

CHAPTER 16

FAQs about Caribbean Parrotfish Management and their Role in Reef Resilience

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Introduction

Research on the biology of coral reef fishes has accelerated rapidly since the development of SCUBA, and has been driven by their diversity and potential use as a model system for testing general ecological concepts (Hixon 2011). More recently, research has embraced concerns about how fish populations respond to stressors such as fishing pressure, habitat degradation, increasing ocean temperatures and acidification, and the introduction of invasive species, and there is an increasing focus on how conservation initiatives may address these threats. This wealth of research has elucidated the functional role of many species, but the role of herbivorous fish has received perhaps the greatest attention. Within the guild of herbivorous fishes, parrotfishes are the best studied taxa and, as can be seen from this book, there is a rapidly growing literature covering all aspects of their biology, management, and importance to coral reefs.

One of the most widely studied functional roles of parrotfishes is their removal of algae that might otherwise compete with corals (McCook et al. 2001). In principle, grazers such as parrotfishes benefit coral populations by facilitating recruitment and reducing the frequency and intensity of competitive interactions with algae. However, as is so often the case in ecological systems, this apparently straightforward concept belies a multitude of complex questions including the relative importance of top-down and bottom-up controls of benthic dynamics, phase shifts and alternative stable states, the degree of functional redundancy amongst herbivores, and resolving the functional versus nutritional aspects of parrotfish feeding (Adam et al. 2015a). In addition, many questions exist concerning the management of parrotfish management, including how harvesting influences the biomass of fish on reefs and their functional role, and how marine reserves affect trophic cascades within food webs.

Research into the nutritional biology of Caribbean parrotfishes has lagged behind that in the Pacific. For example, the emerging picture in the Pacific is that parrotfishes are microphages and detritivores (Crossman et al. 2001, Choat et al. 2004, Clements et al. 2017), which likely also applies to Caribbean species of the genus *Scarus*. However, the nutritional biology of the other major – and endemic – Atlantic genus, *Sparisoma*, has received little recent study. Species of *Sparisoma* differ from *Scarus* in taking a large proportion of bites from fleshy macroalgae (Bruggemann et al. 1994c), and their alkaline intestine helps dissociate protein-tannin complexes in brown algae (Lobel 1981). Furthermore, brown algal secondary metabolites do not seem to affect nutritional assimilation (Targett and Arnold 1998). The degree to which *Sparisoma* derives nutrition from detritus and microalgae remains unclear (but see Bruggemann et al. 1994c). Despite the uncertainty of the nutritional biology of Caribbean parrotfish, many studies have examined the impact of their grazing on coral reef algae, which seems to be strongly negative (e.g. Williams and Polunin 2001, Kramer 2003, Mumby et al. 2006b, Burkepile et al. 2013).

Parrotfishes are among the most abundant and conspicuous of Caribbean coral reef fish, yet comprise just 16 species, and only species from the genera *Scarus* and *Sparisoma* are functionally important grazers on reefs. Furthermore, the functional importance of these genera has increased since the mass mortality of the herbivorous urchin *Diadema antillarum* in the early 1980s (Lessios 1988), so that they are now the major grazers on most reefs in the region. The relative simplicity of this system has allowed the functional role of parrotfishes to be sufficiently well understood that it can be built into predictive models that provide realistic insights into future reef dynamics (Mumby 2006a). Such models have provided a range of new insights into coral reef resilience, which is the probability that a reef will still be able to maintain a trajectory of coral recover after some prescribed period of time during which disturbances occur (Mumby et al. 2007a, 2014).

Through our work on the biology, functional role, and management of Caribbean grazers, we have been exposed to a wide range of questions about the role of parrotfishes. Some of these queries stem from an understandable inability to keep abreast of a diverse literature, but some are driven by misunderstandings over what particular papers actually demonstrate (and we include the wider scientific literature here, not just our own). Indeed, some of the confusion is caused by apparent disagreements in the literature about the roles parrotfishes might play in reef dynamics and resilience. For example, a recent high-profile analysis of coral cover trends in the Caribbean highlighted the importance of overfishing of parrotfishes, and strongly recommended reductions in herbivore fishing (Jackson et al. 2014). This led to comments on international fora (e.g., coral-list) such as “we have parrotfishes on our reefs but coral cover is still declining”, “we have a marine reserve but coral cover is still low”, and “banning parrotfish fishing doesn’t address the threats of climate change”. Such comments reveal several misconceptions about the role of parrotfish in coral population dynamics, and if left unchecked could lead to perceived failures of management that result from unrealistic expectations.

This chapter aims to address some of the most frequently asked questions (FAQs) posed to us by researchers, reviewers, managers, and the general public. It is not intended to be a comprehensive review of Caribbean parrotfishes, but rather attempts to summarise the key literature required to answer specific questions. We begin by addressing questions regarding the basic biology of parrotfishes as this builds a foundation from which to understand their role in reef resilience, and the implications for management.

Parrotfish Biology

FAQ 1. What Controls the Diversity and Abundance of Parrotfishes on Reefs?

The Western Atlantic supports a greater diversity of parrotfishes than the Eastern Atlantic (Floeter et al. 2008, Bonaldo et al. 2014) and in the Western Atlantic the density of herbivorous fishes decreases from tropical to temperate latitudes, possibly because of the physiological challenges of utilising a relatively low-quality food in cooler water (Floeter et al. 2004, but see Clements et al. 2009). The major evolutionary radiation of *Sparisoma* was driven by allopatric processes caused by geographic separation from the Atlantic and riverine barriers (Robertson et al. 2006). Species of the genus *Scarus* likely arrived in the Caribbean through migration from an Indian Ocean source via South Africa and primarily exhibited sympatric radiation on reaching the Western Atlantic (Choat et al. 2012). Within the Caribbean, the biogeography of parrotfishes is not well documented, although there is little evidence that any species have restricted ranges within the region.

