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Ecomorphological convergence in planktivorous surgeonfishes

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Abstract

Morphological convergence plays a central role in the study of evolution. Often induced by shared ecological specialization, homoplasy hints at underlying selective pressures and adaptive constraints that deterministically shape the diversification of life. Although midwater zooplanktivory has arisen in adult surgeonfishes (family Acanthuridae) at least four independent times, it represents a clearly specialized state, requiring the capacity to swiftly swim in midwater locating and sucking small prey items. Whereas this diet has commonly been associated with specific functional adaptations in fishes, acanthurids present an interesting case study as all nonplanktivorous species feed by grazing on benthic algae and detritus, requiring a vastly different functional morphology that emphasizes biting behaviours. We examined the feeding morphology in 30 acanthurid species and, combined with a pre-existing phylogenetic tree, compared the fit of evolutionary models across two diet regimes: zooplanktivores and nonzooplanktivorous grazers. Accounting for phylogenetic relationships, the best-fitting model indicates that zooplanktivorous species are converging on a separate adaptive peak from their grazing relatives. Driving this bimodal landscape, zooplanktivorous acanthurids tend to develop a slender body, reduced facial features, smaller teeth and weakened jaw adductor muscles. However, despite these phenotypic changes, model fitting suggests that lineages have not yet reached the adaptive peak associated with plankton feeding even though some transitions appear to be over 10 million years old. These findings demonstrate that the selective demands of pelagic feeding promote repeated – albeit very gradual – ecomorphological convergence within surgeonfishes, while allowing local divergences between closely related species, contributing to the overall diversity of the clade.

Introduction

Morphological convergence provides powerful evidence for both the adaptability of organisms and the constraints of those adaptations (Losos, 2011). These homoplasious states present a framework by which to evaluate persisting ecological pressures and the underlying utility of shared traits. An array of factors influence the extent to which organisms are capable of converging under the same functional demands. Ranging from developmental processes to behavioural differences or even genetic structure, the way selective pressures shape morphology can be strongly clade dependent (Wake, 1991; Losos, 2011). Localized environmental variables and existing competitors can additionally limit the capacity of species to exploit a resource (Hansen, 1997; Gould, 2002; Langerhans & DeWitt, 2004). Even when the ecological opportunity exists and lineages are capable of responding to the same selective forces, the outcome may differ if there

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are multiple optimized solutions to overcome the same evolutionary challenge (Wainwright *et al.*, 2005; Wainwright, 2007). Despite these restrictions, convergence is regarded as being very common (Mahler *et al.*, 2013; Moen *et al.*, 2015). Independent lineages commonly acquire shared traits, although the magnitude of these physical similarities is variable and often difficult to quantify (Stayton, 2006; Collar *et al.*, 2014).

In fishes, morphological convergence is frequently discovered among species with shared specialized diets. Cichlids have been presented as an example of repeated dietary convergence with studies establishing a relationship between trophic specialization and functional traits such as body size and tooth shape (Rüber & Adams, 2001; Hulsey & García De León, 2005; Montaña & Winemiller, 2013). The relationship between diet and morphology in fishes has been widely studied, including transitions to durophagy (Collar *et al.*, 2014), piscivory (Collar *et al.*, 2009), herbivory (Davis & Unmack, 2014) and zooplanktivory (Cooper & Westneat, 2009). However, the morphological and ecological diversity of coral reef fishes make these assemblages strong candidates for studies of convergence (Lobato *et al.*, 2014). A major component of both coral reef and pelagic communities, zooplanktivory has evolved in virtually every major reef fish lineage including Balistidae, Chaetodontidae, Holocentridae, Labridae, Lutjanidae, Pomacanthidae, Pomacentridae and Serranidae (Hobson, 1991). Traits that have been found associated with zooplanktivory include a general reduction in feeding musculature (Wainwright & Richard, 1995; Wainwright *et al.*, 2002; Hulsey *et al.*, 2007), increased jaw protrusibility (Lazzaro, 1987; Cooper & Westneat, 2009), longer gill rakers (Lazzaro, 1987) and larger eye diameter (Hulsey *et al.*, 2007; Cooper & Westneat, 2009). These changes have been attributed to the functional demand of locating and sucking small (< 3 mm) prey items out of the water column (Lazzaro, 1987). But, not all zooplanktivores fit this model. In a study on labrids, Schmitz & Wainwright (2011) found that whereas most species did possess smaller jaws and longer gill rakers, *Cirrhilabrus solorensis* lacked all typical zooplanktivorous traits, indicating some morphological inconsistencies across this dietary regime. Furthermore, most research has focused on evolutionary shifts from benthic suction feeding to midwater zooplanktivory with few studies considering the functional implications of transitions from biting behaviour to plankton feeding.

Here we focus on the monophyletic Acanthuridae, a group of reef-associated fishes consisting of more than 80 species. Whereas the majority of acanthurid species graze benthically on filamentous algae or macrophytic algae, or consume microbes and detritus, midwater zooplanktivory has evolved at least four separate times within the family, spanning three genera: *Paracanthurus, Naso* and *Acanthurus* (Jones, 1968; Winterbottom & McLennan, 1993; Tang *et al.*, 1999; Klanten *et al.*, 2004). As grazing appears to be the ancestral state in acanthurids, zooplanktivory represents a dramatic evolutionary shift ecologically, behaviourally and functionally from tearing, scraping or nipping algae from the substratum to suction feeding on small, drifting zooplankters (Winterbottom & McLennan, 1993).

Within surgeonfishes, planktivory has been associated with a suite of morphological and physiological modifications including dentition, gill raker spacing, gastrointestinal tract length, gut microbiota and feeding behaviour (Jones, 1968; Purcell & Bellwood, 1993; Choat & Clements, 1998; Wainwright & Bellwood, 2001; Konow *et al.*, 2008; Fishelson & Delarea, 2014; Miyake *et al.*, 2015). Diet-associated morphological plasticity combined with the presence of independent transitions to zooplanktivory from grazing ancestors suggests at the adaptability of surgeonfishes and presents a prime opportunity to investigate convergence. Previous studies of dietary transitions in acanthurids were limited by a lack of phylogenetic resolution for the clade (Winterbottom & McLennan, 1993; Tang *et al.*, 1999), but with phylogenetic progress (Clements *et al.*, 2003; Sorenson *et al.*, 2013) and new insights from palaeontology (Bellwood *et al.*, 2014) has come a better understanding of the evolutionary history of the group. Combining a time-calibrated acanthurid phylogeny, linear morphometrics and evolutionary models, we investigate the following questions in a comparative framework. Have the independent transitions to zooplanktivory resulted in a convergence of feeding morphology and body shape within acanthurids and which functional traits show consistent responses across the planktivore regime? We present an integrated analysis of how functionally demanding trophic states influence trait selection, affect evolutionary rates and ultimately shape phenotypic landscapes.

Materials and methods

Sampling and specimen measurements

A total of 96 ethanol-preserved individuals representing 30 acanthurid species were included in this study (average number of specimens per species = 3.2; range = [1, 5]). Adult specimens were collected for this project with hand spears in the Red Sea, Puerto Rico, Great Barrier Reef and Hawai'i. Seventeen morphological measurements were recorded for each individual. Significant to both feeding and locomotion, these traits were primarily selected for their functional relevance and previous utility in discriminating ecological niches in acanthurids (Jones, 1968) and other reef fishes (Wainwright *et al.*, 2004; Schmitz & Wainwright, 2011). Measured characters were as follows: standard length, total body mass, maximum body depth, maximum body width, lower jaw length (from the mandibular symphysis to the articular–quadrate joint), jaw width at the articular–

quadrate joints, length of the leading edge of the pectoral fin, length of the dentigerous arm of the premaxilla, tooth length (most medial intact tooth on the premaxilla), mass of the adductor mandibulae muscle, eye diameter, gill raker length, ratio of eye depth to total head depth, angle between the centre of the eye and tip of the premaxilla (Jones, 1968), and three distances forming a triangle between the centre of the eye, base of the pectoral fin and the anterior tip of the dentary. The entire adductor muscle of each specimen was excised and stored in 70% ethanol before being weighed using a Mettler Toledo AB204 analytical balance (precision: 0.1 mg). Muscle samples were first blotted on a paper towel and exposed to open air for a standardized time period (1 min) to reduce variation in liquid evaporation before weighing. The adductor mandibulae muscle is responsible for creating the bite force of the lower jaw and mass is a proxy for its power and force capacity (Alfaro *et al.*, 2001; Westneat, 2003).

