



Research

Cite this article: Konow N, Price S, Abom R, Bellwood D, Wainwright P. 2017 Decoupled diversification dynamics of feeding morphology following a major functional innovation in marine butterflyfishes. *Proc. R. Soc. B* **284**: 20170906.
<http://dx.doi.org/10.1098/rspb.2017.0906>

Received: 27 April 2017

Accepted: 26 June 2017

Subject Category:

Morphology and biomechanics

Subject Areas:

biomechanics, ecology, evolution

Keywords:

functional disparity, biting feeding mode, design breakthrough, ecological threshold, key innovation, Chaetodontidae

Author for correspondence:

Nicolai Konow

e-mail: nicolai_konow@uml.edu

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.3825523.v4>.

Decoupled diversification dynamics of feeding morphology following a major functional innovation in marine butterflyfishes

Nicolai Konow¹, Samantha Price^{2,3}, Richard Abom⁴, David Bellwood^{4,5} and Peter Wainwright²

¹Department of Biological Sciences, University of Massachusetts Lowell, Lowell, MA 01852, USA

²Department of Evolution and Ecology, UC Davis, Davis, CA 95616, USA

³Department of Biological Sciences, Clemson University, Clemson, SC 29634, USA

⁴School of Marine and Tropical Biology, and ⁵ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia

NK, 0000-0003-3310-9080; SP, 0000-0002-1389-8521

The diversity of fishes on coral reefs is influenced by the evolution of feeding innovations. For instance, the evolution of an intramandibular jaw joint has aided shifts to corallivory in *Chaetodon* butterflyfishes following their Miocene colonization of coral reefs. Today, over half of all *Chaetodon* species consume coral, easily the largest concentration of corallivores in any reef fish family. In contrast with *Chaetodon*, other chaetodontids, including the long-jawed bannerfishes, remain less intimately associated with coral and mainly consume other invertebrate prey. Here, we test (i) if intramandibular joint (IMJ) evolution in *Chaetodon* has accelerated feeding morphological diversification, and (ii) if cranial and post-cranial traits were affected similarly. We measured 19 cranial functional morphological traits, gut length and body elongation for 33 Indo-Pacific species. Comparisons of Brownian motion rate parameters revealed that cranial diversification was about four times slower in *Chaetodon* butterflyfishes with the IMJ than in other chaetodontids. However, the rate of gut length evolution was significantly faster in *Chaetodon*, with no group-differences for body elongation. The contrasting patterns of cranial and post-cranial morphological evolution stress the importance of comprehensive datasets in ecomorphology. The IMJ appears to enhance coral feeding ability in *Chaetodon* and represents a design breakthrough that facilitates this trophic strategy. Meanwhile, variation in gut anatomy probably reflects diversity in how coral tissues are procured and assimilated. Bannerfishes, by contrast, retain a relatively unspecialized gut for processing invertebrate prey, but have evolved some of the most extreme cranial mechanical innovations among bony fishes for procuring elusive prey.

1. Introduction

The roughly 6000 species of fishes inhabiting coral reefs exhibit tremendous trophic diversity, enabled in part by impressive functional innovations within the feeding apparatus [1,2]. These functional innovations, for instance, include protrusible jaws that provide the mechanical basis for an impressive ability in many fishes to obtain food using a suction feeding mode [3–5]. Moreover, a separate pharyngeal jaw apparatus, set deep within the oral cavity, allows many coral reef fishes to process and transport captured prey [6–8]. Functional innovations can have major evolutionary consequences; they may confer breakthroughs in performance and make new adaptive zones accessible [9–11], and subsequent diversification may be facilitated if the innovation provides access to a previously inaccessible set of resources upon which the lineage can then diversify [8,12–14]. Such subsequent expansion and diversification within a

new adaptive zone may involve functional diversification of the innovation itself [15,16], or secondary diversification of related traits associated with resource specialization [17].

Coral reefs are emblematic high-diversity ecosystems whose bony fish inhabitants compete for resources, or partition them in order to coexist [18–22]. Many reef fish groups have evolved away from suction feeding in the water column to feed on reef-building invertebrates using what broadly can be classified as a biting feeding mode [12,23,24]. By modifying the biting feeding mode into scraping, grazing, nipping or excavating feeding strategies, these reef fishes are able to partition resources including coral.

Here, we examine the evolutionary impact of an extra jaw joint within Chaetodontidae, a group of 129 reef fish species [25] with diverse trophic ecologies that are recognized for their deep-bodied shape, striking colour patterns and close trophic associations with coral. The family consists of two reciprocally monophyletic subfamilies: the butterflyfishes, dominated by the genus *Chaetodon* and their sisters, the bannerfishes. *Chaetodon* taxa transitioned in the Miocene from being largely temperate or deep reef-dwelling organisms into lineages with intimate associations with coral reefs [26]. By contrast, bannerfishes remained loosely reef-associated, do not feed on coral to any major extent and instead consume a wide range of free-living invertebrates.

Members of the Chaetodontidae feed on a wide range of prey, including soft and hard corals, errant and sedentary polychaetes, small benthic crustaceans, algae and various zooplankton [26–29]. Within the radiation of *Chaetodon*, specifically in members of several subgenera forming the clade *Chaetodon* (*Chaetodon*), an intramandibular joint (IMJ) has evolved at least once in the evolutionary history, as a point of flexion between the dentary and articular bones of the mandible [30]. Similar IMJs have evolved in several other lineages of benthic feeding coral reef fishes, including surgeonfishes (acanthurids), angelfishes (pomacanthids), rabbitfishes (siganids), blennies (blennids) and parrotfishes (scarines) [30–32]. The performance benefits and macroevolutionary impacts of IMJs for benthic feeding are incompletely understood. However, the frequency of their evolution in lineages that obtain their prey from bottom surfaces strongly suggests that this innovation improves feeding efficiency when removing attached benthic prey, including algae, sponges or detritus that are nipped, scraped or bitten from the substratum. In some groups, the joint allows biting with the jaws extended [32], whereas in other groups, the joint allows a greater expansion of the mouth [6,18,31]. The latter may serve to increase the area of substrate that can be scraped in a given feeding bout and thus, the amount of material that can be procured per bite. IMJs may also allow fine-scale adjustments of the orientation of the teeth to match uneven feeding surfaces [30].