In contrast to their biogeography, there are major differences in parrotfish diversity and densities among habitat types. For example, one of the most abundant species is *Sparisoma viride*, which is absent in sandy habitat, has densities of <1 fish 100 m⁻² in mangroves, seagrass beds and escarpments, is more common (1–2 fish 100 m⁻²) on gorgonian-dominated pavements and deep *Orbicella*-dominated reefs, and is most common (>2 fish 100 m⁻²) on patch reefs, back reefs, reef crests and shallow *Orbicella*-dominated reefs (reviewed by Harborne et al. 2006). The major abiotic and biotic drivers of this inter-habitat variability are relatively well understood, and reef complexity is typically positively correlated with parrotfish abundance. Refuges within the reef have a range of functions for parrotfishes, including predator avoidance and nocturnal sleeping sites (Tzadik and Appeldoorn 2013). Consequently, across a range of sites and habitats in Belize, the density and biomass of the commonest species (*Scarus iseri*, *Sparisoma aurofrenatum* and *Sp. viride*) were positively correlated with reef complexity, although the abundance of *Sparisoma chrysopterygum* did not appear to be linked to rugosity (Bejarano et al. 2011). Such habitat preferences appear to be established during the settlement and recruitment period of some species (Tolimieri 1998b). Within coral-rich habitats, patches of reef with larger mean heights of coral colonies also appear to support greater biomasses of parrotfishes (Harborne et al. 2012). Critically, although increasing reef complexity increases the grazeable area on reefs, the benefits to parrotfish abundances from increasing rugosity are sufficient to drive higher grazing intensities on rugose reefs (Bozec et al. 2013). Therefore, positive feedbacks are established with increasing rugosity increasing parrotfish abundance and grazing intensity, which reduces macroalgal abundances, facilitating coral settlement and the maintenance and enhancement of processes underpinning high reef complexity (Bozec et al. 2013). Such feedbacks do not occur on flat, hard-bottom habitats where parrotfishes are less abundant and benthic dynamics are largely controlled by physical processes (Mumby 2016).

In addition to reef complexity, other controls of parrotfish populations include decreasing abundances with increasing depth, predominantly because of its effect on algal productivity, but also because of predator abundance and the density of herbivorous competitors (Lewis and Wainwright 1985, Nemeth and Appeldoorn 2009). Wave exposure also has an important influence on the composition of coral reef fish assemblages because varying water velocities favour different fin morphologies (Fulton et al. 2005), although there are limited data available for Caribbean parrotfishes (but see Bellwood et al. 2002). There are also limited data on whether pre- or post-settlement processes are most important

for parrotfish demographics, although factors such as predation risk and refuge availability are more important than larval supply for regulating populations of other territorial species (Hixon et al. 2012). Populations of species such as *Sc. iseri* and *Scarus guacamaia* on reefs are enhanced by nursery habitat availability, particularly mangroves and dense seagrass beds (see FAQ 5). Finally, populations of adult parrotfishes are highly influenced by fishing pressure, but this is outlined in more detail in the Section on 'Parrotfish fisheries management' below.

FAQ 2. Are all Parrotfishes Functionally Equivalent?

When considering the conservation of parrotfishes, an important question is whether the sole target should be increasing fish biomass, or whether herbivore diversity should also be considered to maintain grazing pressure. Answering this question requires an understanding of whether all parrotfishes are functionally equivalent, or whether some species have specialised roles on reefs. Despite the uncertainties concerning their nutritional biology, all parrotfishes remove algae and there is a well-established distinction between the morphology of species that 'excavate' (grazing also removes pieces of the substratum) and those that 'scrape' (food is removed from the surface of the substratum with a non-excavating bite) (Bellwood and Choat 1990). In the Caribbean, *Scarus* species generally target algal turf assemblages, crustose coralline algae, and endolithic algae, while *Sparisoma* species generally target macroalgae (Adam et al. 2015b). More specifically, seven common species have been categorised based on the degree of removal of the substratum and major food sources (Cardoso et al. 2009), and we add our own observations to this list here. *Scarus taeniopterus* and *Sc. iseri* are categorised as 'scrapers' (leave superficial bite marks but remove more turf algae than other species). *Sp. aurofrenatum*, *Sparisoma rubripinne* and *Sp. chrysopterus* are considered 'grazers' (the term grazer is used because these species are not obligate browsers and also scrape the epilithic algal matrix), although *Sp. aurofrenatum* does frequently bite live corals (Miller and Hay 1998) and in some classifications is considered a scraper (Bernardi et al. 2000, Streelman et al. 2002). *Sp. viride* is a 'bioeroder' or 'excavator' (removes both coralline rock and live coral when feeding but feeds extensively on algal turfs and several macroalgae including *Dictyota* spp., Mumby 2006a), and *Scarus vetula* is a 'bioeroder/scrapper' (removes coralline rock but feeds primarily on turf algae). These results suggest significant functional diversity among Caribbean parrotfish (Cardoso et al. 2009, Adam et al. 2015b), especially since the frequently over-fished, large-bodied *Scarus guacamaia* is not included in the classification. A single large-bodied parrotfish species can have key functional roles on reefs, even in the more diverse Indo-Pacific (Bellwood et al. 2003, 2012), although there is some evidence that *Scarus guacamaia* feeds on similar foods to *Sp. viride* (Burkepile and Hay 2011).

The suggestion that there are multiple functional roles within the parrotfish assemblage is supported by experimental evidence that individual species alone may not be able to suppress successional processes resulting in macroalgae that reduce coral growth, or remove established macroalgae that have similar effects (Burkepile and Hay 2008, 2010). These functional roles of individual parrotfish species are further supported by feeding of surgeonfishes (Burkepile and Hay 2008, 2010) and, before their mass mortality, would have complemented grazing by urchins such as *Diadema antillarum* (reviewed by Lessios 1988). However, a study examining the response of the herbivore assemblage to different algal assemblages indicates that while there is complementarity between *Sparisoma* spp. and both the surgeonfishes *Acanthurus* spp. and *Scarus* spp., there may be some redundancy within the latter genera (Burkepile and Hay 2011). Finally, the lack of apparent competition

and aggressive interactions among parrotfish species (Mumby and Wabnitz 2002), also suggests limited niche overlaps and the use of different feeding resources (Fig. 1). This general lack of functional redundancy in Caribbean parrotfishes is consistent with global patterns of functional diversity being highly vulnerable to losses of reef fish species (Mouillot et al. 2014). Therefore, while the absolute biomass of parrotfishes is clearly important to maintain the ecological process of grazing, there is a growing understanding that maintaining the diversity of parrotfish assemblages, and the entire herbivore guild, is also important for the benthic dynamics of reefs.

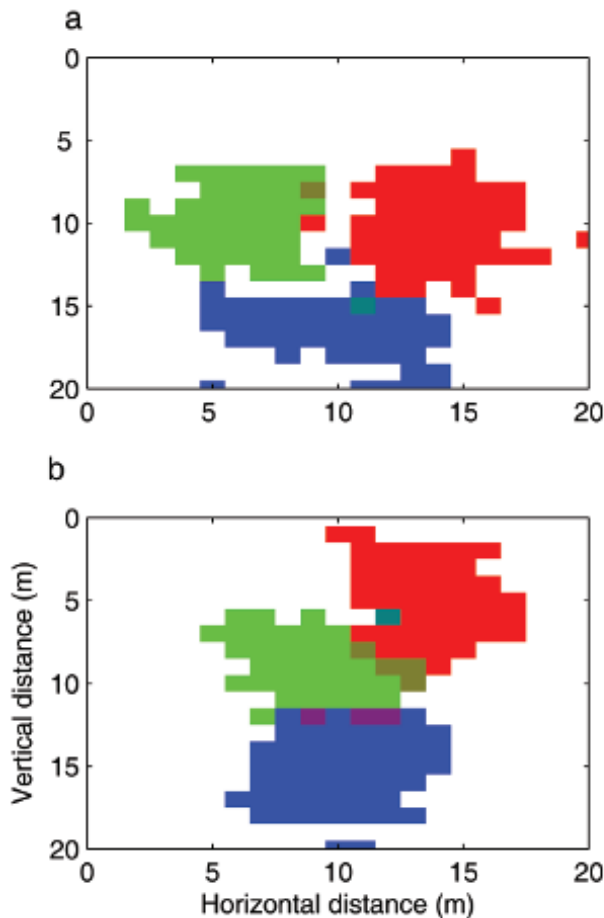


Fig. 1. Species stacking showing three adjacent parrotfish territories for *Sparisoma viride* (a) and *Sparisoma aurofrenatum* (b). Individuals of each species distinguished using red, green, and blue. Intraspecific spatial overlap among territories is infrequent but denoted using purple, olive and turquoise. Note that the territories of different species overlap (stack) in space.

