



Morphological and functional diversity of piscivorous fishes on coral reefs

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Abstract Piscivory is a significant ecosystem function on coral reefs, with up to 53% of species on reefs being regarded as piscivorous. Despite this ecological importance, the species that contribute to this function have not been assessed in a broad comparative, morphological context. We therefore conducted a morphological assessment of piscivorous coral reef fishes based on a comparative analysis of 119 species, linking morphology with ecological traits (habitat and activity). After accounting for phylogenetic relationships, we found that head length, premaxilla–maxilla (pmx–mx) length, body depth, and eye size mark the primary axis of variation among species. Pmx–mx length is strongly correlated with both vertical and horizontal gape size. We identify three distinct ecomorphotypes: diurnal benthic, nocturnal, and pelagic piscivores. Benthic diurnal and nocturnal piscivores display a wide array of pmx–mx lengths, potentially reflecting the large array of prey sizes and shapes in benthic habitats. This diversity highlights the potential for niche partitioning based on maximum ingestible prey sizes. By comparison, pmx–mx lengths in pelagic piscivores are more restricted, suggesting limited variance in prey sizes or restrictions

associated with their feeding mode. Fin shape was also a primary driver of variation between benthic and pelagic predators. The ecomorphotype of nocturnal piscivores suggests that although they are benthic-associated during daytime, these forms leave the reef at night to feed in more open habitats. When analyzing diurnal benthic piscivores alone, we found a major axis of variation between deep-bodied piscivores with large gapes and large head lengths versus fusiform piscivores with high fin aspect ratio values. This continuum appears to describe the relative strength of benthic associations. Overall, we provide a broad quantitative framework for understanding the morphology and potential functions of piscivorous fishes on coral reefs.

Keywords Gape · Fin shape · Nocturnal · Predation · Ecomorphotype

Introduction

Describing the morphological attributes of species dates back centuries (e.g., Darwin 1859), and not without good reason. Morphology has provided invaluable information on the taxonomy, phylogeny, ecology, and life history of species. In more recent decades, the field of functional morphology was established, aiming to causally link specific morphological traits of organisms to the performance of specific tasks (e.g., Wainwright 1991; Motta et al. 1995; Norton et al. 1995). Functional studies enable us to understand not only what functions organisms perform in their environment (e.g., diet), but also how they do it (Bellwood et al. 2019). Ecomorphological or functional morphology studies, in particular, have been able to provide mechanistic links between organisms and their environment (e.g., Wainwright 1988; Turingan 1994; Bellwood

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et al. 2006). A well-studied example is that of the pectoral fin of median paired-fin (MPF) swimmers. Fulton et al. (2005), described a correlation between the pectoral fin shape of coral reef fishes and their swimming mode, which was subsequently causally linked (through experimental performance experiments) to these species being able to access hydrodynamically demanding environments, such as the reef flat (Fulton et al. 2005). This adaptation has since been shown not only to be observable on a global scale (Fulton et al. 2017), but also to facilitate significant trophodynamic pathways on coral reefs (Bellwood et al. 2018). Establishing such links between morphology and ecology has been particularly useful in relation to fish feeding, as such links are directly related to the movement or storage of energy or material in an ecosystem (i.e., ecosystem functions) (Bellwood et al. 2019).

Coral reef ecosystems support a staggering diversity of fish types with morphological attributes that have been linked to numerous feeding modes (Wainwright and Bellwood 2002). Of these feeding modes, some have been studied far more than others relative to their species diversity (Bellwood et al. 2019). For example, a basic, quantitative understanding of piscivorous functional groups is lacking. This is despite piscivory being a major ecological function on coral reefs, with fish communities being strongly influenced by this process (Hixon 1991; Almany 2004a, b; Almany and Webster 2004; Goatley and Bellwood 2016). Furthermore, up to 53% of species on reefs may be regarded as piscivorous (Randall 1967; Hixon 1991). Despite their ecological importance and diversity, piscivorous fishes on coral reefs remain understudied, especially with regard to their morphological or functional characteristics. If we are to understand how different types of piscivorous predators influence coral reef fish communities, we need to first understand how these groups differ from each other, i.e., what are the different types of predators?

The importance of establishing such a framework is revealed when looking at global and coral reef-based fisheries catches in the last decades (Russ and Alcala 1989; Pauly et al. 1998; Myers and Worm 2003). Piscivorous fishes are highly sought after in coral reef fisheries (Jennings and Polunin 1997; Cinner et al. 2009), and the loss of these species from the ecosystem (and thus the ecological function they provide) may result in significant shifts in ecosystem processes (Jackson et al. 2001; Estes et al. 2011). To gain a better understanding of how piscivory may influence ecosystem processes and resilience, we need to know the ecological functions that these species perform. The first step in this endeavor is to understand how they differ from each other with regard to ecomorphological attributes and their functional implications.

