Fifty million years of herbivory on coral reefs: fossils, fish and functional innovations

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The evolution of ecological processes on coral reefs was examined based on Eocene fossil fishes from Monte Bolca, Italy and extant species from the Great Barrier Reef, Australia. Using ecologically relevant morphological metrics, we investigated the evolution of herbivory in surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae). Eocene and Recent surgeonfishes showed remarkable similarities, with grazers, browsers and even specialized, long-snouted forms having Eocene analogues. These long-snouted Eocene species were probably pair-forming, crevice-feeding forms like their Recent counterparts. Although Eocene surgeonfishes likely played a critical role as herbivores during the origins of modern coral reefs, they lacked the novel morphologies seen in modern Acanthurus and Siganus (including eyes positioned high above their low-set mouths). Today, these forms dominate coral reefs in both abundance and species richness and are associated with feeding on shallow, exposed algal turfs. The radiation of these new forms, and their expansion into new habitats in the Oligocene–Miocene, reflects the second phase in the development of fish herbivory on coral reefs that is closely associated with the exploitation of highly productive short algal turfs.

1. Introduction

Biodiversity, or more specifically taxonomic richness, is often used as a metric for describing changes in ecosystems through time. As a result, we have a good understanding of changes in taxonomic richness over time and the underlying drivers of change [1–4]. However, it is increasingly recognized that it is ecological processes, not species, that shape the evolution of ecosystems [5–9]. Although, it is hard to quantify the nature, importance and strength of ecological processes, especially in high diversity systems [10], it is the changes in ecological processes over time that most clearly reveal factors that underpin the establishment and maintenance of today’s ecosystems.

Coral reefs provide a good example. The complexity of these highly diverse ecosystems creates challenges in identifying ecosystem processes and the roles of organisms in shaping them [11,12]. However, one process stands out as critically important: the removal of algae by fishes. Fish-based herbivory has been implicated in many key aspects of coral reef ecology, including coral recruitment, algal growth and coral recovery after climatic disturbances [12,13]. Herbivory appears to be the single most important driver of benthic community composition on coral reefs and is often the main mechanistic link between human activity and coral reef decline [14,15]. Yet, our understanding of the evolution or historical development of reef herbivory is in its infancy. Fossil evidence suggests that fish-based herbivory on coral reefs was established about 50 Ma in the Eocene [16], marking the time when many modern reef fish families are first recorded in the fossil record [17]. These fossils, from deposits in Monte Bolca in northern Italy, coincide with molecular evidence that points to the Eocene divergence of many reef fish groups [4,8]. Thus, Monte Bolca represents a key fossil deposit at the birth of modern coral reefs.

Although phylogenies have provided invaluable insights into the evolution of fish feeding on coral reefs [18,19], including herbivory [20–22], most of the
2. Material and methods

(a) Material examined

The surgeonfishes (Acanthuridae) and their sister group the Moorish idols (Zanclidae) were selected as the main focal group owing to their numerical abundance and functional importance on Recent coral reefs [31,32] and strong representation in the Eocene fossil record. The rabbitfishes (Siganidae), and their sister group the scats (Scatophagidae), were also examined to provide a broader overview of all major herbivorous reef fish groups recorded from the Eocene.

(b) Data collection and analysis

For each specimen examined, fossil and extant, 19 distance and three angle measurements were collected (electronic supplementary material, S2). Measurements were taken from 110 ‘Randall style’ photographs (in a standard presentation with fins pinned) available online [41,42]. All 42 GBR surgeonfish (and a further four individuals of Zanclus cornutus) species were examined [43]. A further 38 specimens from all 13 species of rabbitfish on the GBR (and 11 specimens from three species of scat) were examined to compare patterns. The surgeonfishes were divided into three groups: the monophyletic Naso (sister to all other acanthurid taxa), the Zebrasoma–Pancanthurus–Prionurus group, a paraphyletic group that subtends Acanthurus (combined to provide a group of adequate size for analysis) and the monophyletic Acanthurus (including Ctenochaetus as a junior synonym [44]).
The abundance of GBR surgeonfishes was estimated using two cross-shelf transects and represents the average fish density across four habitats at each of four inner-, mid- and outer-shelf reefs (following [47]). These abundance data were compared to relative abundance data from Monte Bolca, using the fossils held in the museums visited, as an indication of the relative abundance of Eocene surgeonfishes (electronic supplementary material, S1).

