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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

detail is restricted to events during the last 30 Myr when most extant genera arose. Relatively little is known of the earliest origins of herbivory, and it is here that fossils are most useful in revealing both the taxa present and the morphological and inferred functional abilities of fishes at this time. However, so far, our ability to use the evidence from Monte Bolca to explore the historical origins, extent and nature of fish-based herbivory has been limited.

Fortunately, three major advances have opened a window of opportunity. (i) Recent fossil discoveries have markedly increased the number of herbivorous reef fish fossils. Today, in both surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae), the number of fossil genera greatly exceeds Recent taxonomic diversity [23,24]. This is most marked in the surgeonfishes where we have 14 Eocene genera compared to just five genera today [24]. In rabbitfishes, we have three Eocene genera versus one today [23]. These two families dominated piscine herbivory on Eocene reefs as the other major herbivorous taxon on Recent reefs, the parrotfishes, were absent until the Oligocene [8]. The only other potential herbivorous reef fish group known from the Eocene is the damselfishes (Pomacentridae), which is represented by just two specimens, with no indication of herbivory [17,25]. Thus by examining the surgeonfishes and rabbitfishes in the Eocene, we are able to gain insights into not just two families, but fish herbivory in general in this critical period. (ii) Recent functional analyses have revealed a striking relationship between morphology and feeding behaviour in herbivorous reef fishes [26,27], with clear links between feeding mode and head morphology [28]. (iii) Finally, new analytical approaches have provided a means of quantitatively examining changes in the functional morphospace occupied by species or assemblages through time, and the extent of overlap [29,30]. When combined, these advances provide us, for the first time, with the ability to examine the nature of herbivory in the past and to understand the extent to which important ecological processes on coral reefs may have changed through time.

Our goal therefore, is to examine the evolution of fish-based herbivory on coral reefs. Specifically, we wish to identify the role of herbivorous fishes on early reefs. There are three key questions: (i) to what extent has surgeonfish and rabbitfish functional morphospace changed over time and what does this indicate with regard to herbivore feeding abilities? (ii) Does higher taxonomic diversity (generic richness) in surgeonfishes and rabbitfishes equate to broader morphological and functional complexity? (iii) Did Eocene surgeonfishes and rabbitfishes feed in pairs like their modern counterparts? With this information, we will be able to look back on ancient coral reefs and explore how, and where, the fishes fed and what potential role they played in the evolution of coral reef ecosystems.

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.

All fossil fishes were from the Monte Bolca Lagerstätte, Northern Italy [17], with the majority from a single locality (Pesciara; electronic supplementary material, S1). These exceptionally well-preserved Eocene deposits (Ypresian/Lutetian boundary ca 50 Ma) were in the Tethys Sea close to the Eocene centre of marine biodiversity [3]. Although deposited in relatively deep calm water, the adjacent ecosystems appear to have included coastal systems, seagrass beds and coral-bearing hard grounds with connections to the open ocean [17,33].

Extant taxa were based on the Great Barrier Reef (GBR) fish assemblage. This location likewise contains a wide range of habitats from coastal to oceanic systems and lies close to the modern centre of biodiversity for reef fishes [34]. It contains representatives of all extant surgeonfish and rabbitfish genera. Modern reef fish assemblages show extensive overlap between locations [35] and, as such, the GBR supports the full range of modern surgeonfish and rabbitfish morphologies.

Fossil fish measurements were taken from photographic records of material held in major museums (Muséum National d'Histoire Naturelle, Paris; Museo Civico di Storia Naturale (MCSN), Verona; Naturhistorisches Museum, Vienna; the Natural History Museum, London). Specimens were fully articulated and complete, with the sole exception of *Frigosorbinia baldwinae* (MCSNV I.G. 24490) where we substituted the caudal fin of the closely related *Pesciarichthys punctatus* [36,37]. In total, 26 surgeonfish specimens were analysed, encompassing 12 of the 14 currently known Eocene genera and 17 of the 20 known species. Two *Tauichthys* species were excluded as they were based on larval individuals (less than 30 mm standard length [38,39]) and *Sorbinithurus* was excluded as the fossil is incomplete [40]. In a separate analysis, three fossil rabbitfish genera were also examined using the same methods as for the surgeonfishes.

