CHAPTER
2

Innovation and Diversity of the Feeding Mechanism in Parrotfishes

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Introduction

The feeding activities of parrotfishes are one of the fundamental ecological processes in coral reef ecosystems. These activities involve scraping hard rocky surfaces to remove turf algae, detritus, bacteria, and a wide range of encrusting invertebrates. This mixture of dead coral skeletons, the invertebrate and microbial organisms that colonize these surfaces and the detritus of organic debris is then passed to the pharyngeal jaw apparatus of parrotfish where it is mixed with mucous and ground to a fine slurry before being passed to the intestines (Bellwood and Choat 1990, Choat 1991, Choat et al. 2002). Here, nutrients are extracted from the slurry (Crossman et al. 2005) and fine sand is excreted back into the environment (Frydle and Stearn 1978, Bellwood 1995a, 1995b, Bruggenmann et al. 1996). The grazing activities of parrotfishes play a major role in disturbing benthic communities (Burkepile and Hay 2011, Brandl et al. 2014), preventing large algae from getting established and allowing corals and a more diverse community of encrusting organisms to become established and persist. The excretion of sand and concomitant bioerosion of the reef by parrotfishes occurs on a profound level as well, with accounts concluding that parrotfish are the major biological producers of sand in many reef systems (Bellwood 1995a, 1995b, Malella and Fox Chapter 8). Many groups of reef fishes are herbivores, microbiotivores or detritivores but the singular impact of parrotfishes is because they are the only major group that removes the calcareous surface layers of the reef as they graze.

The unique ability of parrotfish to feed in this way is closely linked to the presence of several evolutionary novelties in the feeding mechanism that facilitate their ability to scrape rocky substrates and pulverize these scrapings. In this chapter we will focus on three of these innovations: the parrotfish pharyngeal mill apparatus, the cutting edge of the oral dentition, and the intramandibular joint in the oral jaws. We describe each of the three innovations, review their evolutionary history, their impact on parrotfish feeding abilities, and the impact that each has had on the evolutionary diversification of parrotfishes.

Major Innovations in the Parrotfish Feeding Mechanism

The Pharyngeal Mill Apparatus

Parrotfishes are phylogenetically nested within the Labridae (Westneat and Alfaro 2005). Herbivory appears to have evolved at least three times within Labridae: once in *Pseudodax*, at least once in the odacines (Clements et al. 2004), and once in parrotfish. Parrotfish (Figs 1 and 2) are by far the largest radiation of herbivorous labrids with about 100 described species. All parrotfish share a derived condition of the pharyngeal jaw apparatus, a pharyngeal mill (Fig. 2) that appears to be crucial to their abilities as herbivores (Gobalet 1989, Bullock and Monod 1997). This system is built on a suite of already existing modifications of the pharyngeal jaw system that are shared by labrid fishes (Kaufman and Liem 1982, Bellwood

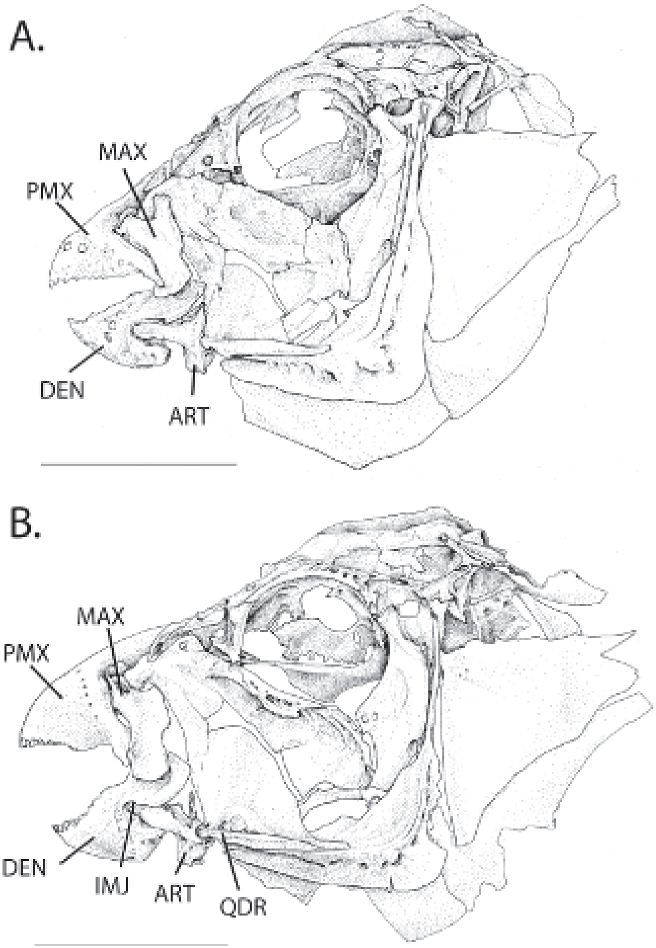

Fig. 1. Diagrams of the skull of parrotfishes prepared by hand from cleared and stained specimens, A. *Cetoscarus bicolor* and B. *Chlorurus sordidus*. Note that while both of these species possess cutting edge dentition on the jaws, *Cetoscarus* lacks an intramandibular joint between the dentary and articular bones while *Chlorurus* has this novel joint. Scale bars = 10 mm. Abbreviations: ART, articular; DEN, dentary; IMJ, intramandibular joint; MAX, maxilla; PMX, premaxilla; QDR, quadrate. Diagrams prepared by Ian Hart.

1994, Wainwright et al. 2012). The labrid condition, termed pharyngognathy, involves three derived features. (1) Fused left and right lower pharyngeal jaw bones (5th ceratobranchials) into a single structural lower jaw that is stronger and able to withstand higher forces. (2) Well developed joints between the underside of the neurocranium and the dorsal surface of the upper pharyngeal jaws that stabilize the upper jaws when the lower jaw is pulled up against them in biting actions. (3) The presence of a direct muscular connection between the neurocranium and the lower pharyngeal jaw that results in a powerful bite (Kaufman and Liem 1982, Stiassny and Jensen 1987).