FAQ 3. Are There Key Spawning Sites that Should be Conserved?

Mass spawning aggregations for species such as groupers and snappers are key sites for protection (Claydon 2004), but most Caribbean parrotfishes do not use the same reproductive strategy (though the bumphead parrotfish in the Indo-Pacific can form aggregations of up to one thousand individuals, Roff et al. 2017). In contrast, terminal phase parrotfishes typically defend territories and spawn daily with a harem of females

(Bruggemann et al. 1994a, van Rooij et al. 1996). However, in shallow water, *Sp. viride* may form non-territorial mixed groups of males and females that have only limited sexual activity, including with territorial males in deeper water (van Rooij et al. 1996). Parrotfishes have long been recognised as undertaking predictable diurnal migrations between resting and feeding sites (Ogden and Buckman 1973), but these movements do not seem to be related to reproductive behaviour. Therefore, protecting parrotfish populations within marine reserves that are sufficiently large to capture diurnal movements are likely to also incorporate spawning sites. However, one exception may be populations of species such as *Sp. rubripinne* that occur at low densities on extensive low complexity hard-bottom and bank areas (Mumby 2016). We have heard anecdotal reports of parrotfishes undertaking spawning migrations to the edge of these habitats (see also the classification of *Sp. rubripinne* as forming spawning aggregations in Nemeth 2012), presumably to release their gametes into more favourable oceanographic conditions at the reef edge. Although population densities of these species are low, the habitats can cover large areas and, therefore, this behaviour may have important demographic consequences. Since spawning migrations may also mean that individuals move either into, or out of, marine reserves, documenting the scale and drivers of this behaviour is a pressing research topic.

FAQ 4. Is It Possible to Increase Parrotfish Recruitment on Reefs?

As might be expected for a species that spawns daily, parrotfish settlement to Caribbean reefs occurs throughout the year, although in some locations there can be a summer peak (e.g. in Florida, Paddock and Sponaugle 2008). Settlement may also be higher around new moons (Tolimieri 1998a) and, like many species, settlement rates vary annually (Paddock and Sponaugle 2008). Settlement densities are also affected by microhabitat availability, with species such as *Sp. viride* having higher densities on the coral *Porites porites*, a pattern that appears to reflect post-settlement survival rather than larval settlement preferences (Tolimieri 1998a). Since survival of recently settled individuals represents a particularly important bottleneck in the demographics of many reef species (Almany and Webster 2006), an important consideration is whether the local breeding biomass of parrotfishes drives a commensurate increase in local settler density (a stock-recruitment relationship). Reef fish stock-recruitment relationships have proven extremely difficult to quantify (Haddon 2011), but are important to identify because protecting adult stocks through the cessation of fishing could potentially lead to a positive feedback: the increased biomass of adults could increase settlement rates and consequently further recovery of the local breeding population. Perhaps the clearest attempt to identify a stock-recruitment relationship in parrotfishes has occurred in Bermuda, where a ban on fishing traps led to an increased biomass of adults that was monitored over a nine-year period (O'Farrell et al. 2015). In contrast to expectations given that Bermuda is a largely demographically closed system, there was no increase in juvenile density as the adult population increased, and this appeared to be linked to an increase in the abundance of the meso-predator *Aulostomus maculatus*. Since large predatory fishes were still being fished in Bermuda, it appeared that *Aulostomus maculatus*, which is rarely caught by fishers, benefited from low predation pressure and an increased abundance of food. Their increased abundance seemed to have limited any potential stock-recruitment relationship. This finding has important implications for management, because the benefits of larval parrotfish spillover from marine reserves may be lost in non-protected areas if meso-predators can respond unchecked to prey enrichment because of the absence of large predators to control their biomass.

FAQ 5. How Important is the Protection of Mangroves and Seagrass Beds for Parrotfishes?

Many reef fish species recruit into 'nursery habitats', rather than directly into their preferred adult habitat, to benefit from lower predation rates or increased food availability. Consequently, a nursery habitat can be defined as an area that supports greater contributions per unit area to the adult population (Beck et al. 2001, see also Adams et al. 2006, Dahlgren et al. 2006). Mangrove stands and seagrass beds are frequently cited as nurseries within tropical marine seascapes, but other shallow habitats such as algal beds can also be important (Nagelkerken et al. 2000). Evidence that Caribbean parrotfish populations are enriched by these habitats is multifaceted. Firstly, juvenile parrotfishes, particularly *Sc. iseri*, are frequently seen in mangrove and seagrass beds (Nagelkerken et al. 2001), which is consistent with the nursery habitat hypothesis. The presence of higher densities of parrotfishes on nearby reefs provides a stronger justification for categorising mangroves and seagrass beds as nurseries, and this has been demonstrated in a number of locations. For example, surveys at different distances from a bay containing mangroves and seagrass beds in Curaçao highlighted that densities of *Scarus coeruleus*, *Sc. guacamaia*, *Sc. iseri*, and *Sp. chrysopteron* were higher close to the bay (Nagelkerken et al. 2000). In contrast, *Sp. aurofrenatum*, *Sp. rubripinne*, and *Sp. viride* were classified as 'reef species' with all life stages, including juveniles, normally found on the reef and not appearing to use nursery areas. However, for reef species such as *Sp. viride*, shallow water habitats such as back reefs and patch reefs represent important sites for juvenile fish (Tolimieri 1998a, c). Subsequent studies have suggested that juvenile parrotfishes are primarily using mangroves and seagrass beds because of increased food availability (Nagelkerken and van der Velde 2004, Verweij et al. 2006).

