**Mihalitsis, Michalis (2022)** ***The functional ecology of fish predation on coral reefs.*** **PhD Thesis, James Cook University.**

# The functional ecology of fish predation on coral reefs

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February 2022

For the degree of Doctor of Philosophy

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Centre of Excellence for Coral Reef Studies and

the Research Hub for Coral Reef Ecosystem Functions,

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## Acknowledgements

I would like to first and foremost, thank my supervisor David R. Bellwood for his guidance, patience, and supervision, not only in the world of academia, but also in my development as a human being. The wisdom and experience I have gained, will stay with me for the rest of my life.

I also want to thank the entire Bellwood Lab/Function Hub for all their help and support throughout my thesis: Orpha Bellwood, Sterling Tebbett, Christopher Hemingson, Renato Morais, Alexandre Siqueira, Robert Streit, Victor Huertas, William Collins, Casey Bowden, Sam Swan, Juliano Morais, Pooven Muruga, Jessica Valenzuela, Jodie Schlaeffer. I will miss the coffees, and all the Friday nights out.

I am greatly appreciative of all the people who helped me in the field: Sterling Tebbet, Helen Yan, Christopher Hemingson, and the staff of Lizard Island and Orpheus Island Research Stations. I also thank the people who helped me out with my experiments at the James Cook University (JCU) MARFU facilities: Katie Motson, Eric Fakan, Jennifer Donnelson, Alexia Dubuc, Rachel Spinks, Taryn Laubenstein, Shannon McMahon, and the entire MARFU staff, especially Andrew Thompson, Simon Wever and Ben Lawes. Your help has been critical in me being able to conduct my work throughout this thesis.

Furthermore, I would like to thank: Christopher H. Goatley, Sean Connolly, Peter Cowman, Pauline Narvaez, Giannis Kapakos, Jake Lowe, Kyle Hillcoat, Augustine Crosbie, and Hanaka Mera for insightful discussions and assistance; Cassandra Karalis, Thomas Bruce, Marta Panero, and Martina Burgo for emotional support. I am deeply grateful for your help whether that having been directly related to my thesis, or to my personal life.

Lastly, I would like to thank my parents George Mihalitsis and Helene Bentsen, and my brother Alexis Mihalitsis, who have supported me immensely throughout this whole journey, and without whom, this thesis would not have been possible.

## Statement of the Contribution of Others

This thesis was supported by funds provided by the Australian Research Council (ARC) to David R. Bellwood (CE140100020 and FL190100062), funds provided to me by the James Cook University (JCU) Graduate Research Scheme (Competitive Research Grant) to myself, and a Fisheries Society of the British Isles (FSBI) Research Grant to myself. Collaborators within this thesis (see below) contributed with a University of New England Postdoctoral Research Fellowship (C.H.R.G below), and a Lizard Island Reef Research Foundation Doctoral Fellowship (R.A.M below).

**Chapter 2**: M.M. and D.B. conceived and designed the study, M.M. carried out the data collection, analyses and prepared the initial manuscript and figures, M.M. and D.B. prepared the final manuscript. Both the authors gave final approval for publication.

**Chapter 3**: M.M. and D.B. conceived and designed the study, M.M. carried out the data collection, analyses and prepared the initial manuscript and figures, M.M. and D.B. prepared the final manuscript. Both the authors gave final approval for publication.

**Chapter 4**: M.M. and D.B. conceived and designed the study, M.M. carried out the data collection, analyses and prepared the initial manuscript and figures, M.M. and D.B. prepared the final manuscript. Both the authors gave final approval for publication.

**Chapter 5**: M.M. and D.R.B. conceived and designed the study; M.M. and C.R.H. carried out the data collection; M.M. analysed the data and prepared the initial manuscript and figures; C.H.R.G. and M.M. conducted the meta- analysis. All the authors contributed towards the final manuscript.

**Chapter 6**: M.M. conceived and designed the study; R.A.M collected the community data; M.M collected the morphological data as well as the data for the metanalysis; M.M. and R.A.M. analysed the data; M.M. prepared the initial manuscript and figures; All authors contributed towards the final manuscript.

All studies were carried out in accordance with the James Cook University Animal Ethics Committee under Ethics numbers A2529, A2181, and A2523. Fieldwork was conducted under the Great Barrier Reef Marine Park Authority (GBRMPA) Permit number G17/38142.1, and the Queensland Government General Fisheries Permit number 200891.

## Abstract

All fishes die. Many, if not most, are eaten by other fishes; a process known as piscivory. Such trophic interactions, despite being widely recognised and functionally important, often lack quantification. This is especially pronounced at the moment of prey capture. Despite being a process lasting milliseconds, how fish feed on other fish can make the difference between life and death. From an ecological perspective, variation in the feeding performance of animals has been shown to shape the niches of animals, which in turn has implications for processes at an ecosystem level. In this thesis, the morphology of piscivorous fishes is quantified, to answer some fundamental questions: 'who are the piscivores on a reef?', and 'how do they feed on other fishes?'.

I address these questions using comparative morphology, functional morphology, and aquarium-based performance experiments. By investigating the overall morphology of piscivorous coral reef fishes (Chapter 1), I found three distinct ecomorphotypes, namely: diurnal benthic, nocturnal, and pelagic piscivores. These fishes are separated along an axis of fin shape, with high variation in their gape size, a proxy for potential prey sizes. A more detailed analysis of the feeding-related morphology of benthic piscivorous fishes, with an emphasis on their dentition and functional traits (Chapter 2), revealed three distinct morphotypes: edentulate, villiform, and macrodont. Edentulate morphotypes have no oral jaw teeth, or teeth so small that they are invisible to the naked eye. Villiform morphotypes have many small teeth, located closely together, sitting in multiple rows. Macrodont morphotypes have few teeth, however, these teeth are large in size, are broadly spaced and located in a single row. An analysis of functional trait space suggests that these morphotypes lie within two functional groups of piscivorous fishes, that feed in fundamentally different ways.

This separation was confirmed by the aquarium-based experiments that showed two distinct functional groups of piscivorous fishes: grabbers and engulfers. Grabbers have macrodont dentition and typically strike at their prey from relatively large distances, from a horizontal position. They usually capture their prey by grabbing it tail-first, and immobilising it through headshaking

behaviours and bites, before spitting it out and re-capturing their prey head-first, followed by ingestion. Engulfers have edentulate or villiform dentition, strike at their prey from relatively short distances, from high angles (above or below the prey). They either fully engulf their prey or capture them head-first, thus preventing escape, followed by ingestion. These two fundamentally different functional groups, also reflect differences in the relative size of their prey; engulfers generally fed on smaller prey.

I then shifted the focus of the thesis to the prey, and its potential role in this predator-prey interaction. I investigated the distribution of anti-predatory functional traits, in a coral reef fish community, and how this may shape relative prey availability for piscivores on a reef. I found that small-bodied (< 5 cm) solitary fishes are primarily associated with the substratum ('sitting' on the substratum), whereas larger-bodied (> 5 cm) solitary fishes roam above, in close proximity to the substratum. Schooling reef-associated fishes are primarily found as planktivores higher up in the water column, with the distance from the reef substratum (i.e. shelter potential) being size-dependent. Based on behaviours shaping location and sociality, and the differences in body size, I identify three distinct functional groups of prey fishes: cryptobenthic substratum dwellers, solitary epibenthic, and social. These groups also display differences in their body depth, and thus, the relative number of predators on a reef that are able to feed on them, due to gape limitations. Furthermore, based on a metanalysis of mortality rates, these groups also display differences in their size-dependent early-life mortality rates. In essence, this Chapter highlights the need to understand the nature of the prey, as well as the predators', when considering predator-prey interactions.

Finally, in Chapter 6, I build a framework to assess the nature of piscivory on coral reefs, at a community level, incorporating functional groups of both predators and prey. I first allocated size-based functional traits that are directly related to predation (e.g. gape size of predator and body depth of prey), to individuals of a surveyed coral reef fish community. A simulation-based approach was then used to estimate the most likely predation events in the community. These results showed

that our perception of reef fish predators was highly skewed. The typical predator on a reef, is not a coral trout, barracuda, or snapper, as previously assumed. It is a small-bodied fish (< 15cm) such as a pseudochromid, plesiopid, or goby. These results call for a paradigm shift in the way we view fish predation in coral reef ecosystems. Furthermore, the application of predator and prey functional groups at a community level, reveals a new view of the relative importance of predation in shaping both prey populations and ecosystem processes.

Overall, this thesis provides a new, nuanced, perspective on how piscivory occurs in coral reef ecosystems, especially at the moment of capture; those few milliseconds determining the difference between life and death. It answers fundamental questions about this process, such as, 'who are the main predators on a reef?', 'how do they feed on other fishes?', and 'what is the role of prey in this interaction?'. With answers to these questions, we can now begin to understand how predation may be shaped by the changes currently occurring on reefs, and how predation itself may help shape the reefs of the future of coral reefs.

## Table of Contents

# List of Tables

# List of Figures

# Chapter 1. General Introduction

One of the most common ways of death in reef fishes is to be eaten by other fish (i.e. piscivory) (Randall 1967a). While piscivory is one of the best known and most widely reported trophic interactions in aquatic environments, it is, at the same time, one of the most logistically challenging to study (Sweatman 1984; Hixon 1991; Matley et al. 2018). Remarkably, quantitative in situ studies of direct piscivory, is relatively rare. While there is a large number of studies that have investigated the subsequent effects of piscivory on ecosystems and fish communities (Hixon & Carr 1997; Steele et al. 1998; Almany 2004b; Albins & Hixon 2008; Stier et al. 2014), there is relatively little documentation of the predation events themselves. As a result, many fundamental questions remain unanswered. How do fish eat fish? Do they all do it the same way? Who are the main predators? And does the nature of the prey fish influence these interactions?

To address these questions, the focal ecosystem should incorporate a wide array of predator and prey 'types', thus allowing a comparative framework to be conducted, strengthening causal links between different forms and functions (Wainwright & Bellwood 2002). Of all ecosystems, coral reefs are perhaps the most promising, due to their exceptional diversity and complexity. The fishes on coral reefs are renowned for their spectacular colours, shapes, and unusual behaviours (Wainwright & Bellwood 2002). Coral reefs, therefore, represent the perfect system for studying the nature of fish predation.

Piscivory on coral reefs has been studied extensively with regards to its influence on demography (e.g., Hixon & Carr 1997; Almany & Webster 2006) and community composition (e.g., Heinlein et al. 2010; Stier et al. 2013; Stier et al. 2017), as well as its indirect effects on fish communities (e.g., Rizzari et al. 2014; Madin et al. 2016; Mitchell & Harborne 2020). These studies have been essential in developing our understanding of how predation shapes reef fish communities and other aspects of coral reef ecosystems. However, while predation is a process occurring daily, in vast numbers on a coral reef, it only lasts milliseconds. This is a remarkably small timeframe, but for the coral reef fishes involved, it is a matter of life and death. How this event occurs can have far-reaching implications. For example, are all prey equally vulnerable? And what constrains a predators' success? There is still, therefore, a need to quantitatively understand the nature of this interaction (i.e., the exact moment of predation). In particular, the extent to which interactions between different species of predators and prey may shape the eventual outcome. In essence, there is a need to identify the different 'types' of predators and prey, before we can ask questions relating to how different predators may influence coral reefs; an important question given the rate at which these piscivorous fishes are disappearing from coral reefs (Dulvy et al. 2004a; Graham et al. 2005; Valdivia et al. 2017). How then, do we quantify this elusive process, for a system governed by vast numbers of different species with different morphologies, behaviours, and life histories?

