinian corals and *Acropora* species (Maida and Ferreira 1997, Leão et al. 2003). The richest region in the province in terms of the number of coral species and reef area size is the Abrolhos bank, off north-eastern Brazil, where coral formations have a particular mushroom shape and reefs do not display the typical zonation pattern observed in other Atlantic coral reefs (Maida and Ferreira 1997, Leão et al. 2003).

Water temperature constrains the development of shallow coral reefs in the south and south-eastern Brazilian coast. As a result, benthic communities in these regions are usually

composed of massive corals and hydrocorals, together with algae, sponges and other benthic organisms that form a veneer on profuse rocky shores. As temperature decreases towards the south of the province, rocky shores become more dominant in relation to biogenic reefs and there is a marked reduction in the taxonomic and functional diversity of tropical reef fish communities (Ferreira et al. 2004, Floeter et al. 2001, 2005).

Reef fish fauna in the Brazilian province mirrors the particular physical conditions and benthic fauna of the system. Approximately 20 percent of the Brazilian reef fishes are endemic to the region, with a number of species closely related to the fauna in the Caribbean (Moura and Sazima 2000, Floeter et al. 2008). Ten parrotfish species have been recorded within the Brazilian province: two *Scarus*, six *Sparisoma*, *Cryptotomus roseus* and *Nicholsina ulsta* (Robertson et al. 2006, Floeter et al. 2008), with assemblages dominated by sparisomatine species ([Fig. 7](#)). Sparisomatine parrotfishes (i.e., *Sparisoma* or seagrass clade) are regarded as having a weaker association to coral reef habitats, especially in comparison to scarinine species (i.e., *Scarus*, or reef, clade; Streelman et al. 2002). Among the sparisomatine parrotfishes *Sparisoma* spp. are dominant on most reefs along the Brazilian coast and oceanic islands (Ferreira et al. 2004, Floeter et al. 2005), while *Cr. roseus*, *N. ulsta* and *Sparisoma radians* inhabit shallow vegetated areas (i.e., seagrass and macroalgae) adjacent to reefs (C.E.L. Ferreira pers. obs.). Although scarinine parrotfishes originated in reef habitats and have been suggested to have closer, and in some cases obligate, association with coral reefs (Streelman et al. 2002), both Brazilian *Scarus* species appear to be doing well on both the tropical coral-rich north-eastern and subtropical coral-poor south-eastern coasts (Ferreira et al. 2001, Cordeiro et al. 2016).

Five of the parrotfish species in the Brazilian province are recently described endemics that were previously confounded with their sister species in the Caribbean (e.g. Moura et al. 2001, Gasparini et al. 2003). Besides morphological resemblances, pairs of sister species in the Caribbean and Brazil often differ in abundance in their respective regions. *Sparisoma viride*, for example, is present in high densities throughout much of the Caribbean (Bruggemann et al. 1994, McAfee and Morgan 1996, Mumby and Harborne 2010), yet its sister taxon, *Sparisoma amplum*, is relatively rare on Brazilian reefs and only occurs in higher densities on the north-eastern coast and oceanic islands (Ferreira et al. 2004, Francini-Filho et al. 2010). The clade formed by *Sp. amplum* and *Sp. viride* may thus be considered as central for coral reefs in the Caribbean, but peripheral for Brazilian reefs. In contrast, while *Sp. rubripinne* and *Sp. chrysopterum* are generally found in low densities on Caribbean reefs (McAfee and Morgan 1996), usually near seagrass beds and other marginal habits, their sister species, *Sp. axillare* and *Sp. frondosum*, respectively, are the most abundant parrotfish species on Brazilian reefs ([Fig. 8](#); Ferreira et al. 2001, Ferreira et al. 2004, Floeter et al. 2007, Francini-Filho et al. 2010, Cordeiro et al. 2016).