The second multivariate analysis (a PCA) was conducted on five key morphological variables that have been found to relate to pairing behaviour [28]. PC1 scores of extant surgeonfishes and rabbitfishes were plotted against the observed pairing frequency [28], with fossil species placed along the regression line corresponding to their PC1 values, to estimate the likely pairing behaviour of fossil species.

3. Results

The Eocene surgeonfishes of Monte Bolca show remarkable similarity to modern day forms (figure 1). Although there are no genera in common between the two time periods, there is an extensive overlap in morphology and inferred functional capabilities. The morphological measurements clearly delineate major morphological groups, with the ordination separating deep-bodied Zanclus, fusiform Naso and long-snouted Zebrasoma from a broad swathe of more generalized surgeonfish morphologies encompassing Prionurus, Acanthurus and Paracanthurus (figure 2a). Thus, both the Eocene and Recent assemblages have representatives in all extreme (specialized) areas of morphospace, with the sole exception of the more extreme areas occupied by Recent Acanthurus. These areas are not occupied by Eocene taxa.

In terms of potential niche overlap, the Eocene surgeonfish fauna overlaps with 98% of the GBR fauna on PCo1 and 57% on PCo2, with a bivariate area of overlap of 55% (figure 2a). Remarkably, despite the Eocene sample having 12 genera, the functional morphospace occupied is similar to that seen in modern forms with just five genera (electronic supplementary material, S3). The extent of overlap between Eocene and Recent groups, however, varies greatly among the modern clades or groups, from almost complete overlap in the basal Zebrasoma–Paracanthurus–Priornurus group, where Eocene species occupy 98% of the area occupied by extant forms, to 53% overlap with Naso and just 11% overlap with Acanthurus.

This variability is further reflected in the nature of the overlap between taxa. The relatively small area of the Zebrasoma–Paracanthurus–Priornurus group is almost entirely nested (92% of overlap owing to nestedness within the larger fossil morphospace), suggesting the near-complete historical presence of the Zebrasoma–Paracanthurus–Priornurus morphospace. By contrast, the area defined by Naso species shows high turnover (21% overlap owing to nestedness), suggesting that Naso encompasses species with unique morphologies, not recorded in the Eocene fossil record. This is even more extreme in Acanthurus, with almost no overlap (3% overlap owing to nestedness) suggesting that modern Acanthurus occupy morphospace not previously occupied on Eocene reefs (electronic supplementary material, S3). Thus, the Eocene fauna appears to have had representatives that occupy similar morphospace to all extant acanthurid genera with the exception of the bulk of the modern genus Acanthurus (including Ctenochaetus). The importance of the novel Acanthurus morphospace to modern surgeonfishes can be seen in the relative abundance plots (figure 2b). Modern surgeonfish assemblages are overwhelmingly dominated by a few species, most of which lie in the modern Acanthurus morphospace. This space encompasses the majority of modern surgeonfish species and most individuals. Morphologically, this space is characterized by fishes with a large distance between their eyes and their low-set mouth and the presence of a deep caudal peduncle (electronic supplementary material, S4).

The rabbitfishes provide further evidence of the changes seen in surgeonfishes except that modern rabbitfishes appear to have completely abandoned the Eocene morphospace (figure 3). Like the surgeonfishes, the Eocene rabbitfishes also lacked the specialized morphologies seen on Recent reefs,

![Figure 1. The morphology of surgeonfish genera: 12 from the Eocene of Monte Bolca, Italy (left; Tauichthys and Sorbinithurus excluded) and five from the Recent Great Barrier Reef (right). Eocene species, top-bottom: Gazolaichthys vestenanovae, Proacanthurus bonatoi, Lehmanichthys lessiniensis, Tyleichthys nuchalis, Acanthuroideos massalongoi, Eoandallius elegans, Metacanthurus venensis, Metaspisurus emmanueli, Padovathurus gaudryi, P. punctatus, Friggorobinia baldwiniae and Protozebrasoma bloti. Recent species, top-bottom: Naso thynnoides, Zebrasoma scopas, Paracanthurus hepatus, Priornurus maculatus and Acanthurus (prev. Ctenochaetus) striatus.](http://rspb.royalsocietypublishing.org/)
with the modern rabbitfish morphospace again being characterized by fishes with a large distance between their eyes and their low-set mouth (electronic supplementary material, S5).