The modifications in parrotfish are substantial and include extensive elaboration of the paired fourth epibranchial bones that sit lateral to the pharnygobranchials (the upper jaw bones that bear tooth plates), holding the upper jaws in a medial position while biting occurs, thus stabilizing them and guiding them during anterior-posterior movements of the upper jaw (Gobalet 1989, Chapter 1). The joints between the upper pharyngeal jaws and the neurocranium are extended anterior-posteriorly and are convex, allowing the upper jaws a long scope as they slide forward and backward while the muscular sling generates a biting action (Fig. 2). It is suspected that the characteristic milling action of parrotfishes is produced by an anterior-posterior motion of the upper jaws while the lower jaw bites against it (Gobalet 1989, Wainwright 2005). The teeth on both the upper jaws

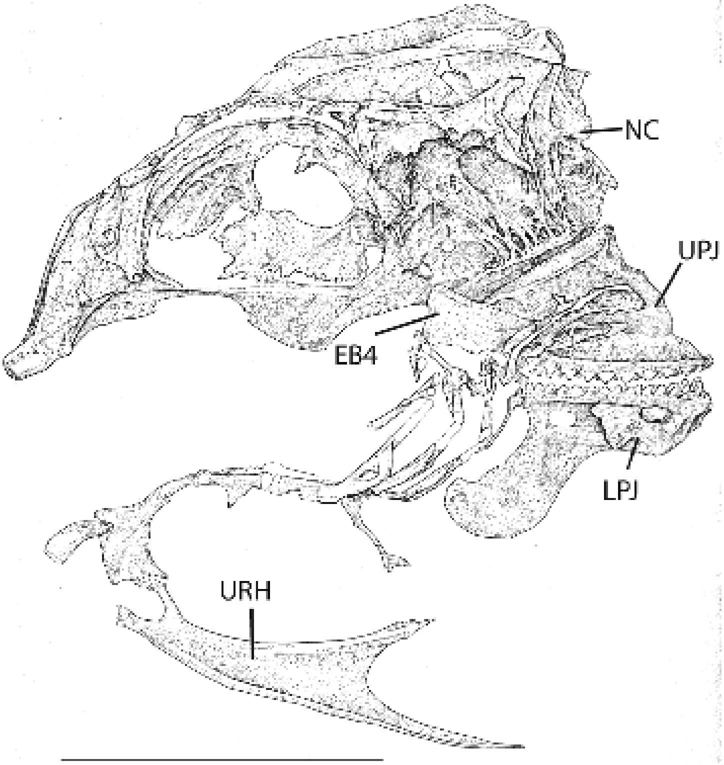

Fig. 2. Diagram of the pharyngeal mill apparatus of the parrotfish *Chlorurus sordidus*, prepared by hand from a cleared and stained specimen. Note the anterior-posterior elongation of the joint between the neurocranium and upper pharyngeal jaw, and the teeth on both the upper and lower pharyngeal mill. Scale bar = 10 mm. Abbreviations for bone names: EB4, fourth epibranchial; LPJ, lower pharyngeal jaw (5th ceratobranchials); NC, neurocranium; UPJ, upper pharyngeal jaw (pharyngobranchial); URH, urohyal. Diagram prepared by Ian Hart.

and lower jaw are organized into anterior-posterior rows with the newest teeth coming in anteriorly and older teeth being moved posteriorly until they are worn away. This characteristic structure of the pharyngeal jaws is found in all parrotfish (Bellwood 1994) though it varies somewhat among genera and species in terms of the extent of the anterior-posterior elongation of the joint with the neurocranium and the size of the grinding surface on the lower pharyngeal jaw (see figure 12 in Bellwood 1994). The major trend within these features is that the grinding surface and the joint with the neurocranium are more elongate in the anterior-posterior direction in the reef-associated group that includes *Bolbometopon, Cetoscarus, Hipposcarus, Chlorurus* and *Scarus*. Functionally, the key consequence of this large suite of derived traits characteristic of the parrotfish pharyngeal mill is that the system is specialized for milling or grinding actions, as opposed to the crushing and winnowing actions that are more typical of pharyngeal jaw function in other labrids (Liem and Sanderson 1986, Wainwright 1988).

Cutting Edge on Oral Dentition

Teeth on the upper and lower oral jaws are coalesced into a cutting edge in *Leptoscarus, Sparisoma, Cetoscarus, Bolbometopon, Hipposcarus, Chlorurus* and *Scarus* (Fig. 1, Bellwood and Choat 1990, Bellwood 1994). Oral jaw teeth in the remaining parrotfish, *Cryptotomus, Nicholsina*, and *Calotomus*, are individual, caniniform teeth as in wrasses, though *Calotomus* has somewhat flattened teeth (Bellwood 1994). Referring to the distribution of this trait on the parrotfish phylogeny (Fig. 3), it is somewhat ambiguous whether the absence of the cutting edge in these taxa is a retained primitive trait or a secondary reversal to this condition. However, a maximum likelihood reconstruction upon the phylogeny favors the interpretation that the cutting edge dentition evolved once and has been lost twice. All parrotfish that lack the cutting edge dentition are occupants of seagrass habitats and all taxa with the cutting edge except some *Sparisoma* are reef-dwellers, suggesting that there is a strong relationship between feeding on rocky substrates and the evolution and use of the cutting edge. The cutting edge gives a distinctive beak-like appearance to the jaws that is the basis of the common name ‘parrotfish’. This structure is key to the ability of parrotfish to scrape the surface of rock or dead coral, removing the characteristic assemblage of coral skeleton, algae, microbes, detritus and encrusting invertebrates that they feed upon. Whether scraping or excavating, the feeding activities of parrotfish on reefs depend critically on this modified dental arrangement (Clements and Bellwood 1988, Bellwood and Choat 1990).