In the last few decades, the identification of functional groups within coral reefs, has gained ground rapidly (Bellwood et al. 2019). This approach is implemented through an established set of steps (Wainwright & Reilly 1994). Within this framework, the first step is an assessment of the features the animal possesses (e.g., morphology) to carry out different tasks (e.g., swimming, feeding). This assessment underpins hypotheses regarding how the animals may use these features through their behaviour (Feilich & López-Fernández 2019). The next step is to carry out performance experiments to test these hypotheses, and assess how the animal is indeed using its morphology or other features to carry out the function of interest. The maximal abilities of the animal in carrying out a certain task, sets its potential niche (Wainwright 1991). Within this set of boundaries, the animal interacts with external factors (e.g., competition, food availability, abiotic factors etc.) to shape its realised niche for that particular function.

This approach has been implemented multiple times for coral reef fishes (e.g., Wainwright 1987; Fulton et al. 2005; Konow et al. 2008; Collins & Motta 2017). Furthermore, the implications of such an approach has been found to be directly linked to emergent general patterns at a global scale

(Fulton et al. 2017). Indeed, this approach has been identified as a particularly promising avenue of research for elucidating patterns in community ecology (McGill et al. 2006) and in ecosystem function (Bellwood et al. 2019). However, this approach has yet to be applied to piscivorous coral reef fishes and their prey, arguably one of the most important trophic interactions on coral reefs.

In this thesis, therefore, I quantify the functional morphology of piscivorous coral reef fishes, and conduct comparative analyses to establish how piscivorous fishes differ in their general morphology (Chapter 2). I then explore their functional morphology that is directly related to feeding (Chapter 2,3), followed by performance experiments and quantification of feeding abilities of piscivorous coral reef fishes (Chapter 4). I subsequently identify functional groups of coral reef fish prey, at a community level (Chapter 5). Finally, I develop a methodology to quantify the process of fish predation on coral reefs, at a community level, and assess the ability of the established functional groups to elucidate patterns of fish predation on coral reefs at broad ecological scales (Chapter 6).

# Chapter 2. Morphological and functional diversity of piscivorous fishes on coral reefs

Published as: Mihalitsis M. & Bellwood D. R. (2019) Morphological and functional diversity of piscivorous fishes on coral reefs. Coral Reefs, 38(5), 945-954.

## 2.1 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 et al. 2006). A well-studied example is that of the pectoral fin of Median Paired-Fin (MPF) swimmers . Fulton, Bellwood and Wainwright (2005), described a correlation in 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, Bellwood & Wainwright 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 have 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 & 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 2004b; Almany 2004a; Almany & Webster 2004; Goatley & Bellwood 2016). Furthermore, up to 53% of species on reefs may be regarded as piscivorous (Randall 1967a; Hixon 1991). Despite their ecological importance and diversity, piscivorous fishes on coral reefs remain understudied, especially with regards to their morphological or functional characteristics. If we are to understand how different types of 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 & Alcala 1989; Pauly et al. 1998; Myers & Worm 2003). Piscivorous fishes are highly sought-after in coral reef fisheries (Jennings & 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 endeavour is to understand how they differ from each other with regards 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 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 & Richard 1995; St. John 1999), and how it is functionally linked to maximum prey size (Mihalitsis & 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 & Nauen 1983; Allen 1985; Heemstra & Randall 1993).

My 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 & Bellwood 1991; Wainwright & Bellwood 2002), by quantifying the morphological diversity of 119 species from 19 fish families. I construct a broad morphospace for piscivorous coral reef fishes and correlate this diversity of morphotypes with basic patterns of activity and habitat use (behavioural traits). I then explore the potential functional implications of these major axes of morphological diversity, and identify distinct ecomorphotypes for further detailed study.

## 2.2 Materials & Methods

In this 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 towards the ecological function of piscivory. The primary focus of my 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 published literature or websites (e.g. Hiatt & Strasburg 1960; Randall 1967b; Froese & Pauly 2014). If diet data was 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, I only included images of sub-adult and adult fishes. A mean of 3 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 & Bellwood 1991; Bellwood & Wainwright 2002). All families and respective species are given in Appendix A along with raw trait values measured (see Appendix A Table 2,3). As some of the morphological traits measured in this study are absent in the Muraenidae (fin ARs), they were excluded from my analyses. For some families, only a few species are considered significant piscivores, such as *Cheilodipterus* within the Apogonidae (Marnane & 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 pre-maxilla to the posterior margin of the maxilla), a potential proxy for the oral gape. These measurements were used as they have been previously found to characterise the ecology of coral reef fishes (Goatley & Bellwood 2009; Claverie & Wainwright 2014). Caudal fin AR was measured based on (Sambilay 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 Appendix A 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*.

I also assessed the relationship between pmx-mx length and gape measurements taken directly from specimens. I measured 65 individuals from 33 species. 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 my 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 the Grafen method (Grafen 1989). Species not placed on the 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 these analyses, is given in Apppendix A Fig. 2.

Following the PPCA, I overlaid ecological traits on the morphospace ordination. These were habitat (benthic/pelagic) and activity (diurnal/nocturnal), and were based on existing literature (e.g. Hobson 1965; Hobson 1972; Goldman et al. 1976; Randall 2005). I identified emergent groupings as ecomorphotypes. Here, I use the term ecomorphotype, as a grouping within a morphology-based ordination (morphospace), that is grouped based on ecological (behavioural) traits. I displayed the 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, Claude & Strimmer

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).

### 2.3 Results

In the Phylogenetic Principal Component Analysis (PPCA) of morphospace, the first two axes explained 47.3 % and 22 % of the total variance respectively (Fig. 2.1). PC1 is mostly correlated with head length, pmx-mx length, body depth, and eye diameter (Table 1, Fig. 2.1); PC2 with pectoral AR and caudal AR (Table 1, Fig. 2.1). When behavioural traits (habitat use, activity) were mapped onto the morphospace using convex hulls, I identified three distinct ecomorphotypes: 1) pelagic predators 2) benthic diurnal predators, and 3) nocturnal predators (for classification of species, see ESM Table 2; I 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, 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. 2.1). 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. 2.2c, 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, my 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).

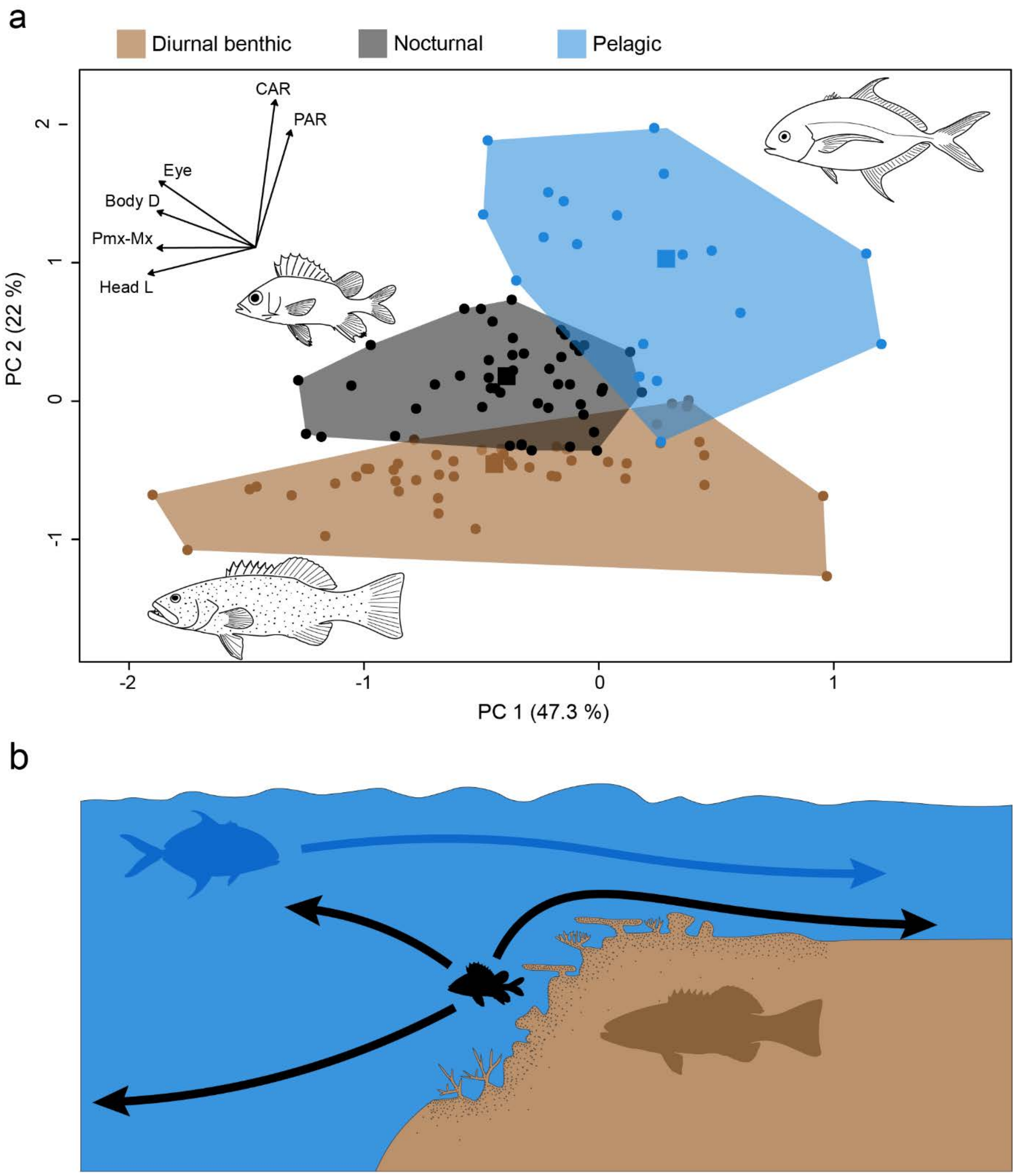


*Figure 2.1* (a) Phylogenetic Principal Component Analysis (PPCA) of piscivorous coral reef fishes. Groups represent associated ecomorphotypes based on activity and habitat association. Brown = diurnal benthic, black = nocturnal, blue = pelagic. Squares within convex hulls represent the centroid, and fish illustrations indicate the species closest to each centroid, respectively *Plectropomus leopardus*, *Sargocentron tiere*, and *Carangoides ferdau*. (b) illustration of each ecomorphotype indicating its association with the reef. Arrows indicate where pelagic and nocturnal ecomorphotypes may be feeding. Abrreviations: 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 Appendix A Fig. 3.

*Table 1* Loading vectors from principal components 1 and 2 (PC1, PC2) of the 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 |

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. 2.1a). 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. 2.2a), suggesting that pmx-mx length is a reasonable 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. 2.1a), reflecting variation in gape sizes (Fig. 2.2b).