The morphology of the Eocene surgeonfishes and rabbitfishes also reveals potential behavioural patterns in the history of the groups. Fitting the fossil fishes to a generalized morphological relationship, which describes the degree of pairing in reef fishes, we see a clear spread in both families from the Eocene. Eocene surgeonfishes exceed the range of morphologies seen in extant surgeonfishes and are relatively evenly spread across PC1. Most notably, there are five Eocene surgeonfishes in the strongly pairing region of PC1 (figure 4a; electronic supplementary material, S6). In the rabbitfishes, just one species has a morphology that would suggest it might have lived in pairs (figure 4b). These Eocene species all share the suite of morphological features that are characteristic of pair-forming species on modern coral reefs. These features include large eyes, more concave foreheads, pointed snouts and deep bodies.

4. Discussion

(a) Taxonomic versus functional diversity in Eocene surgeonfishes and rabbitfishes

Through a morphological analysis of surgeonfishes and rabbitfishes, we were able to examine changes in functionally relevant morphological attributes over the last 50 Myr. From the outset, it was clear that the 12 Eocene surgeonfish genera did not occupy proportionally greater morphospace than their extant relatives in five genera. However, it was the nature of the overlap that revealed the most interesting patterns, with striking ecomorphological stasis. Distinctive long-snouted forms in the modern fauna were matched almost exactly in the Eocene, as were fusiform open-water forms. There was also extensive overlap in more generalized surgeonfish morphologies. However, the morphology that characterizes the modern Acanthurus was conspicuously under-represented in the Eocene, indicating a major shift in habitat occupation on modern reefs. Today, Acanthurus occupies a range of habitats including high-energy, low-cover exposed locations. Furthermore, it is these Acanthurus forms that numerically dominate modern reefs. Overall, ancient reefs had surgeonfish genera that occupied all modern morphospace, but with only limited excursion into...
in the Eocene. It appears that both surgeonfishes and rabbitfishes have acquired new morphologies that have permitted the exploitation of novel resources.

(b) Modern surgeonfishes and rabbitfishes exploit a new reef world

For the first quarter of the Caenozoic, parrotfishes were probably absent [40]. The few damselfishes present in the Eocene showed little evidence of herbivory [17], and the rabbitfishes were relatively large-toothed forms [16] (figure 3) that were probably croppers of low algae or browsers of macroalgae or sea grasses. They are morphologically more robust than their more gracile modern counterparts, most of which feed on small turfing algae [48]. This leaves surgeonfishes as the primary vertebrate herbivores on Eocene coral reefs. Surgeonfishes were the numerically and taxonomically dominant fish herbivores in the critical period during the early Caenozoic when modern scleractinian coral groups first expanded, before becoming the dominant reef builders in the Oligocene–Miocene [49,50]. Remarkably, even at this early date, the inferred abilities of Eocene surgeonfishes broadly overlapped those on modern reefs. Our morphological analyses reveal an extensive overlap in the potential abilities of surgeonfishes on modern and ancient reefs. Thus, a recently described novel feeding mode (crevice-feeding specialists [27,28]) was already in place 50 Ma, as were most general herbivore feeding modes. Eocene surgeonfishes would probably have been able to remove algae from most complex reef surfaces, including both large erect macroalgae (by the Naso analogue Gezochichthys) and short turfs by more Acanthurus-like forms (e.g. Proacanthurus and Frigosorbinia). Indeed, the highly characteristic multidenticate Acanthurus tooth form, which is closely associated with feeding on low heavily cropped algal turfs (or the epilithic algal matrix; EAM [9,51,52]), was already present in both Proacanthurus and Protozebrasoma [9,53,54]. The Eocene fauna thus appears to be functionally complete, at least in terms of major feeding modes. However, the Acanthurus morphospace, which most Recent reef surgeonfish occupy, was remarkably under-represented.

What appears to have been largely missing from the Eocene fish fauna were species that could access exposed EAMs. On modern coral reefs, these surfaces are exploited by a wide range of surgeonfish species and it is likely that feeding on this surface gave rise to the highly modified modern detritus-feeding specialists (traditionally placed in the genus Siganus) and short turfs by more Acanthurus-like forms (e.g. Proacanthurus and Frigosorbinia). Indeed, the highly characteristic multidenticate Acanthurus tooth form, which is closely associated with feeding on low heavily cropped algal turfs (or the epilithic algal matrix; EAM [9,51,52]), was already present in both Proacanthurus and Protozebrasoma [9,53,54]. The Eocene fauna thus appears to be functionally complete, at least in terms of major feeding modes. However, the Acanthurus morphospace, which most Recent reef surgeonfish occupy, was remarkably under-represented.