Recent fish 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−Paracanthurus−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]).

(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 selected that linked morphological characters to functional attributes (e.g. feeding, swimming, sensory). A total of 18 fractions were calculated from the measurements (electronic supplementary material, S2). To correct for allometry, the fraction values for each species were plotted against standard length. Where a significant relationship was found, residuals were calculated. To allow for data transformations, negative values were removed from the residual data by adding a constant (the lowest number in the column +0.01 [45]). The mean of the corrected fractions was then calculated for each species and the data were used to conduct a principal coordinates analysis (PCoA). The PCoA was based on a Gower's dissimilarity matrix [46] to accommodate the heterogeneous nature of the morphological data (a PCoA based on a Bray−Curtis dissimilarity matrix explained 5% more variance overall but was rejected owing to the statistical robustness of the Gower's matrix). The area of morphospace occupied by the Eocene and Recent surgeonfish assemblages was then calculated, and the nature of overlap was quantified [29,30].
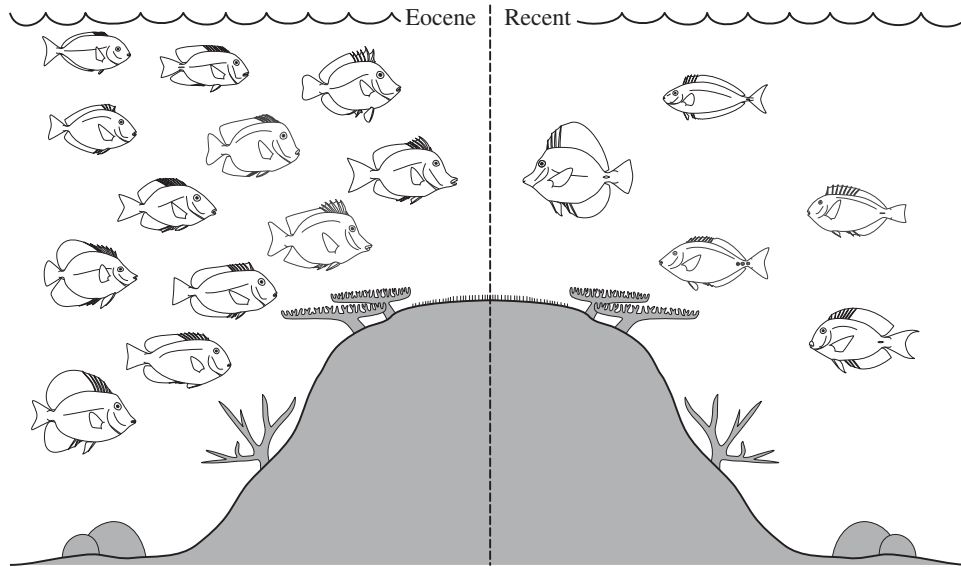
Figure 1. The morphology of surgeonfish genera: 12 from the Eocene of Monte Bolca, Italy (left; *Tauichthys* and *Sorbinithurus* excluded) and five from the Recent Great Barrier Reef (right). Eocene species, top-bottom: *Gazolaichthys vestenanovae, Proacanthurus bonatoi, Lehmanichthys lessiniensis, Tylerichthys nuchalis, Acanthuroides massalongoi, Eorandallius elegans, Metacanthurus veronensis, Metaspisurus emmanueli, Padovathurus gaudryi, P. punctatus, Frigosorbinia baldwinae* and *Protozebrasoma bloti*. Recent species, top-bottom: *Naso thynnoides, Zebrasoma scopas, Paracanthurus hepatus, Prionurus maculatus* and *Acanthurus* (prev. *Ctenochaetus*) *striatus*.