A literature search was undertaken to classify species based on diet composition (Jones, 1968; Robertson & Gaines, 1986; Montgomerey *et al.*, 1989; Hobson, 1991; Choat *et al.*, 2002, 2004; Crossman *et al.*, 2005; Sandin & Williams, 2010). We categorized species as zooplanktivorous if over 25% of their adult diet consists of zooplankton. Whereas some other species present in this study do supplement their diet with zooplankters, they consume more than 75% algae, detritus or both and were categorized as nonzooplanktivorous.

Morphometric analysis

Analyses were conducted using the R statistical computing environment (R Core Team, 2014) and were based on the log10-transformed species means for each morphometric variable; cube roots were first calculated for body mass and adductor weight to make variables dimensionally similar. Phylogenetic regressions (using the function phyl.resid.R in the package ‘phytools’) were run and residuals extracted for each trait against standard length (Revell, 2009, 2010). This removed the confounding effects of body size while accounting for phylogenetic relationships. We used the time-calibrated consensus tree from Sorenson *et al.* (2013) in our analyses. This phylogeny was originally constructed using a concatenated dataset of two mitochondrial and six nuclear loci. We pruned the tree to only include the 30 species of our study and performed a phylogenetic principal components analysis (PCA) on the residuals for the 16 remaining traits to reduce the dimensionality of our data set (Revell, 2012). As a recent study has shown that using phylogenetic PC axes as trait data could bias results (Uyeda *et al.*, 2015) we also implemented a nonphylogenetic PCA. Principal components (PCs) were assessed for significance using the broken-stick model (Macarthur, 1957; Frontier, 1976; Jackson, 1993) implemented in the R package ‘adephylo’ (Jombart & Dray, 2008; Jombart *et al.*, 2010). Those components that contributed a significant portion of trait variation were retained and PC scores adopted as trait input for subsequent comparative analyses.

We projected both the significant PCs and individual trait residual values on a phylomorphospace using the function phylomorphospace.R in the phytools package (Rohlf, 2002; Sidlauskas, 2008; Revell, 2012). This function graphs the phylogeny in a two-dimensional space and reconstructs ancestral states along morphospace axes. It then plots tree tips with their associated branches connecting taxa to their respective ancestral nodes. Thus, we were able to evaluate both interspecific physical similarity (proximity between lineages) and intraspecific phenotypic trajectories (magnitude and directionality of branches).

Adaptive peak-based estimates of convergence

Evolutionary models represent the different possible processes shaping morphological evolution and provide a method of testing predictions for different phenotypic distributions. We assessed the fit of six evolutionary models to both our significant PCs and the residuals of each morphological trait using the function OUwie.R of the package OUwie (Beaulieu *et al.*, 2012; Beaulieu & O’Meara, 2015). As OUwie requires *a priori* assignment of regimes, only two were selected – zooplanktivorous and nonzooplanktivorous. This division allowed us to test for convergence between lineages that have transitioned to diets involving midwater suction feeding to capture small prey, as opposed to the biting morphology seen in benthic grazing acanthurids. The possible ancestral dietary regimes along the internal branches of the phylogenetic tree were determined prior to model selection using Bayesian stochastic character mapping (Huelsenbeck *et al.*, 2003) implemented in the make.simmap function in the phytools package (Revell, 2012). All evolutionary models were run on 1000 stochastically mapped trees to take into account uncertainty in the ancestral dietary regime. Using a model-fitting framework on all stochastic character maps, we estimated how zooplanktivory alters functional traits and their evolutionary rates of change. Single-rate Brownian motion (BM) does not allow for separate regimes and operates under the assumption that trait evolution proceeds as a random walk and trait variance across lineages accumulates proportional to time (Felsenstein, 1985). Increasing in complexity, the single-optimum Ornstein–Uhlenbeck (OU1) model constrains traits to evolve towards one value, essentially incorporating a single selective regime into the model, but there is still no influence of diet upon the trait. OU models differ from BM in that they involve three parameters: the primary trait optima/optimum (θ), the strength of selection towards those optima (α) and the variance of the Brownian random walk (σ^2) (Hansen, 1997; Butler & King, 2004). Multipeak OU models allow these parameters to vary with dietary regime and, as a result, can estimate adaptation and strength of selection towards separate phenotypic optima. The simplest multipeak OU model, OUM, does not permit α or σ^2 parameters to vary between regimes. Among the more complex OU models, OUMA only estimates multiple α parameters, whereas OUMV permits separate σ^2 for each regime. The full OUMVA model allows all parameters (θ, α and σ^2) to vary by regime, but the likelihood often didn't converge with the smaller data set used in this study. As we predict that zooplanktivorous lineages are converging on a separate adaptive peak from their grazing relatives, the best-fitting models for PC1, PC2 and traits under selection should correspond to multipeak OU models (OUM, OUMA, OUMV or OUMVA).

As preliminary analyses indicated that estimates of θ were stabilized by dropping θ_0, we assumed the starting value was distributed according to the stationary distribution of the OU process (root.station = TRUE). Model fit was evaluated using a modified Akaike information criterion (AICc), which incorporates a correction for small sample size (Burnham & Anderson, 2002; Burnham *et al.*, 2011). We confirmed that eigendecomposition of the Hessian were positive for all iterations which indicates that the analyses returned the maximum likelihood estimates. Negative values indicate a saddlepoint and unreliable results; if negative values were detected, the results for that model and tree were discarded from the data set. Additionally, we generated a 95% confidence interval for all model parameters (α, θ and σ^2) using the parametric bootstrapping function OUwie.boot.R (package OUwie). Model parameters for 1000 replicates were determined by those originally estimated under the best-fit model for each morphological character.

To ensure that the complexity of the OU models do not exceed the information contained within our small dataset, we also performed 1000 OUwie simulations for PC1 and PC2 (Boettiger *et al.*, 2012). These simulated data sets were generated with the parameter estimates from the best-fit model in our original data set using OUwie.sim (Beaulieu *et al.*, 2012). Simulated data were then recursively run through all six models in OUwie to determine the extent to which the algorithm could identify the model as well as the parameters that the data were generated under, thereby demonstrating statistical power.

Additionally, to quantify the strength of convergence within zooplanktivorous species, we implemented the Wheatsheaf Index (w), a technique that has been shown to perform well with simulations on smaller phylogenetic trees (Arbuckle *et al.*, 2014). The index primarily relies on phylogenetic relatedness and morphological similarity to estimate pull towards an adaptive peak. Higher scores represent a large distance travelled across an adaptive landscape towards the phenotypic optimum as well as close proximity between focal species (*a priori* designated convergent taxa). Thus, the index measures convergence as a combination of phenotypic similarity within focal taxa and morphological dissimilarity between focal and nonfocal taxa. The Wheatsheaf Index was applied to both trait data and PC scores in R using the package 'windex' (Arbuckle *et al.*, 2014).

Pattern-based estimates of convergence

As a further test of convergence, we quantified the amount of independently evolved similarity within both our trait data and PC scores using the R package convevol (Stayton, 2015). Selected trait data (premaxilla length, maximum body depth, distance between the jaw and eye, tooth length and the angle between the jaw and eye) were used as the convevol function requires fewer variables than the number of focal taxa. We calculated the degree of phenotypic similarity, using both a distance-based approach and a frequency-based measure of convergence. The frequency-based measure quantifies the number of lineages that have evolved into a certain region of morphospace and reports the number of convergent events (C_5) that have occurred, whereas the distance-based measures (C_1–C_4) are calculated between two lineages as a proportion of the distance between both species tips and the largest distance between those taxa throughout their evolutionary history (anywhere between the species tips and their most recent common ancestor). A higher C value indicates stronger convergence. We report four C values representing the proportion of the maximum distance between focal taxa that has been closed by evolution (C_1), this proportion while accounting for the magnitude of change (C_2), and the amount of evolution attributable to convergence between focal taxa (C_3) as well as the smallest clade containing these focal taxa (C_4). We performed 500 simulations of evolution along the phylogeny using BM, calculating convergence measures for each simulation in convevol to determine if the observed C value is greater than would be expected by chance (P-value).

Results

Diet analysis

We were able to obtain morphological data on six zooplanktivorous species among the 30 acanthurids incorporated in this study, spanning four independent transitions to pelagic feeding within the family (Fig. 1). Literature searches, however, revealed variability in the diet composition of zooplanktivorous acanthurids incorporated in this study. *Naso brevirostris* and *N. vlamingii* exhibit ontogenetic shifts from benthic grazing to pelagic feeding (Green & Bellwood, 2009), with both gelatinous zooplankton and filamentous algae composing significant amounts of their adult diets. *N. hexacanthus* is a zooplanktivore specialist, subsisting solely on gelatinous salps and small amounts of inorganic material (Choat *et al.*, 2002). Similarly, *Acanthurus mata* and *A. thompsoni* are strict zooplanktivores, feeding on gelatinous zooplankton (mostly *A. thompsoni*), copepods and crustacean larvae (Hobson, 1974; Choat & Clements, 1998; Crossman *et al.*, 2005). Finally, whereas little literature exists on the exact prey composition of *Paracanthurus hepatus,* this species is generally considered a zooplanktivore, although they are often seen grazing on benthic algae (Winterbottom & McLennan, 1993).

