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RESEARCH

More than one way to be a planktivore: the vast morphospace of plankton-feeding reef fishes

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Abstract Planktivorous reef fishes are thought to possess unique morphological traits to feed on small, evasive prey. Despite the multitude of family-level studies addressing this hypothesis, results remain inconclusive. Our goal, therefore, was to determine whether specialised traits and patterns of morphological convergence are congruent across a comprehensive phylogeny of reef-associated fishes. We measured 15 morphological traits from 815 images of 299 species in 12 globally distributed families. Using phylogenetic comparative methods, we mapped the evolution of plankton-feeding across lineages; assessed the effect of planktivory on body shape; and tested for the presence of morphological convergence among planktivores. We demonstrate that planktivory is evolutionary ubiquitous and occurs in 12 of the most abundant global families. Some morphological trait differences between planktivores and non-planktivores were detected, but there was no difference in overall body shape. Contrary to longstanding assumptions, we show that planktivores have not converged towards distinct morphologies, but instead encompass the entire morphospace of reef fishes. Due to their behavioural, spatial, temporal, and resource heterogeneity, reef fishes of any shape and size can readily navigate the challenges of plankton-feeding.

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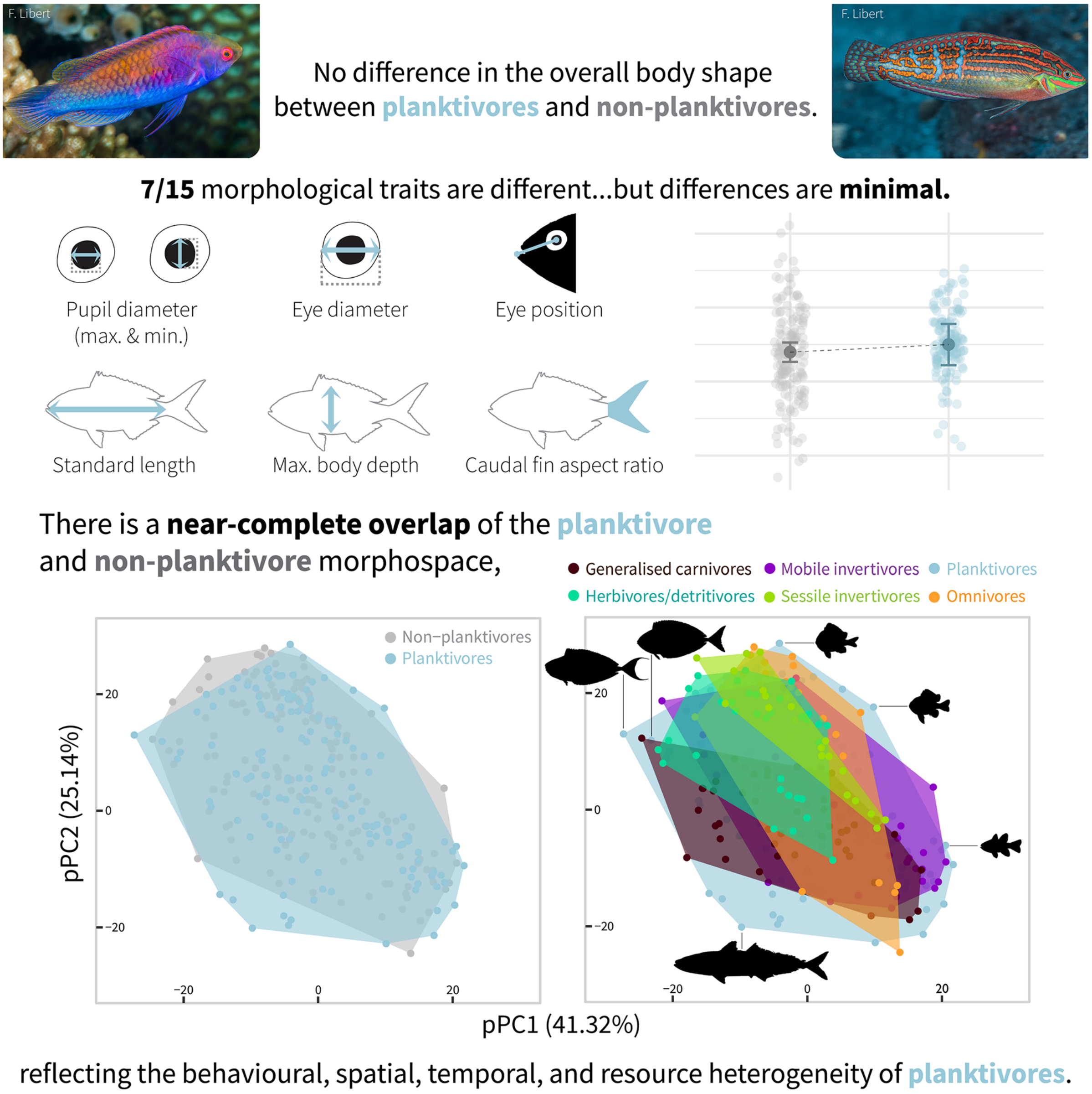
Graphical abstract



Keywords Coral reefs · Evolutionary transitions · Morphological adaptations · Phenotypic convergence · Phylogenetic comparative methods · Trophic ecology

Introduction

Almost every reef-associated fish species begins its life as a planktivore. Prior to settling on the reef, most fish larvae inhabit the pelagic zone, consuming plankton (Leis 1991). These ontogenetic ties likely explain why planktivory is ubiquitous across deep time in marine fishes (Bannikov and Bellwood 2017; Friedman et al. 2010). Regardless of their ancestral diet state, species from nearly all major reef fish families have transitioned to and from planktivory, with the most common transition being toward planktivory (Floeter et al. 2018; Gajdzik et al. 2019; Ng et al. 2024; Siqueira et al. 2020). Today, plankton-feeding fishes make up a disproportional number of the species richness on coral reefs of the Indo-Australian Archipelago, the global marine biodiversity hotspot (Siqueira et al. 2021). This pervasive nature of plankton-feeding among reef fishes across time and space opens multiple avenues to examine patterns of evolutionary convergence. Do different species independently evolve similar phenotypes to exploit a similar niche? This question has been explored since the dawn of evolutionary biology. The ability for taxa to target specific resources is often constrained by certain traits and, over time, selective pressures may result in convergent phenotypic adaptation (Grant & Grant 2006).

Since the 1970s, it has been suggested that plankton-feeding reef fishes are one such example, facing selective pressures resulting in unique morphological traits to feed on small, evasive prey (Davis and Birdsong 1973; Hobson 1975; Hobson and Chess 1978). Planktivorous reef fishes are observed where plankton are abundant in the water column, and often where tidal currents are strong (Hobson and Chess 1978). Specific locomotory traits related to increased swimming performance through the maximisation of thrust and reduction of drag (Webb 1984) are widely hypothesised to be important for planktivorous fishes. These traits include a slender fusiform body, deeply forked or lunate caudal fin (Davis and Birdsong 1973; Hobson 1991; Hobson and Chess 1978), narrow caudal peduncle (Webb 1984), and high fin aspect ratios (Fulton et al. 2005; Wainwright et al. 2002). Feeding on small, evasive prey in the water column is also challenging. Feeding-related traits such as small mouths, protrusible jaws, and smaller adductor mandibulae muscles may facilitate the type of suction feeding required to consume plankton (Lazzaro 1987; Wainwright & Bellwood 2002). The abundance, length, or spacing of gill rakers may also influence the ability for fishes to retain plankton (Davis and Birdsong 1973; Lazzaro 1987). Indeed, longer gill rakers were observed in planktivorous wrasses (Schmitz and Wainwright 2011a). In order to see small plankton particles, reef fishes may have also adapted sharper visual acuity, which is improved by having larger eyes (Caves et al. 2017; Goatley and Bellwood 2009), pupils, and lenses (Schmitz and Wainwright 2011a). Large eyes located close to the mouth are also thought to improve the visual selection of plankton (Hobson 1991). Based on these observations, it appears as though planktivorous reef fishes are undergoing directional selective pressures, converging towards a specific morphotype.