By adding an additional point of flexion to the jaw mechanism, the IMJ confers a trait that is characteristic of a functional innovation [14,17,33]; it increases the mechanical complexity of the jaw system, and thus potentially its functional versatility. A previous study found support for the hypothesis that the introduction of an IMJ in parrotfishes led to increased rates of morphological diversification in the jaws [34]. Here, we test this hypothesis with chaetodontids, asking whether those lineages that possess the IMJ show elevated rates of evolution in trophic morphology. While morphological diversity of the jaws of parrotfishes that possess an IMJ was not found to be

associated with diversification in diet [34], members of *Chaetodon* show nearly the full range of diets found across the family, although many species make extensive use of coral; 60 of 86 studied species of *Chaetodon* are either facultative or obligate coral feeders [35], while coral feeding has only been reported in six members of the family outside this genus [28,35]. This is particularly noteworthy because only 128 species of bony fishes worldwide are known to feed on coral [28], meaning that about half of them belong to this single butterflyfish genus. The high frequency of coral feeding within the clade that possesses an IMJ suggests the possibility that the joint provides particular functional advantages for coral feeding.

To explore the impact of the IMJ on diversification of chaetodontids and its potential role in the evolution of the extensive coral feeding found in *Chaetodon*, we compare rates of morphological diversification between *Chaetodon* and all other chaetodontids. Our comparisons focus on a dataset of functional morphological traits of the jaws and skull, overall body shape as well as the length of the guts, which is known to influence the evolution of niches, including corallivory [36,37].

2. Material and methods

(a) Phylogeny

We used the nucleotide dataset of Bellwood *et al.* [26] because our sampling of taxa was designed to match this tree. The dataset was reanalysed using the same models and time calibration points, but we estimated both the tree topology and branch durations concurrently to generate a Bayesian posterior distribution of time-calibrated trees that exhibited topological variation. Analyses were conducted in BEAST v. 1.6.1 [38]. We ran four independent chains for 10 000 000 generations, sampling every 1000th. Output was examined in TRACER v. 1.6.1. [39], to ensure that the Markov chain Monte Carlo chains had converged, identify burn-in and verify that samples were not auto-correlated. After removing burn-in and concatenating the four runs, we randomly sampled 1000 trees from the Bayesian posterior distribution of trees; pruned these trees to match the morphological dataset and used them in all subsequent analyses to account for phylogenetic (topological and branch length) uncertainty.

(b) Morphological data

We characterized the morphological diversity of the feeding apparatus in 33 members of the Chaetodontidae. The taxa used were carefully selected *a priori* so as not to skew our analyses by sampling closely related species that may only be separated by nuanced colour-pattern variations (a taxonomic phenomenon that appears particularly common within genus *Chaetodon*). We measured 19 feeding apparatus traits (electronic supplementary material, table S1), computed as species averages from three freshly sacrificed (unfixed) individuals per species (electronic supplementary material, table S2). The traits measured included jaw bone lengths and jaw closing muscle masses [3], third-order lever lengths for the lower jaw, which govern mouth opening mechanics [5], and link lengths for the hyoid four-bar linkage model which govern suction generation mechanics [40]. The length of the gently untangled fresh gut was measured from the oesophagus to the vent [36,37]. Body length, width and depth measurements were acquired and body fineness was calculated [22]. All linear measurements were log-transformed to ensure that the magnitude of character change was unrelated to the absolute trait value (larger changes are less likely when trait values are small). Muscle masses were cube-root

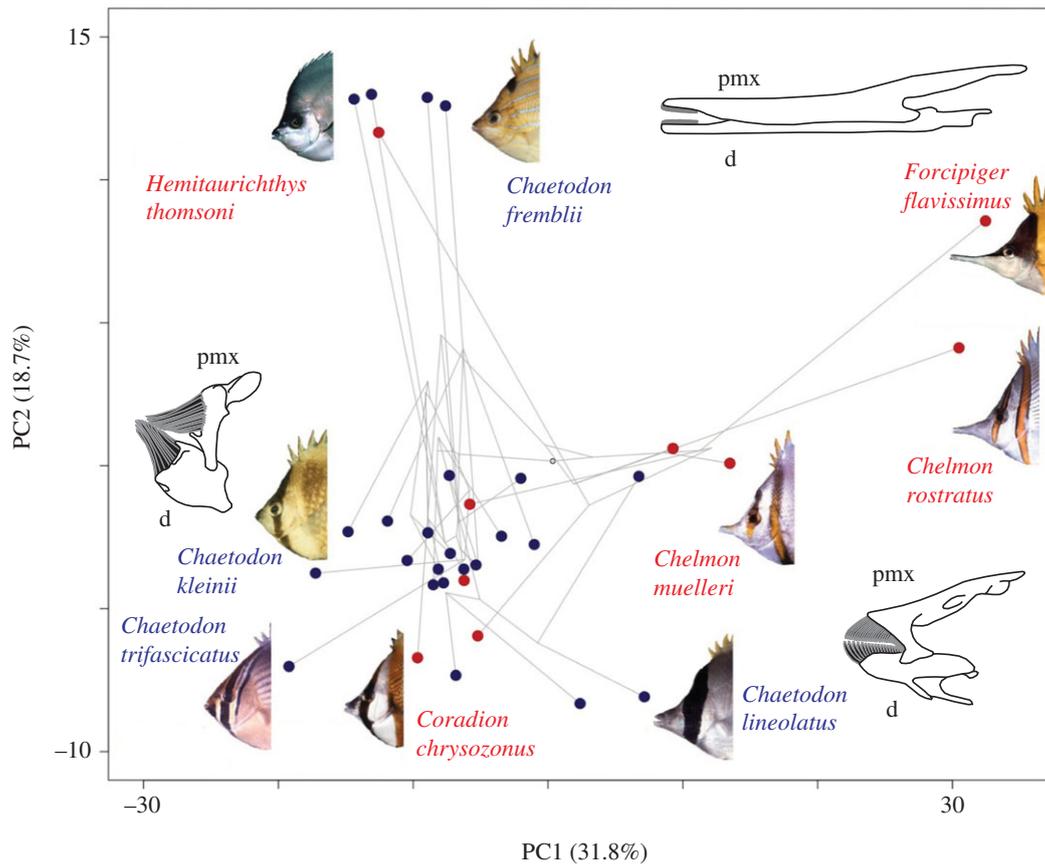


Figure 1. Phylomorphospace for the Chaetodontidae with PC1 versus PC2 and the phylogeny (grey lines) superimposed, using the phylomorphospace function in PHYTOOLS [43]. Names are given for species depicted and subfamily status is shown by colour (blue, butterflyfishes; red, bannerfishes). The main axis of morphological variation within the family is highlighted by representative tooth-bearing jaw bones (pmx, premaxillary; d, dentary) adjacent to their bearers.

transformed prior to log transformation to bring non-ratio traits to the same dimensional scale. Finally, we calculated size-corrected values for all traits across all chaetodontids and ran a phylogenetic principal components analysis to create orthogonal characters [41]. All dataset manipulations and statistics were performed in the R software environment for statistical computing (R Development Core Team 2011) using the *ape* [42] and *phytools* [43] packages.