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–Prionurus* 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–Prionurus* 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–Prionurus* 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).
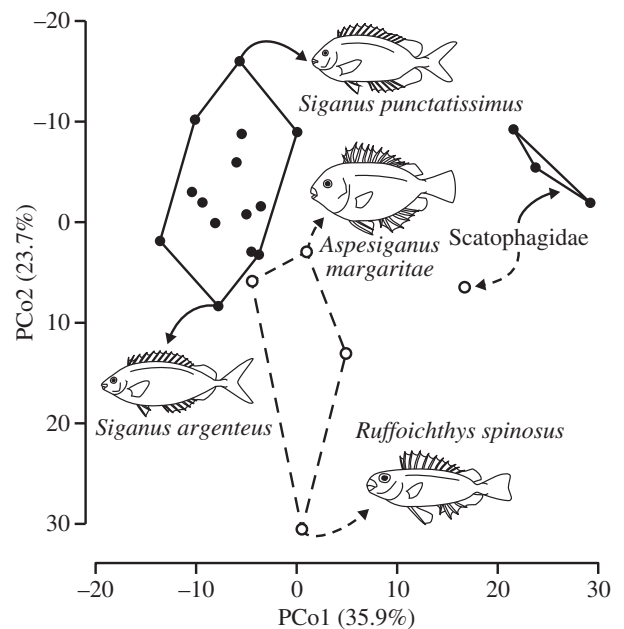
The rabbitfishes provide further evidence of the changes seen in surgeonfishes except that modern rabbitfishes appear to have completely abandoned the Eocene morphospace (figure 3). Like the surgeonfishes, the Eocene rabbitfishes also lacked the specialized morphologies seen on Recent reefs,
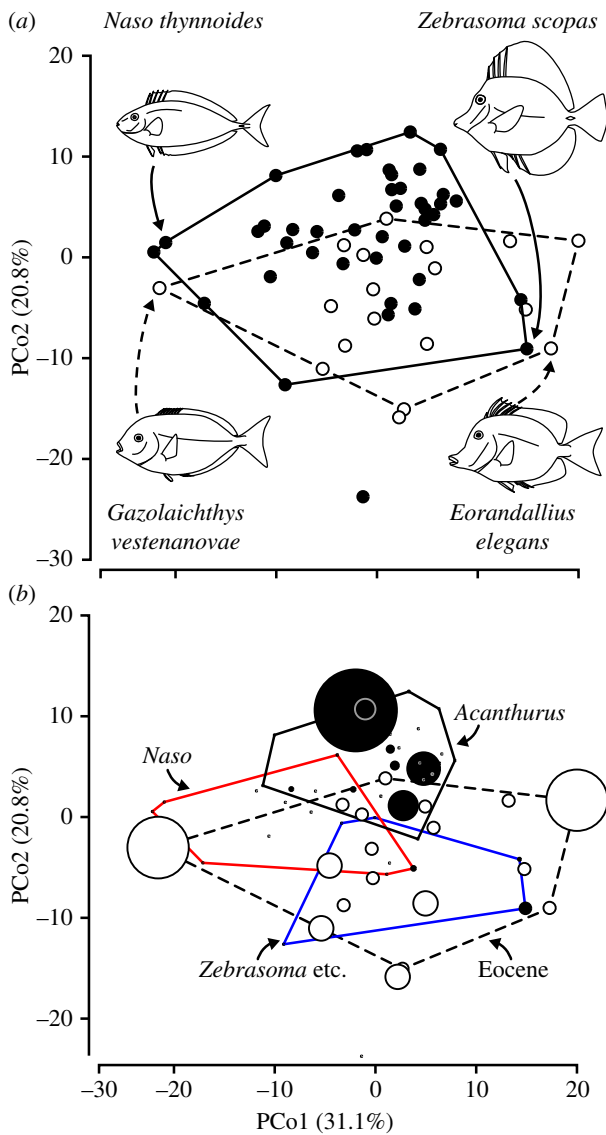
Figure 2. (*a*) PCoA created using 17 morphological fractions from Eocene and Recent surgeonfish (and zanclid) fishes (electronic supplementary material, S2). Filled circles represent Recent fishes and open circles Eocene fishes. The solid line shows the area of morphospace occupied by Recent surgeonfishes and the dashed line the morphospace of Eocene surgeonfishes. *Zanclus cornutus* and its Eocene counterpart *Eozanclus brevirostris* sit outside these polygons with low PCo2 scores. Line drawings of Recent (top) and Eocene (bottom) forms highlight the separation of fusiform and deep-bodied morphologies along PCo1 (vectors and species labels available in the electronic supplementary material, S4). (*b*) The areas of morphospace occupied by the three recent surgeonfish groups: *Acanthurus* (inc. *Ctenochaetus*; black line), *Naso* (red line) and *Zebrasoma*, *Paracanthurus* and *Prionurus* group (blue line). The size of filled circles represents the relative abundance of each species on the GBR and open circles the relative abundance of fossils found at Monte Bolca (scales not comparable between Eocene and Recent; Eocene values range from one to five individuals, Recent 0 to 188 fish ha^{-1}). (Online version in colour.)
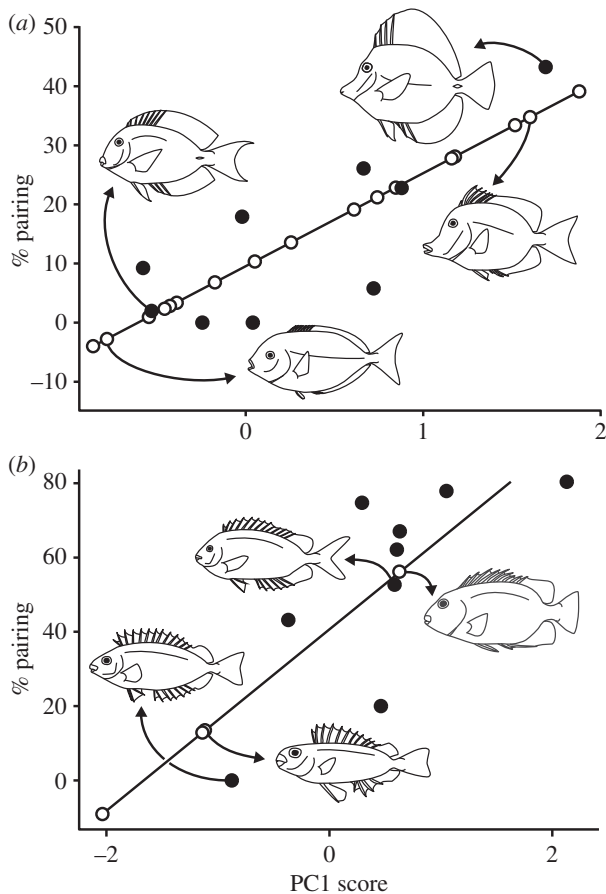
Figure 3. A comparison of Eocene and Recent rabbitfishes (and scats) based on a PCoA of 17 morphological fractions (electronic supplementary material, S2). Filled circles represent Recent fishes and open circles Eocene fishes. The solid line shows the area of morphospace occupied by Recent rabbitfishes, the dashed line Eocene rabbitfishes (vectors and species labels available in the electronic supplementary material, S5).

