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REVIEW ARTICLE

# Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages

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Coral reef ecosystems are remarkable for their high productivity in nutrient-poor waters. A high proportion of primary production is consumed by the dominant herbivore assemblage, teleost fishes, many of which are the product of recent and rapid diversification. Our review and synthesis of the trophodynamics of herbivorous reef fishes suggests that current models underestimate the level of resource partitioning, and thus trophic innovation, in this diverse assemblage. We examine several lines of evidence including feeding observations, trophic anatomy, and biochemical analyses of diet, tissue composition and digestive processes to show that the prevailing view (including explicit models) of parrotfishes as primary consumers of macroscopic algae is incompatible with available data. Instead, the data are consistent with the hypothesis that most parrotfishes are microphages that target cyanobacteria and other protein-rich autotrophic microorganisms that live on (epilithic) or within (endolithic) calcareous substrata, are epiphytic on algae or seagrasses, or endosymbiotic within sessile invertebrates. This novel view of parrotfish feeding biology provides a unified explanation for the apparently disparate range of feeding substrata used by parrotfishes, and integrates parrotfish nutrition with their ecological roles in reef bioerosion and sediment transport. Accelerated evolution in parrotfishes can now be explained as the result of (1) the ability to utilize a novel food resource for reef fishes, i.e. microscopic autotrophs; and (2) the partitioning of this resource by habitat and successional stage. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **00**, 000–000.

KEYWORDS: algae – cyanobacteria – diet – feeding – herbivorous fish – nutrition – pharyngeal anatomy – resource partitioning.

## INTRODUCTION

The flux of carbon from primary producers (autotrophs) to herbivores and detritus is a key process in the structuring of ecosystems (Cebrian, 1999; Lartigue & Cebrian, 2012). High rates of primary production support diverse and abundant herbivore assemblages on coral reefs (Choat & Clements, 1998), where autotroph assemblages are characterized by low biomass (Hatcher & Larkum, 1983; Hatcher, 1988; Goldberg, 2013). The paradox that these systems flourish in oligotrophic conditions, as first noted by Charles Darwin (Darwin, 1842), is partly explained by the highly efficient mechanisms for the uptake and recycling of nutrients in key components of the reef benthos, corals and sponges (de

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Goeij *et al.*, 2013; Rädecker *et al.*, 2015). However, the remarkable biodiversity of today's coral reefs is largely the result of extremely rapid diversification within the last 5 Myr (Bellwood, Goatley & Bellwood, 2016; Renema *et al.*, 2016). How was this requisite efficiency in nutrient transfer and retention maintained while primary production was increasingly partitioned among a rapidly radiating herbivore assemblage (Robertson *et al.*, 2006; Choat *et al.*, 2012; Sorenson *et al.*, 2013) dominated by parrotfishes (Box 1)?

Parrotfishes thus pose two categories of questions. The first involves ecological and nutritional interactions: what are the nature, identity and composition of the autotrophic resources targeted by parrotfishes, what are the mechanisms by which these resources are harvested, processed and assimilated, and how are these food resources partitioned from those of other members of the diverse assemblage of herbivorous fishes on coral reefs? The second category involves processes that are visualized at evolutionary time scales. Phylogenetic reconstruction suggests that rapid diversification into clade-specific foraging and feeding modes occurred during the late Cenozoic at a period when the nature of the benthic biota of coral reefs underwent a comprehensive reorganization (Renema *et al.*, 2016). This supports the argument that parrotfish feeding and abundance cycles are enhanced by substratum disturbance and the exposure of fresh carbonate surfaces over ecological time scales (Russ *et al.*, 2015). The present study focuses on ecological interactions within and among herbivore clades. However, the primary aim is to resolve the nutritional ecology of parrotfishes and thus provide a basis for identifying processes underlying the rapid diversification of this clade in the Pleistocene.

The study of autotroph/herbivore interactions involves two distinct approaches: plant-based and animal-based (Oesterheld & McNaughton, 2000). The former estimates the biomass of plants removed by herbivory, whereas the latter determines consumption by integrating herbivore density and nutritional requirements (Oesterheld & McNaughton, 2000). The plant-based approach is more straightforward but carries more assumptions and is less spatially transferable than the mechanistic animal-based approach (Oesterheld & McNaughton, 2000). Recent work on herbivory in terrestrial systems highlights both the necessity (Ford & Goheen, 2015; Tilman & Borer, 2015) and the benefits (Hempson, Archibald & Bond, 2015; Kartzinel *et al.*, 2015) of the latter mechanistic approach, which is also central to the more general requirement of integrating ecosystem engineering and trophodynamics (Sanders *et al.*, 2014). Developing a mechanistic understanding of the relationships between autotrophs and primary consumers is important for coral reef ecosystems for three reasons: the taxonomic and nutritional complexity of the autotroph community (Hatcher, 1988; Goldberg, 2013), the functional and phylogenetic disparity of the dominant herbivore fauna (Choat & Clements, 1998), and the view that herbivory strongly influences both the biotic composition of the reef benthos (Bellwood *et al.*, 2004; Hughes *et al.*, 2007; Adam *et al.*, 2015a) and the structure of the reef itself (Perry *et al.*, 2015; Morgan & Kench, 2016). We will discuss each of these elements in turn.

## THE AUTOTROPH ASSEMBLAGE OF CORAL REEFS

Much of the primary production on coral reefs is generated by small benthic filamentous algae and microbial autotrophs (Odum & Odum, 1955; Hatcher & Larkum, 1983; Hatcher, 1988; Goldberg, 2013). Epilithic algal turfs and their associated detrital complexes are diverse and heterogeneous assemblages (Connell, Foster & Airoldi, 2014; Harris, Lewis & Smith, 2015), but in addition the porous calcareous substratum of coral reefs is colonized by a diversity of microscopic autotrophic organisms that are collectively known as endoliths, among which euendolithic cyanobacteria and microalgae are known as microborers (Tribollet, Wisshak & Tapanila, 2008a; Verbruggen & Tribollet, 2011; Goldberg, 2013). These endolithic assemblages are also highly productive (Wanders, 1977; Tribollet *et al.*, 2006; Rix *et al.*, 2015). The small size and diversity of the epilithic and endolithic complexes on coral reefs makes it impossible to define the dietary targets of herbivores simply by the observation of feeding activities, leading to terminological problems. The 'Epilithic Algal Matrix' (EAM) is defined as a conglomeration of short, turf-forming filamentous algae (< 1 cm high), macroalgal spores, microalgae, sediment, detritus and associated fauna (Wilson *et al.*, 2003; Bonaldo, Hoey & Bellwood, 2014). The EAM and macroalgae are generally considered as separate, homogeneous categories that comprise the main food resources for herbivorous reef fishes (Bonaldo *et al.*, 2014; Adam *et al.*, 2015a; Graham *et al.*, 2015). This broad approach to dietary classification differs from comparable studies in terrestrial and freshwater systems, where the autotroph resource base is typically considered at a much finer grain (e.g. Genner, Turner & Hawkins, 1999; Sibbing & Nagelkerke, 2001; Shipley, Forbey & Moore, 2009; Kartzinel *et al.*, 2015).

## THE HERBIVOROUS FISH ASSEMBLAGE OF CORAL REEFS

Despite their location in oligotrophic oceans, coral reef ecosystems support diverse and productive

**Box 1.** Problems and inconsistencies between prevailing views of parrotfish nutritional biology and the current literature.

i. **Hindgut fermentation profiles and microbial processing:** The processing of plant diets by microbial gut symbionts in mammalian herbivores produces short-chain fatty acid (SCFA) profiles that predominantly reflect the fermentation of carbohydrates (Stevens & Hume, 1998). In contrast, profiles of SCFA across diverse herbivorous coral reef fishes indicate fermentation of resources that differ considerably in macronutrient composition (Clements & Choat, 1995; Choat & Clements, 1998; Crossman *et al.*, 2005) (Fig. 1). The branched-chain SCFA isobutyrate and isovalerate are produced through fermentation of the amino acids valine and leucine, respectively, and are thus good markers of protein fermentation, which tends to be reduced when carbohydrate substrates are present as in herbivorous diets (Davila *et al.*, 2013). The relatively high proportion of these branched-chain SCFA in parrotfishes and detritivorous surgeonfishes thus indicates fermentation of protein in the hindgut of these fishes, rather than the pattern of carbohydrate fermentation seen in algae-feeding fishes (Fig. 1). Furthermore, the hindgut microbial communities and gastrointestinal macronutrient profiles of parrotfishes resemble those in omnivorous and detritivorous surgeonfishes, rather than surgeonfish species that feed on turfing algae or macroalgae (Crossman *et al.*, 2005; Smriga, Sandin & Azam, 2010; Miyake, Kamanda Ngugi & Stingl, 2015). Combined with the low SCFA concentrations (Fig. 1) and the high proportion of transient bacteria in the hindgut of parrotfishes (Miyake *et al.*, 2015), this indicates a relatively minor role for hindgut fermentation and a diet rich in protein, both of which are inconsistent with feeding on turf algae or macroalgae.

ii. **Fatty acid profiles:** A multivariate analysis of fatty acid composition in 47 species groups of coral reef fish and invertebrates from the Northwestern Hawaiian Islands clearly separated parrotfishes from algae-feeding fishes including unicornfishes, surgeonfishes and kyphosid chubs (Piché *et al.*, 2010). This result appears to be driven by differences in diet rather than phylogenetic relationship (Piché *et al.*, 2010).

iii. **Parallels with trophodynamics in rift lake systems:** The cichlid fishes that inhabit the rocky shores of African rift lakes have diversified as primary consumers resulting in a diversity that rivals that of coral reefs (Fryer & Iles, 1972). These fishes display high levels of resource partitioning in their use of aufwuchs, the epilithic resource that includes cyanobacteria, diatoms and chlorophytes (Reinthal, 1990; Genner *et al.*, 1999; Albertson, 2008), and is thus the freshwater analog of EAM on coral reefs (Bellwood *et al.*, 2014). Nutrient recycling by grazing cichlids in these freshwater communities is thought to favour the growth of diazotrophic autotrophs, i.e. cyanobacteria, which are major components of primary productivity in these systems (Higgins, Hecky & Taylor, 2001; André, Hecky & Duthie, 2003). Primary productivity, nutrient availability, and rates of both nitrogen fixation and grazing are similar between these rift lake systems and coral reefs (Higgins *et al.*, 2001), raising the possibility that herbivorous coral reef fishes partition a similar range of dietary resources including cyanobacteria.