The extent of overlap between the two time periods is emphasized by the quantitative analyses, with almost complete overlap between the Eocene surgeonfishes and the basal Zebrasoma–Paracanthurus–Prionurus group (98%), moderate overlap with Naso (53%) and limited overlap with Acanthurus (11%). These patterns are reinforced by the nature of the overlap, revealing the Zebrasoma group to be almost entirely nested within fossil forms. This suggests that the morphospace occupied by the Zebrasoma group is highly conserved and has been occupied since the Eocene, the two other groups show successively less nestedness and higher turnover (i.e. the emergence of unique morphologies), peaking in 97% of functional turnover defining the dissimilarity between Acanthurus and the fossil assemblage, indicating that these forms are occupying novel morphospace (electronic supplementary material, S3).

The pattern seen in surgeonfishes was even more apparent in the rabbitfishes. The three Eocene rabbitfish genera occupy an area of morphospace that is similar in size to that occupied by the single modern genus. However, there is no overlap: modern rabbitfishes occupy an entirely new area of morphospace, completely abandoning that occupied

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**Figure 4.** The estimated extent of pairing in Eocene (a) surgeonfishes and (b) rabbitfishes based on their morphology. Pairing values for Recent species are based on field observations [28]. PC1 scores are derived from a PCA of five morphological features (electronic supplementary material, S6). Surgeonfish illustrations as per figure 1, Eocene (open circles) rabbitfish illustrations: Acanthopteryx agassizi (top) and Rufiochthys spinosus (bottom), and Recent (filled circles) illustrations: Siganus punctatissimus (top) and S. canaliculatus (bottom; other species labels in the electronic supplementary material, S6).

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**Note:** The text continues with further details and analyses not included in this snippet.
Our data on surgeonfish morphology are supported by molecular evidence, which points to the relatively recent origins of fish groups that exploit this highly productive habitat. This includes surgeonfishes (Acanthurus) at about 26 Ma [44], parrotfishes (Scarus) at about 24 Ma [20] and wrasses (Thalassoma) at 22 Ma [20]. The former two groups exploit the algal or detrital resources in the EAM, the latter feed on crustacea and other invertebrates. All achieve their highest densities on the exposed reef crest or flat [59–61]. Most of this expansion in habitat use appears to have been in the Miocene or later, with surgeonfishes colonizing first, to be joined later by wrasses and parrotfishes. These groups now dominate modern coral reefs and their presence marks the earliest origins of the highly specialized modern coral reef fish faunas and their associated roles in modern reef processes.

It is interesting to note that the parrotfishes appear to follow the same trend as surgeonfishes, with EAM feeding arising before the invasion of shallow waters. In parrotfishes, the oldest lineages encompass a broad range of feeding modes, including EAM-scraping forms, with the taxa that are most closely associated with feeding on the high-productivity reef flat arising within the last 5 Ma [20–22]. In the rabbitfishes, Eocene morphologies have been completely replaced by the modern forms, many of which feed on EAMs, often in exposed reef locations [62].

There are many benefits of accessing such exposed habitats. They often cover huge areas of the reef, thus presenting extensive untapped resources for fishes. They support EAMs, potentially one of the most nutritious food resources on coral reefs [51]. Furthermore, they occur predominantly in shallow water where productivity rates are the highest [63]. It is clear why these areas support the highest densities of herbivores on modern reefs. However, they also represent some of the most dangerous locations. Studies have repeatedly highlighted the limitations to herbivory in these regions as a result of predation risk [48,61] and documented herbivore responses to predation risk are widespread [64–66]. The appearance of morphologies that may reduce predation would thus be expected in association with this expanded into exposed locations. This is entirely consistent with observed morphological changes seen in both surgeonfishes and rabbitfishes.

The main aspects that characterize the ‘new’ acanthurid morphospace are the increased distance between the eye and mouth and a deep caudal peduncle. While the movement of the eye position may initially appear to be counterproductive when locating food, visual acuity is likely to be of limited importance for feeding on a low, 1–5 mm, tightly cropped EAM [45], where the capacity to visually select algae is limited. It may be that EAM feeding is strongly correlated with caudal fin aspect ratio (deep peduncle = low aspect ratio; electronic supplementary material, S2). In a fish that feeds on algae and detritus, the high acceleration inherent in a low aspect ratio fin is thus most likely to be associated with fast starts and a sudden burst for cover, rather than securing prey. This new surgeonfish morphospace, therefore, is characterized by fishes that are likely to be slightly better at both detecting and avoiding predators, a useful combination in exposed locations.