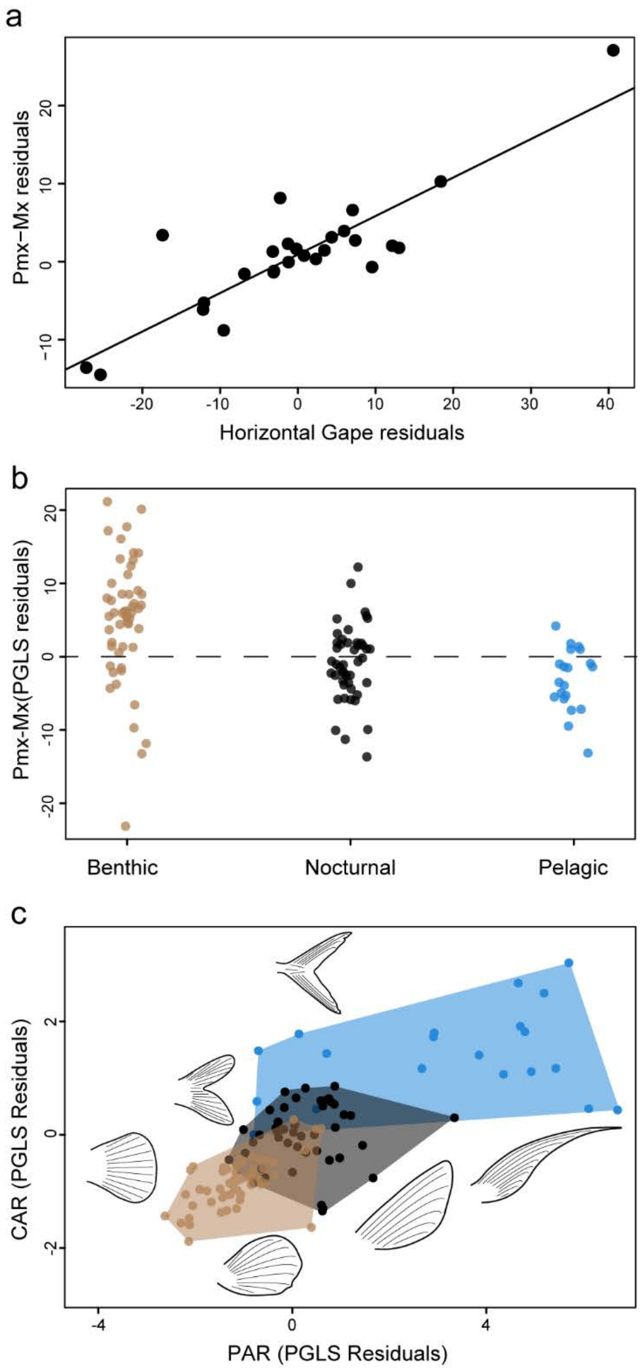


*Figure 2.2* **a** Premaxilla – Maxilla (pmx–mx) length (residuals) plotted against vertical gape (residuals). **b** Pmx–mx length (proxy for gape) (Phylogenetic Least Squares (PGLS) corrected residuals) for each ecomorphotype. **c** caudal aspect ratio (AR) (residuals) plotted against pectoral AR (residuals). Colours represent associated ecomorphotypes respectively, brown = diurnal benthic, black = nocturnal, blue = pelagic.

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

| **Variable** | **Level** | **lambda** | **AIC** | **Estimate** | **St. Error** | **t-value** | **p-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** |

As benthic diurnal piscivores, as an ecomorphotype, displayed the most variance along PC1, I repeated the PPCA as described above (Fig. 2.1a) 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. 2.3a). 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. 2.3). The second axis (PC2) is primarily correlated with caudal AR (CAR) (Table 3, Fig. 3). My 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. 2.3).

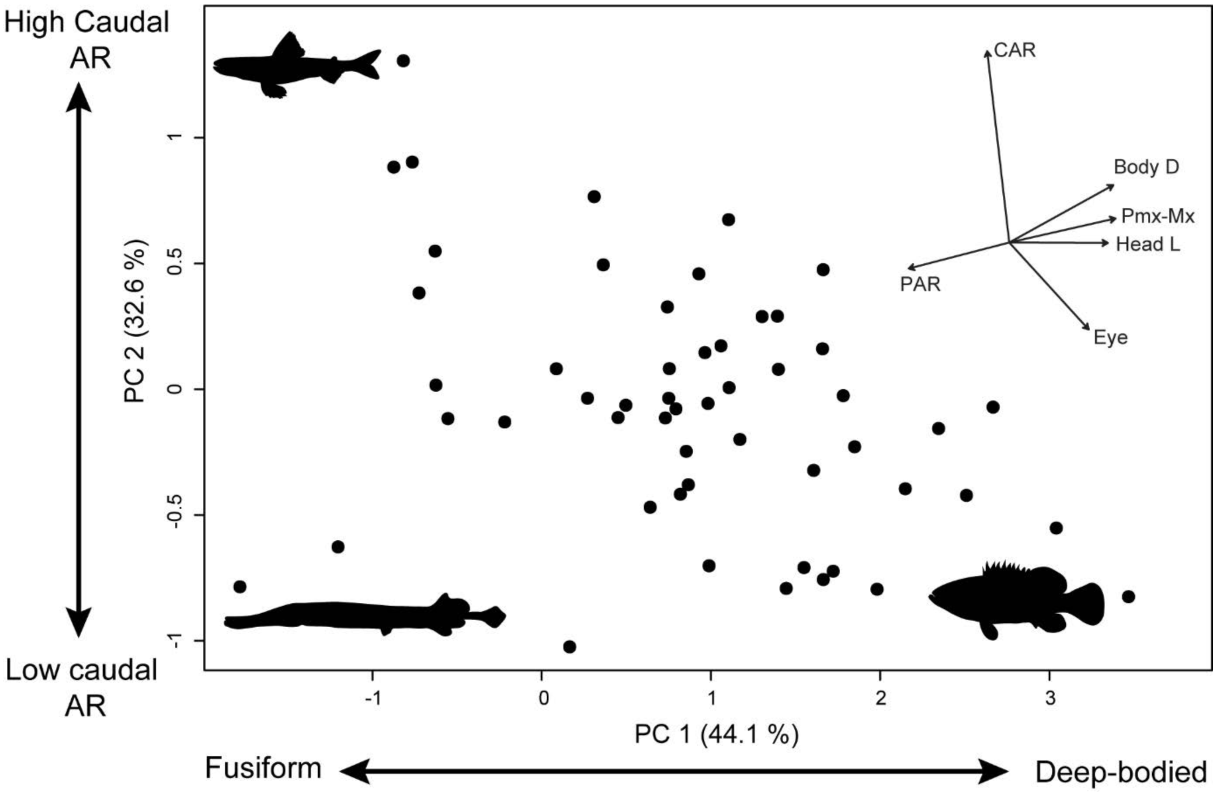


*Figure 2.3* **a** Phylogenetic Principal Component Analysis (PPCA) of benthic diurnal piscivores only, showing the continual axis of variation between fusiform vs. deep-bodied species (PC1) and species with high aspect ratio (AR fins) vs. low AR fins (PC2). Abrreviations: CAR = caudal aspect ratio, 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 Appendix A Fig. 4.

*Table 3* Loading vectors from principal components 1 and 2 (PC1, PC2) of the 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 |

## 2.4 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. I show caudal and pectoral fin morphology to be the primary drivers of variation separating these ecomorphotypes. I 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 behavioural studies.

I found high caudal and pectoral fin ARs in pelagic piscivores and lower ARs in benthic-associated piscivores. However, I found that these fin morphologies also explain a distinct morphotype of nocturnal piscivores, situated directly between benthic and pelagic piscivores (Fig. 2.1a, Fig. 2.3c, Table 1). Pectoral fin AR values, have previously been associated with Median and Paired Fin (MPF) swimming (Walker 2004; Drucker et al. 2005; Fulton, Bellwood & Wainwright 2005). However, I found no evidence of the species investigated to be MPF swimmers in the literature (e.g. Fulton 2007). I therefore argue that the high AR values shown in my 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 & Bellwood 2015). However, species within these families feed at night, and away from the reef (Newman & Williams 2001; Marnane & 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 long-term sustained swimming, which would be 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 & Bellwood 2018; Morais & Bellwood 2019).

However, I suggest that increased values of fin AR (pectoral and caudal) in pelagic morphotypes may also indicate a functional advantage with regards to their ability to feed in high energy environments, such as the reef flat. High fin AR values have been shown to be functionally linked to an increased swimming ability of MPF swimmers (Walker 2004; Fulton & Bellwood 2005). I 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, Welsh & Bellwood 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), I 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 the three ecomorphotypes, which are mostly explained by PC2 (Fig. 2.1, Table 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). These 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 & Richard 1995; Mihalitsis & 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 & Hixon 2008; Morris & Akins 2009)). These 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 2.1a), 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 & Wainwright 2002; Claverie & 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, 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 2.2b), 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 feeding 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 & 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 I did not find 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 vs. 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 & 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, these 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 & Bellwood 2019).

Looking at patterns within benthic diurnal piscivores I found that they primarily differentiate along an axis of high pmx-mx, head length and body depth values vs. high pectoral fin AR values, potentially reflecting variation in their association with the benthos. When further exploring the life history of the species in this study, I 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 & 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, Allen & Steene 1997; Froese & Pauly 2010) (see also Appendix A Fig. 4).

Overall, these 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. The 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.

# Chapter 3. Functional implications of dentition-based morphotypes in piscivorous fishes

Published as: Functional implications of dentition-based morphotypes in piscivorous fishes. R. Soc. Open. Sci. 6: 190040.

## 3.1 Introduction

Vertebrate teeth have been studied for centuries. Their importance in elucidating the life history of organisms has been demonstrated in multiple fields, from paleontology and evolution, to ecology. Usually, the focus is on biomechanics, morphology, and/or behaviour (e.g. Bellwood & Choat 1990; Wroe et al. 2005; Gordon & Prins 2008; Bellwood et al. 2014; Hocking et al. 2017; Torices et al. 2018). However, most studies of vertebrate teeth have been focused on mammals (Valkenburgh & Ruff 1987; Hillson 2005; Ungar 2010; Churchill & Clementz 2015; Foffa et al. 2018). Other vertebrate lineages, although more speciose, have received less attention.

Fishes, and more specifically, teleosts, constitute over half of all vertebrate species (Eschmeyer et al. 2010), however, our understanding of their oral tooth morphology was for a long time primarily at a descriptive level: small/large, conical/villiform/molariform (e.g.(Allen 1985)). In the last decade however, research has begun to elucidate the morphology and potential function of several aspects of fish dentition (Grubich, Rice & Westneat 2008; Grubich et al. 2012; Bellwood et al. 2014; Conway et al. 2015; Ferguson et al. 2015; Corn et al. 2016; Galloway et al. 2016; Bemis et al. 2019). These studies have provided invaluable information on how the tooth morphology of fishes may influence their feeding capabilities. However, if we are to link tooth functional morphology to ecological functions and, more specifically, to how fishes feed in their environment, there is a need to identify functional groups based on full dentition morphologies rather than individual teeth.