Morphometric analysis

Acanthurids display considerable morphological diversity in both facial anatomy and body shape (Fig. 1). The principal components analysis yielded two significant axes responsible for nearly 59% of the variance within the morphological data set (Table 1). Principal component 1 (38% variance explained) revealed differences between diet guilds on the morphospace, with loadings indicating that zooplanktivores tend to have a shallower and narrower body, smaller adductor mandibulae muscles and reduced jaw and facial structure (Fig. 2; Table 1). PC2 (20% variance explained) shows broader overlap between diet regimes, although planktivores all occupy the upper half of the range. PC2 is most positively correlated with gill raker length and negatively with jaw length and body depth (Fig. 2; Table 1). We found few differences between the phylogenetic PCA and nonphylogenetic PCA results (Fig. S1; Table S1), indicating that using phylogenetic PCA axes likely does not have a large effect on our findings.

Phylomorphospaces of trait residuals were constructed in an effort to visualize trends within individual characters

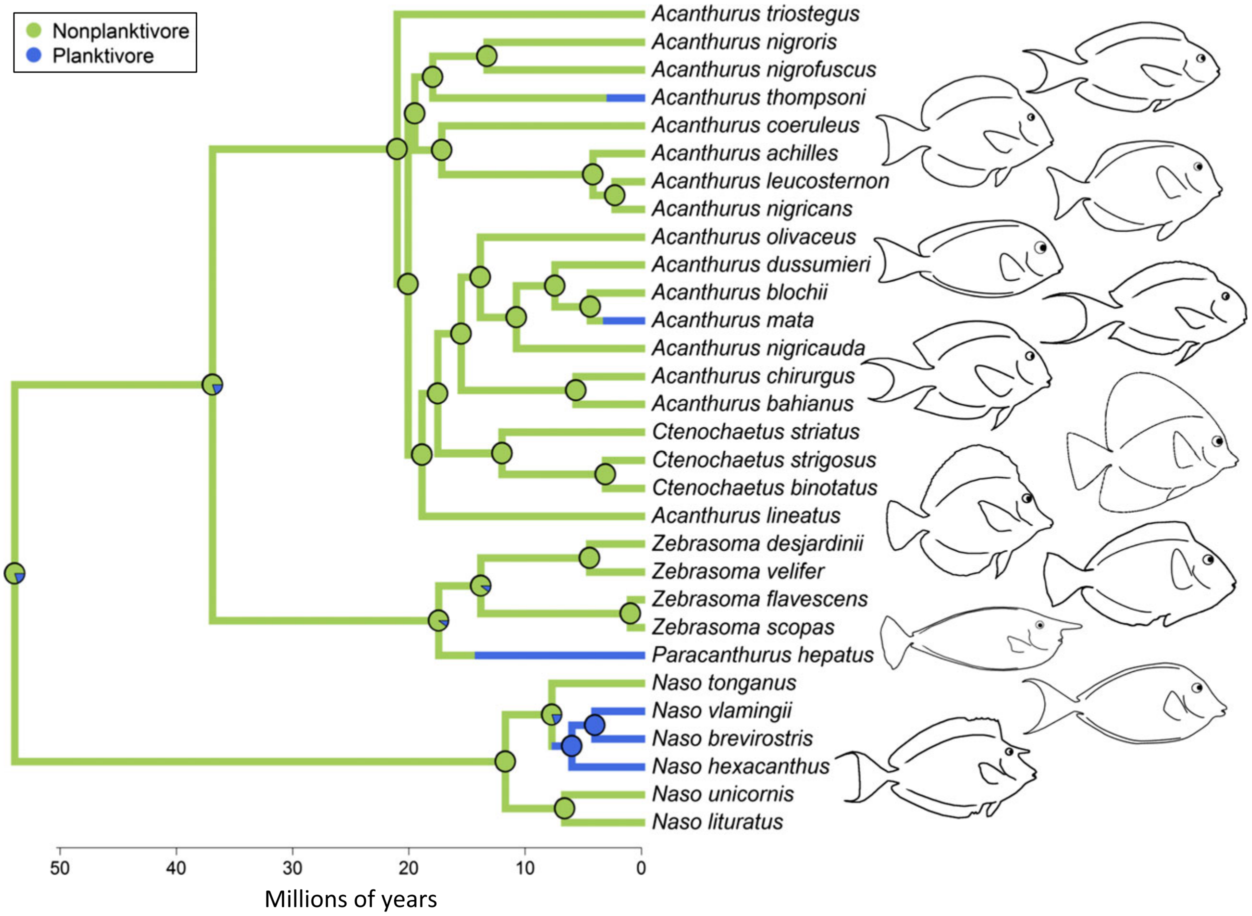

Fig. 1 Time-calibrated phylogeny (adapted from Sorenson *et al.*, 2013) of acanthurid species included in this study with a sample stochastic character map of diet and ancestral state estimates from 500 simmaps indicated at the nodes. Blue and green denote zooplanktivorous and nonzooplanktivorous species, respectively. Fish outlines illustrate morphological diversity within the clade and are identified as follows (from top to bottom): *Acanthurus thompsoni, A. blochii, A. leucosternon, A. mata, A. nigricauda, Ctenochaetus binotatus, Zebrasoma velifer, Z. flavescens, Paracanthurus hepatus, Naso brevirostris, N. lituratus* and *N. unicornis.*

Table 1 Loadings for the 16 morphological traits from a phylogenetic principal components analysis run on body size-corrected residuals. Only PC1 and 2 were found to explain more variance than expected by chance, suiting a broken-stick approach.

Variable	PC1	PC2
Body mass	−0.801	0.012
Eye diameter	−0.466	0.584
Max body depth	−0.773	−0.515
Max body width	−0.819	0.177
Pectoral fin	−0.173	−0.423
Jaw length	−0.183	−0.769
Jaw width	−0.601	−0.405
Premax	−0.646	0.548
Eye to Fin	−0.939	0.031
Fin to Jaw	−0.666	0.182
Jaw to Eye	−0.829	−0.237
Tooth length	−0.441	−0.488
Adductor Weight	−0.869	0.245
Gill Raker Length	−0.157	0.818
Eye depth	0.220	0.472
Jaw to eye angle	−0.414	0.237
% variance explained	38.58	20.05

(Figs 3 and 4). Whereas some traits displayed little visible trend with diet regime, others demonstrated marked parallel movement towards zooplanktivore specific morphologies (Fig. 4). Estimation of the direction of trait change at each transition to planktivory revealed general consistency in the reductions of traits among planktivorous lineages (Table S2).

Adaptive peak-based estimates of convergence

Results from PC model fitting are summarized in Table 2, which provides information regarding fit (log-lik and AICc values) and estimates of diet optima for each of the six evolutionary models averaged over 1000 stochastic reconstructions. Two-peak OU models (OUM, OUMV, OUMA and OUMVA) were substantially favoured for PC1, with OUM models generating the lowest AICc in over 90% of the reconstructions. The OUM model implies that the two diet regimes have separate phenotypic optima, but do not differ in rate of evolution or pull towards their respective adaptive peaks. For PC2, the multiple optima OUMA model yielded the lowest accurate mean AICc value but the preferred model varied substantially across the stochastic reconstructions. The most complex model, OUMVA, did not converge for our PC2 data set and is therefore not reported in the Table. Two parameterized multipeak OU models (OUM, OUMV) were preferred almost equally (~ 30%) across reconstructions and a considerable 18% favoured the single-peak OU model, indicating model estimation difficulties. As over 80% of reconstructions favour some parameterized version of a multipeak OU model, we find weak support for multiple phenotypic optima on PC2.

Results from individual trait parametric bootstraps produced distinct, well supported diet optima for body mass, body depth, pectoral fin length, length of the dentigerous arm of the premaxilla, the triangular facial distances, tooth length, adductor mandibulae mass and the angle between the jaw and the eye (Table 3).