The need for a framework to identify distinct morphotypes of piscivorous fishes is also rooted in the cryptic nature of this ecological function. Compared to herbivory, an ecological function occurring frequently and extensively during daytime, piscivory occurs less frequently, and there is a little evidence of when, where, or how it occurs (but see Sweatman 1984; Khan et al. 2016). The direct quantification of such an ecological function can therefore be logistically challenging. By establishing a framework for the morphological drivers of the diversity among piscivorous fishes, it may be possible to get an indication of the features that are important for driving patterns of piscivory on coral reefs. Furthermore, it may allow us to identify those functions for further studies in an experimental (performance-based) and ecological context. To date, functional traits studied on piscivorous fishes have been largely related to their gape size (e.g., Wainwright and Richard 1995; St. John 1999), and how it is functionally linked to maximum prey size (Mihalitsis and Bellwood 2017). However, there may be other important traits that reveal other axes of variation. Observations on other morphological traits of piscivorous fishes, which may be of potential functional significance (e.g., fin shape), have been largely descriptive (Collette and Nauen 1983; Allen 1985; Heemstra and Randall 1993).

Our goal, therefore, is to provide a quantitative, comparative, overview of the morphology of all major families of piscivorous coral reef teleosts (except for Muraenidae) (Choat and Bellwood 1991; Wainwright and Bellwood 2002), by quantifying the morphological diversity of 119 species from 19 fish families. We construct a broad morphospace for piscivorous coral reef fishes and correlate this diversity of morphotypes with basic patterns of activity and habitat use (behavioral traits). We then explore the potential functional implications of these major axes of morphological diversity, and identify distinct ecomorphotypes for further detailed study.

Materials and methods

In our study, a piscivorous fish is defined as a species in which fishes formed a significant proportion of the diet (usually > 20% occurrence) and are therefore expected to contribute substantially toward the ecological function of piscivory. The primary focus of our study is piscivory as an ecological function, looking at piscivores *sensu lato* rather than exclusive fish eaters (e.g., barracuda or coral trout). Trophic designations are therefore based on the published literature or websites (e.g., Hiatt and Strasburg 1960; Randall 1967; Froese and Pauly 2010). If diet data were unavailable for a species, dietary habits were assumed to be similar to closely related species (e.g., *Cephalopholis aitha*

is assumed to have similar dietary habits to other *Cephalopholis* species). Morphological measurements were taken from images where fish are displayed laterally with fins extended, or from specimens if photographs did not allow for a trait to be measured (e.g., caudal aspect ratio (AR) for *Pterois volitans*). All images were analyzed using the software ImageJ. Only images where fins were clearly visible and spread out were used. To minimize allometric effects, we only included images of subadult and adult fishes. A mean of three individuals per species were analyzed. In total, 348 individuals from 119 species from 19 families were analyzed, incorporating all major piscivorous reef fish families (Choat and Bellwood 1991; Bellwood and Wainwright 2002). All families and respective species are given in the Supplemental Material along with raw trait values measured (see ESM Tables 2, 3). As some of the morphological traits measured in this study are absent in the Muraenidae (fin ARs), they were excluded from our analyses. For some families, only a few species are considered significant piscivores, such as *Cheilodipterus* within the Apogonidae (Marnane and Bellwood 2002), and therefore only these genera within the families were considered.

Morphological measurements were: body depth, caudal fin aspect ratio (AR), eye diameter, head length, pectoral fin aspect ratio, and the premaxilla–maxilla (pmx–mx) length (distance from the tip of the premaxilla to the posterior margin of the maxilla), a potential proxy for the oral gape. Caudal fin AR was measured based on Sambilya Jr (1990) (fin height squared, divided by fin area), whereas pectoral fin AR was modified after Wainwright et al. (2002) (fin length squared, divided by fin area). For details, please see Supplemental Material (ESM Fig. 1). Phylogenetic body size corrections were undertaken following (Revell 2009) using the R packages *nlme* (Pinheiro et al. 2014) and *ape* (Paradis et al. 2004). Phylogenetic least squares (PGLS) models used in this study assumed a Brownian motion pattern of evolution. Residuals were calculated for each trait and were then analyzed using a phylogenetic principal component analysis (PPCA) using the R package *phytools*.