The enrichment of populations of nursery-using parrotfishes on nearby reefs has also been demonstrated at entire reef scales. Across six Caribbean islands, the abundance of *Sc. iseri* was significantly higher on reefs around islands supporting mangrove stands and provides further evidence for this species having a high dependence on mangrove and seagrass nurseries (Nagelkerken et al. 2002). Working within a single biogeographic region (Mesoamerican Barrier Reef) and controlling for reef area, Mumby et al. (2004) demonstrated an increase in the biomass of *Sc. iseri* of 42% in mangrove-rich reef systems compared to mangrove-scarce areas. Furthermore, *Sc. guacamaia* appeared to have a functional dependency on mangroves and had suffered local extinctions after mangrove removal (Mumby et al. 2004). This functional dependency has also been reported from Aruba, where juvenile *Sc. guacamaia* were only observed in mangroves while all adults were observed on reefs (Dorenbosch et al. 2006). For these nursery-using species, the benefits of nursery habitat availability can have greater effects on the abundances of smaller fish (<25 cm) than the cessation of fishing within marine reserves, although protection is more important for larger-bodied individuals (Nagelkerken et al. 2012).

Despite convincing correlative studies, there is still a need for studies that directly observe the ontogenetic migration of parrotfishes from nursery habitats to nearby reefs, which may be aided by increasingly sophisticated methods of tagging fishes. Such research is necessary to fully parameterise models of parrotfish population demographics, including the maximum distance to which nursery habitats enrich adult populations. Currently the best evidence is that mangroves affect fish assemblages up to distances of approximately 10 km (Dorenbosch et al. 2006, Mumby 2006b, Huijbers et al. 2013), but this is likely to vary among species and seascapes. Finally, there is a need to better understand how the enrichment of nursery-using species by nursery habitats affects other components of fish

assemblages. For example, in seascapes where nursery habitats are extensive, the high abundance of nursery-using parrotfishes and piscivores reduces the abundance of other parrotfishes settling directly to reefs because of increased competition and predation, and affects benthic dynamics (Harborne et al. 2016).

FAQ 6. How Fast Do Parrotfishes Grow?

Growth rates are a key parameter for fisheries management, but data on the growth rates of Caribbean parrotfishes are limited. Most of the available data are for *Sp. viride*, which suggests growth in this species best fits von Bertalanffy growth equations (van Rooij et al. 1995, Choat et al. 2003, Paddock et al. 2009). Growth rates vary among size phases, with growth fastest in juveniles, slower in sexually inactive terminal phase males, and slowest in initial phase females and territorial, terminal phase males (van Rooij et al. 1995). These rates suggest that sexually inactive males trade higher growth rates for current reproductive activity in order to obtain a territory that will provide future high reproductive success (van Rooij et al. 1995). Consequently, *Sp. viride* can be categorised as a relatively short-lived species (maximum age ~12 years) with relatively consistent demographic parameters across the Caribbean, although data from Florida and elsewhere suggest that at some spatial scales there may be higher demographic plasticity (Choat et al. 2003, Paddock et al. 2009). Demographic models were recently created for the major Caribbean parrotfish species and tested against independent field data, although it would be advantageous to quantify regional variation in demographic rates in multiple species (Bozec et al. 2016), as has been carried out for *Sp. viride* (Choat et al. 2003).

FAQ 7. What are the Natural Predators of Parrotfishes?

The loss of parrotfishes caused by fishing and invasive lionfish is discussed in subsequent sections, so here we consider the demographic process of mortality caused by native predators. Although data are scarce, predation of parrotfishes can be assumed to decrease significantly with increasing body size, so that survival of new settlers on reefs is critical to replenishing adult populations (as for other species, Almany and Webster 2006). The list of parrotfish predators appears extensive, and they have been found in the stomach of piscivores such as small- and large-bodied groupers, jacks, snappers, and moray eels (Randall 1965, 1967). In addition, the trumpetfish *Aulostomus maculatus* elicits classic anti-predator responses by *Sc. iseri* (group formation) and *Sp. viride* (hiding in corals) (Wolf 1985). Over a time series of nine years in Bermuda following a reduction of parrotfish catches, an increased biomass of trumpetfish, but a stable density of juvenile parrotfishes despite an increased biomass of adults, also suggests this species is an important predator (O'Farrell et al. 2015, see FAQ 4). Interestingly, joining a school occurred less frequently when it contained fewer conspecifics (Wolf 1985), probably because of the increased predation risk for less-abundant species in groups (Almany and Webster 2004). On reefs where *Sp. viride* is relatively rare compared to *Sc. iseri*, such as near nursery habitats, this process may increase the mortality rates of non-nursery species even more than might be expected because of the increased biomass of nursery-using predators (Harborne et al. 2016).

The identity of parrotfish predators is likely to vary considerably with body size and life phase. Meso-predators, such as small-bodied groupers, are probably the most important predators of juvenile parrotfishes. For example, the abundance of recently settled fish, including numerous *Sc. iseri* and *Sp. viride*, were more abundant on patch reefs with higher densities of the large-bodied Nassau grouper, *Epinephelus striatus*, because it reduced the foraging of smaller *Cephalopholis* groupers (Stallings 2008). This experiment suggests

that the indirect effects of Nassau groupers on the predators of juvenile parrotfishes are more important than any direct predation. Similarly, fishing of large-bodied carnivores in Belize was linked to increased densities and changed behaviours of meso-predators, and declines in populations of *Sp. viride* (Mumby et al. 2012). As parrotfishes increase in size, the number of potential predators decreases until only the largest piscivores, such as sharks, are capable of feeding on adult parrotfishes. Parrotfishes are the preferred food of juvenile lemon sharks, *Negaprion brevirostris* (Newman et al. 2010), and have also been found in the stomachs of nurse sharks (Randall 1967), but diet data for other sharks is scarce and mortality rates are very difficult to establish. However, constraining adult parrotfish mortality rates is important for population and resilience modelling because larger-bodied fishes have the largest contribution to grazing and bioerosion. Equally, currently poorly known changes in the behaviour of herbivores when threatened by predators may be more important to benthic dynamics than direct predation events, as demonstrated in both the Caribbean and Indo-Pacific (Madin et al. 2010, 2011, Rizzari et al. 2014, Catano et al. 2016).

A key consideration when establishing marine reserves to protect biodiversity, fisheries, and ecological processes is whether the direct benefits to parrotfishes of a cessation of fishing are greater than the negative effects of increased predation caused by higher abundances of piscivores. A study in one of the largest and oldest marine reserves in the Caribbean demonstrated that even in lightly fished systems, the reduction of parrotfish catches far outweighs increased predation rates, and will increase grazing intensity (Mumby et al. 2006b). This is primarily because large-bodied parrotfishes, which are key grazers, reach a size that dramatically reduces their risk of predation by large-bodied groupers that are a prime beneficiary of marine reserve establishment. However, increased predation inside the park appeared to reduce the mean size of smaller bodied parrotfishes, such as *Sc. iseri* and *Sp. aurofrenatum* (Mumby et al. 2006b). Despite this effect, the long-term impact of Caribbean no-take marine reserves is clearly to enhance grazing.