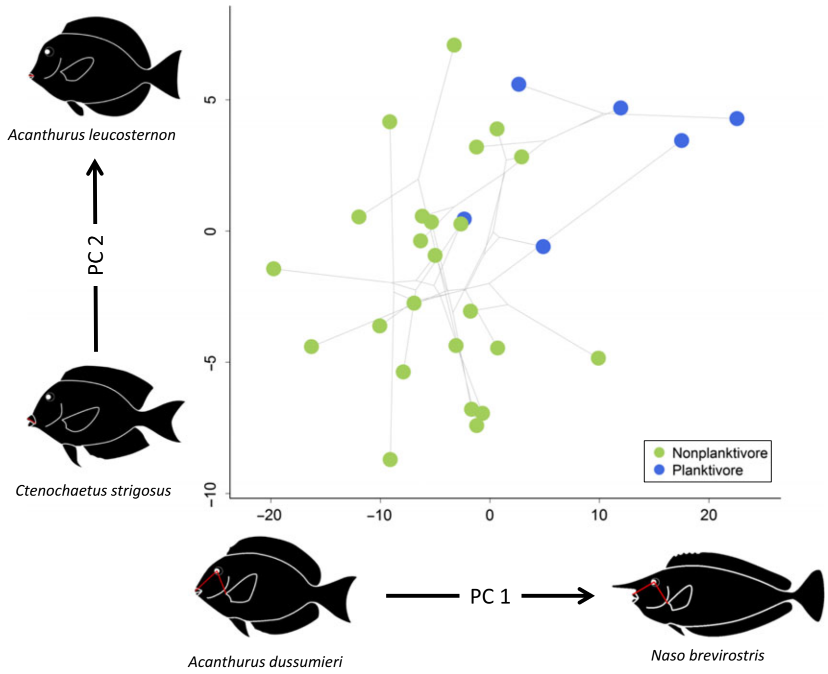

Fig. 2 Phylomorphospace projection of acanthurid species on the first two principal components. Blue and green circles denote zooplanktivorous and nonzooplanktivorous species, respectively. Fish silhouettes illustrate the outlying species on each axis, whereas superimposed red lines designate the traits loading high (> 0.82) on that Principal component (PC) and, therefore, the major sources of variation along that axis. PC1 scores are negatively correlated with adductor mandibulae mass, distances between eye and pectoral fin, and distances between eye and anterior tip of the premaxilla. PC2 scores load negatively with gill raker length (Table 1).

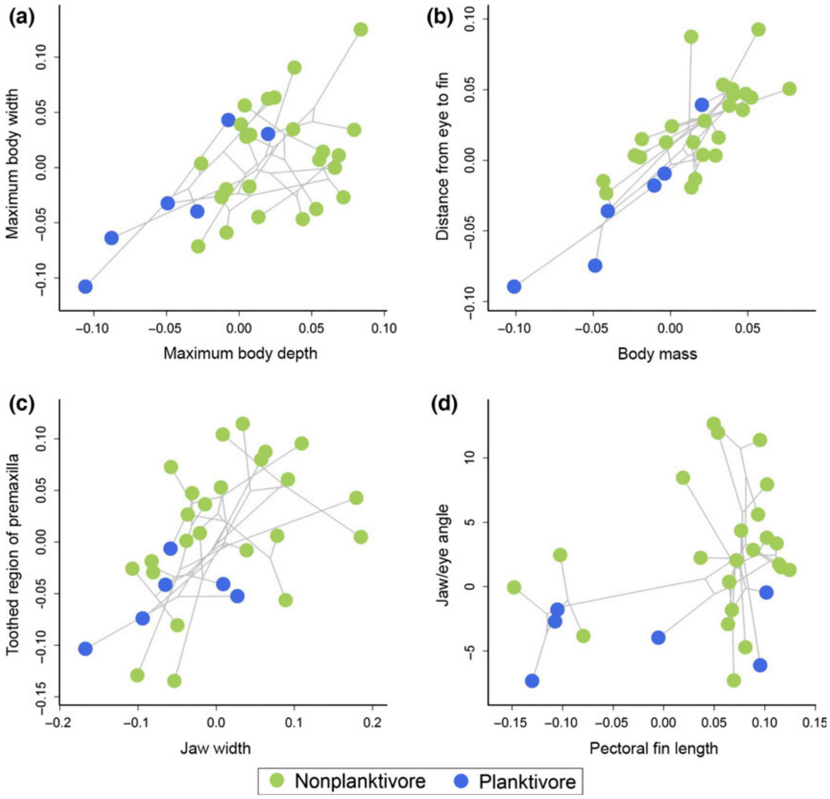

Fig. 3 Representative phylomorphospaces of size-corrected residuals for selected variables. Blue and green circles indicate zooplanktivorous and nonzooplanktivorous species, respectively. In panel d, the clade that occupies a distinct region of morphospace along the horizontal axis is *Naso*, corresponding to a reduction in pectoral fin length.

Whereas other morphological trends shared varying amounts of confidence interval overlap, zooplanktivorous species demonstrated lower average values than nonzooplanktivorous taxa in all 16 variables. There was no difference in alpha parameter between regimes for any trait, which may reflect poor estimation power as demonstrated in the simulations (Figs S5 and S6). Two-peak OU models were preferred as the best-fit model for all but five of the morphological traits, which favoured single-peak OU models (Table 3).

The simulations under our best-fitting OU models demonstrate that our data have the power to distinguish multipeak (OUM, OUMA, OUMV, OUMVA) models from single-rate or single-peak (BM, OU1) models (Fig. S2a, b) and to successfully estimate the placement of the optima (Figs S3 and S4). This is evidenced by the clear division of AICc scores; multipeak models consistently showed a much lower distribution than single-optimum models in the 1000 simulations. Our simulations, however, indicate that we cannot readily distinguish between the more complex OU models on PC1 as the results yielded no universal best-fit model (Fig. S2a). Whereas multipeak OU models are also a better fit on PC2, there were some difficulties distinguishing between all OU models (Fig. S2b). Given our small sample size it is not surprising that neither α nor σ^2 can be reliably estimated on our phylogeny (Figs S5–S8). Nevertheless, we have sufficient statistical power to estimate θ and discriminate between single-peak and multipeak models, which permits conclusions about the placement of the peaks within the adaptive landscape (Figs S3 and S4).

The Wheatsheaf Index (w) yielded relatively low values for both individual traits and PC scores, indicating a weak strength of convergence in the zooplanktivore regime. Despite input of the three traits most strongly correlated with zooplanktivory: adductor mass, distance between jaw and eye, and distance between the eye and fin, we recovered a w of 1.25 (95% CI = [1.196, 1.489]; $P = 0.679$). PC data returned comparable results, with an estimated w of 1.09 (95% CI = [0.926, 1.641]; $P = 0.849$). The high P-values ($P > 0.05$) suggest the strength of convergence is not significantly different than would be expected under randomized trait values interspersed across the tree. Such weak selection implies that lineage-specific factors have stunted adaptation and created variability in evolutionary responses.

Pattern-based estimates of convergence

Analysis from the R package convevol using PC data revealed a C_1 of 0.36, indicating that evolution has closed 36% of the distance between planktivorous taxa, with convergence responsible for 3.2% of the total evolution between planktivorous lineages (Table S3). As the most recent common ancestor between

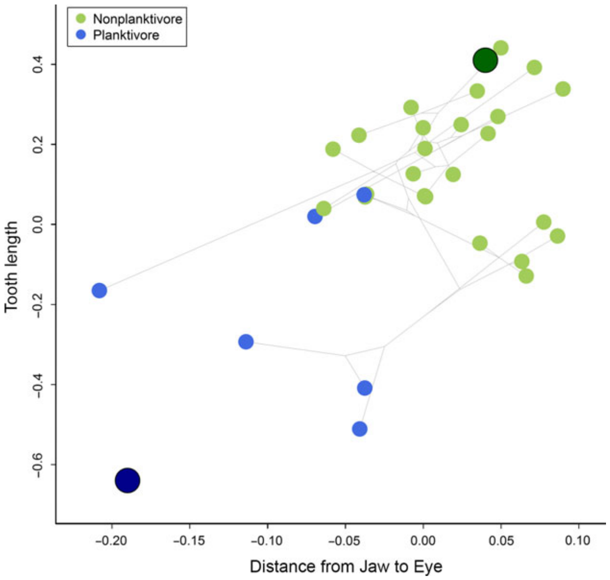

Fig. 4 Phylomorphospace of size-corrected residuals for tooth length and the distance between the centre of the eye and anterior tip of the jaw mapped to the phylogenetic tree from Fig. 1. Blue and green circles indicate zooplanktivorous and nonzooplanktivorous species, respectively. Large circles are colour-coded to denote the location of trait optima (θ) for each diet regime as determined by the best-fitting evolutionary model (Table 2).

Table 2 Comparisons of five evolutionary model fits and primary trait optima (θ) for the first two principal components. Mean Akaike information criterion (AICc) is the averaged AICc over 1000 replications and ΔAICc is the model's mean AICc minus the minimum AICc between models. Final column (%) contains the percentage of 1000 stochastic reconstructions in which each model was favoured. Bolded rows represent the best-fit model as indicated by the lowest AICc score. Estimated θ for zooplanktivore (Z) and nonzooplanktivore (NZ) regimes are displayed where applicable.