iv. **Niche space:** Ecological theory going back to Hutchinson's classic treatise (Hutchinson, 1959) predicts that resources will be partitioned among consumers. The efficiency with which different animals utilize different dietary resources determines feeding success and growth, and this efficiency is driven by differences in trophic mechanisms (Sibbing, 1991). It is thus highly unlikely in theoretical terms that a large proportion of the diverse herbivore assemblage on coral reefs are generalists feeding broadly on EAM. We reiterate that parrotfishes diversified within systems that already contained diverse EAM- and macroalgal-feeding fish taxa (Robertson *et al.*, 2006; Choat *et al.*, 2012; Sorenson *et al.*, 2013).

v. **Relationships between nutritional composition of plants and the digestive system of herbivores:** Terrestrial and aquatic communities both display clear relationships between the nutritional composition of plants and the extent to which production is removed by herbivores (Cebrian, 1999). Phaeophyte macroalgae are generally considered poor quality diets for herbivorous fishes, as they are comparatively low in protein and store carbohydrate in forms that are resistant to digestion (Montgomery & Gerking, 1980; Kumar, Sahoo & Levine, 2015). As a result, phaeophytes are typically eaten by fishes in which algal carbohydrates are fermented to metabolically-useful SCFA by hindgut microbes (Choat & Clements, 1998; Clements *et al.*, 2009; White *et al.*, 2010). It is therefore puzzling that phaeophytes are seen as major dietary components for browsing parrotfishes (e.g. Bonaldo *et al.*, 2014; Adam *et al.*, 2015b; Bozec *et al.*, 2016), which are not hindgut fermenters (Crossman *et al.*, 2005; Fig. 1). Furthermore, recent studies show that cover of macroalgae does not correlate with the abundance of parrotfishes in either the Caribbean (Loh *et al.*, 2015; Suchley *et al.*, 2016) or the Indo-Pacific (Russ *et al.*, 2015).

vi. **Linking bioerosion and nutrition:** Bellwood & Choat (1990) split Indo-Pacific scarinine species into two functional groups based on jaw morphology and feeding behaviour: scrapers that fed predominantly on epilithic materials, and excavators (or biters) that remove significant quantities of coral or calcareous substratum when feeding. The latter group in particular are recognized as key agents of bioerosion and sediment redistribution on reefs (Bellwood, 1995a,b; Tribollet & Golubic, 2005; Bonaldo *et al.*, 2014; Perry *et al.*, 2015; Morgan & Kench, 2016). An excavating feeding mode makes little sense if the dietary targets are epilithic, i.e. turf algae, detritus or EAM as a whole. Indeed, the relationship between the nutrition of excavating parrotfishes and rates of bioerosion has been almost completely ignored, despite the importance of integrating ecosystem engineering and food webs as mentioned elsewhere (Sanders *et al.*, 2014).

vii. **Detritovore feeding mechanisms:** Some previous studies, including our own, categorised Indo-Pacific *Scarus* and *Chlorurus* species as detritivores that target organic detritus and microalgae (e.g. Choat *et al.*, 2002; Wilson *et al.*, 2003; Crossman *et al.*, 2005; Carassou *et al.*, 2008; Price *et al.*, 2010; Bellwood *et al.*, 2016), or more generally as feeding on the EAM (Brandl & Bellwood, 2016). However, feeding on detrital components generally involves a component of suction feeding (Sibbing, 1991), a motor pattern distinct from that in parrotfish feeding (Alfaro & Westneat, 1999).

**Box 1.** Continued.

viii. **Demographic profiles:** Not only are parrotfishes abundant in shallow water habitats subject to high temperatures, they have a capacity for rapid somatic growth rates over the full life span and to undergo opportunistic episodes of accelerated growth (Choat & Robertson, 2002; Taylor & Choat, 2014). Populations of parrotfishes are dominated by small individuals with elevated rates of recruitment and mortality (Choat & Robertson, 2002). Furthermore, most parrotfishes form large residential spawning aggregations with high reproductive outputs, and thus require the capacity to store lipid required to fuel production of mature oocytes (Choat, 2012). In contrast, surgeonfishes with diets dominated by turfing and macroscopic algae (Jones, 1968; Choat *et al.*, 2002) have demographic profiles characterized by asymptotic growth patterns, extended life spans and reduced annual levels of somatic growth and reproduction (Choat & Robertson, 2002; Taylor & Choat, 2014). This comparison suggests a demographically dynamic herbivore assemblage which due to high temperatures and small size incurs considerable size-specific metabolic costs, placing substantial qualitative and quantitative demands on reef resources (Depczynski *et al.*, 2007). Is a carbohydrate-based algal diet sufficient to provide all members of this herbivore assemblage with the protein and lipid necessary to sustain the high rates of somatic growth and reproductive output characteristic of parrotfishes?

populations of herbivorous fishes that maintain high abundances and species richness at local spatial scales (Choat & Clements, 1998; Graham *et al.*, 2015). These assemblages are dominated by three clades containing species that intensively graze the calcareous surfaces of coral reefs: parrotfishes (scarine labrids), surgeonfishes (Acanthuridae), and in the Indo-Pacific, rabbitfishes (Siganidae) (Horn, 1989; Choat & Clements, 1998). These three clades have different evolutionary histories. Parrotfish diversification is recent (late Pliocene to mid Pleistocene) (Choat *et al.*, 2012), while both surgeonfishes and rabbitfishes began major episodes of diversification in the Eocene (Sorenson *et al.*, 2013; Bellwood *et al.*, 2014). Despite the phylogenetic diversity of this grazing assemblage, component species are generally placed into simple feeding categories such as excavators, scrapers and browsers, etc, with their food resources identified only in general terms, such as macroalgae or EAM (e.g. Bonaldo *et al.*, 2014; Adam *et al.*, 2015a; Graham *et al.*, 2015).

### THE ROLE OF HERBIVOROUS FISHES IN CORAL REEF ECOLOGY

Coral reef ecologists have typically employed a plant-based approach to herbivory, and algal removal by herbivores is considered to have a major influence on the ecological functioning and health of reef ecosystems (Mumby, 2006; Hughes *et al.*, 2007; Jackson *et al.*, 2014; Graham *et al.*, 2015; Bozec *et al.*, 2016). It has long been known that the impacts of multiple stressors on coral reefs are complex and interactive (Hughes & Connell, 1999), generating outcomes that are dependent on biotic composition and environmental context (Hughes *et al.*, 2010; Loh *et al.*, 2015). Indeed, an intriguing new hypothesis suggests that differences between the Indo-Pacific and Caribbean in the responses of reefs to overfishing and eutrophication may be related to differences between the two systems in sponge communities and nutrient regimes (Pawlik, Burkepile & Thurber, 2016). This new hypothesis retains the view that parrotfishes protect reefs from algal overgrowth, but adds that in the Caribbean these fishes also contribute to reef health through the consumption of sponges whose pattern of nutrient cycling can contribute to algal overgrowth (Pawlik *et al.*, 2016).

## RECONSIDERING DIETARY RESOURCES FOR HERBIVOROUS REEF FISHES

Our overview of autotroph and herbivore assemblages on reefs, and the perceptions of the interactions between them, prompts a fundamental question of central importance to coral reef trophodynamics, and consequently also to the evolution and management of these systems. Are algal resources sufficient to support the high densities of herbivorous fishes considered necessary to maintain coral reef ecosystems? The available literature provides several grounds for us to question current perceptions of resource partitioning in herbivorous reef fishes in general, and in parrotfishes in particular (Box 1, Fig. 1). An overall assessment of these inconsistencies with the prevailing dietary hypotheses for parrotfishes suggests a novel hypothesis, that the nutritional focus of parrotfishes is likely to be microbial elements of the reef autotroph assemblage. Microscopic epilithic and endolithic autotrophs, rather than epilithic turf, macroalgae or detritus, may represent the primary dietary components for most parrotfishes. Benthic microbial and filamentous autotrophs such as cyanobacteria tend to be fast growing, lack complex support structures and have a higher proportion of protein than macroscopic algae (Nagarkar *et al.*, 2004; McDermid, Stuercke & Balazas, 2007; Angell *et al.*, 2015; Clements & Choat, in press).

Our primary hypothesis is thus that parrotfishes, lacking the capacity to extract sufficient levels of nutrients from macroscopic algae, selectively feed on microscopic benthic autotrophs, especially cyanobacteria. This challenges the prevailing views that most parrotfishes feed primarily on either carbohydrate-rich turfing and macroscopic algae (e.g. Mumby, 2006; Jackson *et al.*, 2014; Graham *et al.*, 2015; Bozec *et al.*, 2016), detrital components of EAM (e.g. Bonaldo *et al.*, 2014; Bellwood *et al.*, 2016), or a combination of the two (e.g. Brandl & Bellwood, 2016). In the next section we evaluate our hypothesis in the context of four lines of evidence: (1) feeding behaviour and gut content analysis; (2) trophic anatomy; (3) fatty acid composition; and (4) stable isotope analysis. Our main questions are:

1. What available data on feeding behaviour and diet unequivocally test hypotheses of food resource use by parrotfishes?
2. How do structural and functional features of the feeding apparatus and biochemical trophic markers characterize parrotfishes compared to other taxa of herbivorous and detritivorous teleosts on reefs? and
3. What does the integrated complex of structural, functional and behavioural characters indicate about the utilization of food resources by parrotfishes?

Much of the information below is assembled from the literature, but has been overlooked or in some cases misinterpreted in the absence of an animal-based approach to reef herbivory. We emphasise that developing a coherent hypothesis for resource use in parrotfishes necessarily involves joining up the dots between disparate sources of information, many of which have not previously been considered in the context of reef herbivory. Our intent is to provide a synthetic overview of food resource use by parrotfishes compared to other herbivorous and detritivorous reef fish taxa, rather than a comprehensive taxonomic treatment of the group itself.