(c) Comparing morphological diversity

Morphological disparity has commonly been measured as the variance or average pairwise distance between species [44]. The Brownian motion (BM) rate parameter, calculated using a time-calibrated phylogeny, can provide an estimate of the ability of a lineage to generate diversity that takes into account both time and phylogenetic structure [45,46]. Under a BM model, variance is proportional to time, so a faster BM rate of evolution generates greater diversity over the same interval.

We estimated rates of morphological evolution using the maximum-likelihood estimate of the BM rate parameter (σ^2) [46] as implemented in the R package OUwie [47]. To test the hypothesis that rates of morphological evolution were higher in *Chaetodon* than in bannerfishes, we compared the fit of two models to each trait, the first model fits a single rate of evolution across all Chaetodontidae, while the second allows different rates of evolution within bannerfishes and *Chaetodon*. We assessed the fit of the one and two-rate BM models using the modified Akaike information criterion (AICc), which accounts for small sample sizes [48]. AICc is a function of the likelihood of the data, given the model, the number of parameters in the model and the size of the sample; thus, the lower the AICc value, the better the fit. To integrate over phylogenetic uncertainty, we repeated these analyses across 1000 trees sampled from the

Bayesian posterior distribution from the BEAST analysis and calculated the difference in the average AICc scores (ΔAICc) to select the best fitting model for each PC axis. An ΔAICc value of 2 or more was accepted as support for one model over the other [48]. Owing to the small number of species in the dataset, we confirmed that any rate differences between *Chaetodon* and other chaetodontids could be distinguished using parametric bootstrapping. The 95% confidence interval around the rate estimates were calculated from 1000 bootstrap replicates run under the best-fitting two-rate model parameters.

3. Results

(a) Principal components analysis

Axes 1 through to 3 from the principal component analysis together summarize 61.5% of the total variance in the dataset. PC1 is the primary axis of morphological variation (after correcting for body size by using residuals from a phylogenetic regression against standard length [41]) and explains 31.8% of the total dataset variance. Traits that are strongly positively correlated with PC1 include upper jaw (premaxillary) protrusion, lower jaw (dentary) protrusion, closed mouth protrusion, the length of the ascending and dentigerous processes of the upper jaw and length of the palatine. Axis 1 describes the full spectrum of jaw lengths, with large positive values describing fishes with elongated jaws (in decreasing order of jaw length, the bannerfish clades *Forcipiger*, *Chelmon*, *Chelmonops*, *Heniochus* and the butterflyfish clade *Chaetodon radophorus*) and large negative values describing truncated snouts (the butterflyfish clade *Chaetodon chaetodon*; figures 1 and 2). PC2 accounts for 18.7% variance and is most highly

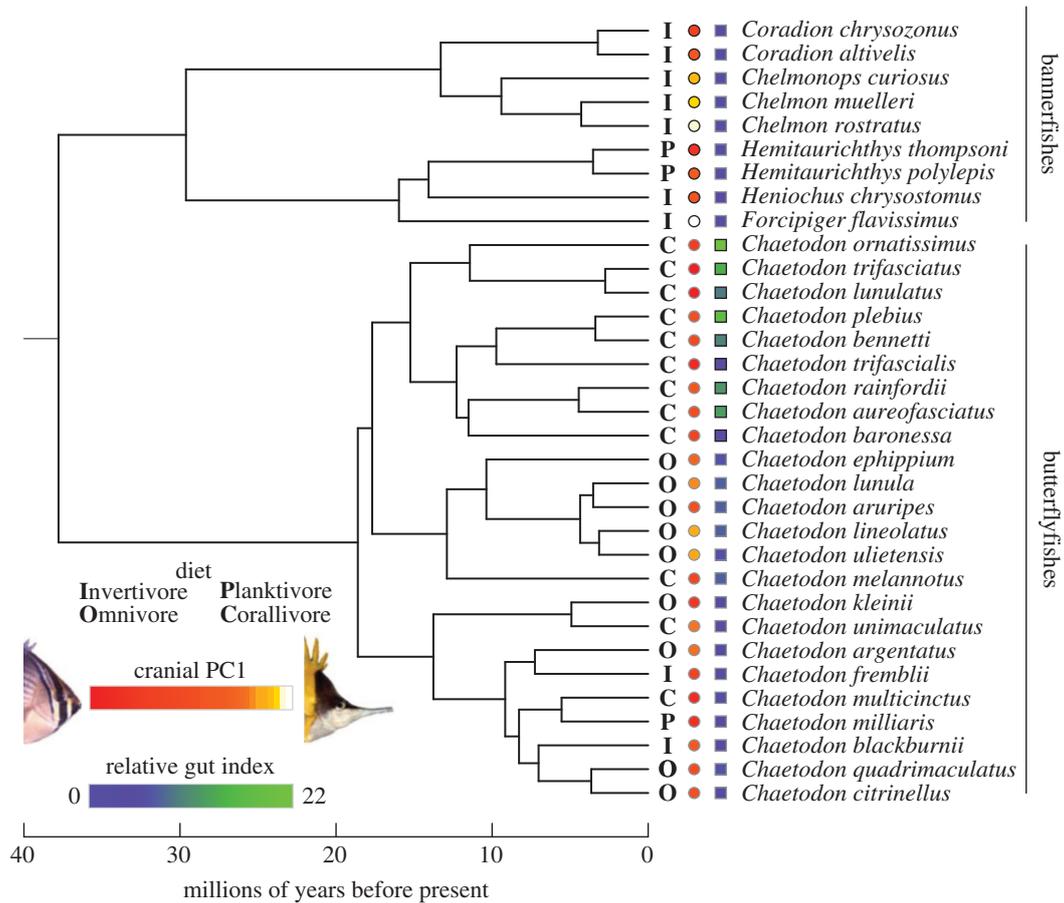


Figure 2. Maximum clade credibility phylogeny generated using the data, methods and calibration points from Bellwood *et al.* [26]. Dietary groups (adapted from [26]) are indicated by capital letters. Coloured circles at the branch tips indicate the value of PC1 for each species, which describes a gradient of jaw lengths (see heat-map) from short (*C. ornatissimus*) to long (*Forcipiger flavissimus*). Coloured squares indicate the value of relative gut index (gut length divided by orbital standard length (OSL)), ranging from 0.4 in *Hemitaurichthys thompsoni* to 21.1 in *C. ornatissimus*.