We also assessed the relationship between pmx–mx length and gape measurements taken directly from specimens. We measured 65 individuals from 26 species (A2529). Vertical oral gape and horizontal oral gape were measured by using a pair of scissors [following Mihalitsis and Bellwood (2017)]. Specimens were subsequently displayed in a lateral position with fins extended, and the pmx–mx length measured from images. Gape residuals and pmx–mx length residuals (both against SL) were calculated and their relationship examined with linear regressions.

As there is currently no phylogenetic tree encompassing all species in our dataset, a phylogenetic tree was

constructed using the Open Tree of Life (OTL) (Hinchliff et al. 2015) and the R package ‘rotl’ (Michonneau et al. 2016). Tree branch lengths were computed using Grafen’s method (Grafen 1989). Species not placed on our phylogenetic tree through OTL were manually inserted by evaluating their topology from other published phylogenetic trees (Alfaro et al. 2018). The phylogenetic tree used in our analyses is given in the Supplemental material (ESM Fig. 2).

Following our PPCA, we overlaid ecological traits on our morphospace ordination. These were habitat (benthic/pelagic) and activity (diurnal/nocturnal), and were based on the existing literature (e.g., Hobson 1965, 1972; Goldman et al. 1976; Randall 2005). We identified emergent groupings as ecomorphotypes. Here, we use the term ecomorphotype, as a grouping within a morphology-based ordination (morphospace) that is grouped based on ecological (behavioral) traits. We displayed our ecomorphotypes using convex hulls based on the *vegan* R package (Oksanen et al. 2013), and tested for significant differences among ecomorphotypes using a phylogenetic multivariate analysis of variance (Phylo-MANOVA) from the *geiger* package (Harmon et al. 2007) (simulations = 1000, test statistic = Wilks). Subsequent post hoc comparisons of traits (response variable) between ecomorphotypes (predictor variable) were undertaken using PGLS models (method = Maximum likelihood), using the *nlme* (Pinheiro et al. 2014) and *ape* packages (Paradis et al. 2004). Models were conducted using both Brownian motion and Pagels’ patterns of evolution and were evaluated based on the Akaike information criterion (AIC). The initial *lambda* parameter was set to 1 and non-fixed. All calculations and analyses were undertaken in the software R (R Core Team 2017).

Results

In our phylogenetic principal component analysis (PPCA) of morphospace, the first two axes explained 47.3% and 22% of the total variance, respectively (Fig. 1). PC1 is mostly correlated with head length, pmx–mx length, body depth, and eye diameter (Table 1; Fig. 1) and PC2 with pectoral AR and caudal AR (Table 1; Fig. 1). When behavioral traits (habitat use, activity) were mapped onto the morphospace using convex hulls, we identified three distinct ecomorphotypes: (1) pelagic predators (2) benthic diurnal predators, and (3) nocturnal predators (for classification of species, see ESM Table 2; we found no published evidence for nocturnal pelagic predators). Subsequent Phylo-MANOVA analysis revealed significant difference in the occupation of morphospace between ecomorphotypes (Wilks’ Lambda = 0.126, $F = 33.522$,

Fig. 1 a Phylogenetic principal component analysis (PPCA) of piscivorous coral reef fishes. Groups represent associated ecomorphotypes based on activity and habitat association. Brown, diurnal benthic; black, nocturnal; blue, pelagic. Squares within convex hulls represent the centroid, and fish illustrations indicate the species closest to each centroid, respectively, *Plectropomus leopardus*, *Sargocentron tiera*, and *Carangoides ferdau*, **b** illustration of each ecomorphotype indicating its association with the reef. Arrows indicate where pelagic and nocturnal ecomorphotypes may be feeding. *CAR* caudal aspect ratio, *PAR* pectoral aspect ratio, *Eye D* eye diameter, *Body D* body depth, *Head L* head length, *pmx–mx* premaxilla–maxilla length. For numbered data points for each species, please see ESM Fig. 3