## FOUR LINES OF EVIDENCE DEFINING THE NUTRITIONAL RELATIONSHIPS OF HERBIVOROUS REEF FISHES

### FEEDING BEHAVIOUR AND GUT CONTENT ANALYSIS

Stomach content analysis is generally adequate to identify the trophic resources of browsing herbivorous fishes, but for many herbivorous taxa on coral reefs the small size of food items, the use of mechanical trituration and the ingestion of inorganic sediment make these methods inadequate (Choat & Clements, 1998). Parrotfishes are particularly problematic in this respect, as they lack a gastric stomach and ingested material is finely ground in the pharyngeal mill (Choat, Clements & Robbins, 2002; Plass-Johnson, McQuaid & Hill, 2013). The majority of gut content analyses conducted on parrotfishes reveal very high proportions of inorganic sediment and microscopic organic material that is referred to variously as unidentifiable matter or detritus (e.g. Choat *et al.*, 2002; Ferreira & Gonçalves, 2006; Dromard *et al.*, 2015). Macronutrient analysis of Indo-Pacific parrotfish gut contents confirms that this material contains high levels of protein, especially in comparison to stomach contents from algivorous reef fishes including surgeonfishes, rabbitfishes and kyphosid chubs (Crossman, Choat & Clements, 2005).

Only a handful of feeding behaviour studies on parrotfishes consider endolithic algae as diet sources (e.g. Bruggemann, Kuyper & Breeman, 1994b; Bruggemann, van Oppen & Breeman, 1994c; Bruggemann *et al.*, 1994a; Bonaldo & Bellwood, 2009; Afeworki, Bruggemann & Videler, 2011), and few differentiate between different elements of the EAM. Afeworki *et al.* (2011) and Bruggemann *et al.* (1994a, b, c) suggest that feeding activity is concentrated on sparse algal turf (Fig. 2A–C) rather than dense algal turf, and assimilation studies highlight the nutritional importance of endolithic autotrophs (Bruggemann *et al.*, 1994a). Parrotfishes have been observed feeding on dead coral surfaces largely devoid of turf (Fig. 2A–C) and directly on epilithic blooms of cyanobacteria (Fig. 2D), demonstrating that epilithic cyanobacteria and euendolithic communities comprising a mix of cyanobacteria and microscopic algae (reviewed by Tribollet, 2008b) were dietary targets rather than epilithic turf algae. Direct evidence of parrotfish feeding on euendoliths is also provided by experimental work on succession in these communities (Tribollet & Golubic, 2005; Grange, Rybarczyk & Tribollet, 2015; Fig. 2E).

Although feeding on live corals and sponges is frequently observed in some parrotfish species (Dunlap & Pawlik, 1998; Goldberg, 2013; Bonaldo *et al.*, 2014), to the extent that they may influence assemblage composition (Loh *et al.*, 2015), it is unclear what is being targeted (Wulff, 1997; Rotjan & Lewis, 2005; Rotjan & Dimond, 2010). Interestingly, although live corals frequently contain dense populations of euendolithic autotrophs including cyanobacteria and the siphonous chlorophyte *Ostreobium* (Lesser *et al.*, 2004; Tribollet, 2008b; Gutiérrez-Isaza *et al.*, 2015), and cyanobacteria can comprise 25–50% of a sponge's cellular volume (Erwin & Thacker, 2008), the hypothesis that these may be the dietary target for parrotfishes feeding on corals and sponges has never been tested. Indeed, potential feeding targets for both excavating and large scraping parrotfishes may involve both microscopic autotrophic euendoliths and boring sponges containing cyanobacteria (Wulff, 1997; Fig. 2F).

While Indo-Pacific scarinine parrotfishes tend to graze over calcareous reef surfaces (Bellwood & Choat, 1990), macroalgae and seagrasses appear to be important as feeding substrata for the Indo-Pacific sparisomatine taxa *Leptoscarus* and *Calotomus* (Nakamura *et al.*, 2003; Gullström *et al.*, 2011; Lim *et al.*, 2015; Lee *et al.*, 2016) and for many parrotfishes in the Atlantic (Bonaldo *et al.*, 2014; Adam *et al.*, 2015a,b; Loffler, Bellwood & Hoey, 2015). However, subtropical and tropical macroscopic autotrophs can carry high loads of epiphytes (Lefèvre & Bellwood, 2010; Fig. 2G and H), including cyanobacteria (Capone & Taylor, 1977; Capone, Taylor & Taylor, 1977; Penhale & Capone, 1981; Barott *et al.*, 2011; Del Río *et al.*, 2016), and thus epiphytes provide potential protein-rich dietary targets for browsing parrotfishes. Studies that delineate

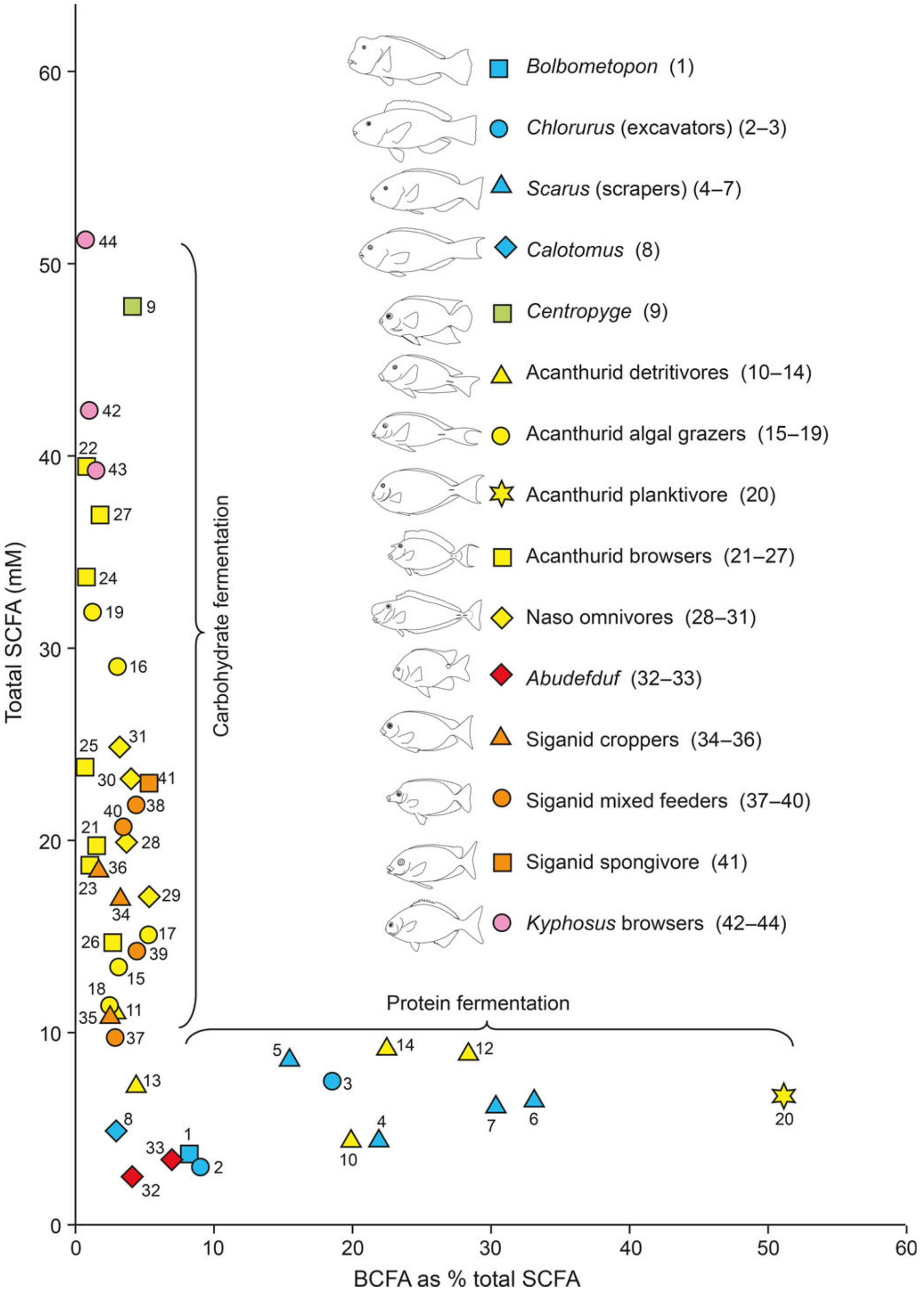


**Figure 1.** Mean total short-chain fatty acid (SCFA) in distal hindgut vs. mean branched-chain fatty acids (isobutyrate and isovalerate) as a percentage of total SCFA in herbivorous reef fishes and related omnivorous and planktivorous taxa. Feeding categories follow Choat *et al.* (2002), Hoey *et al.* (2013) and Bonaldo *et al.* (2014). Data from Clements & Choat (1995) and Clements unpublished. All samples collected from the vicinity of Lizard Island, Great Barrier Reef, Australia, unless indicated otherwise. Taxon symbol key: Scarinae (parrotfishes) – blue; Pomacanthidae (angelfishes) – green; Acanthuridae (surgeonfishes) – yellow; Pomacentridae (damselfishes) – red; Siganidae (rabbitfishes) – orange; Kyphosidae (chubs) – pink. Species key (N): Scarinae (parrotfishes) - 1 *Bolbometopon muricatum* (4)*;* 2 *Chlorurus microrhinos* (4); 3 *Ch. spilurus* (4); 4 *Scarus flavipectoralis* (3); 5 *Sc. niger* (4); 6 *Sc. rivulatus* (3); 7 *Sc. schlegeli* (4); 8 *Calotomus carolinus* (2); Pomacanthidae (angelfishes) - 9 *Centropyge bicolor* (4); Acanthuridae (surgeonfishes) – 10 *Acanthurus blochii* (3); 11 *Ac. dussumieri* (5); 12 *Ac. nigricauda* (5); 13 *Ac. olivaceus* (9); 14 *Ctenochaetus striatus* (9); 15 *Ac. lineatus* (9); 16 *Ac. nigricans* (13); 17 *Ac. nigrofuscus* (11); 18 *Ac. triostegus* (6); 19 *Zebrasoma scopas* (8); 20 *Ac. mata* (10); 21 *Naso brachycentron* (5); 22 *N. lituratus* (12); 23 *N. tonganus* (14); 24 *Naso unicornis* Lizard Island (11); 25 *N. unicornis* Middleton Reef (3); 26 *Prionurus maculatus* Middleton Reef (9); 27 *Zebrasoma velifer* (3); 28 *N. annulatus* (6); 29 *N. brevirostris* (15); 30 *N. hexacanthus* (10); 31 *N. vlamingii* (13); Pomacentridae (damselfishes) - 32 *Abudefduf septemfasciatus* (4); 33 *Ab. sordidus* (4); Siganidae (rabbitfishes) - 34 *Siganus argenteus* (9); 35 *Si. corallinus* (4); 36 *Si. doliatus* (11); 37 *Si. lineatus* (8); 38 *Si. punctatissimus* (3); 39 *Si. punctatus* (8); 40 *Si. vulpinus* (5); 41 *Si. puellus* (4); Kyphosidae (chubs) - 42 *Kyphosus cinerascens* (8); 43 *K. sectatrix* Middleton Reef (6); 44 *K. vaigiensis* (9).