Intramandibular Joint

Parrotfish in the genera *Hipposcarus*, *Chlorurus* and *Scarus* have a well-developed joint between the dentary and articular bones of the lower jaw (Fig. 1b). In these taxa, the large section two of the adductor mandibulae muscle has the derived condition of inserting on the dentary rather than the articular bone and thus has the unusual property of crossing two joints, both the quadrate-articular joint and the articular-dentary joint. In other parrotfish and in wrasses the mandible is a single rigid structure formed by a dentary and articular that are held tightly together by many short ligaments (Fig. 1a). The intramandibular joint permits motion at the quadrate-articular joint, as in other teloests, as well as the joint between the dentary and articular. The introduction of this joint alters the linkage mechanics of the oral jaw system, resulting in a novel four-bar linkage that transmits motion of the lower jaw to the upper jaws (Wainwright et al. 2004). Exactly how the intramandibular joint functions during feeding is not known, although one inferred

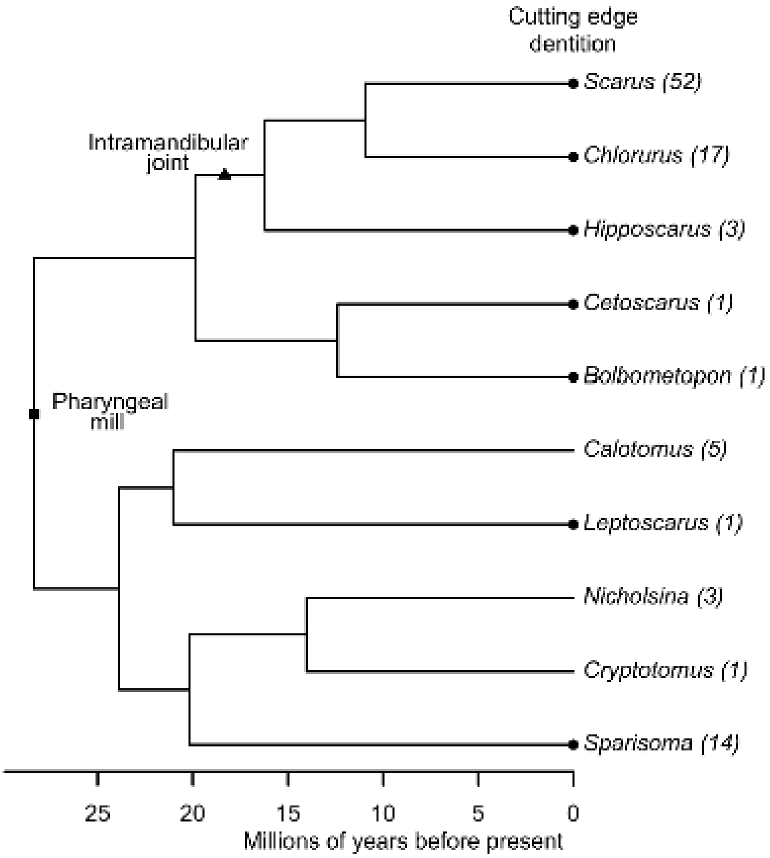

Fig. 3. Time calibrated molecular phylogeny of parrotfish genera (Kazancioğlu et al. 2009). Inferred origins of the parrotfish pharyngeal mill and the intramandibular joint are indicated by a square and triangle respectively. The distribution of the cutting edge dentition among genera is indicated at the tips with dark circle. A likelihood reconstruction of the history of the cutting edge dentition favored a single origin of the trait and two losses.

consequence of the joint and modified attachment of the adductor mandibulae is that the mechanical advantage, or force transmission, of the adductor mandibulae during oral jaw biting is almost twice as high as it is in taxa that lack the joint (Bellwood 1994, Wainwright et al. 2004, see also Gobalet Chapter 1). At present it is also not known if movement occurs at both joints during normal feeding behavior. If movement occurs at both joints during feeding this could allow fish to modulate the orientation of the dentary during biting actions, maintaining a favorable orientation throughout the scrape. Such a function could result in enlargement of the region of contact between the teeth and substrate during scraping. A better understanding of the function of the intra-mandibular joint will be an important goal in future research.

Phylogenetic Distribution of Feeding Innovations

Some lineages of parrotfishes have acquired all three of the innovations described above (Fig. 3). Parrotfish in the group made up by *Scarus*, *Chlorurus* and *Hipposcarus* have the modified pharyngeal mill, cutting edge dentition on their oral jaws, and an intramandibular joint. The possession of all three of these innovations appears to be unique among reef fishes and even among teleost fishes, although none of these traits are unique to parrotfishes.

Remarkably, many of the complex modifications found in the parrotfish pharyngeal mill are also found in the herbivorous wrasse *Pseudodax* (Bellwood 1994). Although a labrid, *Pseudodax* is not closely related to parrotfishes and the presence of the pharyngeal mill has evolved independently in this lineage. This is particularly noteworthy as the pharyngeal mill configuration of the pharyngeal jaws is not known to occur in any teleost outside of Labridae. Cutting edge dentition involving a cement layer around coalesced dentition in the oral jaws is found in another labrid, *Odax* (Clements and Bellwood 1988). *Odax* is a temperate herbivore that feeds mostly on large fucoids and laminarian macroalgae (Clements and Bellwood 1988). The pharyngeal jaws of *Odax* show the typical wrasse condition, lacking the modifications characteristic of the pharyngeal mill seen in parrotfishes and *Pseudodax* (Clements and Bellwood 1988, Bellwood 1994). Similarly, *Pseudodax* lacks the cutting edge dentition made of smaller coalesced teeth, although it does have large, flattened incisiform teeth that provide a different type of cutting edge in the oral jaws (Bellwood 1994). A few other teleost lineages have cutting edge dentition formed by coalesced or fused teeth, including members of Oplegnathidae and Tetraodontidae.

Finally, an intramandibular joint has evolved several times in reef fishes, including some members of Acanthuridae, Pomacanthidae, Chaetodontidae, Blenniidae, Girellidae and Siganidae (Vial and Ojeda 1990, Purcell and Bellwood 1993, Bellwood 2003, Konow et al. 2008, Konow and Bellwood 2005, Ferry-Graham and Konow 2010), and some non-reef lineages: *Helostoma* and some Poeciliidae (Gibb et al. 2008, Ferry et al. 2012). In all cases this trait is associated with feeding by biting the benthos (Konow et al. 2008). Bellwood (2003) noted that these reef lineages, together with parrotfishes, make up the major herbivorous fishes on modern reefs. Given that intramandibular joints have apparently evolved numerous times in benthic feeding reef fishes, there is a need to better understand the functional benefits of this modification in benthic feeding fishes (Konow et al. 2008) and whether the function of the extra joint is similar in each case. Some possible advantages of the additional joint are that it permits (1) a greater angular sweep of the lower jaw, although this trait is normally associated with overall shortening of the lower jaw (Purcell and Bellwood 1993), (2) Modulation of the orientation of the toothed surface of the lower jaw through the sweep of the bite (Price et al. 2010), (3) Effective biting while the upper jaws are protruded (Konow et al. 2008) or (4) that the flexibility and associated complexity in muscular attachments result in greater dexterity in movements of the lower jaw during feeding.