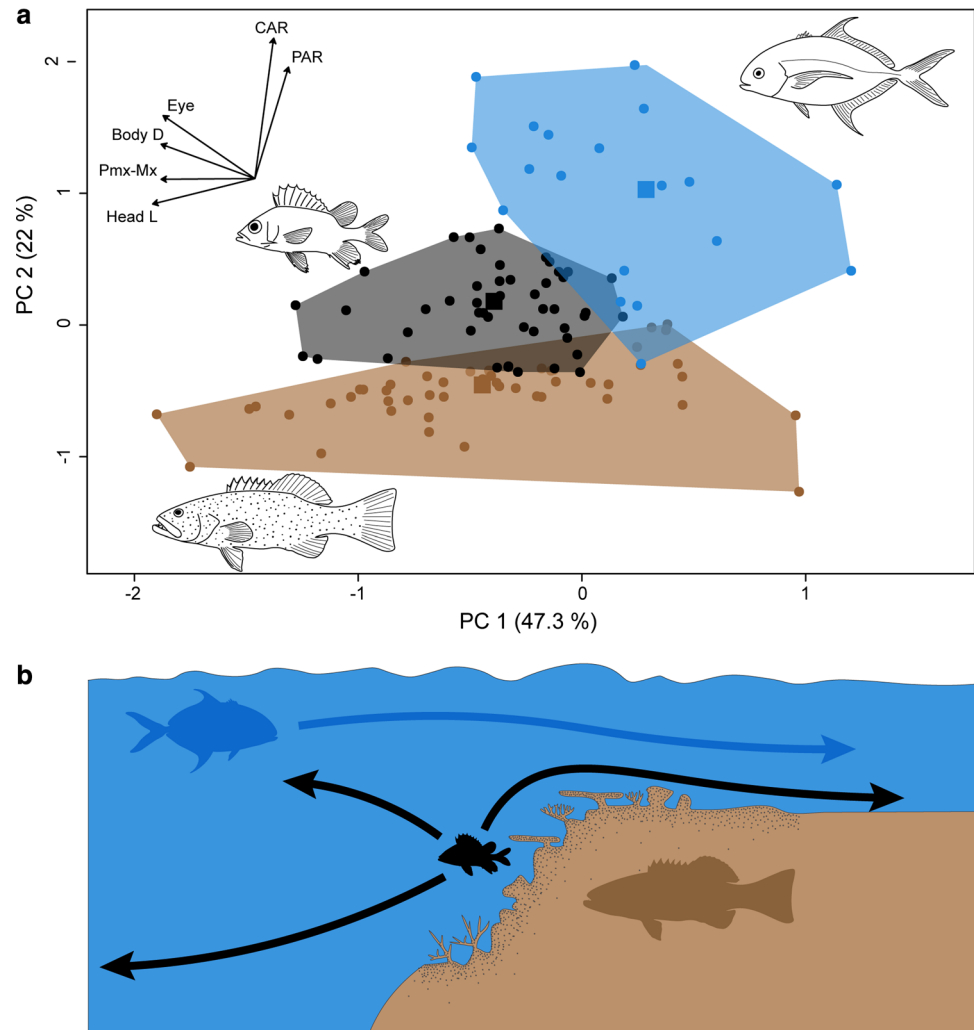


Table 1 Loading vectors from principal components 1 and 2 (PC1, PC2) of our phylogenetic principal component analysis (PPCA)

	PC1	PC2
PAR	0.291	0.659
CAR	0.161	0.827
Eye	− 0.794	0.373
Pmx–mx	− 0.811	− 0.004
Head L	− 0.884	− 0.15
Body depth	− 0.811	0.203

PAR pectoral aspect ratio, *CAR* caudal aspect ratio, *Eye* eye diameter, *pmx–mx* premaxilla–maxilla length, *Head L* head length

$df = 12$, p value < 0.001). The morphospace occupied by nocturnal piscivores is situated between that of the pelagic and benthic piscivores. Groupings appear to be mostly separated along PC2, which is primarily explained by fin shape traits (Table 1; Fig. 1). Nocturnal piscivores appear to have higher fin ARs compared to diurnal benthic

piscivores, but lower fin ARs compared to pelagic piscivores. A phylogenetic least squares analysis (PGLS) showed significant differences between caudal and pectoral AR of benthic diurnal, nocturnal, and pelagic ecomorphotypes (Fig. 2c; Table 2). Additionally, PGLS models found significant differences in eye diameter between ecomorphotypes (Table 2), and higher body depth for nocturnal piscivores compared to diurnal benthic piscivores (Table 2). In essence, our results reveal three ecomorphotypes: diurnal benthic, nocturnal, and pelagic, with significant differences found in caudal AR, pectoral AR, and eye size (traits mostly associated with PC2).