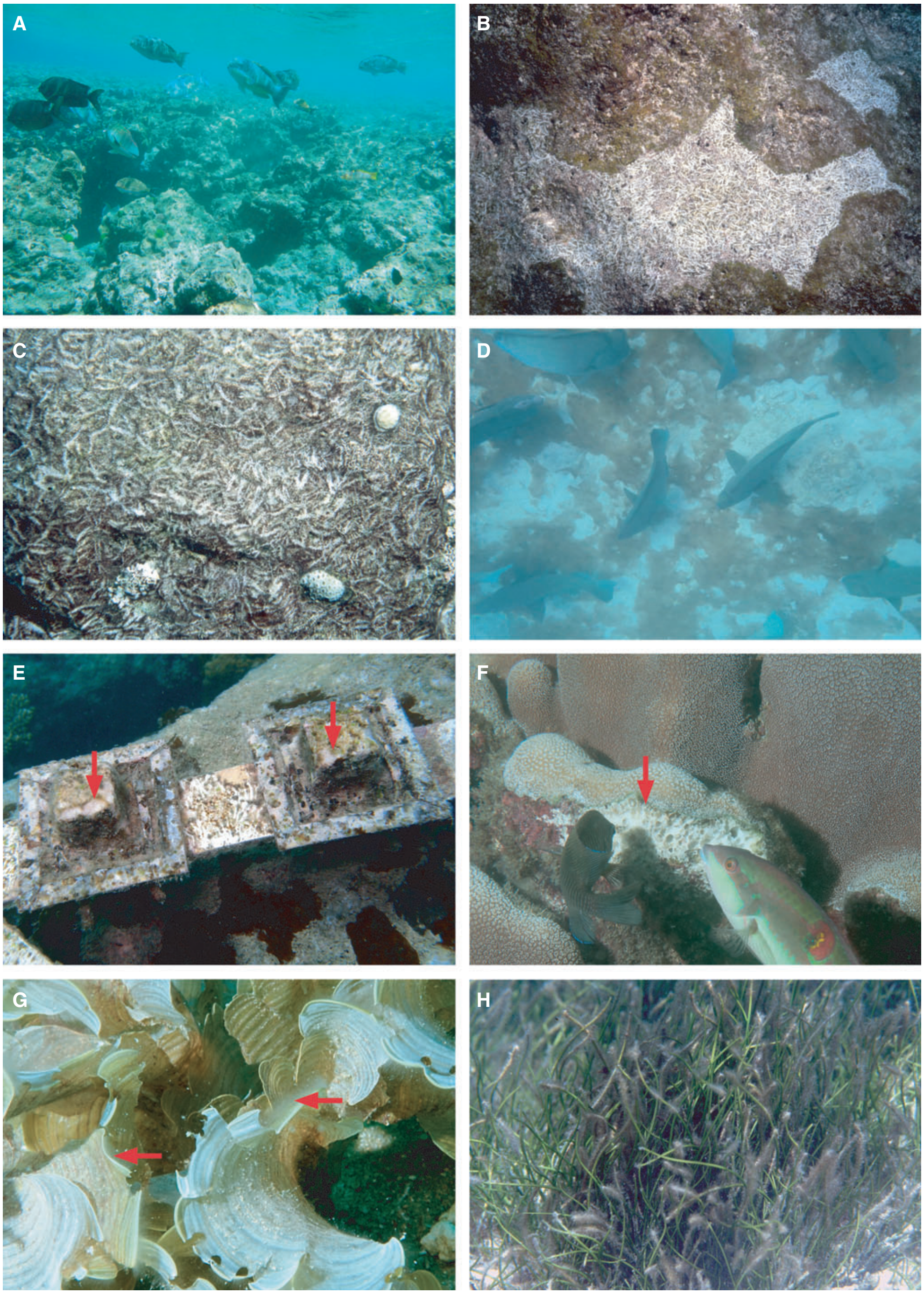
between seagrass and epiphytes typically show that parrotfishes prefer the latter (e.g. Lobel & Ogden, 1981; Van Montfrans, Wetzel & Orth, 1984; Montague *et al.*, 1995; Nagelkerken *et al.*, 2006; Del Río *et al.*, 2016), and epiphytes were the dietary target for a *Scarus* species feeding on *Sargassum* (Lefèvre & Bellwood, 2010). A mechanistic understanding of feeding on macroalgae and seagrasses by parrotfishes requires (a) clearly partitioning different potential food sources (including epiphytes) as dietary targets, and (b) demonstrating that ingested foods provide adequate sources of nutrition. The latter requires experiments that measure nutrient uptake, monitor fish condition over extended periods, or both.

## TROPHIC ANATOMY

Specialized pharyngeal anatomy, and closely-spaced gill rakers in particular, are critical in the retention of microbial dietary elements in suspension-feeding fishes, i.e. species that target detritus or microphytobenthos in sediments (Northcott & Beveridge, 1988; Sibbing, 1991; Guinea & Fernandez, 1992; Sanderson *et al.*, 1996). In such fishes the gill rakers act in concert with specialized mucus glands and sometimes structures on the roof of the pharynx such as the palatal organ to retain microscopic algae and detritus and transport it to the oesophagus or pharyngeal jaws (Northcott & Beveridge, 1988; Sibbing, 1991; Guinea & Fernandez, 1992; Sanderson *et al.*, 1996; Smoot & Findlay, 2010).

Trophic anatomy in parrotfishes is very well characterized in terms of the osteology of the oral and pharyngeal jaws (Bellwood & Choat, 1990; Bellwood, 1994; Wainwright *et al.*, 2004; Carr *et al.*, 2006), and both scraping and excavating feeding modes in parrotfishes generate fine particular organic and inorganic material (Bellwood & Choat, 1990; Bonaldo *et al.*, 2014). In comparison, pharyngeal soft anatomy is known only from a handful of parrotfish species. Gill rakers are very closely-spaced in the scraping and excavating scarinine parrotfish genera *Scarus* and *Chlorurus* (Bellwood, 1994) (Supporting Information, Table S1), with interdigitation of anterior (outer) and posterior (inner) rakers forming a fine sieve (Al-Hussaini, 1945; Board, 1956) (Figs 3 & 4). Counts of rakers on the first gill arch of parrotfishes are comparable to those in detritivorous surgeonfishes, mullet and microalgal-feeding damselfishes, and higher than counts in algal-feeding surgeonfish, unicornfish, rabbitfish and chubs (Randall, 1956; Ciardelli, 1967; Westneat, 2002; Knudsen & Clements, 2013) (Supporting Information, Table 1). The numbers of gill rakers are lower overall in sparisomatine than scarinine parrotfishes, although within the sparisomatines the excavating species have higher counts than the browsing species that ingest less inorganic sediment (Bellwood, 1994; Westneat, 2002) (Supporting Information, Table S1).

Parrotfishes display a characteristic structure on the roof of the pharynx called the pharyngeal valve, which is covered in papillae and contains dense mucus-secreting goblet cells (Al-Hussaini, 1945; Board, 1956; Gohar & Latif, 1959; Fig. 4A–D). The mucus is thought to entrap fine organic material, which the pharyngeal valve then transports back into the pharyngeal jaw along with particles that collect on the gill rakers of the posterior gill arches (Board, 1956). Such a function appears highly likely given the structure of the papillae on the pharyngeal valve and the close juxtaposition of the valve to the floor of the pharynx in both sparisomatine and scarinine parrotfishes (Fig. 4A and B). The overall arrangement resembles that of suspension-feeding fishes that target microalgae and detritus (Northcott



& Beveridge, 1988; Guinea & Fernandez, 1992; Sanderson *et al.*, 1996; Smoot & Findlay, 2010), rather than species that target macrophytes (Horn, 1989; Sibbing, 1991; Sibbing & Nagelkerke, 2001). Scarinine parrotfishes and the sparisomatine genus *Sparisoma*, which collectively represent the bulk of parrotfish diversity, have a sacculated intestine which is thought to separate and retain fine digesta within the intestinal pouches while removing particulate inorganic sediment for excretion (Al-Hussaini, 1945; Board, 1956; Gohar & Latif, 1959; Bellwood, 1994).

### FATTY ACID COMPOSITION

Fatty acid composition differentiated functional groups of Hawaiian coral reef fishes, suggesting differences in diet (Piché *et al.*, 2010). Our species-level

**Figure 2.** Feeding substrata and feeding scars of parrotfishes. A, *Chlorurus microrhinos* in typical habitat on the reef crest at Day Reef, Great Barrier Reef, Australia. Two of the territorial surgeonfish *Acanthurus lineatus* can be seen in the background, with two of the herbivorous rabbitfish *Siganus punctatus* and the parrotfish *Cetoscarus bicolor* at left. (KDC photograph). B, Feeding scars left by intensive parrotfish grazing on dead coral substratum at Nanumea, Tuvalu. The substratum is colonized by endoliths and very short epilithic turfs including cyanobacteria. Note absence of macroalgae and very low biomass of macroscopic algae. (KDC photo). C, Feeding scars left by intensive parrotfish grazing on endoliths and very short epilithic turf (including cyanobacteria) at Maitai Wreck, Rarotonga. (KDC photo). D, The parrotfish *Bolbometopon muricatum* grazing on a cyanobacterial bloom at Lizard Island, Great Barrier Reef, Australia. The substratum of sand and coral rubble was colonized by cyanobacteria following a severe cyclone. (Danni Ceccarelli photo). E. Experimental dead coral blocks exposed for 2–3 months at New Caledonia. The blocks were colonized by the euendolithic chlorophytes *Phaeophila* and *Eugomontia* and the cyanobacteria *Mastigocoleus testarum* and *Plectonema terebrans*. Arrows show feeding scars left by excavating parrotfishes. (AT photograph). F. Feeding scar left on edge of massive coral by large individual of *Scarus perrico*, Perlas Archipelago, Panama. Scar reveals boreholes characteristic of boring (endolithic) bivalves, and green edge between scar and living tissue (arrow) represents microscopic, phototrophic euendoliths (mostly the siphonaceous chlorophyte *Ostreobium*) colonizing the coral skeleton. (KDC photo). G. Detail of the brown macroalga *Padina gymnospora* showing dense coverage of cyanobacterial epiphytes (arrows) at Recife, Brazil. *Sparisoma axillare* were observed grazing this material. (KDC photo). H, Dense cyanobacterial epiphytes on the seagrass *Syringodium isoetifolium* at Tokoriki Island, Fiji. Seagrass-feeding parrotfish appear to target nutritionally-rich epiphytes rather than the more fibrous leaves themselves.