The rabbitfishes present independent evidence for the general trends seen in surgeonfishes. Like their surgeonfish counterparts, modern rabbitfish morphospace is characterized by an increased mouth to eye distance, with the associated potential for predation avoidance. However, modern rabbitfishes do not have a broader caudal peduncle. In the rabbitfishes, venomous spines and behavioural modifications [28,62] may have alleviated the need for the rapid acceleration that is suggested by the surgeonfish morphology.

The use of the reef flat (as an example of an exposed location) has many parallels. Among the Labridae, we see extensive use of this habitat in parrotfishes and Thalassoma [60]. In both cases, the possession of a high-aspect ratio pectoral fin may have been an important precursor, permitting fish to cover great distances or to retain positions in areas of high water flow with greater energetic efficiency [67]. Interestingly, many surgeonfish species, especially Acanthurus, have high-aspect ratio pectoral fins [68], which suggest that this fin shape may have also been important in permitting the colorization of exposed habitats.

It is possible that the lack of Acanthurus-like morphologies in the Eocene is a result of an aspect of the Lagerstätten effect, with a large number of taxa being recovered from a location characterized by a limited range of habitats; perhaps the Bolca region lacked exposed reef habitats. This is unlikely, however, as the deposits are time averaged with numerous biotopes represented, from coastal regions to the open ocean. Fish fossils include open-water forms, such as menids, sphyraenids, scobiromids, carangids and exellids [17,33,69]. The absence of one particular morphology owing to preservation bias also seems unlikely, given the wide range of taxa recovered from the deposits, ranging from small damselfishes and benthic flatfishes to sharks, with no apparent preservation bias (at least for fishes) [17,33]. The fishes were preserved in silty calm basins some distance from the habitats they occupied and the deposits appear to include all benthic fish taxa regardless of their ecology. Furthermore, all surgeonfish groups Acanthurus occupy more habitats and are more abundant in reef and off-reef habitats than any other genus [43]. It may be that Acanthurus-like forms have yet to be found, as many species are based on just one specimen and new Bolca species continue to be discovered. However, the lack of Acanthurus-like morphologies is consistent with current molecular evidence, which suggests that groups with this morphology arose only recently (approx. 21 Ma [44]) Furthermore, the proposed shift in surgeonfish morphologies is supported by the rabbitfishes, where the three Eocene genera and one Recent genus show minimal overlap in morphospace (figures 2 and 3). Like the surgeonfishes, there is a shift from relatively robust jawed morphologies in the Eocene to the more gracile modern forms, a change that may reflect a shift from browsing in areas where macroalgae or sea grass are abundant to cropping more open EAM-dominated areas as seen in many extant rabbitfishes [62].

(c) Did Eocene surgeonfishes and rabbitfishes swim in pairs?

One of the most interesting findings is the early representation of surgeonfishes with elongate snouts. Recently described as a distinct functional group among herbivores on coral reefs [27,28], the presence of an elongate snout has been associated in Recent surgeonfishes and rabbitfishes.
with crevice-feeding and pair-formation; pair-formation being hypothesized as a response to enhanced predation risk when feeding in holes [28].

The presence of five Eocene surgeonfish species and one rabbitfish species with morphologies (large eyes, flat or concave foreheads, pointed snouts, deep bodies) that are consistently associated with pairing in extant reef fish families, including surgeonfishes and rabbitfishes [28], strongly suggests that at least some of these extinct species were pair-forming on the reefs and hard grounds in the vicinity of Monte Bolca 50 Ma. Furthermore, given the strong association between these morphologies and crevice-feeding, there is a very strong possibility that these Eocene species also fed on algae in crevices. Today, crevices may be an important location for the early life-history stages of both corals and algae [27,28,70]. Feeding in these microhabitats in the Eocene may thus have been important in changing the competitive balance between corals and algae at this time. Thus, at the dawn of modern coral reefs, the coral-reefing regions of what is now northern Italy were replete with a broad range of fish herbivores, with surgeonfishes filling almost all herbivorous niches. Overall, morphological analyses established the presence of highly specialized surgeonfishes on early coral reefs. These probably include crevice-feeding pairing fishes, macroalgal browsing forms and species able to feed on short algal turfs (EAMs). However, the Acanthurus forms that numerically dominate modern reefs were conspicuously absent. In these modern forms, a repositioning of the eye and deepening of the caudal peduncle may have been critical to the exploitation of exposed high-productivity locations. Nevertheless, surgeonfishes were probably the most important fish herbivores on Eocene coral reefs where they are likely to have played a central role in mediating coral–algal interactions and in shaping the evolution of modern coral reefs.

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