Differences in the relative abundances of sister taxa between the Caribbean and Brazil likely reflects variations in habitat requirements of these species. The sparisomatine parrotfishes *Sp. amplum* and *Sp. viride* possess a suite of features more characteristic of scarinine parrotfishes, namely robust jaws with simple and strong articulations among elements and well-developed musculature to generate a forceful bite (Bellwood 1994). Consequently, *Sp. amplum* and *Sp. viride* are the only sparisomatine parrotfishes considered to have an excavating feeding mode (Rotjan and Lewis 2005, 2006, Francini-Filho et al. 2008), and appear to represent an example functional convergence with scarinine parrotfishes (Streelman et al. 2002, Robertson et al. 2006). These features may explain the higher abundance of these species in coral reefs in the Caribbean and on tropical reefs of Brazil. In contrast, *Sp. rubripinne / Sp. axillare* and *Sp. chrysopterum / Sp. frondosum* are
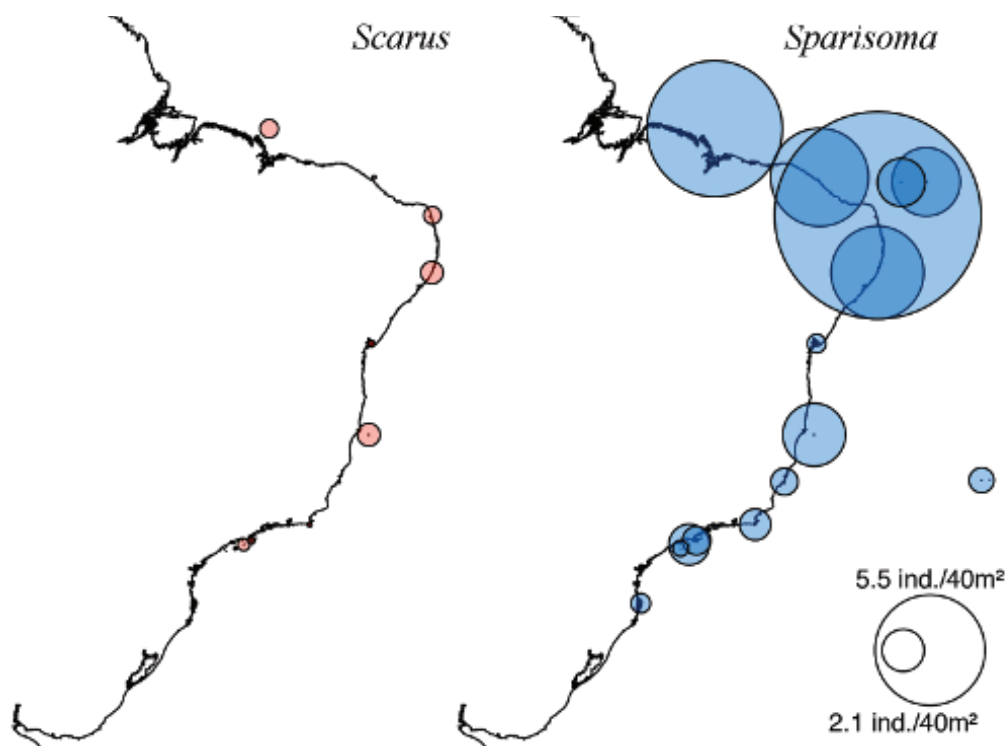
Fig. 7. Spatial variation in the density of scarinine and sparisomatine parrotfishes along the Brazilian coast. Circles are proportional to mean abundances recorded in each location. Data of species abundances based on 20 × 2 m belt transects within shallow (3–15 m) rocky or biogenic (coral/coralline algae) reefs (see details at Floeter et al. 2005).

more representative of typical sparisomatine parrotfishes, feeding on macroalgae and/or associated epiphytic material (McAfee and Morgan 1996, Bonaldo et al. 2006, Ferreira and Gonçalves 2006). Such feeding habits may reduce their reliance on conditions usually associated with coral-rich habitats in favour of the higher abundance of macroalgae on marginal reefs in Brazil.