FAQ 8. What Role are Invasive Lionfish having on Parrotfish Populations?

Perhaps the highest profile invasive species on reefs is the introduction of the Indo-Pacific species *Pterois volitans* and *Pterois miles* (subsequently 'lionfish') into the Caribbean. The history of the invasion is reviewed in detail elsewhere (Côté et al. 2013), but in summary lionfish were recorded in Floridian waters in 1985, entered The Bahamas in 2004, and have colonised the majority of the western Atlantic, Caribbean Sea, and Gulf of Mexico. This rapid spread is driven by a range of factors including high fecundity of well-protected eggs, being habitat generalists, and the limited number of predators (Côté et al. 2013). The ubiquity and high densities of lionfish on many Caribbean reefs has led to concern about their effects on native fishes and invertebrates. These effects may be particularly acute because native species have not evolved anti-predation mechanisms when confronted by the unique hunting style of lionfish: lionfish are stalking predators that use a slow, hovering hunting style with pectoral fins spread out and angled forward (Green et al. 2011, Côté et al. 2013). Consequently parrotfishes may incorrectly assign lower threat levels to lionfish, as has been seen in gobies (Marsh-Hunkin et al. 2013).

A growing literature has demonstrated that the impacts of lionfish on reef fish assemblages are significant (Albins and Hixon 2008, Lesser and Slattery 2011, Green et al. 2012), and these effects include reductions of parrotfish populations. Parrotfishes have repeatedly been found in lionfish stomachs, including adult *Sc. iseri* and *Sp. viride* (Albins and Hixon 2008, Morris and Akins 2009), and juvenile *Sc. iseri*, *Sp. aurofrenatum*, and *Sp.*

viride (Green et al. 2011). This predation pressure reduced the recruitment rate of four out of five parrotfish species (*Cryptotomus roseus*, *Sparisoma atomarium*, *Sp. aurofrenatum*, and *Sp. viride*) settling on patch reefs, as part of an overall 79% reduction of fish recruitment caused by lionfish during a five-week experiment (Albins and Hixon 2008). *Sparisoma aurofrenatum* was also one of 42 small-bodied prey fishes whose biomass declined by 65% during a period of rapidly increasing lionfish abundance on a Bahamian reef (Green et al. 2012). Finally, the lionfish invasion appeared to lead to a local extinction of *Sp. atomarium* on a Bahamian mesophotic reef between 30 and 76 m (Lesser and Slattery 2011).

There are currently few data demonstrating how reductions in parrotfish populations because of lionfish predation translate into changes in grazing rate, and consequently the abundance of algae on reefs. This trophic cascade has been proposed as a potentially important consequence of the lionfish invasion (Albins and Hixon 2013), and there is some evidence that a lionfish-driven phase shift from coral- to algal-domination may have already occurred on some mesophotic reefs (Lesser and Slattery 2011). Lionfish predation particularly targets smaller parrotfishes, and the majority of grazing is typically undertaken by larger individuals. However, an increased mortality of parrotfish juveniles has the potential to reduce the abundance of larger fishes, but the full demographic impact of lionfish predation on prey species has not been documented. In addition, lionfish have sub-lethal effects on parrotfish grazing by altering their foraging behaviour and reducing bite rates (Eaton et al. 2016, Kindinger and Albins 2017). This combination of direct predation and non-consumptive effects on high-lionfish-density reefs in The Bahamas reduced algal removal by 66–80% (Kindinger and Albins 2017).

The Functional Role of Parrotfishes

FAQ 9. Parrotfishes Eat Coral, so Aren't They Bad for the Reef?

Of the Caribbean parrotfishes only species in the genus *Sparisoma* eat coral, and even then live coral comprises a small proportion of bites (<4%) (Bruggemann et al. 1994a). The main corallivores are *Sp. viride* and *Sp. aurofrenatum* (Miller and Hay 1998). The answer to whether these corallivores are bad for the reef depends on the habitat involved. On shallow reef flats and the shallower parts of some forereefs, the consumption of branching corals in the genus *Porites* by parrotfishes is profound, and can lead to local exclusion of this coral (Littler et al. 1989, Miller and Hay 1998). Even the massive *Porites astreoides*, which has a harder skeleton than branching forms, experiences heavy corallivory in this environment, though it is not excluded (Littler et al. 1989).

On forereef habitats, evidence of parrotfish corallivory is common, particularly on large massive species of the genus *Orbicella* (Bythell et al. 1993, Bruckner and Bruckner 1998, Rotjan and Lewis 2005), although the only coral that appears to be preferentially targeted is *Porites porites* (Roff et al. 2011, Burkepile 2012). However, bite lesions can heal rapidly leading to a rapid turnover of scars (Sánchez et al. 2004), with little apparent detrimental impact on the coral. Moreover, although the feeding behaviour of parrotfishes has been implicated in causing mortality in juvenile corals (Birkeland 1977, Box and Mumby 2007), the beneficial role of parrotfishes in removing macroalgae appears to be much more important for corals (Mumby 2009). Consequently, densities of juvenile corals are positively related to parrotfish density, biomass, or grazing in the Caribbean (Mumby et al. 2007b, Burkepile et al. 2013).

Thus, for most Caribbean coral reef environments, the net impact of parrotfishes on coral assemblages appears to be positive, although they might have a net negative

influence on *Porites porites*. In addition to direct effects, an additional negative impact is that corallivory might potentially constrain the ability of *Porites porites* to take advantage of a loss of coral competitors as the cover of massive corals declines on some coral reefs (Roff et al. 2011). Of particular concern, however, is the role of corallivory when coral cover becomes low (Mumby 2009, Burkepile 2012); will predation overwhelm the capacity of corals to grow? There is mixed evidence available to address this question. Roff et al. (2011) found that the intensity of parrotfish corallivory across the Bahamas increased (although weakly) with an increase in coral density. Thus, if a decline in coral cover leads to lower average coral density then rates of corallivory might also decline. In contrast, Burkepile (2012) found that the frequency and intensity of corallivory increased at sites with low coral cover in Florida, but Florida appears to have unusually high levels of corallivory compared to the rest of the Caribbean.

FAQ 10. How much Evidence is there that Parrotfishes are Good for Reef Resilience?