	Model	Loglik	AIC$_c$	Δ AIC$_c$	θ_{NZ}	θ_Z	%
PC1	BM	−110.11	224.66	17.97	—	—	0.00
	OU1	−106.03	218.99	12.30	—	—	0.20
	OUM	**−98.54**	**206.69**	**0.00**	**−4.90**	**1.38**	**90.40**
	OUMV	−98.06	208.62	1.93	−2.12	0.61	1.50
	OUMA	−98.11	208.71	2.03	−4.80	1.25	4.90
	OUMVA	−98.06	211.77	5.08	−2.22	1.07	3.00
PC2	BM	−100.29	205.03	40.52	—	—	0.00
	OU1	−85.75	178.42	13.91	—	—	18.90
	OUM	−82.21	174.22	9.71	−1.89	3.41	30.30
	OUMV	−80.58	168.33	3.83	−2.56	4.63	31.60
	OUMA	**−80.20**	**164.51**	**0.00**	**−1.77**	**4.87**	**15.10**
	OUMVA*	—	—	—	—	—	—

*OUMVA model unable to converge with PC2 data.

planktivorous taxa is the basal node of the phylogeny, convergence also accounted for 3.2% of the total evolution in the clade containing all purportedly convergent taxa. Measurements of convergence computed with selected trait data yielded a C_1 of 0.58, with convergence accounting for 4.5% of evolution between planktivorous taxa. All results from distance-based measures of convergence were significantly higher than would be expected by chance ($P < 0.02$). Frequency-based measures of convergence (number of lineages that evolve into the region of interest) reported a statistically nonsignificant value of 3 for the PC data ($P = 0.39$) and a significant value of 6 for individual trait data ($P < 0.001$). This discrepancy in results between the PC axes and individual variables is probably affected by the increased power provided with the additional individual variables.

Discussion

The combined results of the principal components analysis and evolutionary model fitting support the hypothesis that zooplanktivorous acanthurid species are converging on a separate adaptive peak from their nonzooplanktivorous grazing relatives. The majority of morphological traits and both principal components are best fit by two-peak Ornstein–Uhlenbeck models, indicating a bimodal distribution of traits corresponding to the two diet guilds. Our parametric bootstrapped confidence intervals and simulations have shown that these results are a robust estimation of adaptive peak topology. The pattern-based convevol analyses yielded further support for convergence, identifying significant, independently evolved morphological similarity between zooplanktivorous taxa using both distance- and frequency-based measures of convergence. We conclude that zooplanktivorous surgeonfish species show a consistent trend of reductions in the functional traits included in this study (Figs 3 and 4 and Table S2). Body depth and width, adductor mandibulae mass and the distances between the jaw, eye and fin load highest on the first principal component, which shows strong support for a multipeak OU model, suggesting that these traits hold particular significance in adapting to plankton feeding. These repeated morphological shifts, combined with additional support from the convevol analysis, positive movement along PC1 with every transition (Fig. 2) and similarly oriented trajectories in the individual variables (Figs 3 and 4a, b), are indicative of selection towards a zooplanktivore adaptive peak and are congruent with the distribution expected under convergent evolution (Stayton, 2006; Losos, 2011).

Functional adaptations to zooplanktivory

Trophic diversity across acanthurids is restricted to benthic grazing on algae, microbes and detritus or zoo-

Table 3 Best-fit evolutionary model for size-corrected trait residuals as determined by the lowest scoring Akaike information criterion model that had converged on the maximum likelihood solution. Estimated θ for zooplanktivores (Z) and nonzooplanktivores (NZ) shown with a 95% confidence interval across 1000 bootstraps.

Trait	Best Model	θ_{NZ} [95% CI]	θ_{Z} [95% CI]
Body mass	OUM	0.05 [0.02, 0.08]	-0.09 [−0.15, −0.03]
Eye diameter	OU1	—	—
Max body depth	OUM	0.07 [0.04, 0.10]	−0.11 [−0.18, −0.05]
Max body width	OU1	—	—
Pectoral fin	OUM	0.22 [0.14, 0.30]	−0.24 [−0.32, −0.07]
Jaw length	OUMV	−0.01 [−0.10, 0.09]	−0.09 [−0.15, −0.04]
Jaw width	OU1	—	—
Premax	OUMV	0.03 [−0.02, 0.10]	−0.12 [−0.18, −0.07]
Eye to fin	OUM	0.07 [0.04, 0.10]	−0.10 [−0.17, −0.03]
Fin to jaw	OUM	0.03 [−0.01, 0.07]	−0.07 [−0.15, 0.01]
Jaw to eye	OUM	0.04 [0.00, 0.09]	−0.19 [−0.29, −0.11]
Tooth length	OUM	0.45 [0.32, 0.60]	−0.64 [−0.93, −0.34]
Adductor weight	OUMVA	0.00 [0.00, 0.00]	−0.05 [−0.05, −0.04]
Gill raker length	OU1	—	—
Eye depth	OU1	—	—
Jaw to eye angle	OUM	2.80 [0.74, 4.84]	−4.23 [−8.75, 0.14]

planktivory. With evidence that extant acanthurids (excluding Nasinae) have evolved from benthic grazers (Klanten *et al.*, 2004), transitions to a specialized planktivorous strategy can be expected to alter the selective regime for both locomotion and feeding (Jones, 1968; Winterbottom & McLennan, 1993; Wainwright & Bellwood, 2001).

Most acanthurids bite, tear and manipulate algae that either coat the hard surfaces on reefs or remove the loosely associated microbial epiphytes, consuming them with detritus that accumulate on these surfaces as well. These taxa swim close to the substratum, negotiating the three-dimensionally complex reef environment and interrupting steady locomotion with frequent turning and reorientation to facilitate targeted biting in species-specific microhabitats. Previous research has suggested grazing acanthurids may have evolved deeper bodies in part to enhance manoeuvrability and fast start performance in response to risky feeding behaviour (Bellwood *et al.*, 2014). In contrast, zooplanktivorous taxa forage in midwater, swimming well above the reef to find and suck individual zooplankters that are carried across the reef by water flow. Not only are zooplanktivorous fishes probably subjected to the stronger currents that bring influxes of planktonic material (Hjelm *et al.*, 2001), but the pelagic environment provides little shelter from piscivorous predators and considerable distances are covered as the fish move about in midwater, likely favouring enhanced swimming capacity. The strong expectation in the literature is that benthic-feeding grazers should exhibit agility (Walker, 1997; Ellerby & Gerry, 2011; Bellwood *et al.*, 2014), whereas midwater swimmers emphasize efficiency at relatively high sustained speeds (Fulton *et al.*, 2001; Wainwright *et al.*, 2002; Frédérich *et al.*, 2013). The gravitation towards a more slender body form in zooplanktivores reduces drag experienced during swimming and has been noted in pelagic transitions within other lineages, both between species (Tavera *et al.*, 2012; Frédérich *et al.*, 2013) and intraspecifically (McGee *et al.*, 2013).

Previous studies within Labridae found that zooplanktivores were characterized by high aspect ratio pectoral fins, consistent with increased efficiency at high sustained speeds of swimming (Fulton *et al.*, 2001; Wainwright *et al.*, 2002). Like labrids, many acanthurids propel themselves with their pectoral fins during steady locomotion (Fulton *et al.*, 2001; Bellwood *et al.*, 2014). Given the reliance on pectoral fin swimming and pelagic foraging lifestyle, it is expected that zooplanktivorous acanthurids would present larger fins to maximize swimming capacity. However, an exception to this pattern that we noticed during this study is that species of *Naso* primarily propel themselves by body and caudal fin undulations that are augmented by pectoral fin movements during steady swimming. Whereas we did find evidence of differences in pectoral fin length between the diet regimes, it is likely that the variation along this axis was dominated by differences in mode of locomotion rather than dietary preferences. With greater emphasis on body–caudal undulation in *Naso*, the decreased reliance on pectoral fins is associated with a general reduction of this appendage, skewing the estimated primary optimum for zooplanktivorous acanthurids (Table 3; Fig. 3d).