In addition to differences in parrotfish assemblages between the Caribbean and Brazil, the abundance of parrotfishes in relation to other nominally roving herbivorous fishes differs between these two provinces. While parrotfishes typically dominate herbivorous fish assemblages on Caribbean reefs, surgeonfishes dominate herbivorous fish assemblages on most reefs in Brazil (Floeter et al. 2005). Furthermore, there is a clear decrease in the abundance of parrotfishes and surgeonfishes with increasing latitude along the Brazilian coast. This decline is hypothesized to be related to the physiological constraints of these species to low temperatures, although nutritional hypotheses need to be considered (Ferreira et al. 2004, Floeter et al. 2005). Importantly, feeding pressure by these groups is also reduced at higher latitudes and lower temperatures (Longo et al. 2014, Fig. 9). For example, feeding pressure of *Scarus zelindae* and *Scarus trispinosus* decrease by 95–100 percent from the Abrolhos Archipelago to Arraial do Cabo (Fig. 9). In Santa Catarina, the southernmost region for reefs in Brazil, parrotfishes become less abundant and surgeonfishes vagrant (Ferreira et al. 2004). In this region, species with subtropical-temperate affinities, such
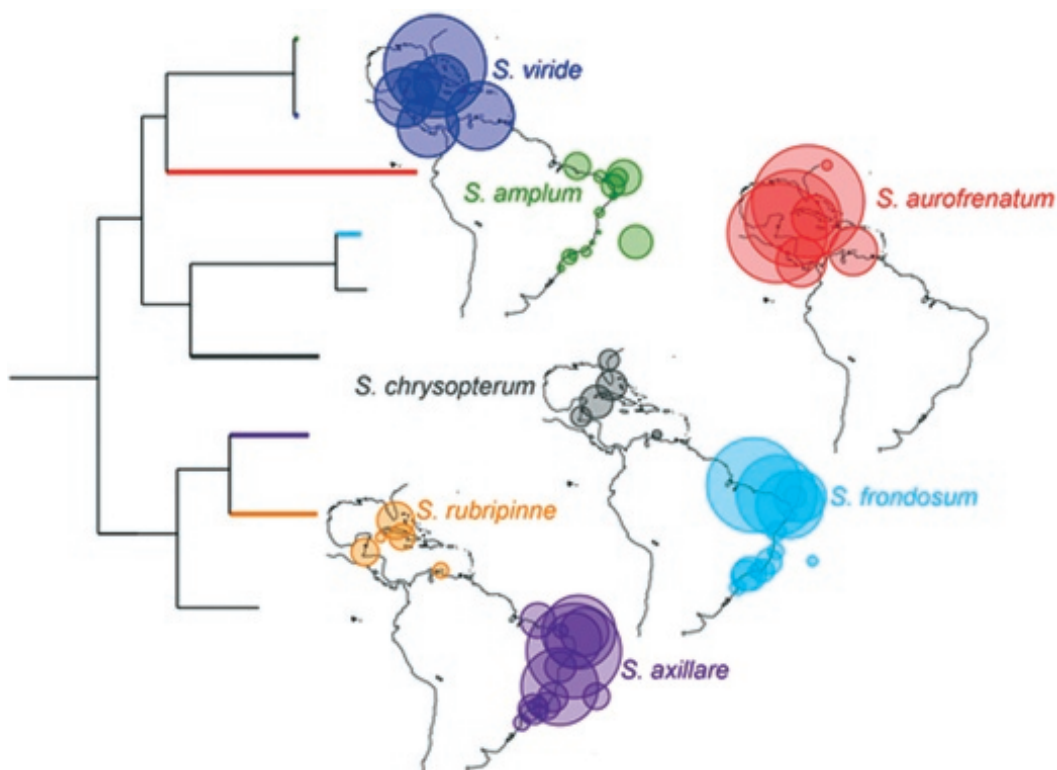
Fig. 8. Phylogeny of *Sparisoma* (modified from Robertson et al. 2006) showing relationships among species and their abundances along the Brazilian coast. Circle sizes representing the mean abundance (square root) of species in the tropical Western Atlantic. Data of species abundances based on 20 × 2 m belt transects within shallow (3–15 m) rocky or biogenic (coral/coralline algae) reefs (see details at Floeter et al. 2005).

as browsing *Kyphosus* spp. and the omnivorous *Diplodus argenteus*, are found in higher densities (Ferreira et al. 2004).