Morphological adaptations to planktivory have been explored in the Acanthuridae (unicorn- and surgeonfishes; Friedman et al. 2016), Chaetodontidae (banner- and butterflyfishes; Hodge et al. 2021), Labridae (wrasses and parrotfishes; Schmitz and Wainwright 2011a, b), and Pomacentridae (damselfishes; Aguilar-Medrano et al. 2011; Cooper et al. 2017; Cooper & Westneat 2009; Frédérich et al. 2008, 2013). However, the generality of a planktivorous morphotype has yet to be tested, comprehensively, at a large-scale, across multiple reef fish families. To address this gap, we first created a dataset of morphological traits from reef fishes belonging to twelve families known to occur across reefs globally: the Acanthuridae, Apogonidae (cardinalfishes), Blenniidae (blennies), Carangidae (trevallies and jacks), Chaetodontidae, Gobiidae (gobies), Holocentridae (soldier- and squirrelfishes), Labridae, Lutjanidae (snappers and fusiliers), Pomacanthidae (angelfishes), Pomacentridae, and Serranidae *sensu lato* (groupers and sea basses). Using the most complete ray-finned fish (Actinopterygii) phylogeny to date (Rabosky et al. 2018), we then modelled the evolutionary history of planktivory across all selected reef fish families. We also tested for, and visualised, the overall body shape variation across 299 species of planktivores and non-planktivores, and investigated the varying effects of planktivory on individual morphological traits and families. Finally, we applied multiple distance-based methods (Arbuckle and Minter 2015; Castiglione et al. 2019) including the recently developed *Ct*-measures (Grossnickle et al. 2024) to test for the presence of morphological convergence in planktivorous reef fishes. We acknowledge the possibility of alternative, specific, hypotheses incorporating multiple adaptations to planktivory, however, our hypothesis is a general one, with the purpose of testing whether the archetypal planktivore morphotype can be detected broadly, across a range of taxa.

We show that planktivory is present in nearly all reef fish families and has arisen multiple times across deep time (~25–50 million years ago). There were unremarkable differences in the morphology of planktivores and non-planktivores, with plankton-feeding fishes occupying the widest breadth of morphospace relative to all other trophic guilds. The lack of morphological convergence detected demonstrates that planktivorous reef fishes of widely varying shapes can, and do, exploit plankton.

Material and methods

Data

Morphological trait selection

We selected 15 morphological traits that characterise the archetypal planktivore body shape. Shape in this context refers to the overall form of the body based on multiple morphological measurements, which are specifically based on previously hypothesised or evidenced characteristics of plankton-feeding fishes (see Introduction; Table S1). These measurements included locomotory traits such as standard length, body depth, head depth at both the point of the pupil and the operculum, 'fusiformness' (i.e. the depth measured at the midpoint from the maximum body depth to the snout), minimum caudal peduncle depth, fineness ratio, caudal fin aspect ratio, and caudal fin shape. Feeding-related traits (lower and upper jaw lengths) and vision-related traits (eye diameter, minimum and maximum pupil diameter, and eye position) were also included. These traits encompass basic body shape, and specific details related to locomotion, feeding, and vision. They thus capture shape in a way that permits subsequent functional interpretation. Extended details on the morphological measurements can be accessed in the Supplementary Material (Fig. S1, Table S1).

Morphological data

We collected morphological data for planktivorous and non-planktivorous species of the consensus reef fish families, given their abundant occurrence across reefs worldwide (*sensu* Bellwood 1996; Bellwood and Wainwright 2002). These 12 families include the Acanthuridae, Apogonidae, Blenniidae, Carangidae, Chaetodontidae, Gobiidae, Holocentridae, Labridae, Lutjanidae, Pomacanthidae, Pomacentridae, and Serranidae *sensu lato*. The family Mullidae (goatfishes) was not included in the morphological analyses due to the lack of planktivorous species.

Morphological measurements were obtained mainly using images sourced from the Smithsonian National Museum of Natural History, Division of Fishes Collections (collections.nmnh.si.edu/search/fishes). Some images of planktivorous fishes were sourced from the taxonomic literature (Table S2), particularly for the Blenniidae and Gobiidae, which were less common in the Smithsonian image collections. To account for variation among images, we sampled mostly John E. Randall's images and up to three images per species where possible. We used the ImageJ software version 1.53a (Schneider et al. 2012) to calculate the lengths and areas of the morphological traits. In total, morphological traits were measured across 991 images and 381 species with an average of approximately 3 images sampled per species.

Measurements were subsequently averaged by species and size-corrected using log-shape ratios following the procedures outlined in Price et al. (2019). Log-shape ratios are generated by scaling each variable using the geometric mean of multiple size-based variables (e.g. standard length and body depth) and log-transforming those values (Klingenberg 2016; Mosimann 1970). We chose to use log-shape ratios because the variables used to size-correct can still be used as individual measurements (Price et al. 2019). These size-corrected values were used as the trait data for all subsequent analyses.

Phylogenies

For all analyses, we used the phylogenetic tree of ray-finned fishes (Actinopterygii) sourced from fishtreeoflife.org (Rabosky et al. 2018). This molecular time tree was fossil-calibrated and constructed with a 27-gene multi-locus alignment. More details on the Actinopterygii phylogeny can be accessed in Rabosky et al. (2018). The morphological dataset was pruned down to match the species sampled in the phylogeny. The final dataset included 815 images across 299 species. To test the sensitivity of our results, we repeated the main analyses using a different phylogeny with another dating scheme (Figs. S2–S4, Tables S3–S5). Following the methods described in Siqueira et al. (2023), we recalibrated the Actinopterygii tree (Rabosky et al. 2018) using the phylogeny of spiny-rayed fishes (Ghezelayagh et al. 2022) as a backbone. This time-calibrated phylogeny was inferred from ultraconserved elements. The congruification approach (Eastman et al. 2013) was applied to ensure similar sampling between the trees, and involved creating a reference tree used to recalibrate the Actinopterygii phylogeny (Rabosky et al. 2018). The reference tree was made by selecting shared nodes among genera between both trees. The results from both trees were broadly comparable, but we chose to infer our findings from the Actinopterygii phylogeny (Rabosky et al. 2018) because the timing of divergences in the recalibrated tree were incongruent with the fossil record.

We acknowledge that the Serranidae *sensu lato* is no longer monophyletic, as it includes lineages from the families Epinephelidae, Anthiadidae, and Serranidae *sensu stricto*, and the genera *Acanthistius* and *Niphon* (Ghezelayagh et al. 2022; Near and Thacker 2024). For our study, we opted to use the Serranidae *sensu lato* to match the primary phylogenetic tree used herein (Rabosky et al. 2018) and because it was highly unlikely to change our results upon the consideration of 11 other reef fish families.