A key difference between the two acanthurid feeding regimes is the reliance on biting actions in the benthic grazers as opposed to suction feeding in midwater. Smaller jaw adductor muscles were found in all transitions to zooplanktivory included in the current study, supporting general expectations about morphological adaptations to this niche (Coughlin & Strickler, 1990; Wainwright & Bellwood, 2001; Holzman & Wainwright, 2009). Other patterns in facial features, such as reductions in jaw dimensions, tooth size and the proportions of the overall feeding apparatus, as indicated by the distances between facial structures (i.e. the eye, pectoral fin and jaw), have been linked to the ability to efficiently feed on pelagic prey items (Davis & Birdsong, 1973). We find no evidence of vertical movement of the eye relative to head depth in zooplanktivores, as there is no discernible separation of diet optima with regard to this trait. Therefore, the reduction in distance between the eye and jaw is primarily driven by movement along the anteroposterior axis of the body, bringing the facial structures closer together. We did, however, find separate adaptive peaks corresponding to a more acute angle between the eye and mouth in planktivorous species. A smaller angle has been suggested to improve feeding ability in zooplanktivores as it would bring the eyes both more proximal to and horizontally aligned with the mouth (Jones, 1968). This morphology may enhance pursuit of small prey directly in front of the fish, as occurs when fish feed on plankton, whereas a wider angle indicates a more ventrally placed mouth that would be advantageous for benthic grazing and browsing herbivores. These trends to reduce the size of the jaws, teeth and overall feeding apparatus have been observed in other reef-associated zooplanktivorous lineages including balistids (Turingan *et al.*, 1995); pomacentrids (Frédérich *et al.*, 2013), haemulids (Tavera *et al.*, 2012), lutjanids (Miller & Cribb, 2007) and labrids (Wainwright, 1988; Wainwright *et al.*, 2002).

It has been postulated that zooplanktivores will have enlarged eyes because a larger lens and longer focal length should increase visual acuity (Lythgoe, 1979; Fernald, 1990). Some studies confirm this expectation in other lineages of reef fishes (Davis & Birdsong, 1973; Cooper & Westneat, 2009), and fishes in other systems (McPhail, 1984; Kassam *et al.*, 2003; Hulsey *et al.*, 2007). Nevertheless, we found no significant differences in eye diameter between zooplanktivorous and benthic grazing acanthurids. Similarly, a study of labrids found no increase in eye size associated with three evolutionary transitions to zooplankton feeding (Schmitz & Wainwright, 2011). Variability in myctophid eye size has also shown no relationship with expected ecological factors, such as bioluminescence and depth patterns (de Busserolles *et al.*, 2013). A more complete evaluation of the relationship between eye size and zooplanktivory in fishes could explore possible reasons for the inconsistency of this relationship.

Another of our patterns seemingly at odds with conventional zooplanktivore functional morphology is the lack of gill raker elongation in pelagic feeding acanthurids. Lengthened gill rakers on the first gill arch in zooplanktivores are thought to improve handling of small mobile prey items by acting as a barrier to retain prey once they are captured and held inside the buccal cavity (Magnuson & Heitz, 1971; Link & Hoff, 1998; Ingram & Shurin, 2009). Whereas some zooplanktivorous species, such as *A. thompsoni* and *P. hepatus*, did display markedly longer gill rakers than closely related grazing species, there was no difference between diet regimes collectively. We noted significant variability in gill raker morphology and meristics both within the family and genera. Nasinae tend to possess blunt, coarse gill rakers, whereas members of *Acanthurus* and *Ctenochaetus* are armed with finer bristles on their gill rakers. One possible factor is that the gelatinous zooplankton on which many planktivorous acanthurids feed do not present the same likelihood of escape as mobile copepods. As gelatinous prey items are not especially mobile, it is unnecessary to augment barriers to escape once they have been successfully engulfed. Furthermore, the planktivorous labrid, *C. solorensis* exhibits a parallel trend, showing no discernible difference in gill raker length (Schmitz & Wainwright, 2011). With these inconsistencies across zooplanktivorous fishes, it is clear that gill raker morphology is another trait that warrants further investigation in conjunction with foraging strategy.

Limitations to convergence

Despite persistent morphological convergence across zooplanktivorous acanthurids, each best-fit evolutionary model estimated the position of the zooplanktivore optimum beyond any observed species values but never exceeding double the current trait value. Whereas grazing taxa were typically clustered around their optima (Fig. 3). Whereas the model fitting and inferred evolutionary trajectories suggest selection towards the adaptive peak associated with plankton feeding in most traits, species have not yet reached the zooplanktivore optima (Fig. 3). As two of the transitions to planktivory appear to be over 10 million years old, this seems to be a remarkably delayed rate of approach towards the adaptive peak. This slow approach may be due to lineage-specific morphological or genetic constraints that prevent species from reaching the phenotypic optimum (Hansen, 1997; Collar *et al.*, 2014). As restricting background factors such as habitat and life history change slowly and vary across species, they not only place limits on the clade as a whole, but differentially influence lineages. Hansen (1997) suggests that these circumstances represent an OU process where individuals within a shared regime are slowed in their approach to the phenotypic optimum by these constraints, creating secondary optima for species. Indeed, we find support that whereas the selective demands of pelagic foraging have pulled lineages closer to their phenotypic optima, zooplanktivorous taxa remain morphologically diverse, failing to congregate on an adaptive peak. Under these circumstances we would expect to find a low α parameter corresponding to a long phylogenetic half-life [$t_{1/2} = \ln(2)/\alpha$] (Hansen, 1997). This half-life is a measure of the time it takes to evolve halfway to the expected phenotype, with a high value implying that lineage-specific constraints are working to delay the rate of approach to the new optimum. Unfortunately, our simulations demonstrate that we lack the statistical power to accurately estimate α (Figs S4 and S5). As an alternative, we used evidence from the Wheatsheaf Index which confirmed that convergence within the zooplanktivore ecomorph was not significantly different than would be expected under a random distribution, suggesting a low strength of selection. We conclude that the combination of a low evolutionary rate and unidentified constraints work to delay acanthurid evolution towards a single zooplanktivore phenotypic optimum.

Consistent with the possibility of taxon-specific secondary optima, we find incongruities in adult diet composition, ontogenetic dietary shifts and foraging habitat across zooplanktivorous lineages. Variation in evasiveness of the plankton species fed on by different planktivorous acanthurids may select for different performance traits. *Acanthurus thompsoni* feed on calanoid copepods which are capable of fast escape responses and are highly adapted to respond to disturbances in the water caused by approaching predators (Coughlin & Strickler, 1990; Kiørboe & Visser, 1999). In contrast, the gelatinous salps consumed by species of *Naso*, are slow, steady swimmers that lack an escape response (Bone, 1985). The functional demands of locating and capturing calanoid copepods and salps may be quite different; there are few challenges to capturing salps once they are located, whereas copepods require a stealthy approach that minimizes water disturbance and a quick, well-timed suction strike (Coughlin & Strickler, 1990; Holzman & Wainwright, 2009). Further adjustments must be made for nonplanktonic prey; some species of *Naso* and *Paracanthurus hepatus* exhibit grazing behaviour and retain the ability to feed by biting the substratum to dislodge algae and the detrital layers that overly algal mats (Hobson, 1974; Choat *et al.*, 2002). Additionally, many species of *Naso* are exclusively benthic grazers as juveniles, an ontogenetic shift that would help perpetuate the generalist feeding morphology and behaviour seen in zooplanktivorous adults. Whereas herbivory emphasizes biting, acanthurids have small jaws and relatively weak jaw adductor muscles compared to large predatory reef fishes (Wainwright & Bellwood, 2001) and durophagous taxa (Turingan *et al.*, 1995). Sucking zooplankton from the water column requires little biting strength, as is evidenced by the trend for smaller adductor mandibulae musculature. The differing demands placed on generalist and specialist diets could be partially responsible for morphological differences within our diet regime, as each feeding mode presents different challenges. Whereas variation in prey-specific zooplanktivore feeding mechanisms has never been observed, it has been proposed as an explanation for some of the morphological diversity within this trophic level (Wainwright & Bellwood, 2001).

Conclusions

Zooplanktivorous acanthurids exhibit strong – although not perfect – convergence in many morphological traits examined in this study. Whereas most traits followed previous functional expectations, eye and gill raker size did not. Despite many functional adaptations to a specialized diet and their clade age, pelagic feeding acanthurids have not yet reached the adaptive peak associated with planktivory. Perhaps variability in prey selectivity and ontogenetic changes in foraging habitat have independently constrained lineages, influencing the extent of convergence under the same functional demands. Nevertheless, we have shown how trophic differences shape adaptive landscapes and can contribute to diversification by facilitating local divergences between closely related species while promoting overall convergence within trophic guilds. This understudied phenomenon likely plays a significant role in preserving morphological diversification through the competing forces of selection and lineage-specific adaptive constraints.

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References

Alfaro, M.E., Janovetz, J. & Westneat, M.W. 2001. Motor control across trophic strategies: muscle activity of biting and suction feeding fishes. *Am. Zool.* **41**: 1266–1279.