In theory, grazing by parrotfishes can reduce the abundance of macroalgae and thick algal turfs and facilitate the recruitment, growth, and fecundity of corals (Mumby 2006a), which is a key mechanism promoting reef resilience following a disturbance (Mumby and Steneck 2008). Empirical evidence to support this hypothesis has been found by comparing the functioning of one of the Caribbean's oldest (60+ years), largest (450 km²), and most effective marine reserves (the Exuma Cays Land and Sea Park in the central Bahamas), to surrounding, unprotected reefs. Enforcement of park regulations since the mid-1980s has fostered a relatively intact fauna with abundant sharks and among the highest grouper biomasses in the entire region (Mumby et al. 2011). A cessation of fishing inside park boundaries means that parrotfish biomass is, on average, twice that outside the park, and the cover of macroalgae is four-fold lower (Mumby et al. 2006b). Density of coral juveniles show a simple linear positive increase with parrotfish grazing (Mumby et al. 2007b), and the trajectory of coral populations over time (2.5 years) was positive in the park but neutral to negative outside its boundaries (Mumby and Harborne 2010). These relationships were robust to other putative mechanisms, such as the possibility of there being natural variation in parrotfish abundance at the scale of the study site compared to controls, elevated coral larval supply to the reserve, changes in reef habitat complexity, differences in the density of damselfishes that can interfere with grazing behaviour, and densities of alternative herbivore groups including urchins or acanthurids. In addition, an experimental manipulation of parrotfish grazing evaluated the impact of fishing larger-bodied parrotfishes on the cover of macroalgae and the recruitment of corals to settlement plates (Steneck et al. 2014). The study was undertaken on two exposed forereefs in Belize, and used stainless-steel rods to prevent access of larger-bodied parrotfishes without the usual problems of caging effects on benthos. This 'removal' of large parrotfishes was sufficient to cause a large macroalgal phase shift and vastly reduce coral recruitment, highlighting the importance of adult fishes.

Other than those in the Bahamas and Belize, few studies have been able to track the relationship between a change in herbivory and consequent effects on algae and corals, but many studies have investigated individual components of this process. Mechanistically, one would first expect a negative relationship between parrotfish biomass or grazing and the cover of macroalgae. Secondly, a negative relationship would be expected between macroalgae and demographic and biological responses of corals. There is plenty of evidence for both. For example, negative relationships between total herbivore biomass or

total parrotfish biomass and macroalgal cover have been found throughout the Caribbean (Williams and Polunin 2001, Kramer et al. 2003, Newman et al. 2006, Burkepille et al. 2013). These studies were mostly undertaken on forereef habitats where the major macroalgal species include *Lobophora variegata* and species of *Dictyota*. The exception appears to be shallow, eutrophic patch reefs inside Glovers Atoll, Belize (McClanahan et al. 2004) where parrotfishes are unable to influence macroalgal growth (McClanahan et al. 2001). A key point is that this habitat is very different to that of forereefs, and the dominant algae are erect and generally unpalatable, including the genera *Sargassum* and *Turbinaria*. A wealth of evidence exists on the competitive interactions between corals and macroalgae in the Caribbean, all of which shows negative impacts on coral, although this can be species and size-specific, with less importance in larger corals (Ferrari et al. 2012). Furthermore, macroalgae can negatively affect the growth and survivorship of juvenile corals (Box and Mumby 2007), coral growth rate (Lirman 2001, Ferrari et al. 2012), partial colony mortality (Lirman 2001, Nugues and Bak 2006), and coral fecundity (Foster et al. 2008).

In short, the evidence for the positive effects of parrotfishes on coral resilience is substantial for forereef environments, but impacts might be absent in environments where algal growth is strongly enhanced by high light and/or high nutrients, such as shallow patch reefs.

FAQ 11. Isn't There a Lot of Evidence of Reserves not Benefitting Corals even though Parrotfishes were Protected?

A few Caribbean studies have found no evidence of protecting parrotfishes improving coral health (Huntington et al. 2011, Toth et al. 2014), yet each has serious difficulties in interpretation. Huntington et al. (2011) compared coral cover in shallow patch reefs between 1998/9 and 2008/9 and asked whether those in a reserve had fared better: they had not. There are a number of problems with this study. First, there was no evidence that the reserves had any positive influence on the biomass of parrotfishes, perhaps because of poaching or the inhospitable nature of the profound macroalgal dominance throughout the study area. (as seen in the Pacific, Hoey and Bellwood 2011). If there was no trophic impact of the reserve then there is no reason to expect any cascading benefit to corals via a reduction in macroalgae. Arguably, the reserve was not functioning successfully for herbivores, and there was no clear mechanism by which the reserve could influence corals either directly or indirectly. Second, the reefs studied were impacted by two bleaching events and three hurricanes between census dates. The authors' study design was unable to resolve the impacts of either event, so it is perhaps not surprising that no systematic effect of reserves on coral cover was found. A more appropriate study design would have tracked the impact-recovery response of individual reefs and asked whether recovery rates were greater in those sites with the greatest herbivore biomass (Fig. 2).

A study of coral trajectories in Florida between 1998 and 2011 found no benefit of reserves on coral trajectories (which mostly declined), nor did reserves affect macroalgal cover (Toth et al. 2014). The authors conclude that reserves have no impact on the health of corals, contrary to other studies such as those described earlier from The Bahamas. Clearly, the reserves studied had no beneficial impact on coral, but the contrasts made with other studies are disingenuous and misleading. First, parrotfishes are protected from commercial exploitation in Florida and there is no evidence that reserves have any impact on herbivory at the study locations: even fished reefs are likely to have supported a parrotfish assemblage close to its carrying capacity. Indeed, the authors of this study did

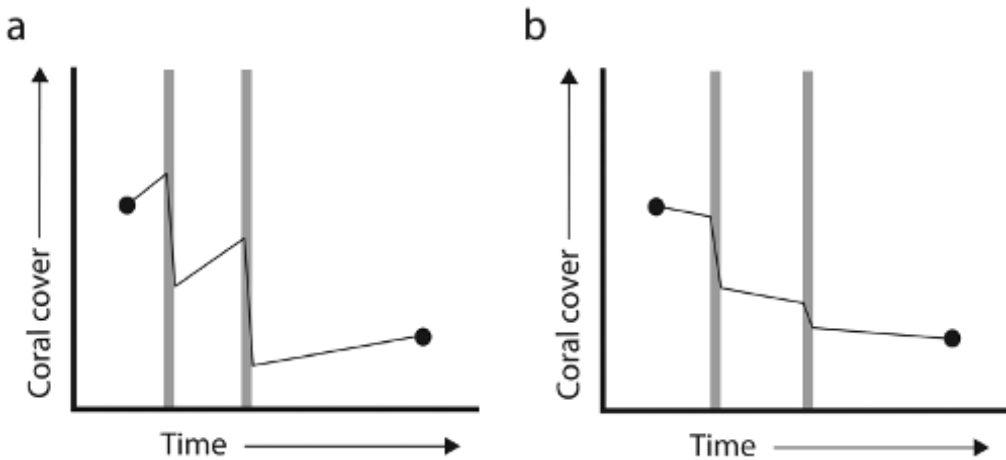


Fig. 2. A schematic representation of the difficulty in assessing coral cover trajectories (black lines) from only two sampling points (black circles) when the reef has experienced disturbance events (grey rectangles): (a) a resilient reef with high parrotfish biomass that experiences increases in coral cover between disturbances, and (b) a reef with low parrotfish biomass which experiences acute and chronic decreases in coral cover.

not even include herbivores in their study design, so we have to assume that herbivore levels were not systematically different between reserves and non-reserves. Under these circumstances, it is not surprising that reserve effects are absent on corals since the reserves have no mechanistic means of influencing corals. In contrast, reserves have a demonstrable benefit to parrotfish biomass where herbivores are the subject of fisheries (Hawkins et al. 2007, Valles and Oxenford 2014). It is under these circumstances that reserves have the potential to benefit coral populations. However, an important point made by Toth et al. (2014) is that coral populations can decline even when parrotfishes are not subjected to fishing. We will return to this issue in the next FAQ.