correlated with three distances between mouth wall bones. These bones form a triangle between the anterior and posterior articulations of the suspensorial mouth wall with the neurocranium and the ancestral mandibular jaw joint formed by the quadrate and articular bones. This axis contrasts fishes with robust and rigid jaw suspension with those that have reduced and motile jaw suspension. High positive values along PC2 distinguish suction-feeding taxa from biting taxa, which load with high negative values along PC2. PC3 explains 11% of variance and is most strongly correlated with variables describing the lateral dimension of the jaws, contrasting fishes with wide versus narrow mouths. Only principal component axes 1 through to 3 have non-trivial and thus interpretable eigenvalues, as determined according to the null expectation for the eigenvalues under a broken stick model [49].

(b) Phylogeny

We used TRACER v. 1.6.1 to examine the log and trees from BEAST and confirm that each independent run had converged, all effective sample size values were greater than 200 and that the first 10% should be discarded as burn-in. After removal of burn-in, the results from the four independent chains were combined using LogCombiner (www.beast.bio.ed.ac.uk/LogCombiner). There were no discernible differences between the maximum clade credibility tree generated in this study (figure 2; electronic supplementary material, figure S1) and

that of Bellwood *et al.* [26]; the topologies are congruent and all node age estimates fall within the 95% of the sampled values (95% highest posterior density) for both analyses.

(c) Comparing morphological diversity

The results of the model-fitting are summarized as medians and 95% confidence intervals for the one- and two-rate models across the 1000 phylogenies in table 1. PC1 is best fitted with a two-rate model that allows morphological diversity in bannerfishes and *Chaetodon* to evolve at different rates (median ΔAICc 4.43). Contrary to our predictions, we found that the rate of jaw length evolution, as represented by PC1, was over four times higher in bannerfishes (median 15.71) than in *Chaetodon* (median 3.55). Gut length is also best fitted by a two-rate model (median ΔAICc 5.85) with rates of evolution nearly eight times faster in *Chaetodon* (median 1.34) compared to bannerfishes (median 0.17). The results from the parametric bootstrapping confirmed that the empirical estimates of the rate in the two clades could be distinguished (electronic supplementary material, figure S2). The 95% confidence interval (CI) were non-overlapping for gut length and although the 95% CI for PC1 do overlap for jaw morphology, the distribution and median estimates clearly differ. However, there is no evidence that the IMJ influences the rate of evolution of body elongation, PC2 and PC3 as they are all best fit by a single rate of morphological evolution across the Chaetodontidae. Phylogenetic uncertainty impacts the rate estimate

table 1 Summary of model fit comparisons and model parameters estimates from all models, averaged across 1000 phylogenies sampled from the Bayesian posterior distribution generated by BEAST. Data are medians with 95% confidence intervals. Best-fitting models are italicized.

		LH single rate	AICc single rate	single rate	LH two rate	AICc two rate	IMJ clade rate	other rate
principal component 1	median	-121.02	246.45	7.31	-116.30	242.02	3.55	15.71
	lower	-122.83	243.18	5.44	-118.01	238.43	2.56	11.35
	upper	-119.39	250.07	9.57	-114.50	245.44	4.77	21.05
principal component 2	median	-113.20	230.79	4.56	-112.51	234.46	3.70	6.44
	lower	-116.92	224.62	3.27	-115.74	228.74	2.61	3.90
	upper	-110.11	238.24	6.41	-109.66	240.90	5.14	10.71
principal component 3	median	-106.89	218.17	3.10	-106.35	222.12	3.37	2.24
	lower	-108.72	215.50	2.35	-108.20	219.37	3.37	1.57
	upper	-105.55	221.85	4.08	-104.97	225.83	4.50	3.06
gut length	median	-88.90	182.20	1.05	-83.46	176.35	1.34	0.17
	lower	-91.70	177.49	0.77	-85.71	172.62	0.98	0.11
	upper	-86.55	187.79	1.39	-81.59	180.85	1.80	0.24
body shape	median	12.42	-20.44	0.00	12.97	-16.51	0.00	0.00
	lower	10.80	-23.31	0.00	11.56	-19.09	0.00	0.00
	upper	13.86	-17.20	0.00	14.26	-13.70	0.00	0.00

slightly but never enough to alter the conclusion (table 1 provides 95% CI).

4. Discussion

High-diversity ecosystems like coral reefs are generally thought to provide opportunities for diversified niche exploitation, in turn accelerating the diversification of feeding morphologies among its occupants. Butterfly and bannerfishes provide a suitable model for probing how morphological and ecological diversity are linked. We discovered differences in the diversification rates of cranial and post-cranial traits with bannerfishes displaying fourfold faster evolution of cranial traits, reflecting frequent jaw elongation, whereas *Chaetodon* butterflyfishes displayed nearly an eightfold faster evolution of gut length. The IMJ in *Chaetodon* appears to facilitate biting feeding modes but does not accelerate craniofacial evolution. The high frequency of coral feeding among *Chaetodon* species suggests that the extra jaw joint enhances the ability of butterflyfish to make use of this food, while dietary diversity in the genus appears to be reflected by rates of evolution of gut length.