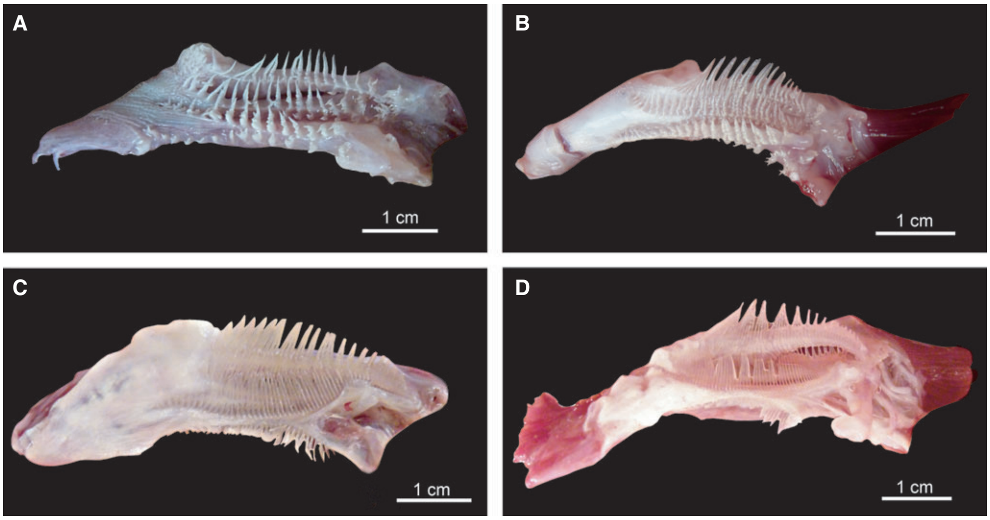


**Figure 3.** Gill arches showing gill rakers from representative parrotfish species. Species: A *Sparisoma frondosum*, a browser; B *Sp. amplum*, an excavating sparisomatine; C *Scarus ghobban*, a scraping scarinine; D *Chlorurus microrhinos*, an excavating scarinine. Scale = 1 cm.

reanalysis of these data (see Supporting Information) split the 15 nominally herbivorous species examined into three clusters: parrotfishes, macroalgal-feeding unicornfishes and chubs, and surgeonfishes (Fig. 5). The eight species of surgeonfishes examined all feed on elements of the EAM (Jones, 1968), but our analysis delineated these species in multivariate space along an axis from species targeting predominantly filamentous algae (e.g. *Acanthurus achilles*, *Zebrasoma flavescens*) through to species targeting microalgae and detritus (e.g. *A. olivaceus*, *Ctenochaetus strigosus*), with species feeding on mixtures of diatoms and filamentous algae in the middle (e.g. *A. nigroris*, *A. leucopareius*) (Fig. 5). Given that fatty acid composition reflects diet (Piché *et al.*, 2010; Kelly & Scheibling, 2012; Cnudde *et al.*, 2015), this result suggests that the scraping and excavating parrotfish species examined fed on resources distinct from both EAM (i.e. including detritus) and macroalgae. Parrotfishes were clearly distinct from all other herbivores examined in having high levels of the monounsaturated vaccenic acid, 18:1n-7 (Piché *et al.*, 2010 Supporting Information), a dietary tracer for bacteria in marine benthic food webs (Kelly & Scheibling, 2012; Cnudde *et al.*, 2015) that is also considered a biomarker for cyanobacteria (Yang

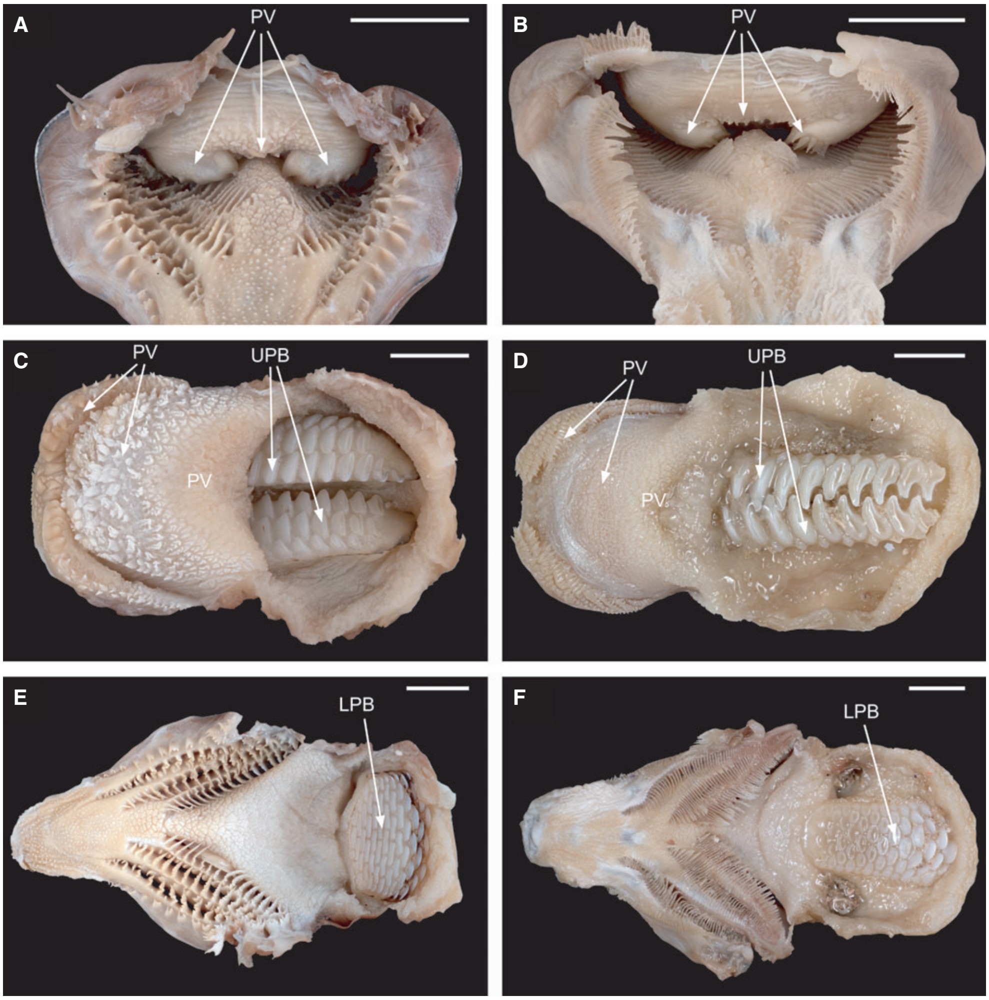


**Figure 4.** Pharyngeal anatomy of *Sparisoma frondosum* (left) and *Scarus zelindae* (right). A and B, Anterodorsal view of intact pharynx showing relationship of the pharyngeal valve on the roof of the pharynx to the gill rakers on the floor of the pharynx; C and D, Ventral view of roof of pharynx roof showing pharyngeal valve on left (anterior) and upper pharyngeal bones on right (posterior); E and F, Dorsal view of floor of pharynx showing arrangement of gill rakers and lower pharyngeal bone. Images taken with a Canon 5D MkII and either a Canon 50 mm f2.5 macro or a Canon 65 mm f2.8 macro lens on a Visionary Digital Passport II imaging system. Canon Remote Capture and Adobe Lightroom v4 was used to control the camera and acquire images, and Helicon Focus Professional software was used to stack and integrate the final images. Scale = 5 mm. Abbreviations: PV pharyngeal valve; LPB lower pharyngeal bone(s); UPB upper pharyngeal bone(s).

*et al.*, 2016). The parrotfishes were distinct from detritivorous surgeonfishes such as *Acanthurus olivaceus* and *Ctenochaetus strigosus* in having lower levels of palmitoleic acid, 16:1n-7, a biomarker for diatoms (Kelly & Scheibling, 2012; Cnudde *et al.*, 2015).

### Stable isotope analysis

Bulk stable isotope analysis (SIA) and compound-specific stable isotope analysis (CSIA) are now standard tools in trophic studies (Shahraki *et al.*, 2014; McMahon *et al.*, 2016). Although these approaches potentially provide valuable insight into the use of microalgae, detritus and algae by herbivorous fishes, they were not considered in recent reviews of parrotfish ecology (Bonaldo *et al.*, 2014; Adam *et al.*, 2015a).