Arbuckle, K., Bennett, C.M. & Speed, M.P. 2014. A simple measure of the strength of convergent evolution. *Methods Ecol. Evol.* **5**: 685–693.

Beaulieu, J.M. & O'Meara, B.C. 2015. OUwie: analysis of evolutionary rates in an OU framework. R package version 1.45. http://cran.r-project.org/web/packages/OUwie/index.html.

Beaulieu, J.M., Jhwueng, D.C., Boettiger, C. & O'Meara, B.C. 2012. Modeling stabilizing selection: expanding the Ornstein-Uhlenbeck model of adaptive evolution. *Evolution* **66**: 2369–2383.

Bellwood, D.R., Goatley, C.H.R., Brandl, S.J. & Bellwood, O. 2014. Fifty million years of herbivory on coral reefs: fossils, fish and functional innovations. *Proc. R. Soc. B Biol. Sci.* **281**: 20133046.

Boettiger, C., Coop, G. & Ralph, P. 2012. Is your phylogeny informative? Measuring the power of comparative methods *Evolution* **66**: 2240–2251.

Bone, Q. 1985. Locomotor adaptations of some gelatinous zooplankton. *Symp. Soc. Exp. Biol.* **29**: 487–520.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theorectic Approach.* 2nd edn. Springer, New York.

Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* **65**: 23–35.

de Busserolles, F., Fitzpatrick, J.L., Paxton, J.R., Marshall, N.J. & Collin, S.P. 2013. Eye-size variability in deep-sea lanternfishes (Myctophidae): an ecological and phylogenetic study. *PLoS ONE* **8**: e58519.

Butler, M.A. & King, A.A. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.* **164**: 683–695.

Choat, J. & Clements, K.D. 1998. Vertebrate herbivores in marine and terrestrial environments: a nutritional ecology perspective. *Annu. Rev. Ecol. Evol. Syst.* **29**: 375–403.

Choat, J.H., Clements, K.D. & Robbins, W.D. 2002. The trophic status of herbivorous fishes on coral reefs I: dietary analyses. *Mar. Biol.* **140**: 613–623.

Choat, J.H., Robbins, W.D. & Clements, K.D. 2004. The trophic status of herbivorous fishes on coral reefs II. Food processing modes and trophodynamics. *Mar. Biol.* **145**: 445–454.

Clements, K.D., Gray, R.D. & Choat, J.H. 2003. Rapid evolutionary divergences in reef fishes of the family Acanthuridae (Perciformes: Teleostei). *Mol. Phylogenet. Evol.* **26**: 190–201.

Collar, D.C., Meara, B.C., Wainwright, P.C. & Near, T.J. 2009. Piscivory limits diversification of feeding morphology in centrarchid fishes. *Evolution* **63**: 1557–1573.

Collar, D.C., Reece, J.S., Alfaro, M.E., Wainwright, P.C. & Mehta, R.S. 2014. Imperfect morphological convergence: variable changes in cranial structures underlie transitions to durophagy in moray eels. *Am. Nat.* **183**: E168–E184.

Cooper, W.J. & Westneat, M.W. 2009. Form and function of damselfish skulls: rapid and repeated evolution into a limited number of trophic niches. *BMC Evol. Biol.* **9**: 24.

Coughlin, D.J. & Strickler, J.R. 1990. Zooplankton capture by a coral reef fish: an adaptive response to evasive prey. *Environ. Biol. Fishes* **29**: 35–42.

Crossman, D.J., Choat, J.H. & Clements, K.D. 2005. Nutritional ecology of nominally herbivorous fishes on coral reefs. *Mar. Ecol. Prog. Ser.* **296**: 129–142.

Davis, W.P. & Birdsong, R.S. 1973. Coral reef fishes which forage in the water column. *Helgoländer Meeresun.* **24**: 292–306.

Davis, A. & Unmack, P. 2014. Evidence for a multi-peak adaptive landscape in the evolution of trophic morphology in terapontid fishes. *Biol. J. Linn. Soc.* **113**: 623–634.

Ellerby, D.J. & Gerry, S.P. 2011. Sympatric divergence and performance trade-offs of Bluegill ecomorphs. *Evol. Biol.* **38**: 422–433.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.

Fernald, R.D. 1990. The optical system of fishes. In: *The Visual System of Fishes* (R. Douglas & M. Djamgoz, eds), pp. 45–61. Springer, Netherlands, London.

Fishelson, L. & Delarea, Y. 2014. Comparison of the oral cavity architecture in surgeonfishes (Acanthuridae, Teleostei), with emphasis on the taste buds and jaw "retention plates". *Environ. Biol. Fishes* **97**: 173–185.

Frédérich, B., Sorenson, L., Santini, F., Slater, G.J. & Alfaro, M.E. 2013. Iterative ecological radiation and convergence during the evolutionary history of damselfishes (Pomacentridae). *Am. Nat.* **181**: 94–113.

Frontier, S. 1976. Étude de la décroissance des valeurs propres dans une analyse en composantes principales: comparaison avec le moddle du bâton brisé. *J. Exp. Mar. Bio. Ecol.* **25**: 67–75.

Fulton, C.J., Bellwood, D.R. & Wainwright, P.C. 2001. The relationship between swimming ability and habitat use in wrasses (Labridae). *Mar. Biol.* **139**: 25–33.

Gould, S.J. 2002. *The Structure of Evolutionary Theory*. Harvard University Press, Cambridge, MA.

Green, A.L. & Bellwood, D.R. 2009. *Monitoring Functional Groups of Herbivorous Reef Fishes as Indicators of Coral Reef Resilience - A practical Guide for Coral Reef Managers in the Asia Pacific Region*. IUCN, Gland, Switzerland.

Hansen, T.F. 1997. Stabilizing selection and the comparative analysis of adaptation. *Evolution* **51**: 1341–1351.

Hjelm, J., Svanbäck, R., Byström, P., Persson, L. & Wahlström, E. 2001. Diet dependent body morphology and ontogenetic reaction norms in Eurasian perch. *Oikos* **95**: 311–323.

Hobson, S. 1974. Feeding relationship of teleostean fishes on coral reefs in Kona, Hawaii. *Fish Bull.* **72**: 915–1031.

Hobson, E.S. 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: *The Ecology of Fishes on Coral Reefs* (P.F. Sale, ed), pp. 69–95. Academic Press, San Diego.

Holzman, R. & Wainwright, P.C. 2009. How to surprise a copepod: strike kinematics reduce hydrodynamic disturbance and increase stealth of suction-feeding fish. *Limnol. Oceanogr.* **54**: 2201–2212.

Huelsenbeck, J.P., Nielsen, R. & Bollback, J.P. 2003. Stochastic mapping of morphological characters. *Syst. Biol.* **52**: 131–158.

Hulsey, C.D. & García De León, F.J. 2005. Cichlid jaw mechanics: linking morphology to feeding specialization. *Funct. Ecol.* **19**: 487–494.

Hulsey, C.D., Mims, M.C. & Streelman, J.T. 2007. Do constructional constraints influence cichlid craniofacial diversification? *Proc. R. Soc. B Biol. Sci.* **274**: 1867–1875.

Ingram, T. & Shurin, J.B. 2009. Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages. *Ecology* **90**: 2444–2453.

Jackson, D.A. 1993. Stopping rules in principal components analysis : a comparison of heuristical and statistical approaches. *Ecol. Soc. Am.* **74**: 2204–2214.

Jombart, T. & Dray, S. 2008. Adephylo: exploratory analyses for the phylogenetic comparative method. *Bioinformatics* **26**: 1907–1909.

Jombart, T., Balloux, F. & Dray, S. 2010. Adephylo: new tools for investigating the phylogenetic signal in biological traits. *Bioinformatics* **26**: 1907–1909.

Jones, R.S. 1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (Surgeonfishes). *PhD Diss. [Honolulu]* **4**: 309–361.

Kassam, D., Adams, D., Yamaoka, K. & Ambali, A. 2003. Body shape variation in relation to resource partitioning within cichlid trophic guilds coexisting along the rocky shore of Lake Malawi. *Anim. Biol.* **53**: 59–70.

Kiørboe, T. & Visser, A.W. 1999. Predator and prey perception in copepods due to hydromechanical signals. *Mar. Ecol. Prog. Ser.* **179**: 81–95.

Klanten, S.O., Van Herwerden, L., Choat, J.H. & Blair, D. 2004. Patterns of lineage diversification in the genus *Naso* (Acanthuridae). *Mol. Phylogenet. Evol.* **32**: 221–235.

Konow, N., Bellwood, D.R., Wainwright, P.C. & Kerr, A.M. 2008. Evolution of novel jaw joints promote trophic diversity in coral reef fishes. *Biol. J. Linn. Soc.* **93**: 545–555.