FAQ 12. If We Protect Parrotfishes, What is a Realistic Expectation for the Future Health of my Reef?

In the continued absence of the urchin *Diadema antillarum*, the current dominance – by biomass – of parrotfishes as the primary herbivore on Caribbean reefs is probably unprecedented. Importantly, although parrotfishes and *Diadema* competed when urchins were common (Carpenter 1988), it would be unrealistic to expect parrotfishes to expand their populations to completely fill the role vacated by urchins. After all, parrotfishes evolved in concert with other herbivores, including sea urchins. Consequently, following the mortality of *D. antillarum*, although densities of herbivorous fishes increased two- to four-fold across four reef zones in the U.S. Virgin Islands, their increased grazing intensity was not sufficient to halt an increase in algal cover and biomass (Carpenter 1990).

The functional importance of parrotfishes as a herbivore depends largely on the productivity potential of the benthos (Steneck and Dethier 1994). In highly productive coral environments exposed to high wave action, parrotfishes appear able to maintain between 30% and 40% of the reef in a grazed state of short algal turfs (Mumby 2006a). In contrast, the cover of macroalgae can become much lower where unexploited parrotfishes forage in low-productivity environments like leeward reefs (Renken et al. 2010). It follows that the response of corals to protection of parrotfishes will depend, in part, on the

productivity of the benthos, which influences the frequency and intensity of competition with macroalgae. If productivity potential is low then parrotfishes are more likely to be effective in preventing macroalgal blooms, even when coral cover is low. This is likely to be a factor in the continued health of coral reefs in Bonaire, which is a leeward reef with high coral cover, high parrotfish biomass, and very little macroalgal cover (Steneck et al. 2007).

Since the positive influence of parrotfishes on corals acts through processes of recovery (enhancing recruitment and growth by reducing macroalgae), the net benefit needs to be weighed against opposing rates of coral mortality. First, if background rates of mortality are high, such as in an area with high prevalence of coral epizootics, then coral populations may show net decline even in the presence of parrotfish protection. This might explain the results of Toth et al. (2014) from Florida. Alternatively, even if rates of recruitment and growth exceed background mortality, the overall rate of recovery may be overtaken by frequent acute mortality events from hurricanes and coral bleaching. In this case, coral cover might show a long-term decline, but at least coral populations can continue to recruit and turnover between disturbances. A desirable aspect of such resilience, even in the face of net reductions in cover, is that it allows coral populations to continue evolving, thereby maintaining a window for adaptation.

Observed rates of coral recovery in the Caribbean are non-existent to low once cover falls below 20% (Connell 1997, Roff and Mumby 2012). Protection of parrotfishes in the Exuma Cays Land and Sea Park (The Bahamas) led to an annual increase of total coral cover of around 1% per year. This is low, but should be viewed in context. Coral cover on these reefs was already heavily depleted by the 1998 coral bleaching event and was only 7% at the beginning of the study. Moreover, it is not unusual for rates of coral recovery to follow a sigmoidal function, being slow when cover is low, and accelerating as adult coral populations increase (although examples are scarce for Caribbean reefs, they are likely to follow patterns documented in the Indo-Pacific by Halford et al. 2004 and Gilmour et al. 2013). By protecting parrotfish populations, it is hoped that the currently slow increases in coral cover in the Bahamian park will also accelerate, but this will only occur in the absence of acute coral-mortality events.

In addition to increasing coral cover, an associated aim of parrotfish protection is to affect net carbonate production ('carbonate budgets'). Carbonate budget states, which are determined by the relative rates of carbonate production and erosion, represent an important tool for understanding the interactions between reef degradation and ecosystem services because they ultimately govern reef structural integrity and growth potential (Perry et al. 2008). Field-tested models of Caribbean population dynamics predict that protection of parrotfishes is vital to maintain positive carbonate budgets towards the end of this century, though this also requires significant action on greenhouse gas emissions (Kennedy et al. 2013). Note that these models include both the 'positive' effects of parrotfishes consuming algae and their 'negative' effects on coral carbonate budgets as a major source of bioerosion. In the absence of action on climate change, models predict that protection of parrotfishes still slow net reef decline by two decades or so, which may buy time for coral acclimation or adaptation to stress.

Parrotfish Fisheries Management

FAQ 13. How Important are Parrotfishes within Fisheries?

Fishing has had significant global impacts on herbivore assemblages, but large-bodied functional groups, such as scraping and excavating parrotfishes are particularly

susceptible (Edwards et al. 2014, Debrot et al. 2008). Parrotfishes are not a primary target of Caribbean fishers, but are increasingly caught as more desirable species from higher trophic levels, such as grouper, become rarer (Mumby et al. 2012). Consequently, there is a clear correlation between fishing pressure and parrotfish abundance (Hawkins and Roberts 2004). Furthermore, even if not targeted directly, parrotfishes are frequently caught in traps primarily placed to catch species such as groupers and snappers. As they are designed to catch large-bodied fishes, traps also remove functionally important large-bodied parrotfishes, such as *Sc. vetula* and *Sp. viride* (Rakitin and Kramer 1996, Hawkins et al. 2007). Traps may be particularly effective in low complexity habitats where they provide refuges that are naturally scarce (Wolff et al. 1999). Large-bodied species, such as *Sc. guacamaia*, are also susceptible to spearfishing (Comeros-Raynal et al. 2012). Since many parrotfishes are caught by artisanal fishers and as bycatch, there are few reliable data for the weight of parrotfishes landed in the region.

FAQ 14. Are Marine Reserves Sufficient to Protect Parrotfishes?

No. If the only investment in parrotfish management constitutes protection in reserves, this will potentially leave harvested reefs with lower resilience. An important implication of this is that the structural complexity of harvested coral reefs will be more likely to decline than protected reefs (Bozec et al. 2015). Because many commercially important reef fish species prefer high complexity reef habitats (Bejarano et al. 2011), a loss of complexity will threaten future yield. Indeed, a model of the effects of lost habitat complexity on Caribbean reef food webs found that reef fisheries productivity could decline more than three-fold (Rogers et al. 2014). Management of parrotfishes throughout the seascape should provide a long-term benefit to reef fisheries. A national ban on parrotfish fishing has been implemented in some Caribbean countries, such as in Belize (Mumby et al. 2012) where compliance has been high (Cox et al. 2013), and there are growing hopes that stakeholders will accept similar restrictions elsewhere. Such species-specific regulations represent one of many additional management tools that will be required, along with marine reserves, to manage Caribbean reefs that may look and function very differently in the future (Rogers et al. 2015).