evenly spread across PC1. Most notably, there are five Eocene surgeonfishes in the strongly pairing region of PC1 (figure 4*a*; electronic supplementary material, S6). In the rabbitfishes, just one species has a morphology that would suggest it might have lived in pairs (figure 4*b*). 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

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

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: *Acanthopygaeus agassizi* (top) and *Ruffoichthys spinosus* (bottom), and Recent (filled circles) illustrations: *Siganus punctatissimus* (top) and *S. canaliculatus* (bottom; other species labels in the electronic supplementary material, S6).

those morphologies that characterize species, which exploit exposed, high-turnover shallow reef habitats: the essence of a high-productivity modern coral reef.

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

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 *Gazolaichthys*) and short turfs by more *Acanthurus*-like forms (e.g. *Proacanthurus* and *Frigosorbinia*). Indeed, the highly characteristic multidenticulate *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 *Ctenochaetus*). Today, a single lineage (*Acanthurus* inc. *Ctenochaetus*) dominates herbivory on coral reefs both numerically and in terms of species richness [55–58]. The observed changes in surgeonfish morphology and inferred abilities strongly support a proposed two-phase development of coral reef ecosystems, with the first wave in the Eocene and the second wave of highly specialized forms arising in the Oligocene or Miocene [8,9,20]. This second phase was originally characterized by the presence of feeding forms with strong links to fast-growing, highly productive components of the reef benthos [8,9,18,20,21]. It also coincided with an expansion of carbonate platforms in the IAA, an increase in the importance of *Acropora* in reef systems, a movement of marine biodiversity to the IAA and the rapid cladogenesis of major reef fish groups [3,4,8]. Based on the evidence from surgeonfishes, this period also appears to mark the invasion of a new reef habitat by fishes: the reef crest and reef flat.