The limited number of more quantitative descriptions of fish dentition, when compared to mammalian dentition, is not without good reason. First, mammals only replace their teeth once throughout their lifetime (diphyodont). Fishes by contrast, along with most other lower vertebrate lineages, constantly replace their teeth (polyphyodont) (Weller 1968; Ungar 2010). Secondly, fishes display significantly higher variance in the distribution of their oral teeth along their jaw when compared to other vertebrate groups (Ungar 2010). For example, mammals primarily have canines on the anterior part of their jaws, and no mammalian species has more than one canine in each quadrant (upper left vs. lower right e.t.c) (Ungar 2010). It is therefore possible to classify mammalian dentition based on the number of teeth of each type using dental formulas. For example, humans have the dental formula $I\frac{2}{2}, C\frac{1}{1}, P\frac{2}{2}, M\frac{3}{3}$, where letters indicate tooth type I=incisors, C=canines, P=premolars, M=molars, and fractions indicate number of teeth on upper and lower quadrants. For fishes, this would be an herculean task, given the extent of variation in form and number. Furthermore, compared to a mammal, like humans, which as seen above have 32 teeth, fish can have thousands of teeth in their mouths (Ungar 2010). Finally, tooth function in mammals, is based on tooth shape and location along the jaw (e.g. canines = large conical teeth anteriorly in the jaw vs. molars = relatively flat teeth located posteriorly). Unlike mammals that have different shaped teeth (heterodont) (Ungar 2010), fishes and other lower vertebrates typically have similarly shaped teeth (homodont) (Hunter 1999). However, these descriptive terms, homodont and heterodont, need to be interpreted with caution, as the term ‘different shaped teeth’ can sometimes be misleading. In this study I follow Liem (Liem et al. 2001), who noted that “…in the majority of vertebrate species, the teeth, although they may differ in size, are structurally alike, a condition called homodont’’. This issue was discussed by (D’Amore et al. 2019) who noted the need for a broader evaluation of tooth form and function.

These terms (homodont/heterodont) offer definitions that provide a coarse framework for the comparative analysis of tooth form. However, tooth form may not be the only trait determining tooth function (Grubich, Rice & Westneat 2008; Ferguson et al. 2015) within lower vertebrates. Overlap among groups is inevitable. There is clearly a need to expand our frame of reference from individual tooth form and function to the entire dentition morphotype and its functional implications.

The importance of establishing such a framework, however, is that it will enable us to begin to link morphological traits with functional morphology, i.e. establishing a functional link between certain anatomical features and how they help the organism perform a specific task (e.g. feeding) (e.g. (Turingan 1994; Wainwright & Richard 1995; Fulton 2007)). These characters/traits, can in turn be linked to the way organisms interact with, and more importantly influence, their surrounding environment (Wainwright & Reilly 1994; Wainwright & Bellwood 2002).

One group of organisms displaying high morphological diversity, and thus making them an ideal study group, are piscivorous coral reef fishes (Chapter 2). This group of fishes displays high morphological diversity related to feeding traits such as gape size (Goatley & Bellwood 2009)(Chapter 2). It has been suggested that this diversity may reflect the potential for niche partitioning on prey of different sizes, or different feeding modes (Chapter 2). However, before beginning to ask such questions, there is a need to first delineate the various dentition morphotypes found within this functional group.

In this study, I provide a quantitative comparative framework of piscivorous fish dentition types, and use the data to identify distinct morphotypes. I then show that these morphotypes are linked to key functional feeding traits. Finally, I show that the location of the largest teeth along the jaw, can have biomechanical, and therefore, functional implications. I argue that some teleost lineages might have evolved a type of functional decoupling where similarly-shaped teeth could have a different function, based solely on their position along the lower jaw.

## 3.2 Materials & Methods

### *3.2.1 Morphological measurements*

In total I measured 61 freshly-thawed specimens of 29 piscivorous teleost fish species (mean=2.1 individuals p. species). Standard length measurements (SL) were taken using calipers or measuring tape for larger specimens. Ontogenetic shifts in dentition were minimised by measuring only sub-adult and adult specimens. Vertical and horizontal oral gape distances were measured using scissors, following the methodology and definitions of Mihalitsis and Bellwood (2017). Specimens were then displayed perpendicular to a camera and photographed, first mouth closed, then mouth open (maximal jaw depression). Upper jaw protrusion was measured as the difference between the distance between the tip of the jaw to the anteriormost point of the eye with the mouth closed and open. While mouths were open, the left lower jaw was photographed laterally, the camera being perpendicular to the teeth. In species with villiform dentition, the teeth were found to be angled medially (lingually). Additional images were therefore taken with the camera at approximately 45°, to capture the whole tooth length. In species with enlarged lips, the lips were pulled downwards and fixed with a pin to reveal the full length of the teeth. Qualitative observations on the upper jaw dentition patterns were also made. Some species (e.g. *Neoniphon sammara*) have numerous teeth, however, they are so small (generally <1mm) and compact to be almost invisible to the naked eye; for the purposes of this study they were classified as edentulate as they were too small to measure. Specimens were acquired from commercial suppliers or from donations.

### ***3.2.2 Analysis***

Traits based on images, were collected using the software ImageJ, and all subsequent data analyses were conducted in the software R (R Core Team 2017). I identified the 5 largest teeth along the lower jaw and measured these teeth sequentially, from front to back along the jaw. Measured traits were: lower jaw length, individual tooth lengths (1-5), distance to jaw tip (1-5), distance between teeth (1-4), largest tooth position from jaw tip, largest tooth width at the base, smallest vs. largest tooth length of the five largest teeth, total number of teeth, and number of tooth rows (1-5 indicates that the trait was recorded for each of the five teeth). These traits were chosen to capture the overall morphology of the teeth, dentition, and their relationship to biomechanical properties (e.g., Wainwright et al. 2004; Bellwood et al. 2014). For a detailed description of these traits see Appendix B Table 1. Throughout the Chapter, the terms largest and smallest teeth is based on tooth length, and therefore also refer to longest and shortest teeth respectively (given the similarity in tooth shapes). I then converted trait measurements to percent standard length. To evaluate allometric relationships, I plotted body-standardized variables against body size (SL), and where regressions were significant, calculated residuals. Before transforming values, I produced positive scores by adding a constant to all values (absolute value of the smallest negative residual +0.1). This treatment eliminates negative residuals (thus allowing transformations) but retains the relationships between scores/trait values.

As morphological variables are not phylogenetically independent, I constructed a phylogenetic tree encompassing all species in the dataset (see Appendix B Fig. 1), using the Open Tree of Life (Hinchliff et al. 2015) and the package '*rotl*' (Michonneau, Brown & Winter 2016). Tree branch lengths were computed using the Grafen method (Grafen 1989). I then conducted Phylogenetic Principal Component Analyses (PPCA) using the package '*phytools*' (Revell 2012). As Principal Component Analysis (PCA) can be sensitive to zeros, and the dataset included zero values describing traits for edentulte (toothless) species, I also analysed the data using a distance-based ordination as opposed to a correlative (PPCA). I conducted a Principal Coordinate Analysis (PCoA) based on a Gowers distance matrix, using the '*vegan'* package (Oksanen et al. 2013). After identifying morphotype groupings in these ordinations, I tested the validity of my groupings, by conducting a clustering analysis (simulations=999, distance method = Euclidean), followed by a Similarity Profile Analysis (SIMPROF) (method= Wards, α=0.01) based on the scores produced from the PPCA (PC1 and PC2), to identify significant clusters using the package '*clustsig*' (Whitaker et al. 2014).

After identifying morphotypes based on tooth morphology, I compared these morphotypes to established functional feeding traits. Functional traits were defined as morphological traits for which specific function(s) have been experimentally shown to aid the organism in carrying out a specific task related to feeding. These traits were: jaw protrusion (Oufiero et al. 2012; Longo et al. 2016), gape size (vertical oral gape and horizontal oral gape) (Wainwright & Richard 1995; Mihalitsis & Bellwood 2017), mouth shape (vertical oral gape/horizontal oral gape) (Lauder 1979), and jaw lever ratios (Wainwright & Richard 1995). For a detailed description of each function see Appendix B Table 2. The same treatment applied to morphological tooth traits (evaluating allometry by calculating residuals) was applied to functional traits, however, functional traits were also log10 transformed to minimize the effect of outliers. Following PPCA ordinations to identify distinct functional groups, we analysed each functional trait (same values used for PPCA) (response variable) between morphotypes (explanatory variable) by using Phylogenetic Least Squares (PGLS) models. PGLS models were conducted to explore the significance (and relationship to morphotypes of each variable individually) of the ordination-based interpretations, and were analysed assuming Brownian motion, and using the Maximum Likelihood method. Models were conducted using the '*nlme*' package (Pinheiro et al. 2014).

During initial analysis, I found that some morphological traits did not conform with morphotype divisions. For example, largest tooth position (relative to jaw length) is uninformative for villiform and edentulate fish, as villiform fish have highly homogenous tooth sizes along their jaw (e.g. Fig. 3.2), and edentulate fish teeth are either exceedingly small teeth or absent. I therefore undertook a second morphological trait-based analysis where I included only macrodont species (i.e. excluding villiform and edentulate species). In this part of the study, I used a different set of morphological traits which were applicable to macrodont species exclusively. Traits used in the analysis of macrodont species were: variance in tooth sizes, smallest vs. largest tooth length of the five largest teeth, mean distance between five largest teeth, and largest tooth position. For a detailed description of each trait see Appendix B Table 1.

## 3.3 Results

The initial Phylogenetic Principal Coordinate Analysis (PPCA), based on tooth-based morphological traits, explained 44.7 % (PC1) and 26.6% (PC2), respectively, of the total variation. Three morphotypes, macrodont, villiform, and edentulate, are primarily separated along PC1 (Fig. 3.1, Fig. 3.2a). Villiform species are described by the high abundance of lower jaw teeth (47 in *Cephalopholis microprion* to 96 in *Epinephelus ongus*), and having three to four tooth rows. Macrodont species are characterised by a higher variance in their teeth sizes (having both large and smaller teeth), with fewer teeth than villiforms (ranging from 4 in *Cheilodipterus* species to 20 in *Hologymnosus annulatus*), usually in a single row. Edentulate species were characterised by having no teeth or teeth which were undetectable with the methods used herein. The Principal Coordinate Analysis (PCoA) revealed similar results to the PPCA, suggesting that the zero values of edentulates had minimal effect on the analysis (see Appendix B Fig. 2). The clustering and SIMPROF analyses, strongly supported the ordination-based groupings (see Appendix B Fig. 3). Upper jaw dentition in villiform and macrodont morphotypes were primarily described by a large caniniform tooth on the anteriormost margin of the premaxilla (usually smaller in species with villiform dentition), followed posteriorly by smaller similarly-shaped teeth (e.g. Fig. 3.6).

*Figure 3.1* Dentition patterns in piscivorous fishes: (a) edentulate (*Taenianotus triacanthus*), (b) villiform (*Epinephelus polyphekadion*), (c) 'back-fanged' macrodont (*Plectropomus leopardus*) and (d) 'front-fanged' macrodont *(Oxycheilinus digramma*).