Even though the ecomorphotypes identified are mostly divided along PC2, PC1 still explains most of the variance, and is dominated by variation in pmx–mx length, head length, body depth, and eye size (Table 1; Fig. 1a). Linear models reveal a strong relationship between pmx–mx length residuals and both vertical ($r^2 = 0.78$, $p < 0.001$) and horizontal ($r^2 = 0.77$, $p < 0.001$) oral gape residuals (Fig. 2a), suggesting that pmx–mx length is a reasonable

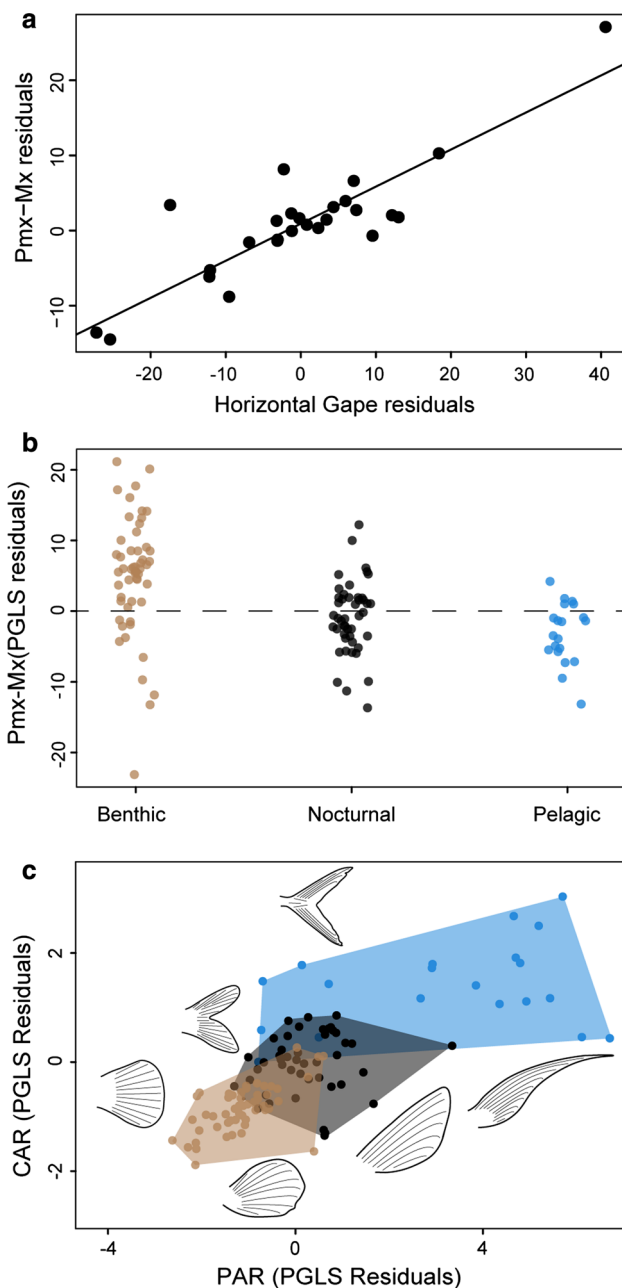


Fig. 2 **a** Premaxilla–maxilla (pmx–mx) length (residuals) plotted against vertical gape (residuals), **b** pmx–mx length (proxy for gape) [phylogenetic least squares (PGLS) corrected residuals] for each ecomorphotype, **c** caudal aspect ratio (AR) (residuals) plotted against pectoral AR (residuals). Colors represent associated ecomorphotypes, respectively, brown, diurnal benthic; black, nocturnal; blue, pelagic

proxy for oral gape. However, a PGLS found no significant differences in pmx–mx length (Table 1) between ecomorphotypes. Gape, therefore, varies extensively within, but not consistently between, ecomorphotypes. However, the extent of the spread along PC1 varies among ecomorphotypes, being least in pelagics and most in benthics (Fig. 1a), reflecting variation in gape sizes (Fig. 2b).

As benthic diurnal piscivores, as an ecomorphotype, displayed the most variance along PC1, we repeated the PPCA as described above (Fig. 1a) but focusing only on diurnal benthic piscivores. When this ecomorphotype is examined in isolation, PC1 and PC2 explained 44.1% and 32.6% of the total variation, respectively (Fig. 3a). The first axis (PC1) is mostly correlated with pmx–mx length, head length, and body depth on one side, and pectoral AR (PAR) on the other (Table 3; Fig. 3). The second axis (PC2) is primarily correlated with caudal AR (CAR) (Table 3; Fig. 3). Our analysis is indicative of a continuum between fusiform species (e.g., *Saurida gracilis* and *Aulostomus chinensis*) with high fin AR values, and more deep-bodied species (e.g., *Antennarius commerson* and *Epinephelus malabaricus*) with high pmx–mx and head length values (Fig. 3).