Although all parrotfish possess the grinding pharyngeal mill, many seagrass-dwelling lineages lack the cutting edge on the oral jaws that is essential for scraping hard surfaces on reefs. Only *Scarus*, *Chlorurus* and *Hipposcarus*, a lineage nested inside a larger clade of reef-dwelling parrotfishes, have the mobile intramandibular joint. As discussed in Bonaldo et al. (2014), the phylogeny suggests that parrotfish may have invaded reef habitats twice, once along the branch below the node uniting *Bolbometopon* and *Scarus*, and a second time within *Sparisoma*. Most parrotfish living in seagrass feed in a different manner from those taxa on reefs because of the absence of the ubiquitous hard substrata that promotes scraping behavior. In seagrass, parrotfish feed on blades of seagrass, epiphytes that live on seagrass and large algal plants. These are taken by a browsing behavior in which they are removed from their holdfast or separated from the rest of the plant by cropping or biting and tearing.

Morphological and Functional Diversity of Parrotfish

The complex phylogenetic distribution of the three innovations discussed above implies the presence of functional diversity among parrotfishes (Fig. 3). There are considerable differences between taxa in their feeding biology, with *Bolbometopon, Cetoscarus* and *Chlorurus* digging deep gashes in the reef during forays (termed excavators by Bellwood and Choat 1990) while *Hipposcarus* and *Scarus* feed with much more superficial scrapes of rock or sometimes sandy surfaces, taking less carbonate while they primarily remove epilithic organisms (Bellwood and Choat 1990). The reef-dwelling *Sparisoma* species appear to be superficial scrapers with *Sparisoma viride* and its sister species, *Sp. amplum*, being informally described as an excavator (e.g. Bellwood 1994) and some authors also categorizing *Sp. chrysopterum* and *Sp. rubripinne* as excavators (Bernardi et al. 2000). Within the lineage that possesses the intramandibular joint there is wide diversity in feeding mode, from superficial scraping to excavating. This suggests that the intramandibular joint may have a general benefit to scraping hard substrate that is not specific to either extreme on the axis from deep excavating to superficial scraping.

A functional morphospace for the parrotfish feeding system can be produced by a principal components analysis summarizing eight functional traits of the feeding mechanism in 34 species, including representatives of all genera except *Nicholsina* (Figs 4 and 5). The traits used in this analysis are described in detail elsewhere (Wainwright

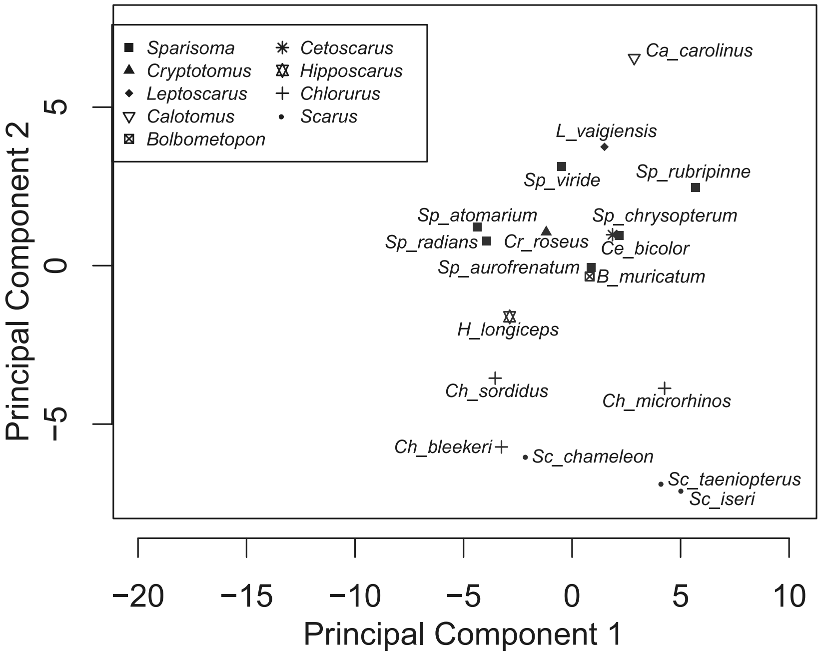

Fig. 4. Plot of Principal Component 1 vs 2 from a phylogenetic PCA run on nine morphological variables associated with the functional morphology of the parrotfish feeding mechanism. The variables included were mechanical advantage of jaw opening and jaw closing, transmission coefficients of the oral jaws and hyoid 4-bar linkages, oral jaw gape distance, maximum upper jaw protrusion distance, and masses of the adductor mandibulae, sternohyoideus, and levator posterior muscles. Average values of each trait for several specimens per species were corrected for body while accounting for phylogenetic relationships where necessary. Data are from Wainwright et al. 2004 and Price et al. 2010.

et al. 2004) but include the horizontal width of the oral gape, maximum premaxillary protrusion distance, the mechanical advantage of jaw opening and closing muscles, and the transmission coefficient of the four-bar linkage that operates the oral jaws (transmission coefficients are the inverse of mechanical advantage), as well as the mass of three major muscles; the adductor mandibulae complex, the sternohyoideus and the levator posterior. The adductor mandibulae is a complex of muscles that function to adduct the oral jaws during biting, the sternohyoideus is involved in ventral depression of the hyoid bar during suction, which is poorly developed in parrotfish, and the levator posterior muscle is a major biting muscle from the pharyngeal jaw system that pulls the lower pharyngeal jaw up against the upper jaw.