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 expansion 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. However, more dorsally positioned eyes are likely to markedly increase the ability of fishes to detect approaching predators when feeding in a head-down position. While high eyes may increase predator detection, a deep caudal peduncle is likely to enhance predator avoidance. Caudal peduncle depth 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 colonization 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, scombrids, carangids and exelliids [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, of 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-forming 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-bearing 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.

References

1. Raup DM, Sepkoski JJ. 1982 Mass extinctions in the marine fossil record. *Science* **215**, 1501–1503. (doi:10.1126/science.215.4539.1501)

2. Alroy J *et al*. 2008 Phanerozoic trends in the global diversity of marine invertebrates. *Science* **321**, 97–100. (doi:10.1126/science.1156963)

3. Renema W *et al*. 2008 Hopping hotspots: global shifts in marine biodiversity. *Science* **321**, 654–657. (doi:10.1126/science.1155674)

4. Cowman PF, Bellwood DR. 2013 The historical biogeography of coral reef fishes: global patterns of origination and dispersal. *J. Biogeogr.* **40**, 209–224. (doi:10.1111/jbi.12003)

5. Vermeij G. 1977 The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* **3**, 245–258.

6. Jablonski D, Sepkoski Jr JJ. 1996 Paleobiology, community ecology, and scales of ecological pattern. *Ecology* **77**, 1367–1378. (doi:10.2307/2265534)

7. Goatley CHR, Bellwood DR, Bellwood O. 2010 Fishes on coral reefs: changing roles over the past 240 million years. *Paleobiology* **36**, 415–427. (doi:10.1666/09035.1)

8. Cowman PF, Bellwood DR. 2011 Coral reefs as drivers of cladogenesis: expanding coral reefs, cryptic extinction events, and the development of biodiversity hotspots. *J. Evol. Biol.* **24**, 2543–2562. (doi:10.1111/j.1420-9101.2011.02391.x)

9. Bellwood DR, Hoey AS, Bellwood O, Goatley CHR. 2014 Evolution of long-toothed fishes and the changing nature of fish–benthos interactions on coral reefs. *Nat. Commun.* **5**, 3144. (doi:10.1038/ncomms4144)

10. Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR. 2013 A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* **28**, 167–177. (doi:10.1016/j.tree.2012.10.004)

11. Done TJ, Ogden JC, Wiebe WJ, Rosen BR. 1996 Biodiversity and ecosystem function of coral reef. In *Functional roles of biodiversity: a global perspective* (eds HA Mooney, JH Cushman, E Medina, OE Sala, E-D Schulze), pp. 393–429. Chichester, UK: John Wiley and Sons, Ltd.

12. Bellwood DR, Hughes TP, Folke C, Nyström M. 2004 Confronting the coral reef crisis. *Nature* **429**, 827–833. (doi:10.1038/nature02691)

13. Hughes TP *et al*. 2007 Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* **17**, 360–365. (doi:10.1016/j.cub.2006.12.049)

14. Hughes TP, Linares C, Dakos V, van de Leemput IA, van Nes EH. 2013 Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends Ecol. Evol.* **28**, 149–155. (doi:10.1016/j.tree.2012.08.022)

15. Roff G, Clark TR, Reymond CE, Zhao J, Feng Y, McCook LJ, Done TJ, Pandolfi JM. 2013 Palaeoecological evidence of a historical collapse of corals at Pelorus Island, inshore Great Barrier Reef, following European settlement. *Proc. R. Soc. B* **280**, 20122100. (doi:10.1098/rspb.2012.2100)

16. Bellwood DR. 2003 Origins and escalation of herbivory in fishes: a functional perspective. *Paleobiology* **29**, 71–83. (doi:10.1666/0094-8373(2003)029<0071:OAEOHI>2.0.CO;2)