Discussion

Our comparative analysis of the external morphology of piscivorous coral reef fishes revealed three distinct morphotypes. Each was linked to existing ecological traits, forming three distinct ecomorphotypes: diurnal benthic, pelagic, and nocturnal piscivores. We show caudal and pectoral fin morphology to be the primary drivers of variation separating these ecomorphotypes. We found pmx–mx, head length, body depth, and eye size to be the major axis of variation among piscivorous coral reef fishes; however, gape varied most within, not between, ecomorphotypes. This suggests that there is a basic division in the various feeding habits (ecomorphotypes) but that within these habits, most among species variation is in gape, and presumably prey size. These differences may lay the foundations for further performance-based experiments and field-based behavioral studies.

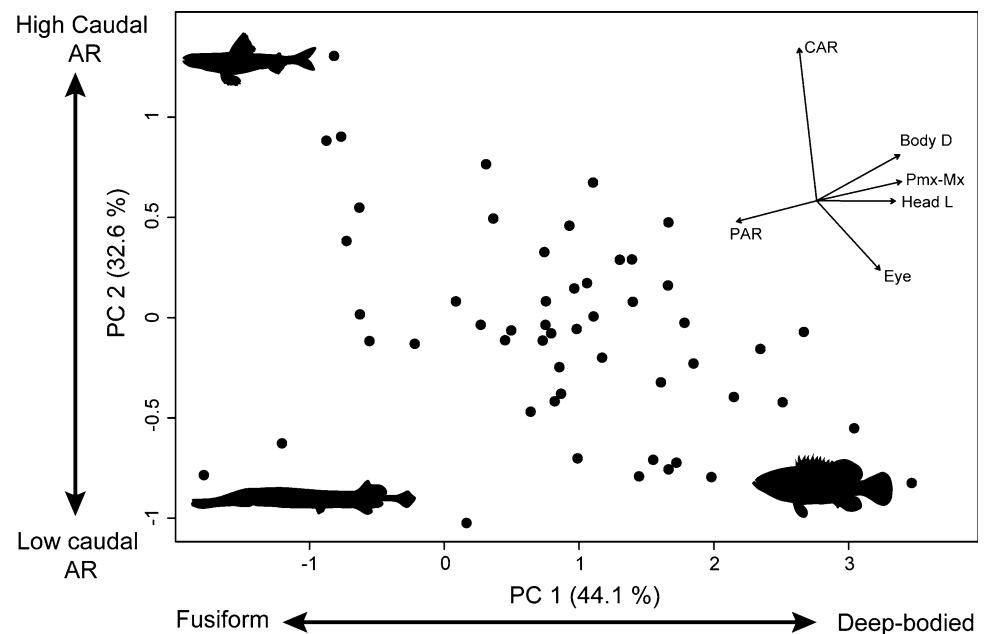
We found high caudal and pectoral fin ARs in pelagic piscivores and lower ARs in benthic-associated piscivores. However, we found that these fin morphologies also explain a distinct morphotype of nocturnal piscivores, situated directly between benthic and pelagic piscivores (Figs. 1a, 3c; Table 1). Pectoral fin AR values have previously been associated with median and paired-fin (MPF) swimming (Walker 2004; Drucker et al. 2005; Fulton et al. 2005). However, we found no evidence of the species investigated to be MPF swimmers in the literature (e.g., Fulton 2007). We therefore argue that the high AR values shown in our study are more likely related to maneuverability (e.g., swift turning when pursuing prey). Nocturnal piscivores are strongly associated with the benthos during the day, hiding in caves, crevices, and under corals on the reef (Kerry and Bellwood 2015). However, species within these families feed at night and away from the reef

Table 2 Phylogenetic least squares (PGLS) models conducted between traits (dependent) and ecomorphotypes (independent)