(a) Decoupled diversification dynamics in cranial versus post-cranial traits

Linking morphology with ecology is complicated by phenotypes being mosaics of traits organized into functional suites and the rate of diversification of different traits not necessarily being directly correlated [50–53]. Feeding ecomorphology may, for instance, be constrained by the locomotor apparatus, with body shape affecting manoeuvrability and stability during foraging, and consequently impacting which microhabitats and food sources can be accessed [54–57]. Across the Chaetodontidae, we found no significant differences in body fineness, suggesting that these laterally compressed, deep-

bodied fishes are generally well adapted to interact with the wave-swept, current-dominated and obstacle-rich reef environments they occupy. Similarly, dental morphology and patterning more directly determine what food resources can be procured. The bristle-shaped iron-tipped teeth in chaetodontid jaws [58] have been proposed to be an ancestral biting adaptation [59,60]. Indeed, this appears to be a generalized trait for chaetodontoid (bristle-toothed) fishes (Chaetodontidae, Pomacanthidae and Micrognathidae) that form a major part of the coral reef ichthyofauna [30].

We also found no support for the idea that diversification of cranial morphology was accelerated by the evolution of the IMJ. Previous observations noted that the origin of *Chaetodon* marked a shift in adaptive zone involving the onset of intimate associations with stony corals [26]. In our phylomorphospace, *Chaetodon* taxa clustered tightly along PC1, indicating that the success of this clade may be best thought of as lineage diversification with a conserved yet versatile jaw mechanism. A similar pattern has been reported for freshwater sunfishes where piscivory similarly has constrained jaw morphological evolution [61], as well as in phyllostomid bats, where the evolution of the ability to eat hard fruit in Stenodermatinae slows subsequent skull evolution, but dietary diversity remains high [62]. Bannerfishes, which mainly suction-feed or selectively pick errant or concealed free-living invertebrates, have evolved some of the most extreme cranial mechanical specialization found in Chaetodontidae [4,63]. Rates of cranial trait diversification in this clade were fourfold higher than in *Chaetodon* along PC1, which describes variation in mandibular jaw length and jaw protrusion ability.

Gut morphology influences the assimilation of nutrients, and it is here that we find considerably elevated rates of diversification in *Chaetodon*. Gut length has diversified at an eightfold higher rate than in bannerfishes, which have a relatively conserved, short gut, underscoring the dominance of a carnivorous niche [64]. We hypothesize that gut length

diversification in *Chaetodon* reflects diversity in the demands of nutrient assimilation from diverse coral-based foods including zooid body walls, tentacles, mucus and endosymbiont algae. Moreover, it may reflect how coral-derived resources impose different mechanical and chemical challenges on digestion. For instance, an extremely long gut, including the 22.1 times standard length seen in *Chaetodon ornatissimus*, is a trait that may facilitate very different specialized niches. Long guts are common in herbivores, and may also support hard coral feeding as well as the ability to assimilate a polysaccharide-rich diet of coral mucus. Interestingly, the trophic status of *C. ornatissimus* varies and depending on geographical location, this species has been reported to use all three of these resources [64–66]. Additionally, the morphology and physiology of the gut may also be important for dealing with noxious anti-predatory metabolites from coral [67]. To understand corallivory in butterflyfishes, future studies may benefit from combining high-speed, high-resolution video on the reef to determine exactly what is ingested, guts analyses from specimens immediately after feeding for contents analyses, and stable isotope and fatty acid profiles for an indication of assimilation patterns [66].

(b) Intramandibular joints as design breakthroughs

Our finding that frequent corallivory in *Chaetodon* is not associated with accelerated evolution of cranial morphology suggests that enhanced diversification of feeding mechanics did not follow the introduction of this innovation. Thus, while it appears that this innovation resulted in a breakthrough that permits efficient corallivory, exceptional diversity in feeding mechanics does not seem to underlie subsequent trophic diversity in *Chaetodon*.

Our results for the IMJ in *Chaetodon* are consistent with findings in the closely related marine angelfishes (Pomacanthidae) where an IMJ has also evolved. Although angelfish skull morphological disparity remains unquantified, it is known that disparity in feeding kinematics is exceptionally low, compared with previously studied bony fish groups [12]. Rather than evolving their feeding apparatus in diverse ways to invade new adaptive zones, the IMJ has permitted angelfishes to negotiate ‘ecological thresholds’, formed by the structural resilience and/or sturdy attachment of their modular invertebrate prey, which include sponges, tunicates and crustose coralline algae. Instead of cranial morphology, it is body size and gut morphology that has diversified in angelfishes, which manage to avoid niche competition by foraging in mixed groups [19,20]. This importance of gut morphological disparity and limited jaw disparity closely parallels our findings for *Chaetodon*. It is interesting that both groups have bristle-like teeth, which may permit trophic breakthroughs [2], whereas subsequent diversification appears to be constrained.

A contrasting result has been found for the IMJ in parrotfishes. Within parrotfishes, a lineage including the genera *Scarus*, *Chlorurus* and *Hipposcarus* has evolved an IMJ [6]. This clade exhibits elevated rates of evolution of jaw functional morphology, although this is not known to be associated with increased ecological diversity [34]. The presence of the IMJ in parrotfishes is also associated with elevated rates of lineage diversification [68]. While the macroevolutionary consequences of an IMJ appear to be quite diverse, the joint can be argued to be an important design breakthrough, given that it appears to aid its bearers in negotiating challenging ecological thresholds [12].

(c) Intramandibular joint-assisted corallivory; an evolutionary dead-end?

Corallivory is extremely rare among coral reef fishes, only occurring in 128 of the roughly 6000 extant reef species and about half of all corallivores belong to *Chaetodon* [69,70]. In the light of our findings, it is tempting to wonder whether the use of coral as a food resource places strong constraints on the functional morphology of fish jaws. Is the feeding morphology and ecology in *Chaetodon* butterflyfishes an evolutionary dead-end? While it appears that the small, biting jaw design and bristled dentition of chaetodontids was pre-adapted for coral feeding [58–60], potential major challenges associated with eating coral may include overcoming their toxic secondary compounds and stinging nematocysts, and extracting nutrients from what may be a very nutritionally poor diet, particularly in the case of coral mucus [67]. It appears that gut anatomy, and possibly gut physiology, is more important in shaping the diversity in the use of coral among *Chaetodon* species. Specializations to teeth and lips may also be important in shaping the abilities of corallivores to harvest digestible elements from the abrasive calcium carbonate matrix of stony corals. Such specializations include bristle-like teeth tipped with iron-invested caps in butterflyfishes [58,59], fused oral beaks for tough gouging bites in parrotfishes [6,34], and fleshy self-lubricating lips for mucus extraction in tube-lipped wrasses [71]. Regardless of the mechanism, *Chaetodon* species have somehow managed to overcome these challenges, allowing the group to enjoy a period of high net-diversification since the Miocene [72].