17. Bellwood DR. 1996 The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. *Coral Reefs* **15**, 11–19. (doi:10.1007/s003380050025)

18. Bellwood DR, Klanten S, Cowman PF, Pratchett MS, Konow N, van Herwerden L. 2010 Evolutionary history of the butterflyfishes (f: Chaetodontidae) and the rise of coral feeding fishes. *J. Evol. Biol.* **23**, 335–349. (doi:10.1111/j.1420-9101.2009.01904.x)

19. Frédérich B, Sorenson L, Santini F, Slater GJ, Alfaro ME. 2013 Iterative ecological radiation and convergence during the evolutionary history of damselfishes (Pomacentridae). *Am. Nat.* **181**, 94–113. (doi:10.1086/668599)

20. Cowman PF, Bellwood DR, van Herwerden L. 2009 Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. *Mol. Phylogenet. Evol.* **52**, 621–631. (doi:10.1016/j.ympev.2009.05.015)

21. Price SA, Wainwright PC, Bellwood DR, Kazancioglu E, Collar DC, Near TJ. 2010 Functional innovations and morphological diversification in parrotfish. *Evolution* **64**, 3057–3068. (doi:10.1111/j.1558-5646.2010.01036.x)

22. Choat JH, Klanten OS, van Herwerden L, Robertson DR, Clements KD. 2012 Patterns and processes in the evolutionary history of parrotfishes (Family Labridae). *Biol. J. Linn. Soc.* **107**, 529–557. (doi:10.1111/j.1095-8312.2012.01959.x)

23. Bannikov AF, Tyler JC, Sorbini C. 2010 Two new taxa of Eocene rabbitfishes (Perciformes, Siganidae) from the North Caucasus (Russia), with redescription of *Acanthopygaeus agassizi* (Eastman) from Monte Bolca (Italy) and a phylogenetic analysis of the family. *Boll. del Mus. Civ. di Stor. Nat. di Verona Geol. Paleontol. Preist.* **34**, 3–21.

24. Tyler JC, Micklich NR. 2011 A new genus and species of surgeon fish (Perciformes, Acanthuridae) from the Oligocene of Kanton Glarus, Switzerland. *Swiss J. Palaeontol.* **130**, 203–216. (doi:10.1007/s13358-011-0016-5)

25. Bellwood DR, Sorbini L. 1996 A review of the fossil record of the Pomacentridae (Teleostei: Labroidei) with a description of a new genus and species from the Eocene of Monte Bolca, Italy. *Zool. J. Linn. Soc.* **117**, 159–174. (doi:10.1111/j.1096-3642.1996.tb02154.x)

26. Goatley CHR, Bellwood DR. 2009 Morphological structure in a reef fish assemblage. *Coral Reefs* **28**, 449–457. (doi:10.1007/s00338-009-0477-9)

27. Fox RJ, Bellwood DR. 2013 Niche partitioning of feeding microhabitats produces a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. *Coral Reefs* **32**, 13–23. (doi:10.1007/s00338-012-0945-5)

28. Brandl SJ, Bellwood DR. 2013 Morphology, sociality, and ecology: can morphology predict pairing behavior in coral reef fishes? *Coral Reefs* **32**, 835–846. (doi:10.1007/s00338-013-1042-0)

29. Villéger S, Novack-Gottshall PM, Mouillot D. 2011 The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecol. Lett.* **14**, 561–568. (doi:10.1111/j.1461-0248.2011.01618.x)

30. Brandl SJ, Bellwood DR. 2014 Individual-based analyses reveal limited functional overlap in a coral reef fish community. *J. Anim. Ecol.* (doi:10.1111/1365-2656.12171)

31. Hoey AS, Bellwood DR. 2009 Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* **12**, 1316–1328. (doi:10.1007/s10021-009-9291-z)

32. Goatley CHR, Bellwood DR. 2010 Biologically mediated sediment fluxes on coral reefs: sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus*. *Mar. Ecol. Prog. Ser.* **415**, 237–245. (doi:10.3354/meps08761)

33. Landini W, Sorbini L. 1996 Ecological and trophic relationships of Eocene Monte Bolca (Pesciara) fish fauna. In *Autecology of selected fossil organisms: achievements and problems*, vol. 3 (ed. A Cherchi), pp. 105–112. Modena, Italy: Bollettino della Società Paleontologica Italiana.