FAQ 15. If it's not Possible to Ban Parrotfish Harvesting, are there any Alternative Management Strategies?

One alternative management strategy that has been proposed is to review the degree to which parrotfish grazing is important for different reef habitats (Mumby 2016). Some habitats, like those with a coral-built framework – often referred to as *Orbicella* reef (formerly *Montastraea* reef) – appear to have the greatest dependence on parrotfishes for controlling algae. Algal populations in some other habitats, such as hardbottom habitats visually dominated by gorgonians, appear to be driven by physical rather than biological processes (Mumby 2016). In these gorgonian-dominated habitats wave-driven scour and dislodgement from resuspended sediments is likely to constrain successful algal colonisation and growth (Torres et al. 2001). Thus, one alternative management strategy is to protect parrotfishes on *Orbicella* reefs where they are functionally critical, but permit exploitation on extensive hardbottom habitats where benthic dynamics will be less affected (Mumby 2016).

A recent study linked fisheries policies to the population dynamics of parrotfishes and their concomitant impacts on resilience of the ecosystem (Bozec et al. 2016). Bozec et al. (2016) found that even low harvest rates led to a large negative effect on ecosystem

resilience. However, the adoption of two relatively simple management practices – a minimum size of 30 cm and ban on fish traps – led to not only a more productive fishery but better outcomes for reef health at a given harvest rate. However, to help mitigate losses of reef resilience it was also necessary to keep harvest rates (the proportion of fishable biomass extracted per annum) to less than 0.1.

FAQ 16. How Quickly do Parrotfish Recover if Fishing is Banned?

There are a number of examples where marine reserves have led to higher biomasses of parrotfishes on reefs compared to unprotected sites (e.g. Polunin and Roberts 1993, Chapman and Kramer 1999, Mumby et al. 2006b). However, there are few long-term data on parrotfish recovery rates after a cessation in fishing. One exception is in Bermuda, where in 1992 the government banned the use of fish traps, which were a major source of parrotfish exploitation. A nine-year data set demonstrated that adult biomasses of parrotfish species increased by a factor of 3.7, and reached this level after around six years, at which point biomass did not recover any further (O’Farrell et al. 2015). Sex ratios may also approach unfished values within 3-4 years (O’Farrell et al. 2016). Recovery trajectories will vary depending on whether initial conditions reflect light or heavy fishing pressure, but the Bermuda data suggest that parrotfish populations can recover relatively quickly following the establishment of protective measures.

FAQ 17. Which Species Should We Protect?

Larger-bodied parrotfishes are particularly susceptible to even modest levels of fishing pressure, as has been demonstrated in both the Caribbean (Debrot et al. 2008) and Pacific and Indian Oceans (Bellwood et al. 2012, Heenan et al. 2016). Consequently, all large-bodied Caribbean parrotfish species should have some form of management because it is particularly important to prevent a limited single-species fishery. The limited functional redundancy among Caribbean parrotfish species (Burkepile and Hay 2008, 2010, Adam et al. 2015b) and apparent weakness of interspecific interactions (Mumby and Wabnitz 2002) implies that there is limited capacity for the loss of one species to be compensated for by others. Therefore, if fishing reduces the abundance of one species it is unlikely that the biomass of other, unfished species would increase to compensate for the lost ecological function.

Despite the importance of large-bodied parrotfishes, most species are important for different reasons. Generally, species in the genus *Scarus* have higher size-specific bite rates than those of *Sparisoma*, making them functionally important in maintaining grazed algal turfs that are suitable for coral recruitment and growth (Bruggemann et al. 1994b, Mumby 2006a, Burkepile and Hay 2011). However, unlike species in the genus *Scarus*, sparisomatines have a broader diet, and are the only reef parrotfishes that routinely consume several macroalgal species once they become established (Mumby 2006a). Sparisomatines are therefore important for both preventing and constraining macroalgal blooms. Within each species, the rate of food consumption (bite size × bite rate) increases with body size, so larger-bodied fish have a disproportionately important impact on grazing (Bruggemann et al. 1994c, Mumby et al. 2006a, Hoey [Chapter 6](#)).

Lastly, although some of the largest parrotfish species, such as *Sc. coelestinus*, are protected in the US Caribbean, their densities are often so low that their functional relevance is questionable. That is not to say that protection is not important – indeed it might be vital to rebuild stocks – but it does not necessarily help restore the ecosystem process of grazing. Moreover, species like *Sc. coelestinus* appear to have low densities even

in areas that had relatively light levels of parrotfish exploitation, such as Belize pre-2000, which implies that the rebuilding of stocks might only achieve modest densities of these species at best. However, the exploitation of large-bodied species such as *Sc. guacamaia* and *Sc. coelestinus* across the Caribbean, and removal of critical mangrove nurseries, means that their natural population levels and functional roles are poorly understood.

Conclusions

Parrotfishes have rarely featured as a model species for generic study, in contrast to the use of damselfish for population biology studies (e.g. Doherty and Fowler 1994), connectivity work with anemone fish (e.g. Almany et al. 2007), or examination of hybridisation in hamlets (e.g. Whiteman et al. 2007). The paucity of studies derives at least partly from the difficulty of working with non-site attached fishes, but also their high sensitivity to being handled means that manipulative studies have been fraught with difficulty. Consequently, although parrotfishes clearly have a critical functional role on Caribbean reefs, there are significant gaps in our knowledge of their basic biology. For example, the majority of studies have focused on *Sp. viride*, and demographic parameters for many other species are severely lacking, even though they have been estimated using a model-fitting approach. The incomplete answers to the FAQs on parrotfish management highlight the urgent need for us to solve these methodological issues and undertake further research. For example, additional data are critical to allow the construction of realistic population models that will provide new insights into the impacts of different fishing strategies on the process of grazing. Furthermore, understanding the impacts of climate change on the abundance and behaviour of herbivores is critical for understanding the stability and functioning of Caribbean reefs (Harborne et al. 2017).

Despite the many gaps in our knowledge, sufficient data exist to allow the incorporation of grazing into spatially explicit models of benthic dynamics, and consequently predict reef resilience on different reefs or under different disturbance regimes (e.g. Mumby 2006a, Mumby et al. 2014). These models provide important support to Caribbean reef managers that is currently unavailable in the Pacific, although similar tools are being developed (Ortiz et al. 2014). However, applying model outputs in real world scenarios relies on stakeholders fully understanding their derivation, limitations, and caveats. Therefore, we encourage everyone concerned with future reef health to frequently ask questions. As the adage says “The only stupid question is the one that is not asked”.

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