Trophic data

We used published trophic data from Siqueira et al. (2020), which defined reef fish trophic guilds, categorising them as planktivores, generalised carnivores, herbivore/detritivores, omnivores, sessile invertivores, and mobile invertivores. We analysed the trophic data in two ways. The first and main method was by categorising reef fishes into planktivores ($n = 142$) and non-planktivores ($n = 157$). The second way was by categorising reef fishes into their specific trophic guilds: planktivores ($n = 142$), generalised carnivores ($n = 43$), herbivore/detritivores ($n = 34$), omnivores ($n = 37$), sessile invertivores ($n = 19$), and mobile invertivores ($n = 24$); this grouping method was only applied to the phylogenetic generalised least squares models and ordination plots.

Analyses

Our analyses were grouped into three main sections. In the first part, we examined the evolutionary history of planktivory across 1592 species belonging to the 13 consensus reef fish families. In the second part, we analysed whether morphological differences exist between planktivores and non-planktivores, across 299 species belonging to 12 reef fish families (all consensus families except for the Mullidae). This was conducted using multiple phylogenetically informed statistical tests and ordination plots to compare: rates of morphological evolution, overall body shape, morphological disparity, morphospaces, and each individual morphological trait. We also examined whether body shape differences occurred at the family-level. Finally, in the third part, we tested for morphological convergence within the planktivorous state.

All analyses were conducted in the R Statistical Environment v.4.3.2 (R Core Team 2023), using the packages “ape v.5.7.1” (Paradis and Schliep 2019), “convevol v.2.0.1” (Brightly and Stayton 2024), “geiger v.2.0.11” (Pennell et al. 2014), “geomorph v.4.0.6” (Baken et al. 2021), “phytools v.2.1.1” (Revell 2024), “RRphylo v.2.8.0” (Castiglione et al. 2019), “Windex v.2.0.8” (Arbuckle and Minter 2015).

Evolution of planktivory across reef fishes

We ran discrete character models using the trophic classification data of reef fishes (Siqueira et al. 2020) and the Actinopterygii phylogeny (Rabosky et al. 2018). Both the dataset and tree were pruned down to encompass the 13 consensus reef fish families (*sensu* Bellwood 1996; Bellwood and Wainwright 2002). Species present in both the dataset and the tree were kept for analysis, resulting in a total of 1592 species. We fit the equal-rates (ER) model and the all-rates-different (ARD) model with a flat prior using the *fitMk* function in the phytools package. The ARD model was selected because it had Akaike information criterion (AIC) values more than two units lower relative to the ER model (Table S6). Stochastic character mapping (Huelsenbeck et al. 2003) was used to visualise the evolution of planktivory. We applied a Bayesian Markov chain Monte Carlo (MCMC) approach to sample character histories from their posterior probability distribution, which enables visualisation of an entire distribution from a sample of stochastic character maps. We ran 1000 stochastic character maps using the *make.simmap* function in the phytools package with the ARD model and an equal root prior. We then used the *densityMap* function in the phytools package to plot the probability density of stochastic histories in each of our mapped trophic states. The posterior probability of each trophic state can be visualised across all the edges and nodes of the phylogeny.

Analyses of shape, traits, and morphospace between planktivores and non-planktivores

Phylogenetic signal and evolutionary rates

Species morphologies are correlated due to common ancestry, meaning that species data points are not independent and thus cannot be directly compared (Garland et al. 2005). To evaluate this, we estimated phylogenetic signal in the overall shape of planktivores and non-planktivores. Phylogenetic signal is the tendency for closely related species to exhibit similar traits as a consequence of their shared evolutionary history (Adams 2014a; Blomberg et al. 2003). We assessed phylogenetic signal using the *physignal* function in the geomorph R package, which calculates a multivariate Blomberg's K statistic (i.e. K_{mult}) that is used to determine whether the data are significantly different from a null model of Brownian motion (Adams 2014a; Blomberg et al. 2003). Statistical significance was evaluated via permutations (1000 iterations).

To investigate whether planktivores exhibit lower rates of shape evolution given the constraints of plankton-feeding, differences in the net rate of shape evolution under Brownian motion between planktivores and non-planktivores were compared using the *compare.evol.rates* function in the geomorph package. Statistical significance was assessed by permutation (10,000 iterations).

Statistical tests comparing shape and specific morphological traits across trophic groups

To evaluate whether trophic groups differ in overall body shape given the phylogeny, we applied multivariate phylogenetic generalised least squares (PGLS) models under Brownian motion evolution using the *procD.pgls* function in the geomorph package (Adams 2014b; Adams and Collyer 2015). We fit a model with trophic group as the independent variable and fish shape (represented by 15 size-corrected morphological traits) as the dependent variable. To test whether there are overall differences in shape when considering both planktivory and families, we fit another PGLS with trophic (planktivores and non-planktivores) and family as the main effects plus an interaction term. We also conducted separate PGLS analyses for each of the 15 morphological traits to evaluate which traits may be driving the differences in shape between planktivores and non-planktivores. These analyses were conducted by (a) combining species from all families and (b) at the family-level. Finally, we conducted separate PGLS analyses of trophic groups (planktivores vs. non-planktivores) on shape within each family. To ensure sufficient sampling, we only ran the analysis on families where more than 10% of the family was sampled (9/12 families). We collated family-level published phylogenetic trees where possible (5/9 families) and the remainder were trimmed from the Actinopterygii phylogeny (Rabosky et al. 2018; Tables S7–S8).

To test whether trophic guilds differed in the amount of shape variation, we used the *morphol.disparity* function in the package geomorph. This function estimates differences in disparity by calculating the variance per group using residuals obtained from the PGLS (Zelditch et al. 2012). Statistical significance of all analyses was evaluated through permutation (10,000 iterations).

Morphospace visualisation

To visualise morphospace differences among trophic guilds, while accounting for phylogenetic nonindependence, we applied phylogenetic principal component analyses (pPCA) with a Brownian motion correlation structure using the function *phyl.pca* in the phytools R package. A correlation structure was preferred over a covariance structure because we size-corrected the measurements using log-shape ratios, which can generate different ranges across some variables. These variables may subsequently dominate the first Principal Components (PC) if a covariance structure is used (Price et al. 2019). The application of log-shape ratios results in the loss of one degree of freedom due to scaling (Claude 2013) such that the first 14 of the 15 PC scores explain the morphospace.

Morphological convergence

We defined evolutionary convergence herein following a broad, pattern-based definition outlined in previous studies, as the evolution of distantly related lineages with high phenotypic similarity (Grossnickle et al. 2024; Losos 2011; Stayton 2015). This definition aligns with those set in the distance-based methods of convergence outlined below. We tested whether planktivorous reef fish species have evolved similar morphological traits by using methods that compare observed convergence to that which is expected by chance: *Ct*-measures (Grossnickle et al. 2024; Stayton 2015), the Wheatsheaf index (Arbuckle et al. 2014; Arbuckle and Minter 2015), and θ (Castiglione et al. 2019). While *Ct*-measures test for convergence directly, the Wheatsheaf index and θ cannot distinguish entirely between convergence (as defined herein) and other evolutionary patterns (e.g. conservatism) that also result in lineages with similar phenotypes (Stayton 2015). However, no single test is perfect, thus multiple convergence measures should be used to confirm patterns (Grossnickle et al. 2024). We used both PC scores and size-corrected morphological trait data as input data for all the convergence tests. A broken-stick model (MacArthur 1957) was applied to select the number of PC axes.