Several isotopic studies are now available that compare parrotfishes from both the Indo-Pacific (Carassou *et al.*, 2008; Page *et al.*, 2013) and Caribbean (Cocheret de la Morinière *et al.*, 2003; Nagelkerken *et al.*, 2006; Lamb, Swart & Altabet, 2012; O'Farrell *et al.*, 2014; Dromard *et al.*, 2015) to other

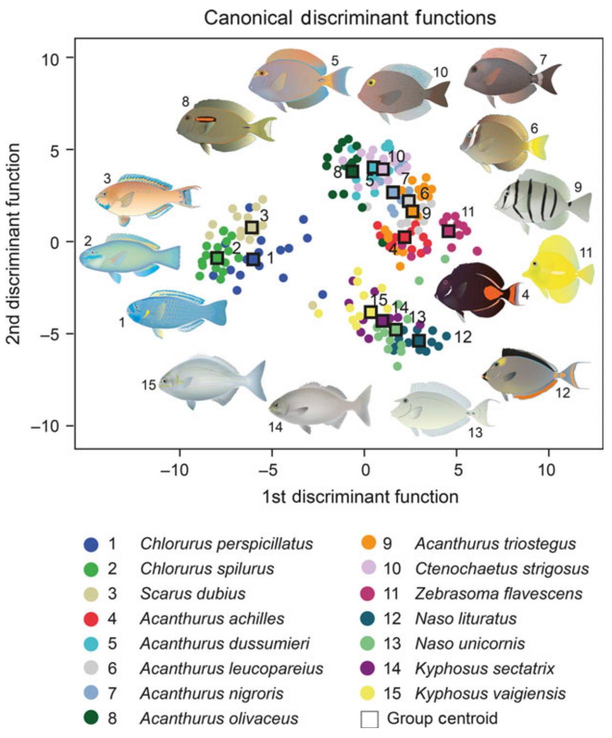


**Figure 5.** Discriminant scores and group centroids for the discriminant function analysis conducted using fatty acid composition data from 15 species of herbivorous reef fishes from the Northwestern Hawaiian Islands. Three clusters are apparent: parrotfishes (1–3), EAM-feeding surgeonfishes (4–11) and browsing unicornfishes and chubs (12–15). The EAM-feeding surgeonfishes include detritus and microalgal-feeding species at the top left of the cluster, turf algal grazers ate lower right of the cluster, and mixed EAM-feeders in between. The fatty acids which accounted for most of the variation (89.6% of total variance) among the 15 herbivorous reef fishes examined were 20:5n-3, 20:1n-9, 18:1n-7 and 16:1n-7. Data reanalyzed from Piché *et al.* (2010).

herbivorous fishes from coral reefs and seagrass communities, although only some of these attempt to resolve diets. A consistent feature of these analyses across both ocean basins is the depleted $\delta^{15}$N signature of most parrotfish species relative to other herbivorous fishes, including macroalgal-feeding chubs and EAM-feeding surgeonfishes (Fig. 6A–C). Depleted $\delta^{15}$N is associated with nitrogen fixation, thus separating (diazotrophic) cyanobacteria from both detrital heterotrophic bacteria (Steffan *et al.*, 2015) and other autotrophs including algae, seagrasses and diatoms (Yamamuro, 1999; Currin *et al.*, 2011; Shahraki *et al.*, 2014). Animal material is enriched in $\delta^{15}$N compared to autotrophs (Yamamuro, 1999; Currin *et al.*, 2011; Plass-Johnson *et al.*, 2013; Dromard *et al.*, 2015), and a depleted $\delta^{15}$N signal is a biomarker of cyanobacteria consumption (Yamamuro, 1999; Currin *et al.*, 2011; Shahraki *et al.*, 2014).

Parrotfishes generally have enriched $\delta^{13}$C signatures relative to other herbivorous fishes, although this trend is less consistent. Enriched $\delta^{13}$C is also a characteristic of cyanobacteria among aquatic autotrophs (Shahraki *et al.*, 2014). SIA was also used to examine dietary diversification in 14 species of Indian Ocean parrotfishes, and identified distinct isotopic clusters for scraping and excavating species, with the former depleted in $\delta^{15}$N compared to the latter (Plass-Johnson *et al.*, 2013) (Fig. 6D). It is important to note that SIA and CSIA mixing models can only retrieve diet sources correctly when these are statistically distinct and all included in the model (Fry, 2013). Failure to do this typically results in an unresolved outcome where all dietary sources contribute to the assumed solution (Fry, 2013).

## SYNTHESIS: BENTHIC CYANOBACTERIA AND MICROALGAE AS FOOD FOR MICROPHAGOUS PARROTFISHES

Integrating the information presented above provides a strong case for the identification of parrotfishes as microphages with a nutritional focus on microscopic, protein-rich autotrophs. Buccal and pharyngeal anatomy indicates that parrotfishes have a unique feeding mechanism with the capacity to retain and triturate microscopic food items (Fig. 7), and thus resemble fishes including certain surgeonfishes and mullet that target diatoms and the microbial/detrital complex, not macroalgae or algal turf. Fatty acid composition and stable isotope data indicate that parrotfish diets are distinct from those of algae- and detritus-feeding fishes such as surgeonfishes and chubs. The high levels of protein and 18:1n-7 fatty acids, relatively low levels of carbohydrate, and the depleted $\delta^{15}$N and enriched $\delta^{13}$C isotopic signals associated with parrotfishes are all characteristic of cyanobacteria rather than organic detritus or non-diazotrophic microalgae such as diatoms (Yamamuro, 1999; Nagarkar *et al.*, 2004; Kelly & Scheibling, 2012; Yang *et al.*, 2016; Clements & Choat, in press).

Cyanobacteria are associated with all of the reported dietary targets of parrotfishes, being important constituents of both EAM (Cruz-Rivera & Paul, 2006; Den Haan *et al.*, 2014; Harris *et al.*, 2015) and euendolithic communities (Tribollet, 2008b; Goldberg, 2013; Grange *et al.*, 2015), dominant epiphytes of both macroalgae (Capone *et al.*, 1977; Penhale & Capone, 1981; Barott *et al.*, 2011) and seagrass (Capone & Taylor, 1977; Bologna & Heck, 1999;

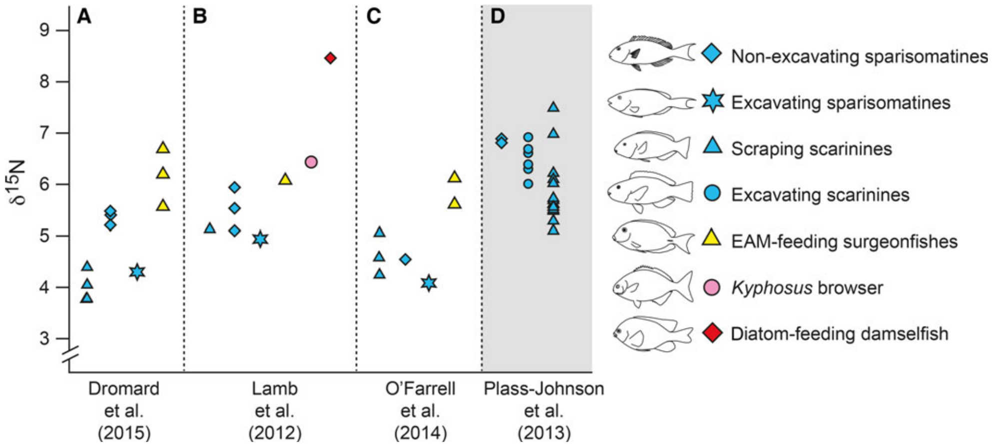


**Figure 6.** Relative $^{15}$N stable isotope positions of herbivorous reef fishes. Each point represents a species mean from Lamb *et al.* (2012), Plass-Johnson *et al.* (2013), O'Farrell *et al.* (2014) and Dromard *et al.* (2015). Species-level data from O'Farrell *et al.* (2014) supplied courtesy of the first author. Sources for feeding modes as in Figure 1. Note that panels A–D cannot be directly compared due to differences in baseline isotopic values for each system. Panel D is shaded to indicate that unlike the previous panels the comparison here is between different feeding modes in parrotfishes, rather than between parrotfishes and other herbivorous taxa.

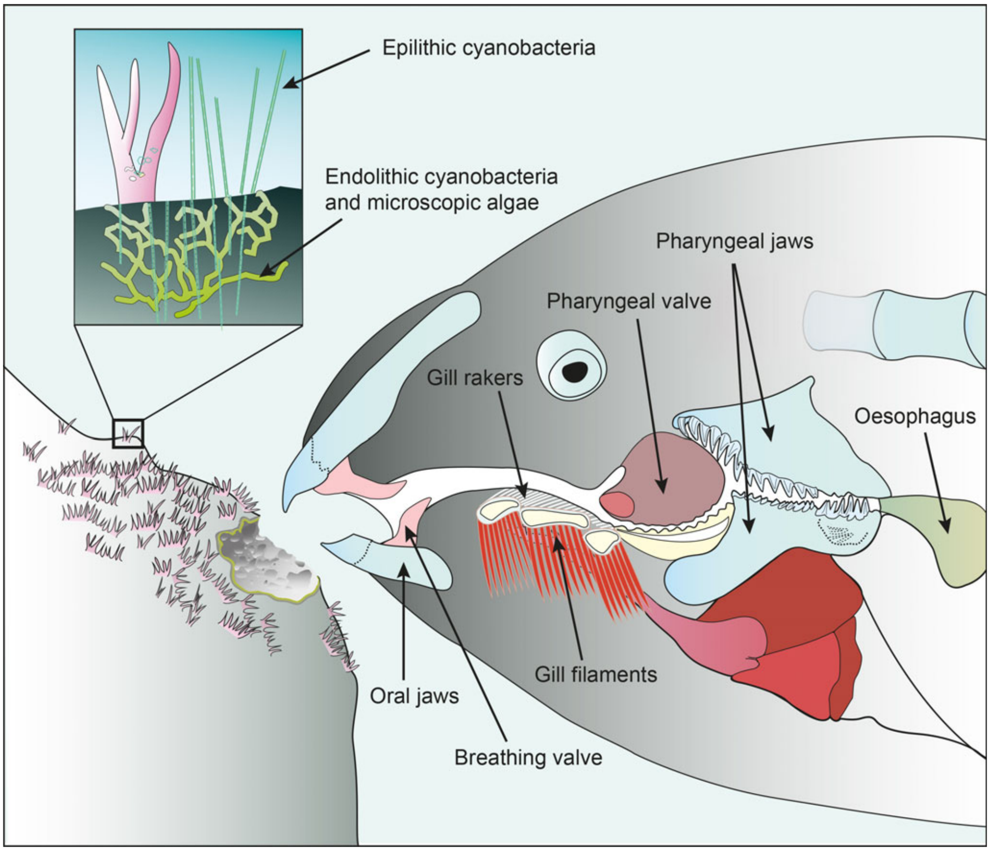


**Figure 7.** Diagrammatic cross-section of parrotfish head showing relationship between various buccal and pharyngeal elements of the trophic apparatus.