Variable	Level	Lambda	AIC	Estimate	SE	<i>t</i> value	<i>p</i> value
Pmx–mx	Benthic (intercept)	0.938	732.505	– 0.531	5.141	– 0.103	0.918
	Nocturnal			1.347	2.152	0.626	0.532
	Pelagic			0.363	2.689	0.135	0.893
Head length	Benthic (intercept)	0.913	892.264	– 2.231	9.286	– 0.24	0.81
	Nocturnal			5.356	4.164	1.286	0.2
	Pelagic			– 1.274	5.125	– 0.248	0.804
Caudal AR	Benthic (intercept)	0.426	188.75	– 0.609	0.217	– 2.806	0.006
	Nocturnal			0.605	0.167	3.608	< 0.001
	Pelagic			2.372	0.215	11	< 0.001
Pectoral AR	Benthic (intercept)	0.851	387.059	– 1.044	0.951	– 1.098	0.274
	Nocturnal			1.427	0.479	2.974	0.004
	Pelagic			2.978	0.585	5.086	< 0.001
Body depth	Benthic (intercept)	0.792	1020.024	– 6.853	12.088	– 0.567	0.572
	Nocturnal			13.254	6.622	2.001	0.047
	Pelagic			14.604	8.11	1.801	0.07
Eye size	Benthic (intercept)	0.747	567.986	– 3.201	1.672	– 1.913	0.058
	Nocturnal			5.872	0.966	6.074	< 0.001
	Pelagic			4.304	1.19	3.617	< 0.001

Bold values indicate significant *p* values

Fig. 3 a Phylogenetic principal component analysis (PPCA) of benthic diurnal piscivores only showing the continual axis of variation between fusiform versus deep-bodied species (PC1) and species with high aspect ratio (AR fins) versus low AR fins (PC2). *CAR* caudal aspect ratio, *PAR* pectoral aspect ratio, *Eye D* eye diameter, *Body D* body depth, *Head L* head length, *pmx–mx* premaxilla–maxilla length. For numbered data points for each species, please see ESM Fig. 4



(Newman and Williams 2001; Marnane and Bellwood 2002; Appeldoorn et al. 2009; Leray et al. 2012; Khan et al. 2017). Such frequent migrations to and from the reef suggest high energetic demands due to the long-term sustained swimming required for such migrations. It is likely that high caudal fin ARs in nocturnal piscivores primarily reflect a morphological adaptation for a wide-ranging lifestyle (migrations) during the nocturnal feeding period (cf. Khan et al. 2017). High fin AR values in pelagic and

nocturnal piscivores may provide further evidence of the potential ecological and evolutionary importance of off-reef habitats and their link to coral reefs (Frédérich et al. 2016; Hemingson and Bellwood 2018; Morais and Bellwood 2019).

However, we suggest that increased values of fin AR (pectoral and caudal) in pelagic morphotypes may also indicate a functional advantage with regard to their ability to feed in high-energy environments, such as the reef flat.

Table 3 Loading vectors from principal components 1 and 2 (PC1, PC2) of our phylogenetic principal component analysis (PPCA) on benthic species exclusively

	PC1	PC2
PAR	− 0.803	− 0.123
CAR	− 0.176	0.907
Eye	0.634	− 0.412
Pmx–mx	0.849	0.114
Head L	0.787	− 0.002
Body depth	0.831	0.272

PAR pectoral aspect ratio, CAR caudal aspect ratio, Eye eye diameter, pmx–mx premaxilla–maxilla length, Head L head length

High fin AR values have been shown to be functionally linked to an increased swimming ability of MPF swimmers (Walker 2004; Fulton and Bellwood 2005). We suggest that increased fin AR values may also aid in the maneuverability of body and caudal fin (BCF) swimming fishes when pursuing prey. Indeed, previous studies have found BCF swimming piscivores (e.g., *Caranx ignobilis*) to be feeding on the reef flat (Khan et al. 2016). Reef flats are characterized by high flows and low structural complexity (Bellwood et al. 2018). Based on these habitat traits, and the requirements for different feeding modes (see below), we suggest that pelagic and nocturnal ecomorphotypes may be better adapted to be feeding on the reef flat than benthic ecomorphotypes.

The results discussed so far have been primarily associated with our three ecomorphotypes, which are mostly explained by PC2 (Fig. 1; Tables 1, 2). However, the primary axis of variation for piscivorous coral reef fishes (PC1) was associated primarily with pmx–mx length and to a lesser extent with head length, body depth, and eye size (Table 1). Our results suggest that gape size is a major axis of variation among piscivorous fishes. Gape size has been shown to be of functional importance, by determining the maximum ingestible prey size for fish that swallow their prey whole (Wainwright and Richard 1995; Mihalitsis and Bellwood 2017). Field studies likewise suggest that gape limitation may be a restrictive trait in the feeding ecology of these species (St. John 1999; Albins and Hixon 2008; Morris and Akins 2009). Our results, therefore, strongly suggest that piscivores exhibit significant niche partitioning, with prey size being the main axis of variation. This partitioning can be observed along PC1, especially within benthic and nocturnal ecomorphotypes (Fig. 1a), suggesting extensive size-based partitioning of prey in these ecomorphotypes. Variation in prey size appears to be far less in pelagic piscivores [cf. Domenici et al. (2014)].