Ct-measures

Due to recent research revealing high Type I Errors (the percentage of false positives) in *C*-measures (Stayton 2015), we decided to use the newly improved *Ct*-measures, which were implemented with the *convSigCt* function in the R package convevol (Grossnickle et al. 2024). Convergence is measured by calculating the phenotypic distances in the phylomorphospace between putatively convergent lineages. Statistical significance is measured based on simulations demonstrating differences to a Brownian motion model of evolution. $Ct1$ is the proportion of the maximum morphological distance between putatively convergent taxa that has been reduced by evolution; $Ct1 = 1$ represents complete convergence and $Ct1 = -1$ represents divergence. $Ct2$ follows $Ct1$ but accounts for the absolute magnitude of evolutionary change within the dataset; the larger the $Ct2$ value, the more the convergence. $Ct3$ is calculated by standardising $Ct2$ using the sum of the morphological distances from the ancestors to the descendants of the putatively convergent taxa. $Ct4$ is calculated by standardising $Ct2$ using the sum of the morphological distances along each branch in the smallest putatively convergent clade (Grossnickle et al. 2024).

We grouped certain morphological traits to test specific hypotheses instead of using the entire morphological dataset, as non-convergent traits might weaken the signal of convergent traits (Grossnickle et al. 2024). Two hypotheses were defined based on groups of morphological traits: (1) a visual system hypothesis, which included pupil diameter (minimum and maximum), eye diameter, and eye position; and (2) a swimming performance hypothesis, which included standard length, head depth (across both the pupil and operculum), maximum body depth, fusiformness, minimum caudal peduncle depth, caudal fin shape, caudal fin aspect ratio, and fineness ratio. We did not include a feeding hypothesis because it would only include the lower and upper jaw lengths, and neither were notably different between planktivores and non-planktivores (Table S9). We ran the *convSigCt* function with 100 simulations using both subsets of morphological traits and the PC scores. To test the sensitivity of the number of simulations on the results, we ran the analysis with the PC score data through both 100 and 300 simulations, of which there was no difference in the results (Table S3). Since our purpose was to test for morphological convergence among independent origins of planktivory, we assigned groups within the *convSigCt* function. Groups were based on the planktivore lineages that share a most recent common ancestor, such that one group represents an independent origin of planktivory. Groupings were validated using the *pwCheck* function.

Wheatsheaf index

We applied the function *windex.sim.test* in the windex package, which calculates the Wheatsheaf index and tests if it is greater than expected from a Brownian motion model of evolution. The Wheatsheaf index measures the strength of convergence by calculating the phenotypic distances between the putatively convergent taxa and the phenotypic distances between putatively convergent to non-convergent taxa, while incorporating phylogenetic relatedness. Significance testing was based on the number of simulations of which we ran at both 1000 and 5000.

Θ_{real}

We used the *search.conv* function within the RRphylo package to test whether planktivorous species are more morphologically similar than expected by their phylogenetic distance (Castiglione et al. 2019). The Θ_{real} measure is the angle of the phenotypic vectors between pairs of focal species and is therefore a measure of phenotypic similarity; smaller angles represent similar phenotypes. We report the average angle obtained by all combinations of species pairs evolving under the planktivorous state (mean Θ_{real}) and standardised by the time distance between the tip pairs (mean $\frac{\Theta_{\mathrm{real}}}{\mathrm{distance}}$). Significance tests compare standardised Θ_{real} and $\frac{\Theta_{\mathrm{real}}}{\mathrm{distance}}$ values of the putatively convergent taxa to the values computed for randomly selected lineages. Assessing significance using the p-value for mean $\frac{\Theta_{\mathrm{real}}}{\mathrm{distance}}$ is preferable, however, if the phylogeny in use is substantially incomplete and if putatively convergent taxa are distributed distantly in the tree space, then p(mean Θ_{real}) is preferrable.

Results

Evolutionary history of planktivory across reef fishes

Planktivory was recorded in all consensus reef fish families, except for the Mullidae (goatfishes) (Figs. 1, 2, S2). Plankton-feeding has arisen at least 19 times, from as early as 53 Million years ago (Ma), in the Serranidae, to as recent as about 2 Ma in *Heniochus* in the Chaetodontidae (Figs. 2, S5). There were at least seven transitions to planktivory which occurred during deep evolutionary time (~25–53 Ma) but most (approximately 12) transitions to planktivory took place more recently, in the last 20 Ma (Figs. 2, S5). Through ancestral reconstructions, we estimated an average number, across 1000 stochastic maps, of about 126 evolutionary shifts between trophic states, with 55 changes to planktivory and 71 changes to non-planktivory. This suggests that the number of transitions towards planktivory were comparable to the number of transitions away. The average posterior probability that each internal node was in the planktivorous state (i.e. the average total time spent in the planktivorous state) was about 18%. Overall, these results indicate a relatively high incidence of planktivory within the evolutionary history of reef fishes.

Planktivory is widespread and is the dominant trophic guild in the Pomacentridae (121/217 species in the phylogeny, 55.8% of the family) and the Apogonidae (38/69, 55.1%) (Figs. 2, S5). Planktivorous species are also common in the Holocentridae (13/42, 31.0%), Acanthuridae (16/67, 23.9%), Carangidae (27/114, 23.7%), and Lutjanidae (16/72, 22.2%). The Serranidae (28/207, 13.5%), Pomacanthidae (5/54, 9.3%), Chaetodontidae (8/96, 8.3%), Gobiidae (13/188, 6.9%), Labridae (20/331, 6.0%), and Blennidae (1/105, 0.95%) have remarkably fewer planktivorous species (Fig. 2). The planktivorous state is relatively conserved within genera, most notably in the Holocentridae (genus *Myripristis*), Pomacanthidae (genus *Genicanthus*), Lutjanidae (genera *Caesio*, *Pterocaesio*, and *Paracaesio*), and Serranidae (Fig. 2). Phylogenetic conservatism of planktivory within the Serranidae is likely due to the inclusion of the primarily planktivorous Anthiadidae family. Planktivory in other families such as the Apogonidae, Pomacentridae, and Labridae is not as phylogenetically conserved, and there are even reversals to non-planktivory (Figs. 2, S5).

Analyses of shape, traits, and morphospace between planktivores and non-planktivores

We found a significant phylogenetic signal ($p=0.001$) in fish shape with trophic group (planktivores and non-planktivores), indicating that shape variation among species can, in part, be explained by their phylogenetic relationships. The phylogenetic signal ($K_{\mathrm{mult}}=0.148$), however, was much lower than expected under a Brownian motion model of evolution. A K_{mult} less than one suggests homoplasy, and that shape variation may be influenced by other factors such as species ecology. Due to the detection of a significant phylogenetic signal in shape, we analysed our morphological data using a phylogenetically informed framework.