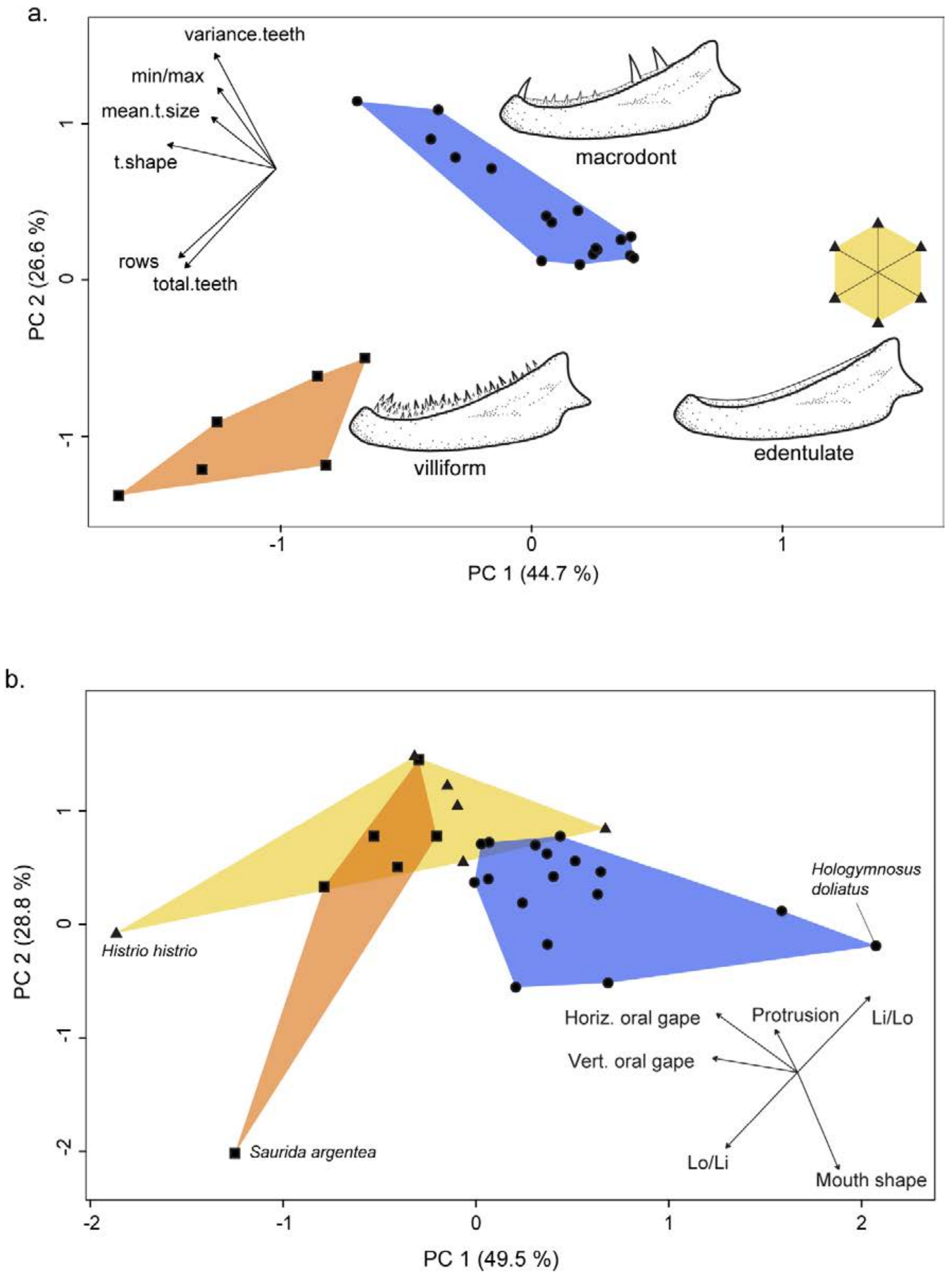


*Figure 3.2* PPCA based on (a) teeth traits and (b) functional feeding traits. Colours/shape scores represent villiform (orange/squares), macrodont (blue/circles) and edentulate (yellow/triangles) species. Lines within the edentulate species polygon are drawn to show that all dots/specimens are in the same location in the ordination. For vector loadings on the principal components, see

Appendix B Table 3. For detailed descriptions of traits (tooth and functional), see Appendix B tables 1 and 2, respectively.

In contrast to the morphological trait PPCA, the functional trait PPCA, revealed more overlap between tooth morphotypes, especially between edentulate and villiform morphotypes. These two morphotypes, were mostly separated from macrodonts by having larger gape sizes (Fig. 3.2a). Macrodonts were characterized by smaller gape sizes, and higher Lo/Li values (velocity advantage) (Fig. 3.2a). Both gape sizes and Lo/Li traits were significant in the PGLS models (Appendix B Table 4). Mouth shape (ratio of vertical oral gape/horizontal oral gape) is vertically oval in macrodont species, whereas edentulate and villiform species were characterized by more rounded mouths; this was, however, not significant in PGLS models (Appendix B Table 4). Jaw protrusion appears to be mostly associated with edentulate and villiform morphotypes; this was, however, not significant in PGLS models (Appendix B Table 4). One species, *Saurida argentea*, does not fit the functional pattern of the rest of villiforms, as it is characterized by a high velocity advantage jaw (high Lo/Li ratio), but no protrusion (Fig. 3.1b). In essence, the results show edentulate and villiform morphotypes to be characterised by larger gape sizes and lower velocity advantage in jaw closing, whereas macrodonts were characterized by smaller gape sizes and higher velocity advantage in jaw closing. It appears that while there may be three tooth morphotype groups, functionally, there are probably only two groups, macrodonts vs. villiform/edentulate.

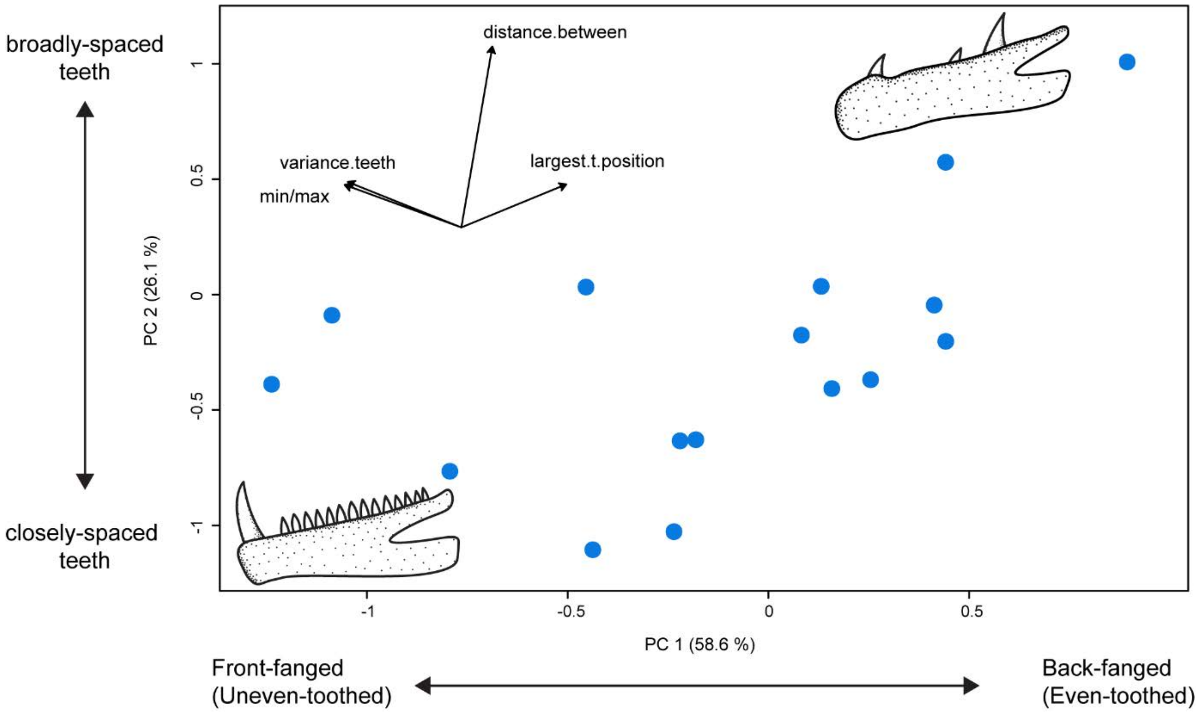


*Figure 3.3* PPCA of macrodont piscivores. For vector loadings on principal components, see Appendix B Table 3. For detailed description of scores, see Appendix B Fig. 6.

When macrodonts were analysed exclusively, *Cheilodipterus macrodon* was an outlier and was therefore removed from the analysis (for an ordination including this outlier see Appendix B Fig. 3.4). Excluding *Cheilodipterus*, the macrodont-based PPCA explained 58.6% (PC1) and 26.1% (PC2) respectively, of the total variation (Fig. 3.3). PC1 is mostly associated with ‘variance in tooth sizes’ and ‘min/max ratio’, and ‘position of largest tooth’. This axis suggests a continuum between species with one large tooth (sometimes two teeth) located anteriorly on the jaw followed posteriorly by smaller teeth vs. species with similar-sized teeth (note this refers to the five largest teeth, not all teeth), where the largest tooth is located posteriorly on the jaw (occasionally a similar-sized caniniform tooth is present in the anteriormost point of their jaw). Extremes of this continuum are hereby termed ‘front-fanged’ and ‘back-fanged’ respectively. PC2 is mostly associated with ‘distance between teeth’, indicating an axis of variation between ‘broadly-spaced’ vs. ‘closely-spaced’ teeth. In essence, the results suggest a continuum between ‘front-fanged’ dentition types which have a large anterior tooth, with teeth being unevenly sized and tightly spaced vs. ‘back-fanged’ dentition types which have a large posterior tooth, with broad tooth spacing, and even tooth sizes. If tooth force potential (based on lever-ratio mechanics) is calculated for anteriormost vs. posteriormost caniniform teeth in back-fanged dentition types, posteriormost teeth were found to have an average 42.1% increase in force (Fig. 3.4). These potential morphotypes appear to be independent of body size and jaw length, as both morphotypes were distributed along the entire range of the sampled body sizes and jaw lengths (Appendix B Fig. 5).

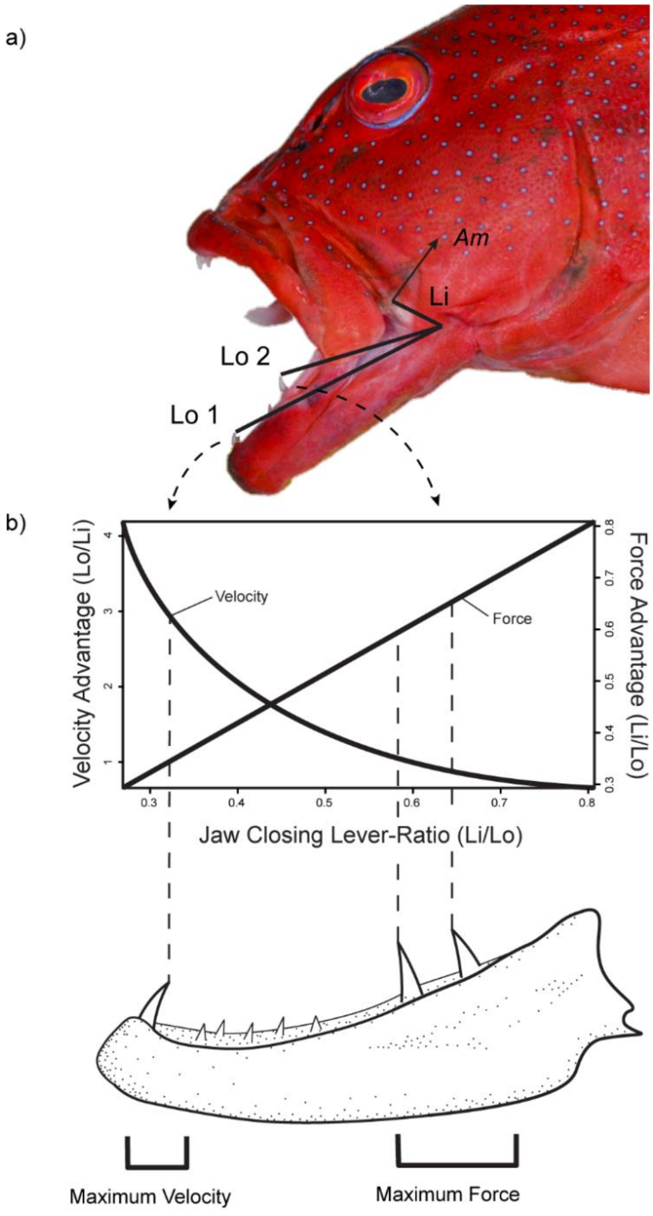


*Figure 3.4* Lever-ratio biomechanics for teeth of a back-fanged macrodont piscivore (*P. leopardus*): (a) change in force between anteriormost versus posteriormost teeth. Li, in-lever; Lo1, out-lever to the anteriormost tooth; Lo2, out-lever to the posteriormost largest tooth; Am, adductor mandibulae muscle. (b) Relationship between velocity advantage and force advantage when calculating lever ratios (modified after [29]) and the functional ramifications of this principal for anteriorly versus posteriorly positioned canines.