34. Bellwood DR, Hughes TP, Connolly SR, Tanner J. 2005 Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecol. Lett.* **8**, 643–651. (doi:10.1111/j.1461-0248.2005.00763.x)

35. Bellwood DR, Hughes TP. 2001 Regional-scale assembly rules and biodiversity of coral reefs. *Science* **292**, 1532–1535. (doi:10.1126/science.1058635)

36. Sorbini L, Tyler JC. 1998 A new species of the Eocene surgeon fish genus *Pesciarichthys* from Monte Bolca, Italy, with comments on caudal peduncle armature and supraneurals in acanthurids. *Stud. e Richerche sui Giacimenti Terziari di Bolca, Mus. Civ. di Stor. Nat. di Verona Misc. Paleontol.* **7**, 21–34.

37. Bannikov AF, Tyler JC. 2012 Redescription of the Eocene of Monte Bolca, Italy, surgeon fish *Pesciarichthys punctatus* (Perciformes, Acanthuridae), and a new genus, Frigosorbinia, for *P. baldwinae*. *Stud. e Richerche sui Giacimenti Terziari di Bolca, Mus. Civ. di Stor. Nat. di Verona Misc. Paleontol.* **14**, 19–30.

38. Tyler JC. 1999 A new genus and species of surgeon fish (Acanthuridae) with four dorsal-fin spines from the Eocene of Monte Bolca, Italy. *Stud. e Richerche sui Giacimenti Terziari di Bolca Mus. Civ. di Stor. Nat. di Verona, Misc. Paleontol.* **8**, 257–268.

39. Tyler JC, Bannikov AF. 2000 A new species of the surgeon fish genus *Tauichthys* from the Eocene of Monte Bolca, Italy (Perciformes, Acanthuridae). *Boll.*

del Mus. Civ. di Stor. Nat. di Verona Geol. Paleontol. Preist. **24**, 29–36.

40. Tyler JC. 1999 A new genus and species of surgeon fish (Acanthuridae) with a unique dorsal-fin pterygiophore arrangement from the Eocene of Monte Bolca, Italy. *Stud. e Richerche sui Giacimenti Terziari di Bolca, Mus. Civ. di Stor. Nat. di Verona, Misc. Paleontol.* **8**, 245–256.

41. Froese R, Pauly D. 2013 FishBase, ver. 10/2013. See www.fishbase.org.

42. FishwisePro. 2013 Fishwise Pro. See www.fishwisepro.com.

43. Randall JE, Allen GR, Steene RC. 1997 *Fishes of the great barrier reef and coral sea*. Honolulu, HI: University of Hawai'i Press.

44. Sorenson L, Santini F, Carnevale G, Alfaro ME. 2013 A multi-locus timetree of surgeonfishes (Acanthuridae, Percomorpha), with revised family taxonomy. *Mol. Phylogenet. Evol.* **68**, 150–160. (doi:10.1016/j.ympev.2013.03.014)

45. Goatley CHR, Bellwood DR. 2013 Ecological consequences of sediment on high-energy coral reefs. *PLoS ONE* **8**, e77737. (doi:10.1371/journal.pone.0077737)

46. Gower JC. 1971 A general coefficient of similarity and some of its properties. *Biometrics* **27**, 857–874. (doi:10.2307/2528823)

47. Wismer S, Hoey AS, Bellwood DR. 2009 Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Mar. Ecol. Prog. Ser.* **376**, 45–54. (doi:10.3354/meps07790)

48. Hay ME. 1981 Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat. Bot.* **11**, 97–109. (doi:10.1016/0304-3770(81)90051-6)

49. Wood R. 1999 *Reef evolution*. Oxford, UK: Oxford University Press.

50. Kiessling W. 2009 Geologic and biologic controls on the evolution of reefs. *Annu. Rev. Ecol. Evol. Syst.* **40**, 173–192. (doi:10.1146/annurev.ecolsys.110308.120251)

51. Wilson SK, Bellwood DR, Choat JH, Furnas MJ. 2003 Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanogr. Mar. Biol. Annu. Rev.* **41**, 279–309.