The ongoing loss of corals on reefs is already resulting in marked changes to butterflyfish communities, and corallivores appear to be particularly vulnerable [73,74]. The unusual jaws of butterflyfishes underpin an intimate relationship between these fish and corals. However, this opportunity appears to have resulted in a dependency leading butterflyfishes to face a challenging future in the face of rapidly declining coral resources.

5. Conclusion

Our results show that an important feeding innovation in butterflyfish jaws (IMJ) may have provided an ecological breakthrough with respect to coral feeding, but did not stimulate subsequent functional morphological diversification of the feeding mechanism. By contrast, gut length has diversified greatly in *Chaetodon*, varying from five to 12 times body length. This contrast in evolutionary dynamics of different parts of the feeding system underscores the importance of evaluating comprehensive character-sets in ecomorphology. *Chaetodon* butterflyfishes offer an intriguing example where high rates of coral feeding and speciation are not founded upon high rates of morphological evolution. Instead, acquisition of an IMJ appears to have rendered the generalized jaw mechanism sufficiently versatile to allow for considerable variation in prey type without extensive changes in shape.

Ethics. All results reported here were generated via research endorsed by a Great Barrier Reef Marine Park collection and research permit (G01/257_1) and by a James Cook University Ethics Approval (A657/01).

Data accessibility. DNA Sequences: GenBank accession numbers (ETS2: FJ167730–FJ167792; S7I1: FJ167793–FJ167846, FJ167848–FJ167856;

cyt b: FJ167682–FJ167709, FJ167711–FJ167719, FJ167721–FJ167729). Sequence alignments, BEAST xml files and R-scripts used for phylogenetic analyses are available at Dryad: <http://dx.doi.org/10.5061/dryad.t0910> [75]. Morphological data: uploaded as electronic supplementary material.

Authors' contributions. Designed the study: N.K. and P.W.; collected the data: N.K. and R.A.; contributed molecular data: P.W. and D.B.; analysed the data: N.K. and S.P.; drafted the MS: N.K.; edited and approved the MS: all authors.

Competing interests. We declare we have no competing interests.

Funding. This research was supported by the Danish Research Agency (SNF-642-00-0229) to N.K., National Science Foundation grant DEB-1061981 to P.W., and the Australian Research Council to D.B.

Acknowledgements. We thank colleagues and staff at several Great Barrier Reef research stations, Australian Institute of Marine Science research vessels as well as commercial operators, collection managers and wholesalers in Hawaii, Singapore, Taiwan, Okinawa, South Africa and Denmark for help with specimen sourcing and processing. We also thank two anonymous reviewers for insightful comments on an earlier version of the manuscript.