### 3.4 Discussion

The analyses identified three major tooth-based morphotypes in piscivorous fishes: edentulate, villiform, and macrodonts. I found that tooth shape, relative tooth size, and number of teeth (along with tooth rows), were the primary distinguishing features of these morphotypes (Fig. 3.1a). Also, when analysed in a context of functional feeding traits, edentulate and villiform morphotypes were found to be overlapping, whereas macrodonts were distinct (Fig. 3.1b). Edentulate and villiform fishes were characterised by larger gape sizes and lower velocity advantage in jaw closing, and to a lesser extent, more rounded mouth openings. Macrodonts were characterized by smaller gape sizes and higher velocity advantage, and to a lesser extent, more oval shaped mouths (Fig. 3.1b). When macrodonts were analysed exclusively, I found a distinct axis of variation, which may reflect functional divergences in the oral teeth of fishes and other homodont lower vertebrates. I suggest that tooth function for some lower vertebrates might differ not based on tooth shape, but solely by position along the jaw. In other words, even if organisms are homodont (like the vast majority of vertebrate species), functional diversification is still possible.

As the functional traits used in the study are key to the prey capture and/or post capture processing of prey, it is likely that edentulate and villiform fishes will display similar feeding behaviours, that are quite distinct when compared to macrodonts. However, for these behaviours to be displayed, and quantified accurately, these organisms may need to be tested in a maximal performance-based context (Wainwright & Reilly 1994; Motta, Norton & Luczkovich 1995; Mihalitsis & Bellwood 2017). For example, Reimchen (1991) showed that capturing and processing behaviour for a predatory fish was random for small sized prey, but shifted to head-first processing when predators were fed prey with body diameter over half their gape. Mihalitsis and Bellwood (2017) likewise found *Cephalopholis urodeta*, a piscivore with villiform dentition and a relatively large gape, captured prey head-first, whereas *Paracirrhites forsteri*, a macrodont with a smaller gape, captured prey mid body or tail first. Based on the observed morphologies and behaviour, I suggest that edentulate and villiform species, with larger gape sizes, might be more efficient in 'engulfing' their prey through ambush predation, whereas macrodonts, with smaller gape sizes but larger teeth, might be more efficient at 'grabbing' their prey after a short-distance lunge and/or longer pursuit. This axis of variation may also reflect varying contributions from suction vs. ram in engulfing vs. grabbing species (Ferry et al. 2015; Longo et al. 2016; Collins & Motta 2017).

After prey capture, Mihalitsis and Bellwood (2017) found that *P.forsteri* conducted a series of head shaking movements when processing prey, potentially to slash/lacerate prey by using their teeth. This feeding behaviour of head shaking is similar to that seen in non-teleostean fish groups e.g. chondrichthyans (Springer 1961), especially when feeding on prey too large to swallow whole (Frazzetta & Prange 1987). Interestingly, this behaviour is also observed in other lower vertebrates (e.g. lizards) (Gans 1961; Van Damme et al. 1991; Schwenk 2000).

When analysing macrodonts exclusively, I found the main axis of variation (PC1) displayed a continuum, with the extremes being 'front-fanged' and 'back-fanged' species. Teeth used to penetrate prey, are strongly linked to the biomechanical property of stress (e.g.(Whitenack et al. 2011; Anderson 2018)) , that is, the force applied to an object relative to the area over which it is applied ($\sigma$ = force/area, SI= newton/meter$^2$) (Vogel 2013; Ferguson et al. 2015). Having a single large caniniform tooth followed (or surrounded) by small teeth maximizes the stress the large tooth will exert on prey tissues, just like having multiple similar-sized teeth but positioned further apart (Fig.

3.5). In villiform dentition, similar shaped teeth in large numbers, are likely to act like a 'bed of nails' which may be able to grip rather than puncture (Fig. 3.5). This observation highlights the need to look past single-tooth morphology alone, and integrate full dentition-based studies when elucidating the life history of organisms.

Furthermore, I suggest that 'back-fanged' dentition patterns, may have key functional implications based on lever-ratio biomechanics. By having a large caniniform tooth posteriorly in their jaw, these species gain, on average, a 42 % force advantage when compared to a same sized tooth positioned at the anterior-most point of the jaw (Fig. 3.4) (see also Ferguson et al. 2015). This value mirrors differences reported in anterior vs. posterior jaw bite pressure, calculated in (Ferguson et al. 2015) for King Mackerel (*Scomberomorus cavalla*). This increase in force advantage could provide the predator with the force required to deeply pierce prey. I suggest that back-fanged morphotypes, could be exhibiting a form of functional decoupling, with the anteriormost canines (higher speed/less force) being used for grabbing prey whereas posteriorly positioned canines (lower speed/higher force) are used for post capture processing (Fig. 3.4), such as deeply piercing and/or lacerating prey, especially when using the slashing behaviour described above. This is further highlighted by the lack of back-fanged tooth distributions on the upper jaw (Fig. 3.6).

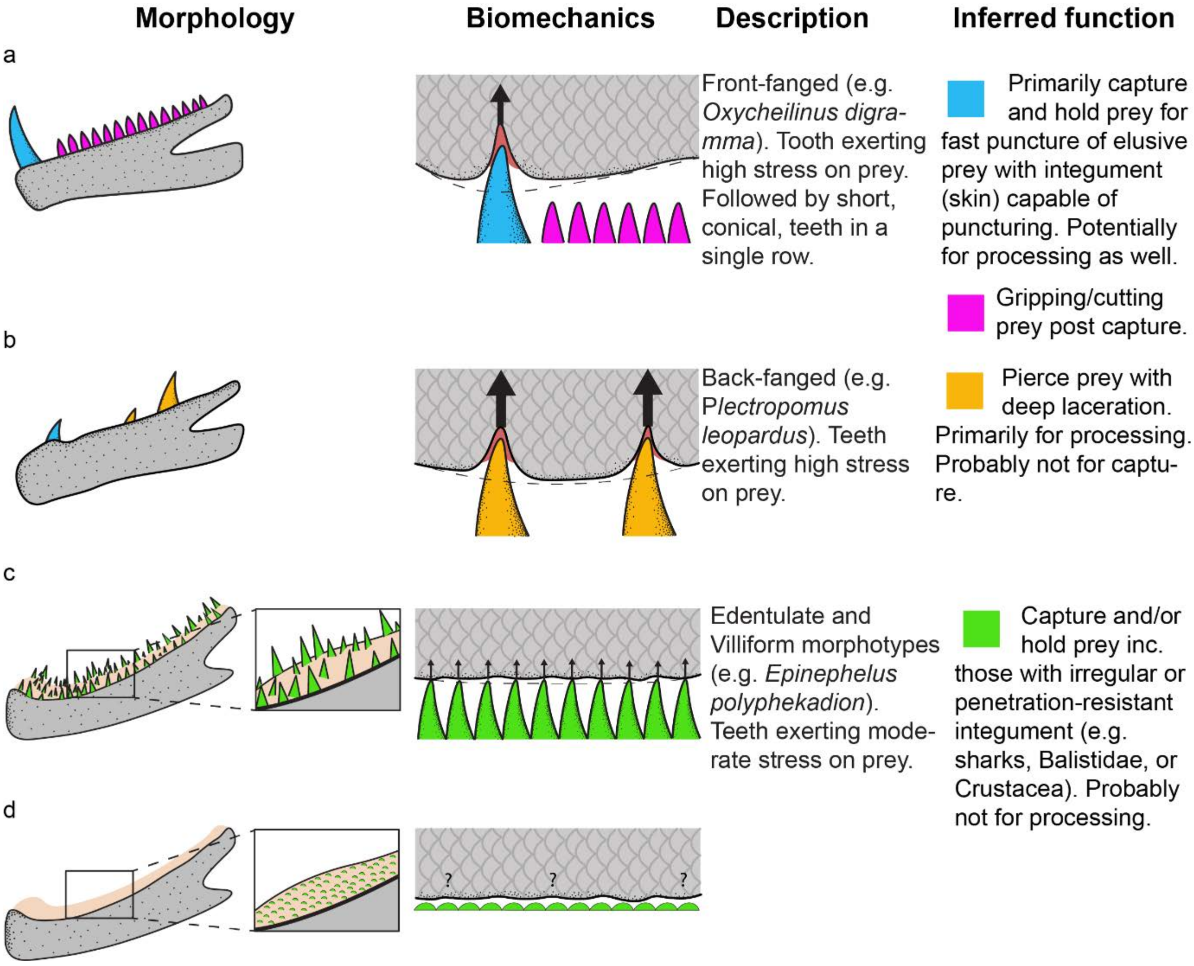
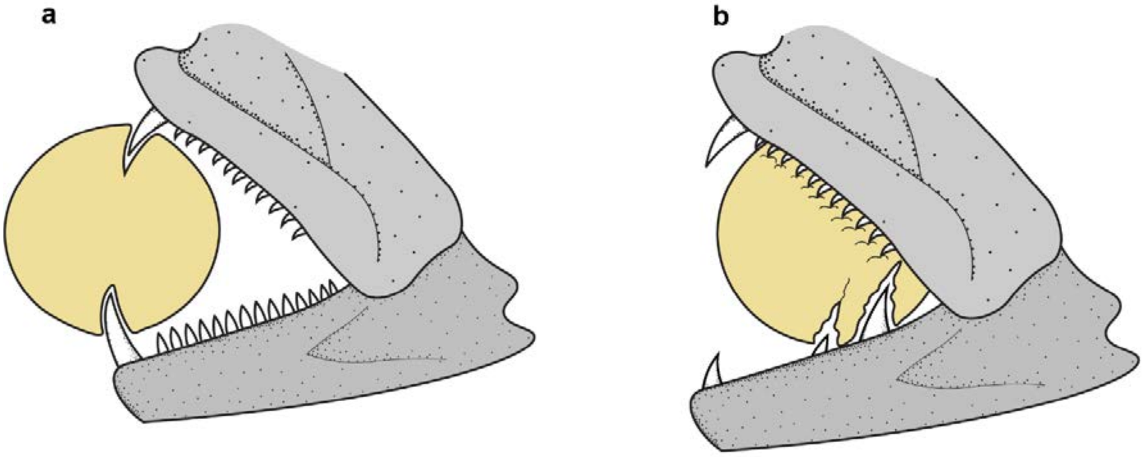


*Figure 3.5* Dentition morphotypes displaying individual tooth morphology, biomechanical properties, description and inferred function based on tooth size, position along the jaw, number of teeth, number of teeth rows and distance between teeth: (a) front-fanged macrodont, (b) back-fanged macrodont, (c) villiform and (d) edentulate.