Studies on behavior and ecology of reef fishes, including parrotfishes, are relatively recent in Brazil (e.g. Ferreira et al. 1998, Floeter et al. 2005, Bonaldo et al. 2006, Francini-Filho et al. 2008, Francini-Filho et al. 2010), and several aspects of the ecology of parrotfishes are still to be elucidated, especially regarding the impact of these species on benthic communities and the influence of benthic communities in shaping parrotfish populations. On coral reefs, the balance between live coral colonies and benthic algae is fundamentally important, as corals provide the basis of the structure and dynamics of these systems. In this scenario, parrotfishes along with other reef herbivores are considered key in mediating coral-algal interactions since they can directly influence the structure of benthic communities (Lewis 1986, Bellwood et al. 2006, Burkepile and Hay 2008). On Brazilian reefs where low coral cover and high abundance of other benthic organisms naturally characterize the benthic community, the importance of parrotfishes in the structure and dynamics the reef benthos remains to be evaluated. Conversely, there is emerging evidence of the importance of bottom-up processes in shaping parrotfish populations (e.g., Heenan et al. 2016, Hamilton et al. 2017). Given the differences in the feeding ecology among parrotfishes and the geographical distribution of species in the group, the extrapolation of
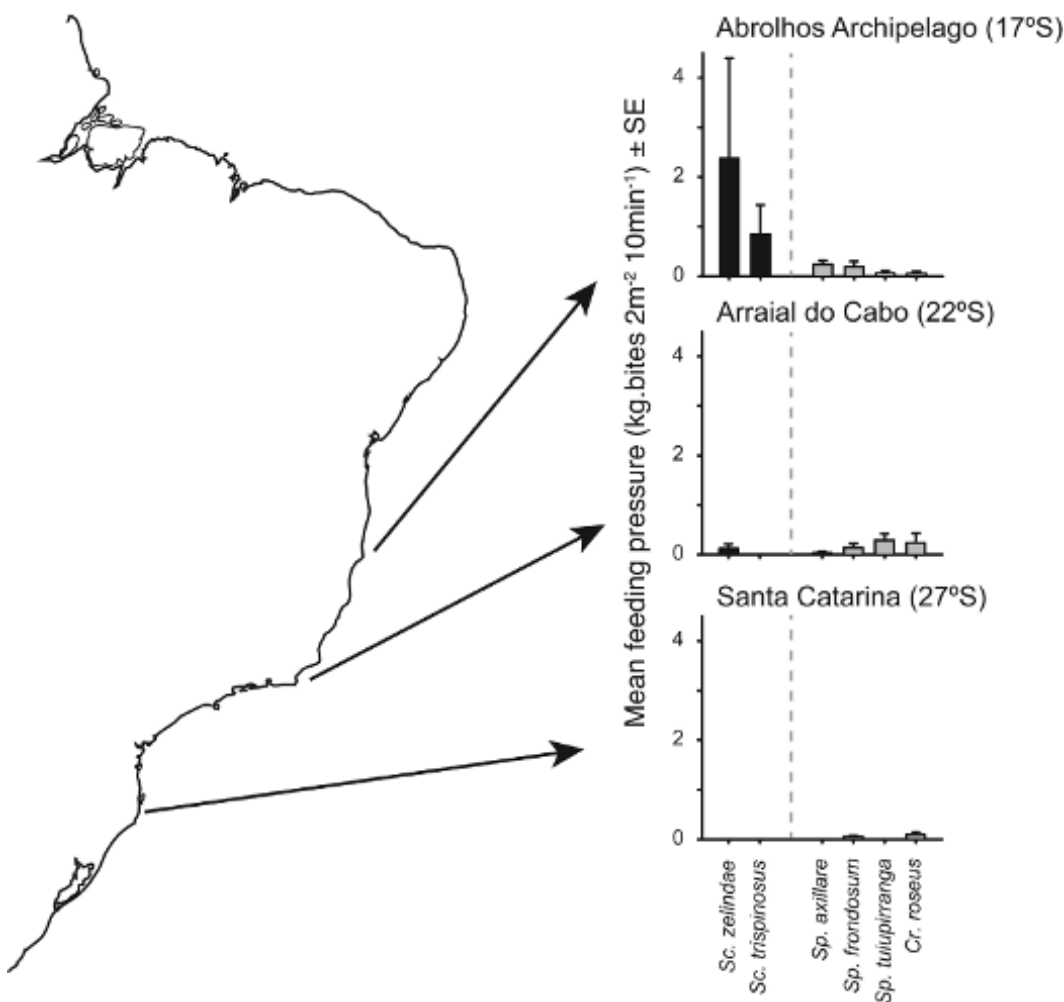
Fig. 9. Mean feeding pressure of parrotfishes at three study sites spanning 10º of latitude along the Brazilian coast (Abrolhos Archipelago, 17°S, Arraial do Cabo, 22°S, and Santa Catarina, 27°S). Data collected with remote filming of 2 m² plots (79–121 10–min videos per site) (see Longo et al. 2014).