We did not detect a difference in the rates of shape evolution between planktivores and non-planktivores ($p=0.282$). Morphological disparity between

Fig. 1 Examples of morphological similarities within families (horizontal) and differences among families (vertical) between planktivorous and non-planktivorous reef fishes. Of the 13 consensus reef fish families, 12 are included in this figure as the Mullidae (goatfishes) do not have any planktivorous species. Species pictured: **a** *Acanthurus mata*, **b** *Acanthurus xanthopterus*, **c** *Ostorhinchus cyanosoma*, **d** *Ostorhinchus nigrofasciatus*, **e** *Plagiotremus laudandus*, **f** *Plagiotremus rhinorhynchos*, **g** *Decapterus macarellus*, **h** *Caranx ruber*, **i** *Chaetodon trichrous*, **j** *Chaetodon citrinellus*, **k** *Bryaninops yongei*, **l** *Pleurosicya micheli*, **m**, *Myripristis berndti*, **n** *Sargocentron caudimaculatus*, **o** *Cirrhilabrus solorensis*, **p** *Halichoeres cosmetus*, **q** *Caesio xanthonota*, **r** *Aphareus furca*, **s** *Genicanthus caudovittatus*, **t** *Pomacanthus xanthometopon*, **u** *Pomachromis fuscidorsalis*, **v** *Pomacentrus coelestis*, **w** *Pseudanthias squamipinnis*, **x** *Serranus tabacarius*. Photographs provided by Athila Bertoncini / Projeto Ilhas do Rio (**g**), François Libert (**b**, **d**, **h**–**p**, **r**, **s**, **u**, **v**, **x**), Isabelle Ng (**a**, **c**, **f**, **q**, **t**, **w**), and Klaus Stiefel (**e**), with permission

planktivores and non-planktivores was detected ($p<0.001$), with non-planktivores exhibiting higher shape variation (3.94) compared to planktivores (2.81). This result was unsurprising, given non-planktivores encompass all other trophic guilds. When comparing planktivores to each individual trophic guild, morphological disparity was only detected ($p<0.01$) between planktivores and two other trophic guilds: sessile invertivores and omnivores (Table S10). Furthermore, no difference was detected in the morphological disparity between planktivores and non-planktivores at the family-level (Table S8).

After accounting for phylogenetic relatedness, there was no statistically significant difference in the overall body shape of planktivores and non-planktivores, and the phylogenetic generalised least squares (PGLS) model could only explain 0.5% of the total variation in the body shape data (Table S11). Similar results were found when dividing species into six trophic guilds (Table S12). Overall, these results provide no evidence for a difference in overall body shape between planktivores and other trophic groups. We also found that family and the interaction between family and planktivory were not important predictors of overall fish shape (Table S13). Upon running a separate PGLS per family, only two families exhibited body shape differences between planktivores and non-planktivores (Fig. S6, Table S7): the Apogonidae and Lutjanidae. However, distinct morphospaces between planktivores and non-planktivores appear to only be present in the Lutjanidae (Fig. S6). The models nevertheless could only explain about

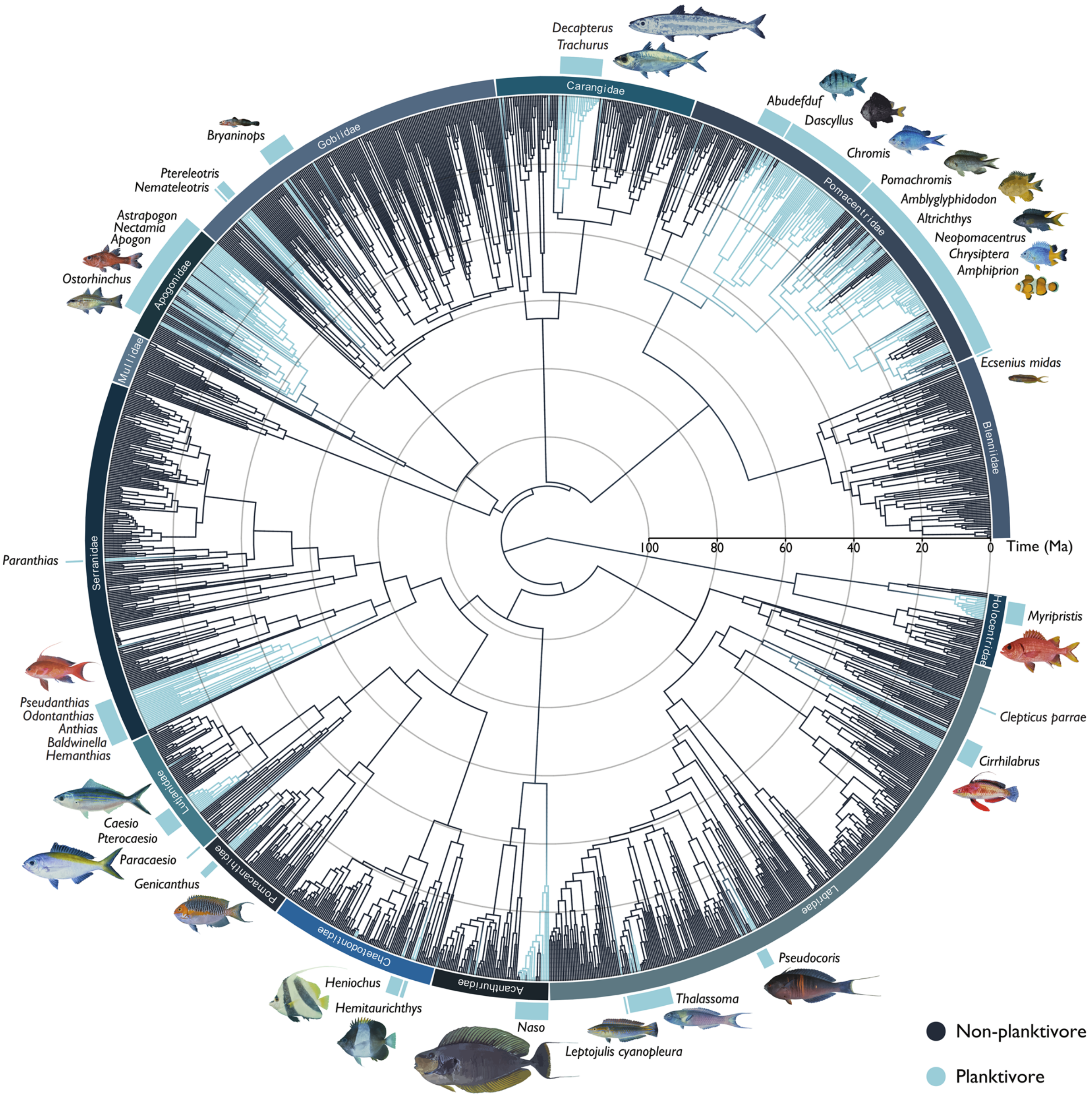


Fig. 2 The evolutionary history of planktivory across reef fishes. The posterior probability distribution across 1000 stochastic maps is represented, where the internal branches are coloured with the trait state that had the highest posterior probability at that given node. The outer ring around the phylogeny represents the 13 consensus reef fish families and the inner concentric rings represent 20 million-year (ma) increments. Planktivorous genera are highlighted in the outermost light blue arcs surrounding their given reef fish family. Examples of planktivorous species are represented with silhouettes which were digitised using John E. Randall's Fish Photos (pbs.bishopmuseum.org/images/JER). The phylogeny with the exact posterior probabilities at the nodes can be accessed in the Supplemental Material (Fig. S5)

12–32% of the total variation in overall body shape of these families (Table S7). We also detected overlap between planktivores and non-planktivores when comparing specific morphological traits (Figs. 3, S3; Table S9). While seven of the 15 traits demonstrated statistically significant differences between plankton-feeders and other trophic groups, the extensively overlapping 95% confidence intervals between these