References

- Wainwright PC, Longo SJ. 2017 Functional innovations and the conquest of the oceans by Acanthomorph fishes. *Curr. Biol.* **27**, R550–R557. (doi:10.1016/j.cub.2017.03.044)
- 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**, 3144–3150. (doi:10.1038/ncomms4144)
- Wainwright PC, Bellwood DR, Westneat MW, Grubich JR, Hoey AS. 2004 A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biol. J. Linn. Soc.* **82**, 1–25. (doi:10.1111/j.1095-8312.2004.00313.x)
- Ferry-Graham LA, Wainwright PC, Bellwood DR. 2001 Prey capture in long-jawed butterflyfishes (Chaetodontidae): the functional basis of novel feeding habits. *J. Exp. Mar. Biol. Ecol.* **256**, 167–184. (doi:10.1016/S0022-0981(00)00312-9)
- Hulsey DC, Wainwright PC. 2002 Projecting mechanics into morphospace: disparity in the feeding system of labrid fishes. *Proc. R. Soc. Lond. B* **269**, 317–326. (doi:10.1098/rspb.2001.1874)
- Bellwood DR. 1994 A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidae), with a revision of genera. *Rec. Aust. Mus. Suppl.* **20**, 1–86. (doi:10.3853/j.0812-7387.20.1994.51)
- Mehta RS, Wainwright PC. 2007 Raptorial jaws in the throat help moray eels swallow large prey. *Nature* **449**, 79–82. (doi:10.1038/nature06062)
- Wainwright PC, Price SA. 2016 The impact of organismal innovation on functional and ecological diversification. *Integr. Comp. Biol.* **56**, 479–488. (doi:10.1093/icb/icw081)
- Lautenschlager S, Witmer LM, Altangerel P, Rayfield EJ. 2013 Edentulism, beaks, and biomechanical innovations in the evolution of theropod dinosaurs. *Proc. Natl Acad. Sci. USA* **110**, 20 657–20 662. (doi:10.1073/pnas.1310711110)
- Heers AM, Dial KP. 2015 Wings versus legs in the avian bauplan: development and evolution of alternative locomotor strategies. *Evolution* **69**, 305–320. (doi:10.1111/evo.12576)
- Schnitzler H.-U., Moss CF, Denzinger A. 2003 From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**, 386–394. (doi:10.1016/S0169-5347(03)00185-X)
- Konow N, Bellwood DR. 2011 Evolution of high trophic diversity based on limited functional disparity in the feeding apparatus of marine angelfishes (f. Pomacanthidae). *PLoS ONE* **6**, e24113. (doi:10.1371/journal.pone.0024113)
- Frédérich B, Olivier D, Litsios G, Alfaro ME, Parmentier E. 2014 Trait decoupling promotes evolutionary diversification of the trophic and acoustic system of damselfishes. *Proc. R. Soc. B* **281**, 20141047. (doi:10.1098/rspb.2014.1047)
- Simpson GG. 1944 *Tempo and mode in evolution*. New York, NY: Columbia University Press.
- Fry BG, Scheib H, van der Weerd L, Young B, McNaughtan J, Ramjan SFR, Vidal N, Poelmann RE, Norman JA. 2008 Evolution of an arsenal: structural and functional diversification of the venom system in the advanced snakes (Caenophidia). *Mol. Cell. Proteomics* **7**, 215–246. (doi:10.1074/mcp.M700094-MCP200)
- Hulsey CD, Roberts RJ, Lin ASP, Guldberg R, Streelman JT. 2008 Convergence in a mechanically complex phenotype: detecting structural adaptations for crushing in cichlid fish. *Evolution* **62**, 1587–1599. (doi:10.1111/j.1558-5646.2008.00384.x)
- Liem KF. 1973 Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Syst. Zool.* **22**, 425–441. (doi:10.2307/2412950)
- Purcell SW, Bellwood DR. 1993 A functional analysis of food procurement in surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). *Environ. Biol. Fishes* **37**, 139–159. (doi:10.1007/BF00000589)
- Eagle JV, Jones GP, McCormick MI. 2001 A multi-scale study of the relationships between habitat use and the distribution and abundance patterns of three coral reef angelfishes (Pomacanthidae). *Mar. Ecol. Prog. Ser.* **214**, 253–265. (doi:10.3354/meps214253)
- Frédérich B, Santini F, Konow N, Schnitzler J, Lecchini D, Alfaro ME. 2017 Body shape convergence driven by small size optimum in marine angelfishes. *Biol. Lett.* **13**, 20170154. (doi:10.1098/rsbl.2017.0154)
- Clements KD, German DP, Piché J, Tribollet A, Choat JH. In press. Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. *Biol. J. Linn. Soc.* (doi:10.1111/bij.12914)
- Price SA, Tavera JJ, Near TJ, Wainwright PC. 2012 Elevated rates of morphological and functional diversification in reef-dwelling haemulid fishes. *Evolution* **67**, 417–428. (doi:10.1111/j.1558-5646.2012.01773.x)
- Cooper WJ, Westneat MW. 2009 Form and function of damselfish skulls: rapid and repeated evolution into a limited number of trophic niches. *BMC Evol. Biol.* **9**, 24. (doi:10.1186/1471-2148-9-24)
- Ferry-Graham LA, Wainwright PC, Westneat MW, Bellwood DR. 2002 Mechanisms of benthic prey capture in wrasses (Labridae). *Mar. Biol.* **141**, 819–830. (doi:10.1007/s00227-002-0882-x)
- Froese R, Pauly D (eds). 2017 FishBase. World Wide Web Electronic Publication. See <http://www.fishbase.org>.
- 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)
- Harmelin-Vivien ML, Bouchon-Navaro Y. 1983 Feeding diets and significance of coral feeding among Chaetodontid fishes in Moorea (French Polynesia). *Coral Reefs* **2**, 119–127. (doi:10.1007/bf02395282)
- Cole AJ, Pratchett MS, Jones GP. 2008 Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish Fisheries* **9**, 286–307. (doi:10.1111/j.1467-2979.2008.00290.x)
- Pratchett MS. 2007 Dietary selection by coral-feeding butterflyfishes (Chaetodontidae) on the Great Barrier Reef, Australia. *Raffles Bull. Zool. Suppl.* **14**, 171–176.
- Konow N, Bellwood DR, Wainwright PC, Kerr AM. 2008 Evolution of novel jaw joints promote trophic diversity in coral reef fishes. *Biol. J. Linn. Soc.* **93**, 545–555. (doi:10.1111/j.1095-8312.2007.00893.x)
- Vial CI, Ojeda FP. 1990 Cephalic anatomy of the herbivorous fish *Girella laevis* (Osteichthyes, Kyposidae). Mechanical considerations of its trophic function. *Rev. Chil. Hist. Nat.* **63**, 247–260.
- Konow N, Bellwood DR. 2005 Prey-capture in *Pomacanthus semicirculatus* (Teleostei, Pomacanthidae): functional implications of intramandibular joints in marine angelfishes. *J. Exp. Biol.* **208**, 1421–1433. (doi:10.1242/jeb.01552)
- Vermeij GJ. 1973 Adaptation, versatility, and evolution. *Syst. Biol.* **22**, 466–477. (doi:10.2307/2412953)
- 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)
35. Cole AJ, Pratchett MS. 2013 Diversity in diet and feeding behaviour of butterflyfishes: reliance on reef corals versus reef habitats. In *Biology of butterflyfishes* (eds M Pratchett, MI Berumen, BG Kapoor), p. 107. Boca Raton, FL: CRC Press.
 36. Berumen M, Pratchett M, Goodman B. 2011 Relative gut lengths of coral reef butterflyfishes (Pisces: Chaetodontidae). *Coral Reefs* **30**, 1005–1010. (doi:10.1007/s00338-011-0791-x)
 37. Elliott JP, Bellwood DR. 2003 Alimentary tract morphology and diet in three coral reef fish families. *J. Fish Biol.* **63**, 1598–1609. (doi:10.1111/j.1095-8649.2003.00272.x)