patterns and processes derived from coral reefs in the Caribbean or Indo-Pacific to other areas should be done with care.

In spite of the unique nature and high endemism of reef fishes of the Brazilian province, reef ecosystems in this area are threatened by several anthropogenic activities, such as overfishing, pollution and habitat destruction. In the specific case for parrotfishes, a number of species have been suffering severe declines in their abundance and body size (Floeter et al. 2006, 2007, Bender et al. 2014). The largest endemic parrotfish in Brazil, *Sc. trispinosus* (maximum length 70 cm), for instance, used to be abundant on reefs along the north-east and south-east coast, but has been heavily fished during the last two decades. As a consequence, the species has suffered marked reductions and local extinctions throughout most of its historic range (Floeter et al. 2007, Bender et al. 2014) and has been recently classified as endangered by the IUCN Red List of species (Ferreira et al. 2012). Other large parrotfishes are facing similar declines, especially as populations of former

targets of spearfishers, such as groupers (Serranidae) and snappers (Lutjanidae), have collapsed on Brazilian reefs. Studies on population dynamics and ecology of parrotfishes in the Brazilian Province, especially on demography, nutritional ecology, and the role of this group in shaping local benthic communities, are fundamentally important to promote management and conservation of these unique species and habitats.

Summary

This chapter has explored how the variable and sometimes extreme environmental conditions of marginal reefs influence the structure of parrotfish assemblages and their interactions with the reef environment, and the challenges such conditions pose. In doing so, this chapter has raised many questions but answered few. Declines in the abundance and diversity of parrotfishes with latitude are widespread, and pronounced among scarinine, especially excavating, parrotfishes. It has been previously suggested that declines in tropical herbivorous fishes, including parrotfishes, with latitude are related to the effects of temperature on digestive physiology, or reductions in the quantity and quality of algal and detrital food sources in marginal environments (reviewed by Choat 1991). We do not discount the potential importance of nutritional ecology in shaping these patterns, rather we offer an additional mechanism for the near absence of parrotfishes in some marginal environments; the inability to penetrate the hard substratum of marginal reefs when feeding. Scarinine parrotfishes scrape and/or excavate portions of the reef substratum when feeding, presumably targeting endolithic phototrophs (Clements et al. 2017). In marginal environments with limited coral reef development benthic communities often occur as a veneer over harder granitic or basaltic substratum, essentially a rocky reef. The feeding apparatus of scraping and excavating parrotfishes, while effective at gouging into calcareous substrata on coral reefs does not have the capacity to penetrate these rocky substrata, and attempts to do so often result in damage to the oral jaws.