After size-correcting traits by calculating residuals of species means from Log-Log regressions on the cube root of body mass the position of 34 species in principal component space reveals major features of the morphological diversity (Figs 4 and 5). Principal component one (PC1) is negatively correlated with all morphological traits and represents an axis that captures species at one extreme with relatively large muscles, a large mouth, high protrusion distance, and high values of four-bar transmission coefficients and jaw lever mechanical advantage, and species at the other extreme with small values of these traits (Table 1; Fig. 4). Principal component two (PC2) primarily involves a trade-off between jaw lever mechanical advantage and the gape width. In bivariate plots of PC1 vs 2 and PC3 vs 4 a group composed of species of *Scarus* is apparent, and a second group made up of all other parrotfishes with the excavators *Chlorurus* and *Bolbometopon* somewhat is set apart from this group (Figs 4 and 5). Two interesting points are that *Sp. viride* is

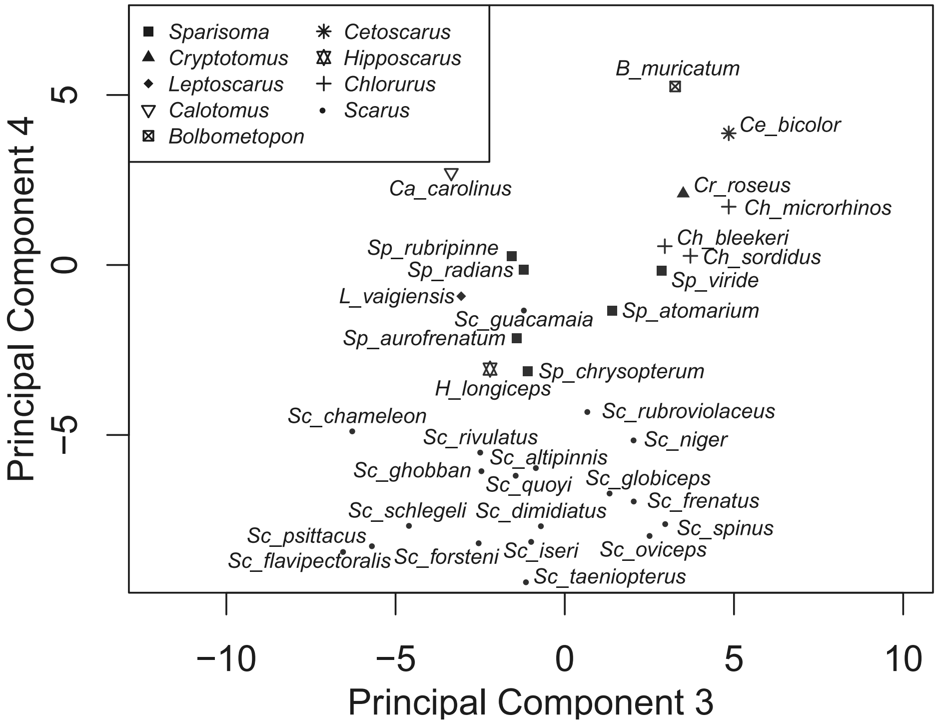

Fig. 5. Plot of Principal Component 3 vs 4 from a phylogenetic PCA run on nine morphological variables associated with the functional morphology of the parrotfish feeding mechanism. See Fig. 4 legend for member variables and Table 1 for loadings and variance explained. Data are from Wainwright et al. 2004 and Price et al. 2010.

intermediate between the excavator group and other *Sparisoma*, and *Hipposcarus* does not fall with *Scarus* or *Chlorurus*, but is intermediate between *Scarus* and *Sparisoma*. This last observation again points to the fact that the intramandibular joint, present in *Scarus, Chlorurus* and *Hipposcarus*, is not associated with a narrow range of functional morphology, but instead supports considerable diversity.

Table 1. Principal Component loadings from a phylogenetic PCA run on morphological traits of parrotfishes.

	PC1	*PC2*	*PC3*	*PC4*
Gape Distance	-0.354	0.652	-0.435	0.152
Protrusion Distance	-0.705	0.182	-0.031	-0.435
Adductor Mass	-0.772	0.068	0.539	0.015
Sternohyoideus Mass	-0.924	0.049	0.087	0.148
Levator Posterior Mass	-0.572	0.013	-0.320	0.649
Jaw Closing Lever	-0.186	-0.764	-0.347	-0.170
Jaw Opening Lever	-0.368	-0.767	-0.067	0.204
Oral Jaw KT	-0.620	0.046	-0.592	-0.391
Hyoid KT	-0.766	-0.089	0.416	-0.089
Cumulative Variance Explained	0.393	0.576	0.714	0.813

Bivariate plots of individual variables are also revealing. A plot of jaw closing lever ratio against mass of the levator posterior muscle sets *Scarus* apart from all other taxa (Fig. 6). Species of *Scarus* have extremely high jaw closing mechanical advantage of the oral