52. Purcell SW, Bellwood DR. 1993 A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). *Environ. Biol. Fishes* **37**, 139–159. (doi:10.1007/BF00000589)

53. Blot J, Tyler JC. 1990 New genera and species of fossil surgeon fishes and their relatives (Acanthuroidei, Telesostei) from the Eocene of Monte Bolca, Italy, with application of the Blot formula to both fossil and recent forms. *Stud. e Richerche sui Giacimenti Terziari di Bolca, Mus. Civ. di Stor. Nat. di Verona Misc. Paleontol.* **6**, 13–92.

54. Sorbini L, Tyler JC. 1998 A new genus and species of Eocene surgeon fish (Acanthuridae) from Monte Bolca, Italy, with similarities to the Recent *Zebrasoma*. *Stud. e Richerche sui Giacimenti Terziari di Bolca, Mus. Civ. di Stor. Nat. di Verona Misc. Paleontol.* **7**, 21–34.

55. Choat JH, Bellwood DR. 1985 Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. *Mar. Biol.* **89**, 221–234. (doi:10.1007/BF00393655)

56. Choat JH, Axe LM. 1996 Growth and longevity in acanthurid fishes: an analysis of otolith increments. *Mar. Ecol. Prog. Ser.* **134**, 15–26. (doi:10.3354/meps134015)

57. Bellwood DR, Wainwright PC. 2002 The history and biogeography of fishes on coral reefs. In *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. PF Sale), pp. 5–32. San Diego, CA: Academic Press.

58. Jones GP, McCormick MI, Srinivasan M, Eagle JV. 2004 Coral decline threatens fish biodiversity in marine reserves. *Proc. Natl Acad. Sci. USA* **101**, 8251–8253. (doi:10.1073/pnas.0401277101)

59. Russ G. 1984 Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser.* **20**, 23–34. (doi:10.3354/meps020023)

60. Bellwood DR, Wainwright PC. 2001 Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* **20**, 139–150. (doi:10.1007/s003380100156)

61. Fox RJ, Bellwood DR. 2007 Quantifying herbivory across a coral reef depth gradient. *Mar. Ecol. Prog. Ser.* **339**, 49–59. (doi:10.3354/meps339049)

62. Hoey AS, Brandl SJ, Bellwood DR. 2013 Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. *Coral Reefs* **32**, 973–984. (doi:10.1007/s00338-013-1043-z)

63. Steneck RS. 1988 Herbivory on coral reefs: a synthesis. In *Proc. 6th Int. Coral Reef Symp., Townsville, Australia*, pp. 37–49. Ithaca, NY: Cornell University.

64. Randall JE. 1965 Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* **46**, 255–260. (doi:10.2307/1936328)

65. Madin EMP, Madin JS, Booth DJ. 2011 Landscape of fear visible from space. *Sci. Rep.* **1**, 14. (doi:10.1038/srep00014)

66. Hoey AS, Bellwood DR. 2011 Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecol. Lett.* **14**, 267–273. (doi:10.1111/j.1461-0248.2010.01581.x)

67. Fulton CJ, Bellwood DR, Wainwright PC. 2001 The relationship between swimming ability and habitat use in wrasses (Labridae). *Mar. Biol.* **139**, 25–33. (doi:10.1007/s002270100565)

68. Fulton CJ, Bellwood DR. 2005 Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnol. Oceanogr.* **50**, 255–264. (doi:10.4319/lo.2005.50.1.0255)

69. Monsch KA. 2006 A revision of scombrid fishes (Scombroidei, Perciformes) from the Middle Eocene of Monte Bolca, Italy. *Paleontology* **49**, 873–888. (doi:10.1111/j.1475-4983.2006.00566.x)

70. Brandl SJ, Hoey AS, Bellwood DR. 2013 Micro-topography mediates interactions between corals, algae, and herbivorous fishes on coral reefs. *Coral Reefs*. (doi:10.1007/s00338-013-1110-5)