Langerhans, R.B. & DeWitt, T.J. 2004. Shared and unique features of evolutionary diversification. *Am. Nat.* **164**: 335–349.

Lazzaro, X. 1987. A review of planktivorous fishes: their evolution, feeding behaviors, selectivities, and impacts. *Hydrobiologia* **146**: 97–167.

Link, J. & Hoff, M.H. 1998. Gill raker characteristics to retention probabilities of zooplankton prey. *J. Freshw. Ecol.* **13**: 55–65.

Lobato, F.L., Barneche, D.R., Siqueira, A.C., Liedke, A.M.R., Lindner, A., Pie, M.R. *et al.* 2014. Diet and diversification in the evolution of coral reef fishes. *PLoS ONE* **9**: 1–11.

Losos, J.B. 2011. Convergence, adaptation, and constraint. *Evolution* **65**: 1827–1840.

Lythgoe, J.N. 1979. *The Ecology of Vision*. Clarendon Press, Oxford.

Macarthur, R.H. 1957. On the relative abundance of bird species. *Proc. Natl. Acad. Sci. USA* **43**: 293–295.

Magnuson, J. & Heitz, J. 1971. Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. *Fish. Bull.* **69**: 361–370.

Mahler, D.L., Ingram, T., Revell, L.J. & Losos, J.B. 2013. Exceptional convergence on the macroevolutionary landscape in island lizard radiations. *Science* **341**: 292–295.

McGee, M.D., Schluter, D. & Wainwright, P.C. 2013. Functional basis of ecological divergence in sympatric stickleback. *BMC Evol. Biol.* **13**: 277.

McPhail, J.D. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): morphological and genetic evidence for a species pair in Enos Lake, British Columbia. *Can. J. Zool.* **62**: 1402–1408.

Miller, T.L. & Cribb, T.H. 2007. Phylogenetic relationships of some common Indo-Pacific snappers (Perciformes: Lutjanidae) based on mitochondrial DNA sequences, with comments on the taxonomic position of the Caesioninae. *Mol. Phylogenet. Evol.* **44**: 450–460.

Miyake, S., Ngugi, D.K. & Stingl, U. 2015. Diet strongly influences the gut microbiota of surgeonfishes. *Mol. Ecol.* **24**: 656–672.

Moen, D.S., Morlon, H. & Wiens, J.J. 2015. Testing convergence versus history: convergence dominates phenotypic evolution for over 150 million years in frogs. *Syst. Biol.* **65**: 146–160.

Montaña, C.G. & Winemiller, K.O. 2013. Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable isotope analysis. *Biol. J. Linn. Soc.* **109**: 146–164.

Montgomerey, W.L., Myrberg, A.A.J. & Fishelson, L. 1989. Feeding ecology of surgeonfishes (Acanthuridae) in the northern Red Sea, with particular reference to *Acanthurus nigrofuscus*. *J. Exp. Mar. Biol. Ecol.* **132**: 179–207.

Purcell, S.W. & Bellwood, D.R. 1993. A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). *Environ. Biol. Fishes* **37**: 139–159.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Revell, L.J. 2009. Size-correction and principal components for interspecific comparative studies. *Evolution* **63**: 3258–3268.

Revell, L.J. 2010. Phylogenetic signal and linear regression on species data. *Methods Ecol. Evol.* **1**: 319–329.

Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223.

Robertson, D.R. & Gaines, S. 1986. Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* **67**: 1372–1383.

Rohlf, F.J. 2002. Geometric morphometrics and phylogeny. *Syst. Assoc. Spec. Vol.* **64**: 175–193.

Rüber, L. & Adams, D.C. 2001. Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. *J. Evol. Biol.* **14**: 325–332.

Sandin, S.A. & Williams, I. 2010. Trophic classifications of reef fishes from the tropical U.S. Pacific. *Scripps Inst. Oceanogr.* http://eprints.cdlib.org/uc/item/5394f7m3

Schmitz, L. & Wainwright, P.C. 2011. Ecomorphology of the eyes and skull in zooplanktivorous labrid fishes. *Coral Reefs* **30**: 415–428.

Sidlauskas, B. 2008. Continuous and arrested morphological diversification in sister clades of characiform fishes: a phylomorphospace approach. *Evolution* **62**: 3135–3156.

Sorenson, L., Santini, F., Carnevale, G. & Alfaro, M.E. 2013. A multi-locus timetree of surgeonfishes (Acanthuridae, Percomorpha), with revised family taxonomy. *Mol. Phylogenet. Evol.* **68**: 150–160. Elsevier Inc.

Stayton, C. 2006. Testing hypotheses of convergence with multivariate data: morphological and functional convergence among herbivorous lizards. *Evolution* **60**: 824–841.

Stayton, C.T. 2015. The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution* **69**: 2140–2153.

Tang, K.L., Berendzen, P.B., Wiley, E.O., Morrissey, J.F., Winterbottom, R. & Johnson, G.D. 1999. The phylogenetic relationships of the suborder Acanthuroidei (Teleostei: Perciformes) based on molecular and morphological evidence. *Mol. Phylogenet. Evol.* **11**: 415–425.

Tavera, J., Acero, A., Balart, E.F. & Bernardi, G. 2012. Molecular phylogeny of grunts (Teleostei, Haemulidae), with an emphasis on the ecology, evolution, and speciation history of New World species. *BMC Evol. Biol.* **12**: 57.

Turingan, R.G., Wainwright, P.C. & Hensley, D.A. 1995. Interpopulation variation in prey use and feeding biomechanics in Caribbean triggerfishes. *Oecologia* **102**: 296–304.

Uyeda, J.C., Caetano, D.S. & Pennell, M.W. 2015. Comparative analysis of principal components can be misleading. *Syst. Biol.* **64**: 677–689.

Wainwright, P. 1988. Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* **69**: 635–645.

Wainwright, P.C. 2007. Functional versus morphological diversity in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* **38**: 381–401.

Wainwright, P. & Bellwood, D. 2001. Ecomorphology of feeding in coral reef fishes. In: *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (P.F. Sale, ed), pp. 33–55. Academic Press, San Diego.

Wainwright, P. & Richard, B. 1995. Predicting patterns of prey use from morphology of fishes. *Environ. Biol. Fishes* **44**: 97–113.

Wainwright, P.C., Bellwood, D.R. & Westneat, M.W. 2002. Ecomorphology of locomotion in labrid fishes. *Environ. Biol. Fishes* **65**: 47–62.

Wainwright, P.C., Bellwood, D.R., Westneat, M.W., Grubich, J.R. & Hoey, A.S. 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.

Wainwright, P.C., Alfaro, M.E., Bolnick, D.I. & Hulsey, C.D. 2005. Many-to-one mapping of form to function: a general principle in organismal design? *Integr. Comp. Biol.* **45**: 256–262.

Wake, D.B. 1991. Homoplasy: the result of natural selection, or evidence of design limitations? *Am. Nat.* **138**: 543.

Walker, J. 1997. Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape. *Biol. J. Linn. Soc.* **61**: 3–50.

Westneat, M.W. 2003. A biomechanical model for analysis of muscle force, power output and lower jaw motion in fishes. *J. Theor. Biol.* **223**: 269–281.

Winterbottom, R. & McLennan, D.A. 1993. Cladogram versality: evolution and biogeography of Acanthuroid fishes. *Evolution* **47**: 1557–1571.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Morphospace projection of acanthurid species on the first two principal components using a non-phylogenetic PCA.

Figure S2 AICc values for all evolutionary models from 1000 simulated data sets under the best fit model parameters for PC1 (A) and PC2 (B).

Figure S3 Distribution of theta values for nonplanktivores (green) and planktivores (blue) for all evolutionary models over 1000 simulations on PC1.

Figure S4 Distribution of theta values for nonplanktivores (green) and planktivores (blue) for all evolutionary models over 1000 simulations on PC2.

Figure S5 Distribution of alpha values for nonplanktivores (green) and planktivores (blue) for all evolutionary models over 1000 simulations on PC1.

Figure S6 Distribution of alpha values for nonplanktivores (green) and planktivores (blue) for all evolutionary models over 1000 simulations on PC2.

Figure S7 Distribution of sigma squared values for nonplanktivores (green) and planktivores (blue) for all evolutionary models over 1000 simulations on PC1.

Figure S8 Distribution of sigma squared values for nonplanktivores (green) and planktivores (blue) for all evolutionary models over 1000 simulations on PC2.

Table S1 Loadings for the 16 morphological traits from a non-phylogenetic principal components analysis run on body size corrected residuals.

Table S2 Summary of the direction each trait has moved since each lineage's transition to planktivory.

Table S3 Results from the convevol analysis. All values have statistically significant *P*-values ($P < 0.05$) unless indicated with an asterisk.

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