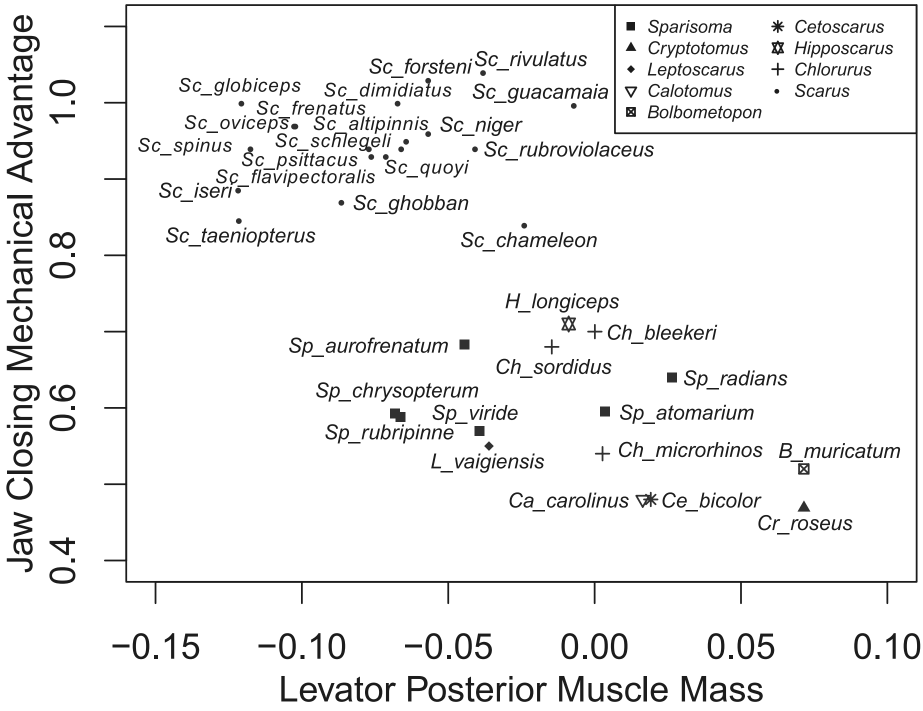

Fig. 6. Plot of jaw closing mechanical advantage versus levator posterior muscle mass in 34 species of parrotfishes. Levator posterior muscle mass is expressed as a residual from a body size correction regression. Data are from Wainwright et al. 2004 and Price et al. 2010.

jaw mandible but extensive diversity in the size of the levator posterior muscle from the pharyngeal jaws. The excavators, *Chlorurus, Bolobometopon* and *Cetoscarus* have very large levator posterior muscles and relatively low jaw closing mechanical advantage, placing them in the lower right region of this plot with *Calotomus*. The large levator posterior muscle may reflect that excavators often remove solid pieces of reef carbonate that must be reduced in the pharyngeal mill before being swallowed. The remaining species are intermediate in the two traits, except *Cryptotomus* which has the largest levator posterior muscle and lower jaw closing mechanical advantage of all parrotfish. This is interesting because *Cryptotomus* is the smallest parrotfish, about 75 mm adult body size.

Curiously, although *Scarus* species all have very high mechanical advantage of jaw closing, they have moderate to very high transmission coefficient in the oral jaw four-bar linkage (Fig. 7). This indicates that while *Scarus* transfer a large amount of adductor muscle force to the cutting edge of the lower jaw during biting, many of them also generate a large amount of movement in the upper jaw for a given amount of rotation of the lower jaw. This appears to be an unusual case where a 'force modified' linkage system operates in series with a second system that is 'displacement modified'.

When the transmission coefficient of the oral jaw 4-bar linkage is plotted against mechanical advantage of jaw opening (Fig. 7), the major pattern is once again the high diversity found in *Scarus* and *Chlorurus*. The mechanical advantage of jaw opening ranges from 0.19 to 0.38 among species of *Scarus* and the most extreme values of 4-bar transmission coefficient are found in *Scarus* or *Chlorurus*. *Sp. viride* has a very low 4-bar transmission

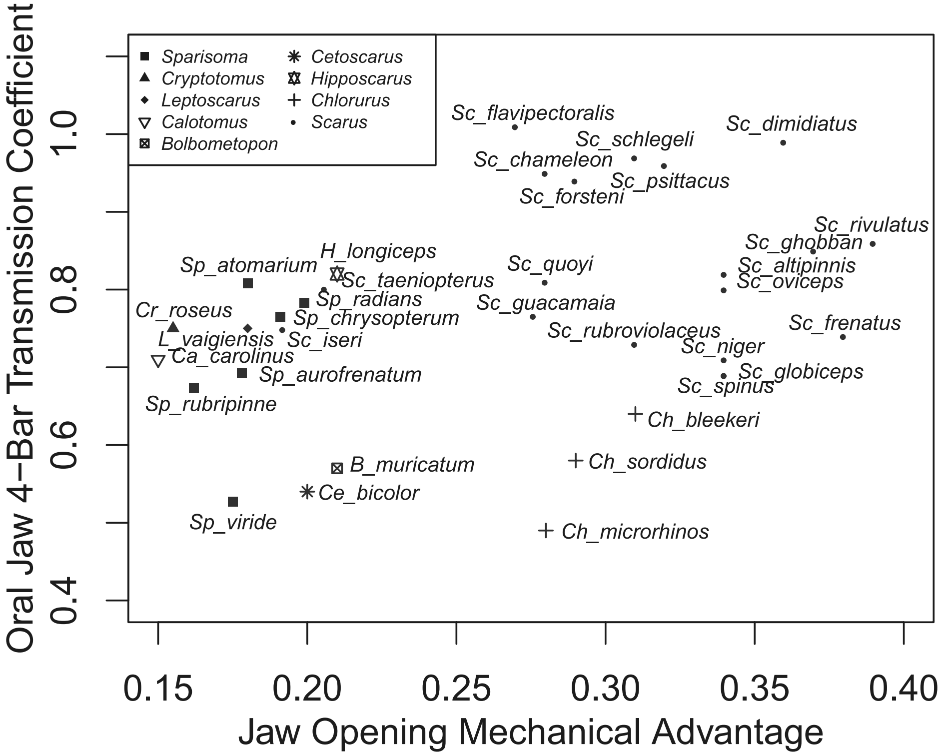

Fig. 7. Plot of transmission coefficient of the 4-bar linkage of the oral jaws versus jaw opening mechanical advantage in 34 species of parrotfish. Data are from Wainwright et al. 2004 and Price et al. 2010.

coefficient, like all other excavators (*Chlorurus*, *Bolbometopon* and *Cetoscarus*). Most of the species of *Sparisoma, Calotomus, Leptoscarus, Hipposcarus* and *Cryptotomus* are clumped in a region with intermediate values of 4-bar transmission coefficient and low jaw opening mechanical advantage.

A plot of adductor mandibulae mass against width of the oral jaw gape continues the trend of separating *Scarus*, excavators and the other taxa (Fig. 8). Once again, *Scarus* shows high diversity in adductor mass, with species spanning most of the range seen across all parrotfishes. As expected, the largest adductor muscles are found in the excavators, *Chlorurus, Bolbometopon* and *Cetoscarus*, but they are joined by three species of *Scarus* that also have large adductors. The smallest adductor muscles are found in some *Sparisoma, Leptoscarus, Calotomus* and some *Scarus*. The width of the oral gape is highest in *Sparisoma, Calotomus* and *Leptoscarus* and smallest in some *Scarus*.