Yamamuro, 1999), and endosymbionts of both corals (Lesser *et al.*, 2004; Gutiérrez-Isaza *et al.*, 2015) and sponges (Weisz *et al.*, 2007; Erwin & Thacker, 2008). Despite this apparent ubiquity of cyanobacterial associations on reefs, cyanobacterial biomarkers were not apparent in the other reef fish groups examined to date that are known to feed on EAM and macroalgae, e.g. surgeonfishes and chubs. A dietary target of cyanobacteria and associated microbial elements thus provides a coherent hypothesis for the apparently diverse benthic biota ingested by parrotfishes, and explains the suggestion that parrotfish foraging patterns reflect small-scale patchiness in EAM and endolithic community composition (Tribollet, 2008b; Nash *et al.*, 2012; Grange *et al.*, 2015). This hypothesis also explains why the density of parrotfishes and macroalgal cover are not strongly correlated (Loh *et al.*, 2015; Suchley, McField & Alvarez-Filip, 2016), with the caveat that isotopic data are the only biochemical parameters available for sparisomatine parrotfishes.

Contradicting the cyanobacteria hypothesis are numerous papers suggesting that herbivorous fishes, including parrotfishes, are deterred by cyanobacterial secondary metabolites (e.g. Thacker, Nagle & Paul, 1997; Nagle & Paul, 1999). We question the generality of this view, as (1) at least some of the work on this is equivocal, with deterrent effects being dependent upon the state of the consumer and the availability of other food resources (e.g. Thacker *et al.*, 1997); (2) only mat-forming or tufting cyanobacteria such as *Lyngbya* have been examined, and the palatability of diverse and abundant non-bloom forming epilithic and endolithic cyanobacteria remains untested; (3) many reef fishes do eat significant quantities of cyanobacteria, including damselfishes (Sammarco, 1983), surgeonfishes (Robertson & Gaines, 1986; Montgomery, Myrberg & Fishelson, 1989), rabbitfishes (Hoey, Brandl & Bellwood, 2013) and parrotfishes (Fig. 2D); and (d) parrotfishes are known to accumulate cyanobacterial toxins (Laurent *et al.*, 2008).

Another potential caveat is the suggested use of seagrasses and some macroalgae by the sparisomatine taxa *Nicholsina*, *Leptoscarus* and *Calotomus* (e.g. Prado & Heck, 2011; Lim *et al.*, 2015). It is possible that these parrotfishes obtain adequate nutrition from seagrasses, chlorophytes or rhodophytes by using a rate-maximising feeding strategy (Sibly, 1981; German *et al.*, 2015) that salvages soluble carbohydrate, starch and protein with little reliance on microbial digestion as occurs in macrophyte-feeding freshwater fishes such as grass carp (Sibbing, 1991; Clements *et al.*, 2014), but this remains to be tested. We stress that such a strategy is (1) inconsistent with the low feeding rate observed in *Calotomus carolinus* (Hamilton *et al.*, 2014); (2) incompatible with the digestion of phaeophytes, which requires a yield-maximising strategy (Sibly, 1981; German *et al.*, 2015) involving microbial digestion to access energy from refractory carbohydrates (Choat & Clements, 1998; Clements, Raubenheimer & Choat, 2009; White *et al.*, 2010), and (3) inconsistent with information on the feeding mechanism and stable isotope signatures available for *Sparisoma* species (see above).

An overview of all the available evidence thus suggests that parrotfishes are microphages that target mainly protein-rich autotrophic microorganisms, predominantly cyanobacteria, that are epilithic, epiphytic, endolithic, or endosymbionts of sessile invertebrates (Fig. 8). There is no doubt that parrotfishes ingest other epilithic and endolithic material in the course of feeding, and the enriched $^{15}$N isotopic signal in a couple of species (see Plass-Johnson *et al.*, 2013) indicate an omnivorous or even carnivorous diet. The data-deficient sparisomatines in particular are likely to obtain some nutrition from epilithic algae and detritus, especially the ‘browsing’ species that ingest epiphytic material associated with macroalgae and seagrass. This feeding mode corresponds to the ‘peanut butter and nutritionally unsuitable crackers’ analogy used to explain the mechanism used by aquatic insects to harvest microbial biomass from leaf litter in streams (Cummins, 1974; Smoot & Findlay, 2010). With parrotfishes the crackers correspond to seagrasses and phaeophyte macroalgae, both of which largely consist of material that is generally refractory to the digestive system of parrotfishes (a possible exception is *Dictyota*, which contains unusually high levels of lipid for a macroalga; McDermid *et al.*, 2007). The peanut butter corresponds to the protein-rich epiphytes including cyanobacteria (Yamamuro, 1999). A similar trophic strategy is seen in wood-eating catfishes, which harvest and assimilate biofilm from submerged wood, but cannot digest the cellulose in the wood (German & Miles, 2010).

We believe that this novel, synthetic view of the trophic biology of parrotfishes is more than the flipside of the ‘cyclones as herbivores’ paradigm of algal removal (see Clements *et al.*, 2009), i.e. that considering parrotfishes as microphages is just a nutritionally-focused view consistent with current understanding of their ecological roles. To the contrary, our synthesis of parrotfish feeding biology suggests that we currently underestimate the complexity of the resource base for herbivorous reef fishes. Our results hint at previously unrecognized spatial and temporal dynamics in primary production and consumption on reefs. We explore this in

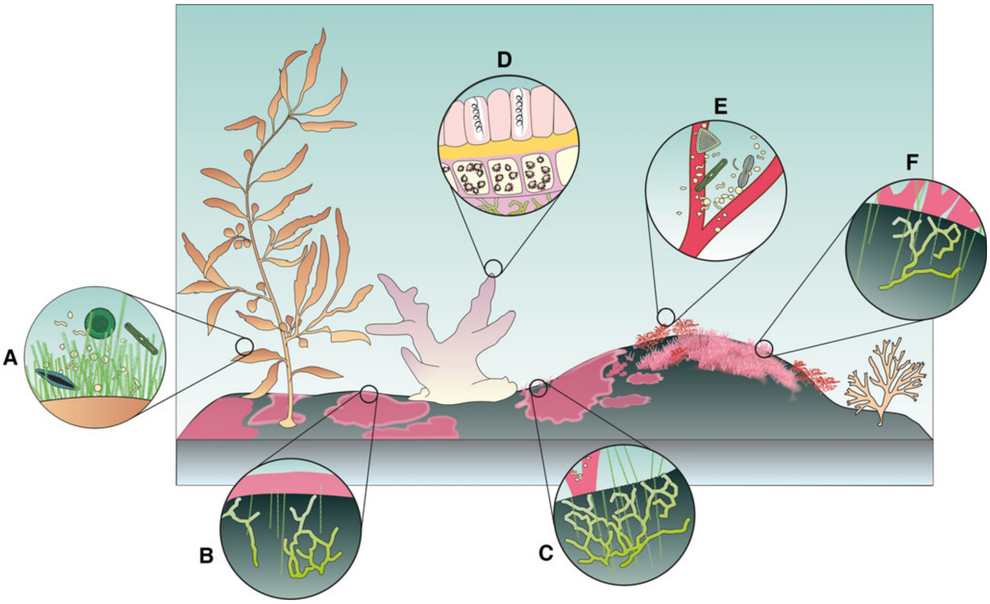


**Figure 8.** Schematic showing microscopic dietary targets of parrotfishes on reefs. A, Epiphytic cyanobacteria on macroalgae. B, Sparse euendolithic cyanobacteria and *Ostreobium* under crustose coralline algae. C, Dense euendolithic cyanobacteria and *Ostreobium* under sparse algal turf. D, Endosymbiotic dinoflagellates and microborers including cyanobacteria, *Ostreobium* and fungi within living coral. E. Detritus and microalgae associated with algal turf. F, Sparse euendolithic cyanobacteria and *Ostreobium* under dense algal turf.

the following section, firstly by comparison with grazing ungulates to consider parallels in resource partitioning and successional dynamics.

## PARROTFISHES AND SUCCESSIONAL DYNAMICS ON REEFS

Resource partitioning in Serengeti ungulates is a strong driver of succession in plant communities (Murray & Brown, 1993), and can lead to feeding facilitation where grazing by some species stimulates regrowth of vegetation that improves forage quality for other species (Arsenault & Owen-Smith, 2002). This can involve the generation of 'grazing lawns' of nutritious, early successional stages of vegetation that are maintained by grazing (McNaughton, 1984; Murray & Brown, 1993). We are not the first to suggest that such systems bear parallels to turf algal communities on coral reefs (e.g. Sammarco, 1983; McNaughton, 1984; Carpenter, 1986; Burkepile, 2013), but our results indicate that successional dynamics on reef substrata may be more complex and important than previously recognized, especially in the sense that we now link parrotfish nutrition (cf. feeding substrata) directly to bioerosion and sediment processing of calcareous substrata (Bonaldo *et al.*, 2014; Perry *et al.*, 2015; Morgan & Kench, 2016).

The view that scarinine and excavating sparisomatine parrotfishes target epilithic and endolithic microbial autotrophs is consistent with the pattern of intensive feeding by these fishes on reef surfaces with sparse algal cover, where endoliths are most dense (Bruggemann *et al.* (1994a, b, c)). Feeding activity by individuals of both excavating and scraping species is often concentrated over small, core areas (Nash *et al.*, 2012; Welsh & Bellwood, 2012; Adam *et al.*, 2015b; Fig. 2A–C), suggesting that particular sites are targeted repetitively, and indicating that feeding is focused on biota on the surface of or within the calcareous reef matrix. Even many epilithic cyanobacteria erode calcareous substrata, forming grooves or pits at the surface (Goldberg, 2013). Direct evidence for feeding on euendoliths is provided by the excellent work of Bruggemann and colleagues (Bruggemann *et al.* (1994a, b, c); Afeworki *et al.*, 2011) and experiments showing that grazing parrotfishes control succession in euendolithic communities (Carreiro-Silva, McClanahan & Kiene, 2005, 2009; Tribollet & Golubic, 2005; Grange *et al.*, 2015).