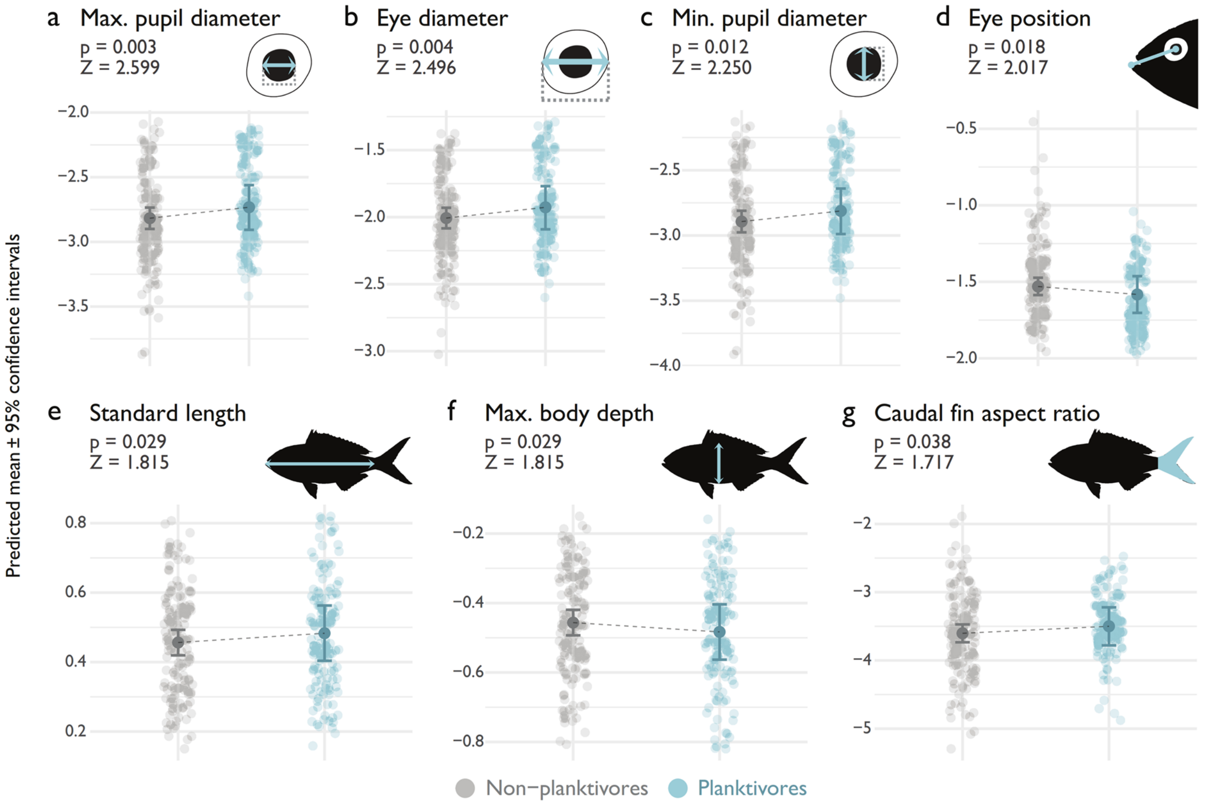


Fig. 3 Morphological trait differences between planktivorous and non-planktivorous reef fishes. Predicted means ± 95% confidence intervals of the seven morphological traits which demonstrated significant differences between planktivores and non-planktivores from the phylogenetic least squared residuals (PGLS) analyses. The darker points represent the model predicted mean, the bars represent the model predicted 95% confidence intervals, and the lighter points in the background represent the size-corrected data. Morphological traits (a-g) are ordered from highest to lowest Z-scores (i.e. effect sizes) and smallest to largest p-values

groups would suggest that planktivores are not markedly distinct (Fig. 3; Table S9). Planktivores demonstrate larger and overlapping 95% confidence intervals in all cases compared to non-planktivores (Fig. 3). The seven traits included all the visual traits (maximum and minimum pupil diameter, eye diameter, and eye position) and traits relevant to swimming performance (standard length, depth, caudal fin aspect ratio (Table S9). PGLS model-predicted values suggest that planktivores have larger pupils and eyes, shorter distances from the eyes to the snout (i.e. eye position), more elongated bodies, narrower body depths, and higher caudal fin aspect ratios relative to non-planktivores (Fig. 3). These statistically significant results were restricted to seven of the 15 traits and even in these, only marginal differences were observed. Finally, the family-level PGLS analyses for each of the 15 morphological traits revealed inconsistencies in the importance of certain traits across multiple families (Table S14).

The extensive overlap between planktivores and non-planktivores was most clearly visualised in the ordination plots (Figs. 4a, S4). The first two pPC axes explained 66.46% of morphospace variation, with pPC1 accounting for 41.32% and pPC2 accounting for 25.14% (Fig. 4). More distinction can be observed when mapping all trophic guilds, but it further confirms that planktivores have the broadest morphospace and encompass the morphospace of every other trophic guild (Fig. 4b). The variation along pPC1 was mostly correlated with the pupil diameter (minimum and maximum), eye diameter, caudal fin shape, minimum caudal peduncle depth, caudal fin shape, and fineness ratio. Variation along pPC2 was