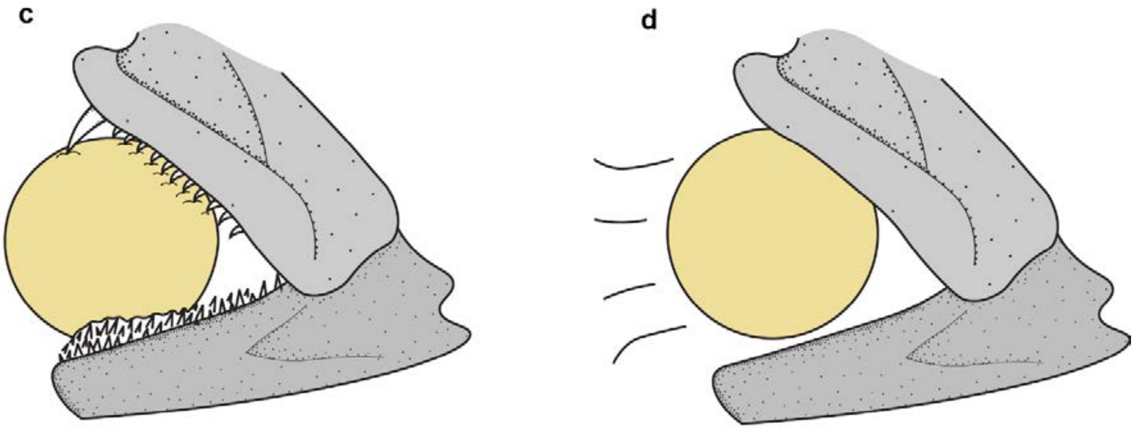
Functional decoupling has long been suggested to provide an evolutionary advantage, for example, in the fused pharyngeal jaws of cichlids (i.e. pharyngognathy) (Liem 1973; Hulsey et al. 2006; Wainwright et al. 2012; Burress et al. 2013). Pharyngeal jaws in piscivorous cichlids, have been identified multiple times as a means of processing/lacerating prey (Fryer & Iles 1972; Liem 1978; Hellig et al. 2010), suggesting that piscivorous cichlid species might not use their oral teeth for processing, only capturing. By contrast, the influence of pharyngeal jaws on prey processing in non-pharyngognath piscivores, has been suggested to be negligible (Fryer & Iles 1972). This could suggest that while pharyngognath piscivores may capture prey using their oral teeth, and process it using their pharyngeal jaws, non-pharyngognath piscivores may both capture and process prey with their oral jaws. In this regard, I note that back-fanged species do not seem to be represented in pharyngognath piscivorous cichlids (Cichlidae) (Greenwood 1981; Kullander et al. 2012), offering support for the suggestion that back-fanged oral teeth in non-pharyngognath species could have a similar function to that of the pharyngeal jaw teeth of pharyngognaths (i.e. lacerating/processing prey). Based on previous observations, and the results from this study, I suggest that some form of functional decoupling could be present within the oral jaws of fishes, and not just between oral vs. pharyngeal jaw systems.

If back fanged species represent a functional decoupling of the oral teeth, separating fast grabbing anterior teeth from slower but deeply penetrating posterior teeth, a longer lower jaw would maximize both the velocity advantage of the anterior tooth, and the force advantage of the posterior tooth (relative to the anterior tooth). Interestingly, lower jaw elongation has arisen on multiple occasions and has been widely associated with increased piscivory (Fryer & Iles 1972; Barnett et al. 2006; McGee et al. 2015). It has been suggested that the mechanistic function underlying jaw elongation is an increase in gape size, and creating a larger contact area between predator and prey for prey manipulation (Grubich, Rice & Westneat 2008; Ferry-Graham et al. 2010). Here, I suggest that the mechanistic function of jaw elongation, may be to facilitate a separation of front fangs, for capture, from back-fangs, with increased pressure/stress output, for prey manipulation and processing.



Capture of elusive prey for further processing prior to digestion.

Processing of prey post capture.



Aiding in the capture of prey/ processing

Suction of prey

*Figure 3.6* Full dentition morphotypes (both upper and lower jaws) displaying inferred functional capabilities based on biomechanical properties: (a) front-fanged macrodont, (b) back-fanged macrodont, (c) villiform and (d) edentulate. Note the absence of the back-fanged dentition in upper jaws.

Overall, I provide a quantitative framework for identifying dentition morphotypes in lower vertebrates, especially piscivorous fishes, and provide a putative functional interpretation of these distinct morphotypes. I identify three distinct dentition morphotypes (edentulate /villiform/macrodont) that appear to be encompassed by just two functional groups, broadly classified as ‘engulfers’ vs. ‘grabbers’. Also, within macrodonts I identify a continuum between front-fanged and back-fanged species, and explore the functional implications separating teeth involved in procurement (grabbing) vs. processing (laceration). I highlight the potential for functional decoupling in fish teeth, based not on the shape of the tooth, but their relative position along the jaw.

## Chapter 4. Functional groups in piscivorous fishes

Published as: Mihalitsis, M., & Bellwood, D. R. (2021). Functional groups in piscivorous fishes. *Ecology and evolution*, *11*(18), 12765-12778.

### 4.1 Introduction

Predation is a fundamental process in all ecosystems. It is a key process through which energy and nutrients are transported between organisms. Humans have been aware of terrestrial-based predation since the Pleistocene, when early hominin species, were still part of the food chain (Brantingham 1998; Berger 2006; Treves & Palmqvist 2007). Yet, aquatic predation, has been present for considerably longer and is likely to strongly shape the life history of aquatic animals. While humans have been aware of aquatic fauna for millennia (Elkin 1952), it is only in the last few decades that technology has allowed humanity to unravel its mechanistic basis and to quantify its impact on ecosystems.

Today, almost every aquatic ecosystem has been examined with regards to predation. For example, multiple studies have demonstrated the ability of predators in upper trophic levels (i.e., fishes) to influence food webs through top-down control (Carpenter et al. 2001; Jeppesen et al. 2003; Hansson et al. 2007). Nevertheless, while this concept has been found to operate in relatively simple ecosystems, such as lakes, recent work in more diverse aquatic ecosystems have not found similar patterns (Rizzari et al. 2015; Grubbs et al. 2016; Roff et al. 2016; Casey et al. 2017; Desbiens et al. 2021; Malakhoff & Miller 2021). Part of this may be the complexity (i.e., functional diversity) of the predators. Therefore, there may be a need to first establish how piscivores influence their prey (i.e., the exact niche axis on which their function is expressed), before attempting to scale up potential effects at an ecosystem level.

Previous work has shown that different 'types' of predators (Hobson 1979; Juanes et al. 2002), can have different influences on communities (Hixon & Carr 1997). This becomes particularly relevant given the taxonomically heterogenous nature of predator assemblages within different habitats and ecosystems (Winemiller 1989; Burress et al. 2013), not only due to biogeography (Hemingson & Bellwood 2018), but also due to direct anthropogenetic impacts (e.g., overfishing, invasive species) (Graham et al. 2005; Albins & Hixon 2008; Green & Côté 2014; Valdivia, Cox & Bruno 2017). Yet, we know little of the ecological impacts of these heterogenous predator assemblages. Do they deliver different types of predation on the communities they live in? In essence, there is a need to understand the different types of predators in aquatic ecosystems, the effect of each predator type on its prey, and ultimately, on its community and ecosystem in general (i.e. functional groups sensu Bellwood et al. (2019)).

To date, multiple studies have described different 'types' of piscivorous fishes (i.e. fish feeding on fish). Hobson (1979) described four major behaviours of piscivores with regards to prey capturing, namely: 1) running down prey, 2) ambushing, 3) habituating prey to an illusion that they are non-aggressive, and 4) stalking. Hixon and Carr (1997) further classified piscivores as 'resident' or 'transient', based on whether the predator inhabits the same habitat as its prey or regularly swims between habitats. Indeed, there is a wide range of terms from ambush and sit-and-wait, to pursuit. By searching the literature, I found a total of 13 different terms in common use, mostly based on behaviour with the same species often having multiple classifications (Appendix C Table 1). In Chapter 2, I identified three major ecomorphotypes of piscivores: diurnal benthic, nocturnal, and pelagic, while in Chapter 3, I identified three distinct morphotypes, based on their dentition and feeding traits: edentulate, villiform, and macrodont morphotypes. Essentially, there appear to be major differences between piscivorous fishes, suggesting high within-group variation in feeding capabilities and behaviours. However, this raises the question: Do these different predator types also reflect differences in their feeding performance, behaviour, and, ultimately, their impact on associated ecosystems?

The goal of this study, therefore, is to quantify aquatic predation by piscivorous fishes through performance-based feeding experiments. Using these data I explore their potential impact on prey populations/communities, placing their functional abilities in an ecological context, through a meta-analysis of relative prey sizes found in piscivorous fishes from multiple aquatic habitats.

## 4.2 Materials & Methods

I conducted performance-based feeding experiments to assess the implications of morphological variation on the performance of piscivorous fishes when capturing and ingesting prey. Feeding events were filmed and the videos analysed to extract quantitative measurements of the approach, strike capture, and subsequent handling of prey. I used piscivorous coral reef fishes as a study group.

### *4.2.1 Performance experiments*

Performance experiments were carried out in a climate-controlled room (27 °C), between 2018-2021 at James Cook University (JCU). Housing and experimental protocols were in accordance with the JCU Animal Ethics Committee (A2523). Holding and experimental tanks were connected in a flow-through filtration system, with halogen lighting above tanks between 9am and 6pm. When not in experimental trials, prey fish were fed commercially available flake and pellet food, while predators were fed commercially-available pieces of prawn. I used predators of all three benthic-associated morphotypes: edentulate, villiform, macrodont (sensu Chapter 3), from a range of different families. I used a minimum of three different predator species within each morphotype, 1-4 individuals of each predator species (depending on availability), and for each individual I recorded a minimum of 3 feeding events (range 3-10). Predator body sizes ranged from 51mm Standard Length (SL), to 290mm SL. In total, I examined 32 fish from 19 species, encompassing the majority of piscivorous coral reef fish families (Chapter 2). Experiments were carried out in 20L aquaria for small-sized or 'sit-and-wait' predators, and 120L aquaria for large-bodied or more 'active' predators. Only one predator was held in an aquarium at a time, and was acclimatised for at least one week prior to experiment initiation.

Predators were starved for 24-hours prior to experimental feeding. Prior to experimentation, an opaque tank separator divided the tank into two arenas, to ensure predator and prey could not see each other. A single prey fish (*Acanthochromis polyacanthus*) was then measured for its SL and Body Depth (BD) in a zip-lock bag (to avoid skin contact and to prevent potential effects of handling on predator behaviour due to olfactory cues). The prey fish was then introduced to the empty side of the aquarium and was allowed a minute to orient itself (fish rapidly stabilised after introduction) before the tank separator was removed. The subsequent feeding event was filmed using a Go-Pro (Hero 4) camera in real time, and a Sony RX100 IV to capture the predators' strike in slow motion. Prey fish were removed after one minute if the predator failed to strike. If the predator made a non-lethal strike, the prey was immediately removed from the tank, and euthanised using a clove oil anaesthetic and ice-water slurry. A successful capture by the predator was designated as the predator capturing and holding prey in its mouth for ≥ 3 sec. After a successful feeding event, the predator had to fully digest the prey before another feeding trial could commence. This usually took two to four days, and was assessed by visually inspecting for swelling in the stomach area of the predator, and the behaviour of the predator upon a researcher approaching the tank. A similar range of relative prey sizes was used across all predator morphotypes (based on prey body depth to predator gape). The majority (93%) of prey had a body depth over 45% of the predators gape, following (Mihalitsis & Bellwood 2017), to ensure predators performed close to their maximal abilities (Wainwright & Reilly 1994).