There are two potential explanations for this variation in size-based niche partitioning among ecomorphotypes. Firstly, benthic coral reef habitats likely host a greater

array of species (and thus potential prey sizes and shapes), when compared to pelagic habitats adjacent to coral reefs (e.g., Bellwood and Wainwright 2002; Claverie and Wainwright 2014). Benthic, and to a lesser extent, nocturnal piscivores, may therefore have the potential to specialize in hunting varying prey sizes. By comparison, pelagic prey such as Clupeidae, Engraulidae, and Atherinidae are less diverse in body shape, with most species being elongate and of a relatively uniform morphology. Prey shape may therefore be less likely to be influencing gape size variation on pelagic piscivores. Secondly, this pattern could be attributed to different capture modes (Grubich et al. 2008; Oufiero et al. 2012; Longo et al. 2016). Benthic piscivores can include ambush piscivores engulfing prey and ram piscivores snapping prey using their teeth. By comparison, pelagic piscivores are considered to rely primarily on pursuit, or high-speed strikes, reaching considerably higher ram speeds (Wardle et al. 1989; Svendsen et al. 2016) when compared to benthic piscivores (Oufiero et al. 2012). The lack of a large relative gape in pelagic piscivores (Fig. 2b) could therefore reflect a negative effect on the hydrodynamics required for a high-speed ram chase/strike by acting as a resisting force. A large gape may prevent high-speed capture. The largest relative pmx–mx length in a pelagic piscivore was found in *Scomberomorus munroi* (15.2% SL). This could suggest that high-speed ram feeding reaches a maximum threshold at this relative pmx–mx length. However, a more comprehensive analysis on all pelagic/high-speed ram species (tunas, bonitos, billfishes, etc.) and their gape morphology is needed. It may be noteworthy in this respect that some of the largest and fastest pelagic predators use elongate bills to stun or damage prey, which may then be consumed at slower speeds (Scott and Tibbo 1968; Domenici et al. 2014; Habegger et al. 2015). Also, the likely nature of high-speed ram (high speed and high precision) could be the reason we did not find the evidence in the literature of nocturnal pelagic piscivory, as light could be a limiting factor for this feeding mode.

Our results suggest an axis of large prey eaters versus small prey eaters. Body size is a strong driver in fisheries catches, with large body sizes being more preferred (Graham et al. 2005). Furthermore, overfishing has been shown to result in a significant reduction in the body size of available fishes (Pauly et al. 1998; Myers and Worm 2003). The disproportionate removal of large prey eaters or small prey eaters may therefore have significant implications on the size structuring of coral reef ecosystems. In essence, our results suggest that fisheries models (and management) may have to consider not only the size of the fish caught when implementing fisheries regulations, but also how the removal of predatory fish may subsequently influence the size-structuring abilities of fishes that remain within the

ecosystem. Changing fish size structures can have far reaching implications for reef ecosystem processes (Brandl et al. 2019; Morais and Bellwood 2019).

Looking at patterns within benthic diurnal piscivores, we found that they primarily differentiate along an axis of high pmx – mx , head length, and body depth values versus high pectoral fin AR values, potentially reflecting variation in their association with the benthos. When further exploring the life history of the species in our study, we noticed fusiform piscivores to either be site-attached, but on sandy/rubble, low-complexity habitats (e.g., *Saurida gracilis*, *Parapercis clathrata*), or to be species that spend a significant amount of time roaming over the benthos (e.g., *Aulostomus chinensis* or *Rachycentron canadum*) (Randall et al. 1997; Froese and Pauly 2010). By contrast, more deep-bodied species, such as species within the Epinephelidae or Antennariidae (*Antennarius commerson*), generally tend to be more site-attached on complex substrata (Randall et al. 1997; Froese and Pauly 2010) (see also Supplemental Material Fig. 4).

Overall, our results identified three morphotypes that are closely linked to ecology through fin ecomorphologies. Pmx – mx length was best at explaining variance within ecomorphotypes; however, fin shape was best at explaining differences among ecomorphotypes. Our results suggest: (a) niche partitioning reflecting different prey sizes within benthic and nocturnal piscivores, and (b) that fin shape is likely to be the strongest predictor for how and where piscivores feed.

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Compliance with ethical standards

Ethics All measurements were carried out in accordance with the James Cook University Animal Ethics Committee (A2529).

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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