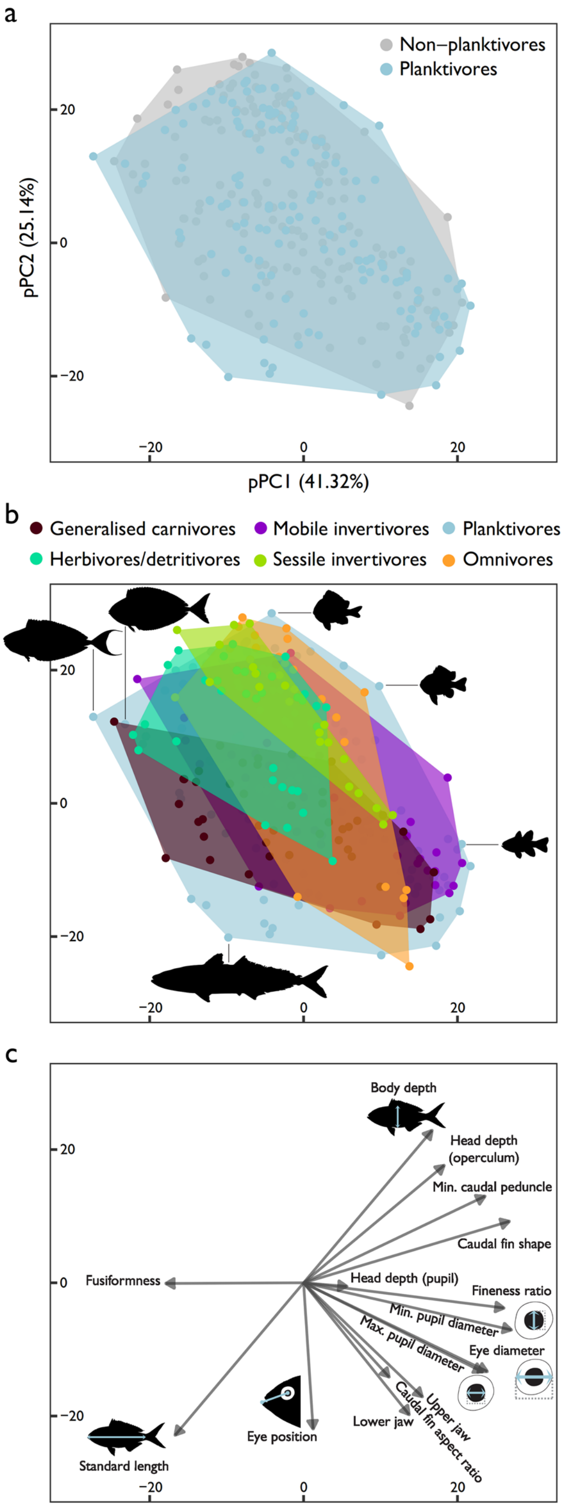


Fig. 4 Reef fish morphospace occupied by planktivores and ▶ non-planktivores. Phylogenetic principal components analysis (pPCA) conducted on morphological traits of 299 species between **a** planktivores and non-planktivores only and **b** among six reef fish trophic guilds, with **c** vector loadings of all 15 morphological traits. Convex hulls indicate the morphospace occupied by the species belonging to each trophic guild. Silhouettes plotted demonstrate examples of the shape variation along each PC axis. Silhouette species at the top from the left to right are *Naso fageni*, *N. hexacanthus*, *Dascyllus flavicaudus*, and *D. melanurus* and at the bottom from left to right are *Decapterus muroadsi* and *Nectamia bandanensis*

mostly correlated with maximum body depth, eye position, and standard length (Fig. 4c, Table S15).

Morphological convergence

The small differences between planktivores and non-planktivores and the vast morphospace of planktivores highlighted previously were further corroborated by the lack of evidence of morphological convergence found among planktivorous reef fishes. *Ct*-measures from the *convSigCt* function suggest that plankton-feeding reef fishes have not converged morphologically, and the results were the same when applying either the PC data or size-corrected morphological trait data (Tables 1, S3). This was supported by findings from the *windex.sim.test* function, whereby the Wheatsheaf index was no greater than expected relative to morphological traits evolving under a Brownian motion model (Tables 1, S5). These findings remained the same regardless of the data type and the number of simulations (i.e. 1000 or 5000; Table S5). On the other hand, Θ_{real} measures from the *search.conv* function demonstrate slightly different results (Tables 1, S4). We conducted hypothesis testing using the p-value for mean Θ_{real}, as it was preferable in our case (see Methods). While the results were largely consistent across the various numbers of simulations (i.e. 1000, 5000, or 10,000) and whether de-clustering was applied (Table S4), convergence was detected when using the PC scores but was not detected when using trait data (Table 1). However, Θ_{real} may not be able to distinguish convergence from other evolutionary processes. The significant result from the PC scores is likely to be an artefact of this effect and thus may be a signal for another evolutionary process such as conservatism. Overall, *Ct*-measures remain the most reliable method of convergence testing, so our

Table 1 Test results for morphological convergence among planktivorous reef fishes

Convergence test	Data type	Measure		p-value
Ct-measures	PC scores	$Ct1$	− 0.022	0.89
	Visual traits	$Ct1$	0.030	0.59
	Swimming traits	$Ct1$	0.031	0.18
Θ_{real}	PC scores	Mean Θ_{real}	83.554	0.014*
	Traits	Mean Θ_{real}	11.483	0.078
Wheatsheaf index	PC scores	Wheatsheaf index	0.984	0.823
	Traits	Wheatsheaf index	1.061	0.063

PC scores from the first three axes (79.07% of the shape variance) and size-corrected morphological trait data were used as input data for all three tests. Measures and associated significance level (p-value) from each convergence test is reported. Statistical significance is denoted with an asterisk (*). Full tables can be accessed in Supplementary Material (Tables S3–S5)

conclusions were largely based on those results. Altogether, our results showcase a lack of morphological convergence among planktivores.

Discussion

It has long been assumed that planktivorous reef fishes are converging towards a distinct body plan that is streamlined and fusiform, including key features like deeply forked caudal fins and large eyes close to their small mouths. Some of these morphological traits and patterns of convergence have been reported in specific families of planktivorous reef fishes, such as the Acanthuridae (Friedman et al. 2016), Chaetodontidae (Hodge et al. 2021), Labridae (Schmitz & Wainwright 2011a), and Pomacentridae (Aguilar-Medrano et al. 2011; Cooper et al. 2017; Cooper & Westneat 2009; Frédérich et al. 2008, 2013). There are even unique instances whereby planktivorous species demonstrate features distinct to their congenerics. Within the grouper genus *Cephalopholis*, for example, the planktivorous sister clade of *C. furcifer* and *C. colonus* (previously classified in their own genera, *Paranthias*) exhibit forked caudal fins and form a sister pair with the carnivorous *C. fulva*, which has rounded caudal fins (Floeter et al. 2018). However, these cases are generally rare, and upon considering the 12 most abundant fish families located in reefs globally, we found no difference in the overall body shape between planktivores and non-planktivores and no evidence for planktivores converging on a distinct morphotype (Table 1). Instead, we discovered that planktivores occupy the broadest morphospace of all trophic guilds and thereby, the entire morphospace of reef fishes (Fig. 4). Since plankton-feeding is observed across nearly all reef fish families (Fig. 2; planktivores [$n = 12$ families], generalised carnivores and omnivores [$n = 8$], herbivore/detritivores and mobile invertivores [$n = 6$], and sessile invertivores [$n = 5$]), and is the most common evolutionary transition destination among reef fish species (Floeter et al. 2018; Ng et al. 2024; Siqueira et al. 2020), it makes sense that planktivores encompass a vast range of morphologies.

The evolutionary prevalence of planktivory in reef fishes may also be due to their ontogeny, which is strongly associated with plankton. Most reef-associated species start their lives as larvae in the plankton, feeding on other plankton for survival before settling on the reef (Hobson 1991; Leis 1991). The effect of this can be observed in reef fishes of other trophic guilds, such as the mobile invertivore *Parablennius pilicornis* (SRF, pers. obs.) and the herbivore-detritivore *Acanthurus xanthopterus* (ACS, IN, pers. obs.), which opportunistically feed on plankton. This establishes that reef fishes of any size, form, and even trophic guild, are capable of consuming plankton. Overall, our results overwhelmingly supported minimal morphological differences between planktivores and non-planktivores (Figs. 3, 4; Tables S8–S13). Some evidence of within-family variation was observed (Table S14), with differences between the overall body shape of planktivores and non-planktivores in the Apogonidae and Lutjanidae (Fig. S6, Table S7). This could be explained by the phylogenetic clustering of planktivory within specific genera, particularly in the mid-water fusiliers (e.g. *Caesio* and *Paracaesio*) (Fig. 2), which are distinct in morphospace to the other predominantly benthic carnivorous lutjanids (Fig. S6). The remaining six families tested did not demonstrate strong differences between planktivore and non-planktivore morphologies (Table S7), suggesting that the morphological signal of planktivory both within and among families is inconsistent.