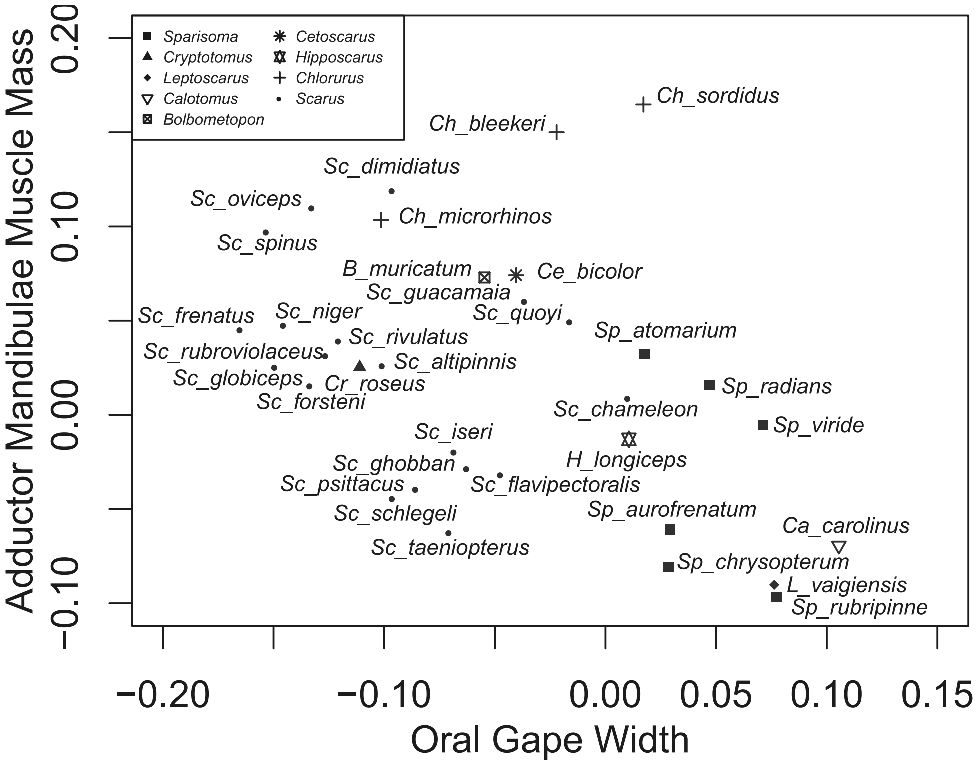

Fig. 8. Plot of adductor mandibulae muscle mass versus oral jaw gape width in 34 species of parrotfishes. Data are from Wainwright et al. 2004 and Price et al. 2010.

Evolutionary Implications of Feeding Innovations

The evolutionary history of the three feeding innovations as seen in Fig. 3 suggests a structure for posing questions about the effect that they have had on parrotfish macroevolution. Two of the innovations, the modified pharyngeal mill and the intramandibular joint, have apparently each evolved only once in parrotfish, while the cutting edge of the oral jaws has a more ambiguous history, with the strongest support for a single origin and two independent losses. Both cutting edge dentition and the intramandibular joint are distributed such that lineages with and without the innovation can be compared, but because all parrotfish have the pharyngeal mill, studies of its effect on diversification must be made between parrotfish and other labrids.

Previous studies have explored macroevolutionary impacts of the pharyngeal mill and the intramandibular joint. A study of lineage diversification rates in labrids revealed a significant correlation between possession of the parrotfish pharyngeal mill and increased rates of speciation (Alfaro et al. 2009) although the influence of co-distributed characters cannot be ruled out. More detailed explorations have revealed that elevated rates of diversification are found only in the clade that includes *Scarus* and *Chlorurus* (Alfaro et al. 2009, Kazancioğlu et al. 2009, Cowman and Bellwood 2011) and the higher rate seen across parrotfish as compared to wrasses appears to be due to a trickle-down effect of the high rate in *Scarus* and *Chlorurus*. Thus, while the highest diversification rates across Labridae are found in the *Scarus*/*Chlorurus* clade, even moderately elevated rates of diversification are not seen in other parrotfishes (Alfaro et al. 2009, Cowman and Bellwood 2011). Interestingly, this shift in diversification on the branch leading to *Scarus*/*Chlorurus* is very close to the inferred origin of the intra-mandibular joint on the branch leading to *Scarus*/*Chlorurus*/*Hipposcarus* (Fig. 3). Most authors have concluded that the higher diversification rate seen in *Scarus*/*Chlorurus* is more likely related to strong sexual selection in this clade, as reflected by strong dichromatism, than to functional innovations of the feeding mechanism (Streelman et al. 2002, Alfaro et al. 2009, Kazancioğlu et al. 2009, Cowman and Bellwood 2011). Sexual selection, or change in the strength of sexual selection, is one of the most commonly found factors that influences diversification rate (Coyne and Orr 2005). It is important to emphasize, however, that in spite of the popularity of this hypothesis, formal analyses of the relationship between sexual selection and diversification rate in parrotfishes, or more broadly in labrids, have not yet been conducted.

What about functional and ecological diversity? Is there a relationship between the three parrotfish innovations and diversity in the functional morphology of the feeding system, the food they eat, and where and how they eat it? Unfortunately, there may not be enough detailed information about the micro-habitat feeding locations and diet in individual species of parrotfish to evaluate diversity in these traits. But, when the diversity of morphological traits is viewed in the context of the time-calibrated molecular phylogeny of parrotfishes a very interesting pattern becomes immediately apparent. *Scarus*, although very diverse in terms of feeding functional morphology (Figs 4-8), is a young lineage, roughly 5-10 million years old crown age (Smith et al. 2008, Kazancioğlu et al. 2009, Cowman and Bellwood 2011, Choat et al. 2012). Furthermore, the lineage that also includes *Chlorurus* and *Hipposcarus* is even more morphologically diverse (Figs 4-8). High diversity evolving over a relatively short period of time implies that the rate of evolution has been high. Indeed, this intuition was confirmed in a model-fitting study where the estimated rate of evolution of feeding traits in the *Scarus*/*Chlorurus*/*Hipposcarus* clade was found to be much higher relative to other parrotfishes (Fig. 8; Price et al. 2010). The jaw closing and opening mechanical advantage, oral jaw 4-bar transmission coefficient and mass of the adductor mandibulae muscle have all evolved between 4 and 23 times faster in this clade than in other parrotfish (Fig. 9).