Like epilithic algal communities (Sammarco, 1983; Carpenter, 1986), euendolithic communities undergo distinct successional stages following colonization of bare substratum (Chazottes, Le Campion-Alsumard & Peyrot-Clausade, 1995; Tribollet, 2008b; Grange *et al.*, 2015). Euendolithic cyanobacteria (e.g. *Hyella* sp., and *Mastigocoleus testarum*) and chlorophytes (other than *Ostreobium* such as *Phaeophila dendroides*) dominate pioneer microboring communities; so called immature communities (Tribollet, 2008b). The chlorophyte *Ostreobium* dominates microboring communities in dead reef substrates after a few months of exposure to colonization (mature communities), and is the main agent of carbonate biogenic dissolution (Tribollet, 2008b; Grange *et al.*, 2015). As euendolithic cyanobacteria require high light levels they can only penetrate a few hundred μm beneath the reef surface (Chazottes *et al.*, 1995; Tribollet, 2008b). In contrast, the euendolithic chlorophyte *Ostreobium* is well adapted to low light intensities, and can thus bore a few mm into the reef matrix (Radtke, Le Campion-Alsumard & Golubic, 1996; Grange *et al.*, 2015). This pattern explains why scraping parrotfishes have depleted $\delta^{15}$N compared to excavators (Plass-Johnson *et al.*, 2013) (Fig. 6): scrapers ingest a higher proportion of the more superficially-distributed diazotrophs.

It is clear that the relationships between parrotfishes and euendolithic microbial communities are synergistic: microboring euendoliths weaken the upper layers of the substratum and provide food for parrotfishes, while grazing by parrotfishes removes the substratum and extends the depth to which euendoliths can penetrate (Tribollet & Golubic, 2005). The effects of parrotfish feeding on succession are hinted at in a recent study in which rates of grazing on experimental euendolithic communities greatly increased after *Ostreobium* started dominating microboring communities (Grange *et al.*, 2015). Subsequent rates of substratum removal by parrotfishes and biogenic dissolution of carbonates by microborers, especially *Ostreobium*, were strongly negatively correlated in a pattern that repeated every 2 months. The removal of reef substrate surfaces by grazing parrotfish allows (a) euendolithic pioneer cyanobacteria to establish again as new surfaces are created, and (b) remaining *Ostreobium* filaments to extend in depth into substrates until they reach their new depth of compensation (Tribollet & Golubic, 2005). Given that excavating parrotfishes appear to prefer euendolithic microbial communities with a high ratio of *Ostreobium*/cyanobacteria (i.e. based on their $\delta^{15}$N signal), this pattern would be consistent with the fish targeting an area about once every 2 months after mature microboring communities had developed with *Ostreobium* dominant and a lower density of cyanobacteria (see Grange *et al.*, 2015; Figs 3and 7). Highly repetitive feeding over the same surfaces by scraping parrotfishes is likely to maintain communities at an earlier stage, when cyanobacteria predominate (Grange *et al.*, 2015). Such a pattern is consistent with the observed foraging movements (Nash *et al.*, 2012; Adam *et al.*, 2015b), high bite rates (Bellwood & Choat, 1990; Bellwood, 1995a, b), depleted $\delta^{15}$N isotope signatures (Carassou *et al.*, 2008; Plass-Johnson *et al.*, 2013) and feeding scars (Bonaldo & Bellwood, 2009; Fig. 3B–D) of scraping parrotfishes.

These predictions on the effects of parrotfishes on microboring community succession remain to be rigorously tested, but they imply previously unrecognized dimensions to resource partitioning. Generic terms such as algal turfs, EAM and detritus overly simplify the complexity of resource partitioning and trophodynamics on reefs. To return to the Serengeti ungulate analogy, in terms of the spatial scale of resource partitioning our current understanding of primary consumption on reefs is akin to what would be known of the complex relationships between African ungulates and co-occurring vegetation had their trophic biology been studied from a hot-air balloon.

## CONCLUSION: A NEW LOOK AT RESOURCE USE AND TROPHIC MORPHOLOGY IN PARROTFISHES

Our integration of disparate data pertaining to resource partitioning in herbivorous reef fishes demands a reconsideration of the ecological roles and evolutionary diversification in these fishes. The view of parrotfishes as microphages provides a unified explanation for seemingly disparate feeding modes and their apparent dietary targets, i.e. excavating and scraping of coral substrata, browsing on seagrasses and macroalgae, and predation of live coral and sponges. The rapid and recent diversification of these fishes (Price *et al.*, 2010; Choat *et al.*, 2012) coincided with major changes in reef structure (Renema *et al.*, 2016), but they evolved into a system already occupied by diverse algae-feeding fishes (Bellwood *et al.*, 2016). We can now potentially explain accelerated evolution in *Scarus* and *Chlorurus* (Price *et al.*, 2010) as the result of: (i) the ability to utilize a novel food resource for reef fishes, i.e. microscopic autotrophs encased in a calcareous matrix (Fig. 2B–F) or epiphytic on macroalgae (Fig. 2G) and seagrasses (Fig. 2H); and (ii) the partitioning of this resource by habitat (Brandl & Bellwood, 2014; Adam *et al.*, 2015b) and successional stage. This view explains why parrotfishes are biochemically distinct from other herbivorous fishes on coral reefs, stressing the importance of work at a level that encompasses digestion, assimilation and metabolism, i.e. an animal-based view (Oesterheld & McNaughton, 2000). This view also highlights the nutritional significance of microorganisms to herbivorous reef fishes in general, either as ingested food or as vectors for nutrient supply through hindgut fermentation, thus stressing the importance of microorganisms in recycling nutrients on coral reefs (Ferrer & Szmant, 1988; de Goeij *et al.*, 2013).

The parrotfish feeding system combines osteological elements of a fused beak, additional jaw articulation and powerful pharyngeal apparatus (Price *et al.*, 2010) with complex soft pharyngeal anatomy involving a retention apparatus consisting of closely-set, interdigitating gill rakers and the pharyngeal valve (Board, 1956; Fig. 7). It is likely that the modified intestine then selectively retains soluble and particulate nutrient-rich material in the sacculae while large low-nutrient or inorganic fragments (e.g. inorganic material and algal cell walls) are removed down the lumen. The parrotfish feeding mechanism stands as a unique development of the actinopterygian trophic apparatus that underpinned the overall radiation of euteleost fishes (Bellwood *et al.*, 2015), enabling the diverse scarinines in particular to harvest nutritionally dense microbial resources associated with hard, inorganic material. As a consequence, parrotfishes play a critical role in destructive and constructive processes on coral reefs by serving as major agents of bioerosion and sediment transport, respectively (Tribollet & Golubic, 2005; Bonaldo *et al.*, 2014; Perry *et al.*, 2015; Morgan & Kench, 2016). Our view of parrotfish feeding thus integrates the ecosystem engineering roles of these fishes with reef trophodynamics (Sanders *et al.*, 2014), a linkage that while not completely novel (e.g. see Bruggemann *et al.* (1994a, b, c)) has nonetheless been obscured by the prevailing view that parrotfishes target EAM, detritus and/or macroalgae.

The role of parrotfishes in regulating the benthic biota on reefs is thus much more complex and nuanced than the removal of epilithic algae and the creation of bare substrata. Indeed, recent reports indicate that parrotfish populations in the Indo-Pacific respond positively to major disturbances that create bare substratum (Lamy *et al.*, 2015; Russ *et al.*, 2015). This is consistent with our view that many parrotfishes target pioneer colonists of such substrata, i.e. epilithic and euendolithic cyanobacteria (Wilkinson & Sammarco, 1983; Williams, Davies & Nagarkar, 2000; Grange *et al.*, 2015), as is the more general view that the most palatable resources for herbivores in aquatic systems tend to be early successional species associated with disturbance (Elger *et al.*, 2004). We suggest three immediate priorities for future work:

i. A reassessment of the comparative trophic anatomy of herbivorous reef fishes that examines relevant functional traits (including soft tissues such as the pharyngeal valve, gill rakers and gastrointestinal tract) within a quantitative and phylogenetic framework.
ii. Extending the biochemical analyses of diet and fish tissues (e.g. SIA, macronutrient and FA analysis) to include a wider range of Indo-Pacific and Atlantic taxa.
iii. Detailed sampling of the substrata grazed by particular parrotfish taxa. Large excavators appear to target discrete grazing areas in an early stage of succession (Grange *et al.*, 2015), and SIA suggests that several Indo-Pacific scraping species including *Sc. frenatus*, *Sc. tricolor* and *Sc. ghobban* appear to target distinct resources (Plass-Johnson *et al.*, 2013).

Nutritional quality of primary production is a consistent indicator of the extent of top-down control of the biomass of primary production and detritus and nutrient recycling in aquatic and terrestrial ecosystems (Cebrian, 1999; Cebrian & Lartigue, 2004). We will not understand the interactions between primary production, herbivorous fishes, sessile invertebrates and bioerosion on coral reefs until we have clearly defined the nutritional relationships between autotrophs and primary consumers, e.g. herbivorous reef fishes and urchins, an outcome that is unlikely to emerge from the current paradigm of reef herbivory which is plant-based and largely ignores a highly productive component: autotrophic microbes. The highly dynamic diversification of some clades of reef fishes (Alfaro *et al.*, 2009; Choat *et al.*, 2012) clearly did involve functional innovation, contrary to recent suggestion (Bellwood *et al.*, 2016), and this will need to be incorporated into an evolutionary framework. A comprehensive appreciation of how herbivores interact with and depend upon the complex autotroph resources available on reefs is also key to how these systems will respond in the future to climatic and anthropogenic stressors. Environmental factors such as eutrophication (Carreiro-Silva *et al.*, 2005, 2009) and ocean acidification (Tribollet *et al.*, 2009; Reyes-Nivia *et al.*, 2013; Enochs *et al.*, 2015) are likely to stimulate the growth of microbial euendoliths, especially that of the chlorophyte *Ostreobium*, and therefore accelerate the biogenic dissolution of carbonates. The present study indicates that changes in the composition of microboring communities (see Grange *et al.*, 2015) are likely to have critical effects both on parrotfish populations and on overall rates of reef bioerosion through the interactions between grazers and microbial euendoliths (Tribollet & Golubic, 2005; cf. Enochs *et al.*, 2015), making these urgent priorities for future research.

## AUTHOR CONTRIBUTIONS

Conceptualization, K.D.C. and J.H.C.; Formal analysis, K.D.C., J.H.C. and J.P.; Investigation, K.D.C. and J.H.C.; Resources, K.D.C. and J.H.C.; Writing-Original Draft, K.D.C. and J.H.C.; Writing-Review & Editing, K.D.C., D.P.G., J.P., A.T. and J.H.C.; Visualization, K.D.C., D.P.G., J.P., A.T. and J.H.C.; Supervision, K.D.C. and J.H.C.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

**Table S1:** Gill raker counts in herbivorous reef fishes.