Sparisomatine parrotfishes appear to be better suited to marginal coral reef environments, are abundant on rocky reefs along the Brazilian coast, and one species, *Sp. cretense*, is largely restricted to temperate reef environments. Sparisomatines are widely regarded as browsers of macroalgae (e.g., Streelman et al. 2002) and are often observed taking bites from macroalgae and seagrass (e.g., Adam et al. 2015), however, it has recently been hypothesized that the majority of species are targeting protein rich epiphytic phototrophs on the surfaces of macrophytes (Clements and Choat Chapter 3). Such a feeding mode alleviates the need to gouge hard surfaces when feeding and may explain the less pronounced decline in this group at higher latitudes. Although it should be noted that the excavating *Sp. amplum* and larger-bodied individuals of other *Sparisoma* spp. regularly takes bites on hard substrata, and such a feeding habit has been shown to cause dentition damage on the basaltic reefs of Fernando de Noronha Archipelago, north-eastern Brazil (Bonaldo et al. 2007).

Perhaps the biggest challenges for parrotfishes inhabiting marginal reefs are the extreme and variable environmental conditions, namely temperature. Cellular processes, metabolism, energy requirements, and individual performance (activity, growth, reproduction) of ectotherms, including parrotfishes, are all linked to environmental temperature. In turn, these effects of temperature on individuals will manifest as changes in parrotfish populations and communities, and ultimately their functional impact. For example, the mean maximum of length and longevity of *Ch. spilurus* varies across latitude, with individuals at low latitude sites being smaller and having shorter life spans than those at high latitudes (Taylor et al. Chapter 4). It is unclear if such relationships will

hold for other parrotfish species, or in regions that experience both extremely high and low temperatures (i.e., the Arabian Gulf). The limited data on latitudinal and seasonal differences in feeding presented in this chapter also point toward the potential importance of environmental temperature in influencing the performance of parrotfishes. Any latitudinal or seasonal patterns, however, are not solely attributable to temperature. Many other factors, including productivity and the nutritional quality of dietary resources, are likely to covary with temperature and need also to be considered. Notwithstanding, a greater understanding of the effect of temperature on the physiology and performance of parrotfishes will not only allow us to better understand the factors that shape parrotfish assemblages on marginal reefs, but also enable us to better predict likely changes in the distribution and ecology of parrotfishes under climate change.

Throughout this chapter we compare the abundance of parrotfishes among locations and latitudes. One problem of such an approach is that it doesn't account for any differences in body size or longevity. If the latitudinal patterns in maximum body size and longevity of *Ch. spilurus* are representative of other parrotfish species, then the shorter life spans at lower latitudes suggest that these populations would have higher rates of turnover. Conversely, those at higher latitudes would have lower turnover, and populations would be composed of individuals from numerous cohorts, and may be extremely susceptible to disturbances or fishing.

Based on the phylogenetic reconstruction of the evolutionary history of 61 species of scarinine parrotfish, Choat et al. (2012) suggest that the ancestral habitats of *Scarus* were rocky reefs (Choat et al. 2012). Despite this, however, it appears that marginal reefs are not the realm of extant parrotfishes. Although some species are endemic to regions of marginal reef (Arabian Sea: *Sc. zufar, Sc. arabicus;* Eastern Pacific: *Scarus perrico, Scarus hoefleri;* Mediterranean: *Sp. cretense*), and others (i.e., *Sc. ghobban* species complex) are regularly found on marginal reefs, the majority of parrotfish species are rare or absent from marginal environments. Parrotfishes often dominate herbivore biomass on low latitude reefs, especially in areas of high turf algal cover and low topographic complexity (Fox Chapter 13), and are viewed as critical to maintaining the balance between corals and algae. Within high latitude marginal reef systems, however, parrotfishes appear to be relatively minor players, with subtropical acanthurids and urchins dominating herbivore assemblages.

Acknowledgments

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