Parrotfish with the intramandibular joint show high rates of evolution in the functional morphology of the oral jaw feeding apparatus. It is interesting that these elevated rates are restricted to aspects of the oral jaws, where the intramandibular joint occurs. Neither mass of the sternohyoideus nor the levator posterior muscle evolve at different rates in the two groups of parrotfish (Fig. 9; Price et al. 2010). These two muscles are not directly associated with the oral jaw system. Price et al. (2010) suggested that the elevated rates

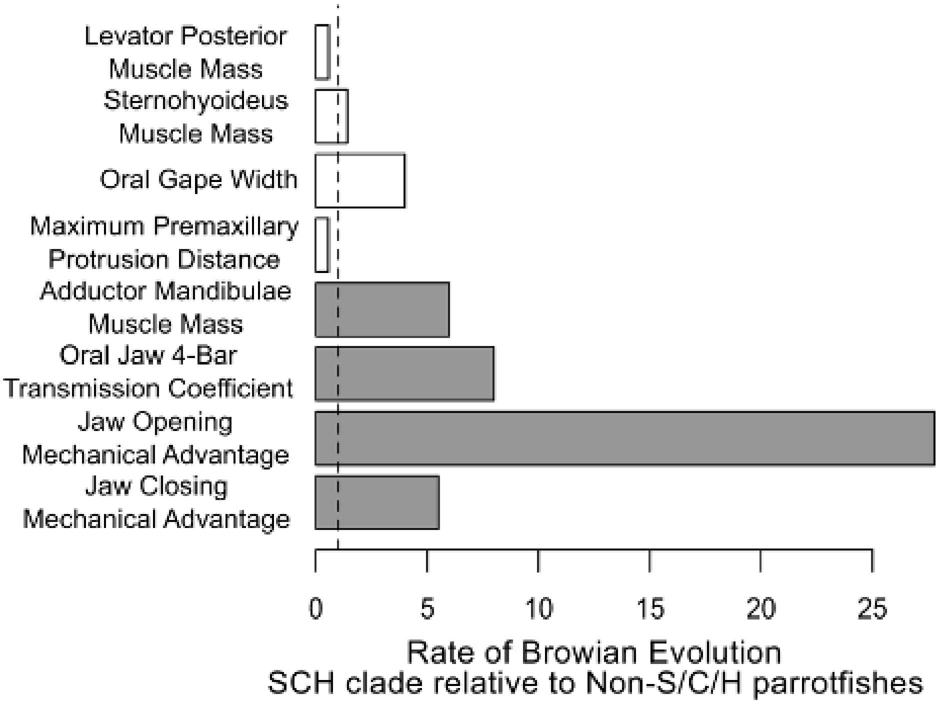

Fig. 9. Bar diagram depicting the rates of evolution of functional morphological traits of the parrotfish feeding apparatus. Rates of evolution of traits are expressed as a ratio of rate of its evolution in the clade that possesses the intramandibular joint (*Scarus*, *Chlorurus* and *Hipposcarus*) and the rate in all other parrotfishes. The dashed line indicates equal rates in both clades (which occurs at a relative rate of 1). Color indicates whether the difference in rates between the clades is significant (grey) or not (white) according to the p-value derived from parametric bootstrapping. Jaw closing and opening mechanical advantage, oral jaw transmission coefficient, and mass of the adductor mandibulae all evolve faster in the intramandibular joint clade, while the sternohyoideus and levator posterior muscles show no difference between groups.

of evolution found in oral jaw traits in the *Scarus*/*Chlorurus*/*Hipposcarus* clade may have come about because of the increased mechanical complexity of the jaws that is produced by the introduction of the second jaw joint. The introduction of the novel joint may increase the range of configurations that can function effectively, thus removing a constraint on diversification. One difficulty with this interpretation is that we would expect functional diversity to reflect variation in feeding ecology, and yet, it is thought that this clade exhibits relatively little diversity in feeding ecology beyond the well-documented differences between the excavating *Chlorurus* and scraping *Scarus* (Bellwood and Choat 1990). Nevertheless, some evidence of ecological diversity and community complementarity has been described (e.g. Rasher et al. 2013). It may be worth future studies generating more detailed data on the microhabitat grazing locations on reefs, where each species feeds and the way in which they scrape the substrate, to determine if the high functional morphological diversity, seen particularly in *Scarus*, is associated with ecological variation. This sort of ecological variation in the substrate that species feed on has been found in surgeonfishes (Brandl et al. 2014, Brandl and Bellwood 2014) where there is considerable variation among taxa in the surface topography of the hard substrate that is grazed and the diversity of substrates grazed by single species. Parrotfish typically occur in high diversity systems with many other species of parrotfish. Species of *Scarus* and *Chlorurus* in the Indo-Pacific can be found feeding in groups with other species and *Scarus* frequently occupy microhabitats with more than six congeners (Russ 1984, Hoey and Bellwood 2008).

It is possible that functional diversity among species of parrotfish on reefs, beyond the difference between excavators and scrapers, may result in ecological diversity (Choat et al. 2002), such as that which facilitates complementarity (Burkepile and Hay 2008, 2011) and the coexistence of so many species. However, no such axis of ecological diversity has yet been identified. The presence of high rates of evolution in oral jaw functional morphology in the *Scarus*/*Chlorurus*/*Hipposcarus* clade is therefore something of a conundrum. One interesting possibility is that both the high rate of functional morphological evolution and the high speciation rate in this group are both a secondary result of strong sexual selection. The high rates of morphological evolution may be tied to sexual selection for aspects of head shape. However, it is difficult to imagine that the variation in size of the adductor mandibulae muscle seen among species of *Scarus* (Fig. 4), which spans most of the range found in parrotfishes, does not have consequences for the feeding ecology of these species. The interplay between sexual selection, functional variation and ecological diversification in parrotfishes remains an area deserving of continued investigation.

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