Morphological variation within and among families of planktivorous reef fishes has been observed in previous studies. Contrary to expectations, plankton-feeding acanthurids and labrids did not exhibit larger eyes (Friedman et al. 2016; Schmitz and Wainwright 2011a). However, the large eye hypothesis was supported in the Pomacentridae (Cooper and Westneat 2009) and Chaetodontidae (Hodge et al. 2021). Variation was also observed in body shape traits, with reduced body depths observed in planktivorous acanthurids (Friedman et al. 2016) but not in the Chaetodontidae (Hodge et al. 2021). Similarly, feeding-related traits varied. Among planktivorous labrids, *Clepticus parrae* and *Halichoeres pictus* possessed long gill rakers, while the fairy wrasse species (*Cirrhilabrus solorensis*; Fig. 1o) did not exhibit any of the hypothesised traits (Schmitz and Wainwright 2011a). However, planktivorous *Cirrhilabrus* species have unique anatomical features (i.e. increased mucus secretion) which putatively aid in the consumption of gelatinous plankton (Huertas and Bellwood 2020). We acknowledge that the variation in results between our study and others may be because some of these anatomical features were not within the scope of our study. Nevertheless, the combination of our findings and previous family-level research clearly demonstrate that reef fishes carry a suite of morphological solutions to exploit plankton (*sensu* Losos 2011), and that these solutions vary both within and among families.

Inability to capture distinct adaptations to planktivory may also be due to the overgeneralisation of the term 'planktivore'. Labelling 'planktivore' as a trophic guild means that species "exploit the same class of resources in a similar way" (i.e. definition of a guild; Stroud et al. 2015). Contrary to this assumption, planktivorous reef fishes target different planktonic resources using varied feeding strategies and partition their foraging across space and time. Plankton-feeding fishes encompass deep water angelfishes (*Genicanthus*) feeding high above the substratum (Randall 1975), fairy wrasses (*Cirrhilabrus*) foraging in aggregations (Layton and Fulton 2014) along rubble slopes (Tea et al. 2018), site-attached damselfishes (Pomacentridae) feeding on plankton above their live coral hosts, and schooling fusiliers (Caesioninae) consuming off-reef plankton at the turbulent reef edge (Hamner et al. 1988). These habitats are spread vertically along various depths and horizontally across various reef zones. Each of these locations is hydrodynamically unique, requiring varying locomotory demands, and thus, varying shapes and sizes. Body size ultimately places restrictions on the capacity for a species to forage in a specific way or place. For example, semi-pelagic fusiliers and pelagic *Decapterus* carangids grow to lengths of 50 cm, allowing them to forage in strong currents. Conversely, 3 cm-long *Bryaninops* cling onto whip corals and *Trimma* pygmy gobies remain close to their caves (Depczynski & Bellwood 2004) feeding on plankton passing by (Saeki et al. 2005).

An intersection in the foraging behaviour of planktivorous reef fishes also exists between space and time (Hobson & Chess 1978). At night, planktivorous apogonids form a 'blanket of mouths', travelling up to 145 m off-reef to feed on emerging plankton (Collins et al. 2024). This is contrary to diurnal fishes, which form a 'wall of mouths', feeding on off-reef plankton along the reef edge (Hamner et al. 1988). Primarily nocturnal families such as the Holocentridae and the predominantly planktivorous Apogonidae tend to have larger eyes (Schmitz and Wainwright 2011b), which may be a morphological adaption to meet both functional demands of greater light sensitivity and visual acuity to feed on zooplankton at night. Thus, nocturnal fishes may have experienced stronger selective pressures on their visual system traits relative to diurnal fishes, which can partially explain the large variability in the eye traits of reef fishes (Fig. 3).

Finally, planktivores may preferentially target the gelatinous or non-gelatinous fraction of zooplankton (Hamner et al. 1988; Huertas and Bellwood 2020), and this could be due to differences in prey size classes (Gardner 1981) or levels of nutrient delivery (Gahan et al. 2024). Indeed, planktivorous fishes prefer larger size classes and often ignore < 2 mm non-gelatinous prey (Gardner 1981), meaning sharper visual acuity may not necessarily increase fitness across all species. Prey size may also lead to other internal anatomical adaptations in the lenses, gill rakers (Schmitz and Wainwright 2011a), dentition (Lazzaro 1987), and adductor muscles (Wainwright and Bellwood 2002) of planktivorous fishes. Ultimately, the abundance and availability of plankton across reefs likely explains why the planktivorous diet does not have strong, unified selective pressures on the morphology of reef fishes. Planktivory is a broad dietary category which primarily refers to a feeding location (in the water column), meaning morphological adaptations and convergence may only be detected in planktivores once specific divisions are identified. These divisions must further account for the varying selective pressures arising from different behavioural, space, time, and prey specialisations. For example, morphological convergence associated with transitions to the water column was indeed detected within the planktivorous fusiliers of the Lutjanidae (Rincon-Sandoval et al. 2020).

Among reef fishes, planktivory is a relatively old trophic state that arose independently on at least seven occasions more than 25 million years ago (Ma). We highlight the earliest reconstructed appearance of planktivory nearly 53 Ma during the Eocene, the birth of many fish lineages on modern coral reefs (Fig. 2; Bellwood 1996). This is corroborated by the oldest fossil record of a putative reef fish planktivore: *Zorzinilabrus furcatus* (family Labridae) from approximately 50 Ma of the Lower Eocene in Monte Bolca, northern Italy (Bannikov and Bellwood 2017). Pomacentrids, a predominantly planktivorous reef fish family, were also found in the Monte Bolca fossil deposits (Bellwood 1996), with the earliest pomacentrid transition towards planktivory dated approximately 35 Ma during the Eocene (Fig. 2). Given the occurrence of planktivory since the birth of modern reef fish families, it is possible that present-day lineages have retained their ancestral morphs, thereby affecting their response to selection. Ancestral body plans may have been ‘good enough’ for reef fishes to meet the functional demands of plankton-feeding. Each species has a specific set of phenotypes and varying levels of genetic variation and constraints within their ancestral population. When taxa are introduced to a new selective environment, their standing genetic variation can lead to a myriad of evolutionary routes (Losos 2011), which may in turn have contributed to the striking suite of morphologies seen across reef fish planktivores today (Figs. 1, 4). Nevertheless, the low phylogenetic signal detected in our results suggests that shape variation among reef fishes is influenced by other external factors, such as the heterogeneity of ecological traits described above.

Herein, we challenge the longstanding assumption that planktivorous reef fishes have converged towards a similar, specialised body plan. We suggest that there is no distinct point for planktivores to converge on due to their diverse set of evolutionary pathways, habitats, foraging behaviour, activity time, and resource preferences. We show that planktivores encompass the entire morphospace of reef fishes, and differences in the overall body shapes between planktivores and non-planktivores are minimal and inconsistent across families. Planktivorous reef fishes, for the most part, do not appear to have diverged far from their ancestral body forms, and thus demonstrate various morphological solutions to overcome the collective challenges of plankton-feeding. Plankton-feeding reef fishes represent an assemblage of species with diverse characteristics matching the stunning array of their forms. They demonstrate varying foraging behaviours, inhabit nearly any and every section of the reef, represent both diurnal and nocturnal fishes, and partition varying prey resources. Ultimately, our study has led to a fundamental re-evaluation of what it means to be a planktivore: that is, there is more than one way to be a planktivore.

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Data availability The morphological data generated for this study is publicly available at Zenodo (DOI https://doi.org/10.5281/zenodo.15015293) This paper also analyses existing, publicly available data accessible at [DOI https://doi.org/10.1038/s41467-020-16498-w] and phylogenetic trees accessible at [DOI https://doi.org/10.1038/s41586-018-0273-1 and DOI https://doi.org/10.1038/s41559-022-01801-3].

Declarations

Conflict of interest The authors declare no competing interests.

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