 38. Drummond AJ, Rambaut A. 2007 BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **7**, 214. (doi:10.1186/1471-2148-7-214)
 39. Rambaut A, Drummond A. 2007 Tracer v1.6.1. See <http://beast.bio.ed.ac.uk/Tracer>.
 40. Konow N, Sanford CPJ. 2008 Biomechanics of a convergently derived prey-processing mechanism in fishes: evidence from comparative tongue bite apparatus morphology and raking kinematics. *J. Exp. Biol.* **211**, 3378–3391. (doi:10.1242/jeb.023564)
 41. Revell LJ. 2009 Size-correction and principal components for interspecific comparative studies. *Evolution* **63**, 3258–3268. (doi:10.1111/j.1558-5646.2009.00804.x)
 42. Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
 43. Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-210X.2011.00169.x)
 44. Foote M. 1997 The evolution of morphological diversity. *Annu. Rev. Ecol. Syst.* **28**, 129–152. (doi:10.1146/annurev.ecolsys.28.1.129)
 45. Hutcheon JM, Garland T. 2004 Are megabats big? *J. Mammal. Evol.* **11**, 257–277. (doi:10.1023/b:jomm.0000047340.25620.89)
 46. O'Meara BC, Ane C, Sanderson MJ, Wainwright PC. 2006 Testing for different rates of continuous trait evolution using likelihood. *Evolution* **60**, 922–933. (doi:10.1111/j.0014-3820.2006.tb01171.x)
 47. Beaulieu JM, Jhwueng D-C, Boettiger C, O'Meara BC. 2012 Modeling stabilizing selection: expanding the Ornstein–Uhlenbeck model of adaptive evolution. *Evolution* **66**, 2369–2383. (doi:10.1111/j.1558-5646.2012.01619.x)
 48. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information theoretic approach*. New York, NY: Springer-Verlag.
 49. Jackson DA. 1993 Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology* **74**, 2204–2214. (doi:10.2307/1939574)
 50. Strelman JT, Danley PD. 2003 The stages of vertebrate evolutionary radiation. *Trends Ecol. Evol.* **18**, 126–131. (doi:10.1016/S0169-5347(02)00036-8)
 51. Cooper WJ, Parsons K, McIntyre A, Kern B, McGee-Moore A, Albertson RC. 2010 Benthic-pelagic divergence of cichlid feeding architecture was prodigious and consistent during multiple adaptive radiations within African rift-lakes. *PLoS ONE* **5**, e9551. (doi:10.1371/journal.pone.0009551)
 52. Sallan LC, Friedman M. 2012 Heads or tails: staged diversification in vertebrate evolutionary radiations. *Proc. R. Soc. B* **279**, 2025–2032. (doi:10.1098/rspb.2011.2454)
 53. Glor RE. 2010 Phylogenetic insights on adaptive radiation. *Annu. Rev. Ecol. Evol. Syst.* **41**, 251–270. (doi:10.1146/annurev.ecolsys.39.110707.173447)
 54. Gerstner CL. 1999 Maneuverability of four species of coral-reef fish that differ in body and pectoral-fin morphology. *Can. J. Zool./–Rev. Can. Zool.* **77**, 1102–1110. (doi:10.1139/z99-086)
 55. Webb PW. 1984 Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* **24**, 107–120. (doi:10.1093/icb/24.1.107)
 56. Fulton CJ. 2007 Swimming speed performance in coral reef fishes: field validations reveal distinct functional groups. *Coral Reefs* **26**, 217–228. (doi:10.1007/s00338-007-0195-0)
 57. Walker JA, Alfaro ME, Noble MM, Fulton CJ. 2013 Body fineness ratio as a predictor of maximum prolonged swimming speed in coral reef fishes. *PLoS ONE* **8**, e75422. (doi:10.1371/journal.pone.0075422)
 58. Motta PJ. 1987 A quantitative analysis of ferric iron in butterflyfish teeth (Chaetodontidae, Perciformes) and the relationship to feeding ecology. *Can. J. Biol.* **65**, 106–112. (doi:10.1139/z87-016)
 59. Motta PJ. 1989 Dentition patterns among Pacific and Western Atlantic butterflyfishes (Perciformes, Chaetodontidae): relationship to feeding ecology and evolutionary history. *Environ. Biol. Fishes* **25**, 159–170. (doi:10.1007/BF00002209)
 60. Carnevale G. 2006 Morphology and biology of the Miocene butterflyfish *Chaetodon fischei* (Teleostei: Chaetodontidae). *Zool. J. Linn. Soc.* **146**, 251–267. (doi:10.1111/j.1096-3642.2006.00203.x)
 61. Collar DC, Wainwright PC, Near TJ. 2009 Piscivory limits diversification of feeding morphology in centrarchid fishes. *Evolution* **63**, 1557–1573. (doi:10.1111/j.1558-5646.2009.00626.x)
 62. Dumont ER, Dávalos LM, Goldberg A, Santana SE, Rex K, Voigt CC. 2012 Morphological innovation, diversification and invasion of a new adaptive zone. *Proc. R. Soc. B* **279**, 1797–1805. (doi:10.1098/rspb.2011.2005)
 63. Ferry-Graham LA, Wainwright PC, Hulsey CD, Bellwood DR. 2001 Evolution and mechanics of long jaws in butterflyfishes (family Chaetodontidae). *J. Morphol.* **248**, 120–143. (doi:10.1002/jmor.1024)
 64. Motta PJ. 1988 Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Environ. Biol. Fishes* **22**, 39–67. (doi:10.1007/BF00000543)
 65. Konow N, Ferry LA. 2013 Functional morphology of the Chaetodontidae. In *The biology of butterflyfishes* (eds MS Pratchett, MI Berumen, BG Kapoor), pp. 19–47. Enfield, NH: Science Publishers Inc.
 66. Nagelkerken I, Van Der Velde G, Wartenbergh SLJ, Nugues MM, Pratchett MS. 2009 Cryptic dietary components reduce dietary overlap among sympatric butterflyfishes (Chaetodontidae). *J. Fish Biol.* **75**, 1123–1143. (doi:10.1111/j.1095-8649.2009.02303.x)
 67. Wylie CR, Paul VJ. 1989 Chemical defenses in three species of *Sinularia* (Coelenterata, Alcyonacea): effects against generalist predators and the butterflyfish *Chaetodon unimaculatus* Bloch. *J. Exp. Mar. Biol. Ecol.* **12**, 141–160. (doi:10.1016/0022-0981(89)90053-1)
 68. Alfaro M, Brock C, Banbury B, Wainwright P. 2009 Does evolutionary innovation in pharyngeal jaws lead to rapid lineage diversification in labrid fishes? *BMC Evol. Biol.* **9**, 255. (doi:10.1186/1471-2148-9-255)
 69. Cole AJ, Lawton RJ, Wilson SK, Pratchett MS. 2011 Consumption of tabular acroporid corals by reef fishes: a comparison with plant–herbivore interactions. *Funct. Ecol.* **26**, 307–316. (doi:10.1111/j.1365-2435.2011.01935.x)
 70. Rotjan RD, Lewis SM. 2008 Impact of coral predators on tropical reefs. *Mar. Ecol. Prog. Ser.* **367**, 73–91. (doi:10.3354/meps07531)
 71. Huertas V, Bellwood DR. 2017 Mucus-secreting lips offer protection to suction-feeding corallivorous fishes. *Curr. Biol.* **27**, R406–R407. (doi:10.1016/j.cub.2017.04.056)
 72. 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)
 73. Graham N, Wilson S, Pratchett M, Polunin N, Spalding M. 2009 Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. *Biodivers. Conserv.* **18**, 3325–3336. (doi:10.1007/s10531-009-9633-3)
 74. Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC. 2006 Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Glob. Change Biol.* **12**, 2220–2234. (doi:10.1111/j.1365-2486.2006.01252.x)
 75. Konow N, Price S, Abom R, Bellwood D, Wainwright P. 2017 Data from: Decoupled diversification dynamics of feeding morphology following a major functional innovation in marine butterflyfishes. Dryad Digital Repository. (<http://dx.doi.org/10.5061/dryad.t0910>)