Upon completion of feeding trials, the predator was euthanised using a clove-oil anaesthetic and an ice-water slurry and the following morphological traits were measured: SL, Total Length (TL), and horizontal oral gape (sensu Mihalitsis & Bellwood 2017). I also photographed the predator with its mouth closed, and fully protruded, to quantify (using ImageJ) the predators' ability to protrude its upper jaw. I note that the predator *Epibulus insidiator*, at maximal jaw protrusion, is unable to close its jaws and thus use its teeth; it was therefore classified as functionally edentulate. Photos were also used to measure the eye size, which was later used as a scale in perpendicular strike videos (see below). Finally, the lateral head integument was removed, to reveal the structure of the predators' adductor muscles (responsible for jaw closing). I recorded the extent of fusion between subdivisions of the Adductor Mandibulae (AM) (A1, A2 and A3), and their respective insertion sites. The AM complex was then removed and weighed to the nearest 0.001g.

### *4.2.2 Image Analyses*

I extracted two datasets from the feeding videos. In the first, I recorded the capturing and processing behaviour of piscivorous fishes. Traits quantified were: body part struck, engulf vs. grab, whether the predator used head shaking behaviour post-capture, number of times the predator spat out and re-ingested prey, and the direction of the preys' body upon ingestion. Engulfing was defined as the majority of the prey body being within the predators' oral cavity upon a strike; grabbing was defined as the predator holding the prey between its oral jaw teeth on capture. In total, I recorded 90 successful feeding events.

In the second dataset, I analysed only videos for which the predators' strike was perpendicular to the camera, thus allowing the quantification of strike angle, strike distance, and the distance travelled by the predator post-capture. Distance travelled post-strike by the predator, was only quantified if the strike did not appear to be influenced by potential interactions with the aquarium. Three snapshots were taken from each video recording: 1) just before strike initiation, 2) the moment at which prey was captured (for successful events) or predator strike was at maximal gape (for unsuccessful events), and 3) the furthest point reached following capture (see Appendix C Figure 1). I then used the software Adobe Illustrator to join the snapshots together. I tilted and aligned the images, so that distances could be measured as straight horizontal lines (see Appendix C

Figure 1) using the software ImageJ. Images were scaled by the predator eye size. In total, I recorded 68 such feeding events.

### *4.2.3 Feeding performance, and prey size in aquatic ecosystems: a meta-analysis*

I conducted a meta-analysis of 2,209 published prey-predator size ratios (PPSR) in natural marine and freshwater ecosystems from published literature. I used the search engine Google Scholar, and searched for terms relating to aquatic predation, and predator and prey size (for published studies used please see raw dataset provided). This analysis specifically examined prey body depth vs. predator gape size; the key functionally relevant measurements for piscine predators (Mihalitsis & Bellwood 2017). Data were only included if represented in terms of predator gape size vs. prey body depth, and in predators that were benthic rather than pelagic (sensu Chapter 2). This ensured that species in the meta-analysis had similar habitat association to those examined in my experiments. I extracted the data using the software WebPlotDigitiser (Rohatgi 2017) and classified the predators in the meta-analysis based on the functional groups identified herein. If Total Length (TL) was not provided in the study, the recorded body size measurement, was converted to TL using published morphometric relationships (Froese & Pauly 2014).

### *4.2.4 Statistical Analyses*

All models and analyses were undertaken in the software R (R Core Team 2017), using the packages *effects* (Fox 2003; Fox & Weisberg 2019), *emmeans* (Lenth 2019), *car* (Fox & Weisberg 2019), *ggplot* (Wickham 2016), *nlme* (Pinheiro et al. 2014), *MuMIn* (Barton & Barton 2019), *glmmTMB* (Brooks et al. 2017), and *stats* (R Core Team 2017). Initially I assessed whether there was a significant allometric effect on the morphological variables by plotting their body size (SL or weight) standardised values across body size (SL or weight respectively). I found no evidence of significant allometry, and therefore used standardised values. Morphological variables were also assessed in a phylogenetic context to evaluate the strength of phylogenetic influences. Phylogenetic tree construction was undertaken following Michonneau, Brown and Winter (2016), and Phylogenetic Generalised Least Squares (PGLS) analyses follow Revell (2012) and Orme et al. (2012). To account for the effect of body size on morphological traits, Adductor mandibulae (AM) mass was standardised through a PGLS regression of body mass vs. AM mass, whereas remaining morphological traits were standardised through PGLS regressions with SL. The residuals of these relationships were then tested for differences between morphotypes. Lambda was estimated based on Maximum Likelihood, and evolution was assumed to follow a Brownian motion pattern (for phylogenetic tree used, see Appendix C Figure 2). These results can be found in Appendix C Figure 3.

Strike angles (response variable) were also modelled using GLMMs following a gaussian distribution and an identity link function, with individual id, nested within species, being the random effect. Strike angles (response) were modelled against morphotype (explanatory) and having species as a random effect.

For strike distance I tested for a potential allometric effect with a linear model between body size (SL) and relative strike distance (strike distance/SL), and found no allometric effect (GLM; p-value = 0.52). Strike distance was standardised to the predators' body size (SL) to account for differences in predator body sizes. Analysis of strike distance was modelled using a GLMM, with a Gamma distribution, a log link function, and species being a random effect. Capture behaviour among morphotypes was analysed using a GLMM with a binomial distribution, a logit link function, and species being a random effect.

For all models, I used the Akaike Information Criterion (AIC) to determine the best model fit, following (Zuur et al. 2013). Model validation (residual plots, Cooks' distance etc.) followed (Zuur et al. 2013); only suitable models were considered.

For the meta-analysis I modelled PPSRs (dependent variable) between the two functional groups identified herein, and predator body size (independent variables), in a Bayesian framework.

The model used a gamma distribution, a log link function, and default priors. Model estimation was performed using Markov Chain Monte Carlo (MCMC) sampling. Three chains, with 5000 iterations, a warmup of 2000, and a thinning factor of 5 was used. The model was run using the *rstanarm* (Goodrich et al. 2018) and *brms* (Bürkner 2017) packages in R. Model residuals were simulated using the posterior predictive distribution and plotted using the *DHARMa* R package (Hartig 2019), and model fit and assumptions were assessed using trace, autocorrelation, rhat, and effective sample size plots.

## 4.3 Results

### *4.3.1 Morphology*

We found significant differences in the feeding morphology of the three fish morphotypes (edentulate, villiform, macrodont). Specifically, I found significant differences between the adductor mandibulae (AM) mass of macrodont and edentulate piscivores, with macrodonts having significantly larger AM (GLM; $p<0.01$, Figure 4.1d). AM shape also varied among groups. Macrodonts displayed separated AM subdivisions (except for *Oxycheilinus sp.*) attaching at two primary locations on the maxillo-mandibular ligament (Figure 4.1), whereas edentulate and villiform species displayed fused AM subdivisions (A1 and A2/A3), attaching along the entire length of the maxillo-mandibular ligament (Figure 4.1). I also found significant differences in the jaw protrusion of macrodont and edentulate piscivores, with edentulate morphotypes having a significantly higher jaw protrusion ability (GLM; $p<0.05$, Figure 4.1d). Essentially, from a morphological perspective, macrodonts had large, subdivided AM muscles, and low jaw protrusion ability, whereas edentulate morphotypes displayed small, fused AM muscles, and high jaw protrusion ability. Villiform morphotypes had an intermediate form between macrodont and edentulate morphotypes. These morphological differences strongly suggest that the three morphotypes will also exhibit distinct feeding performances. Experiments confirmed that this was the case.

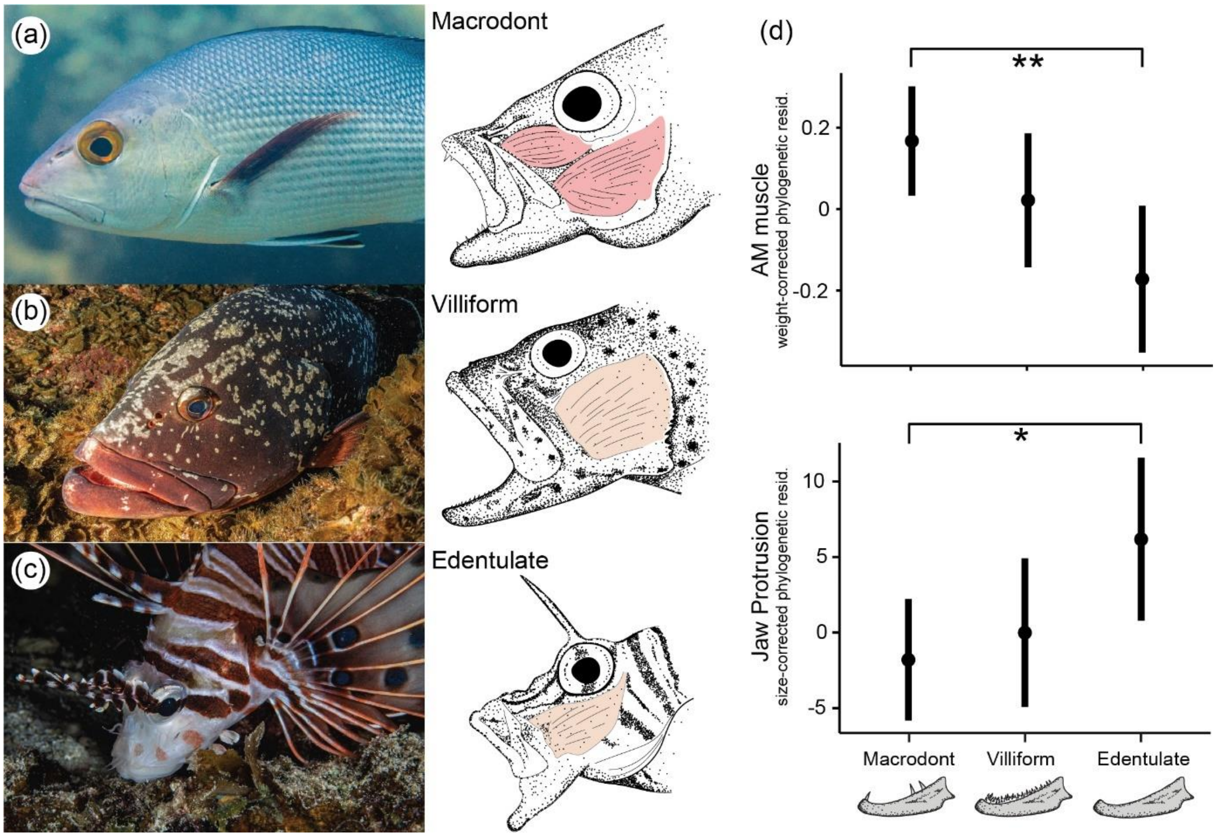
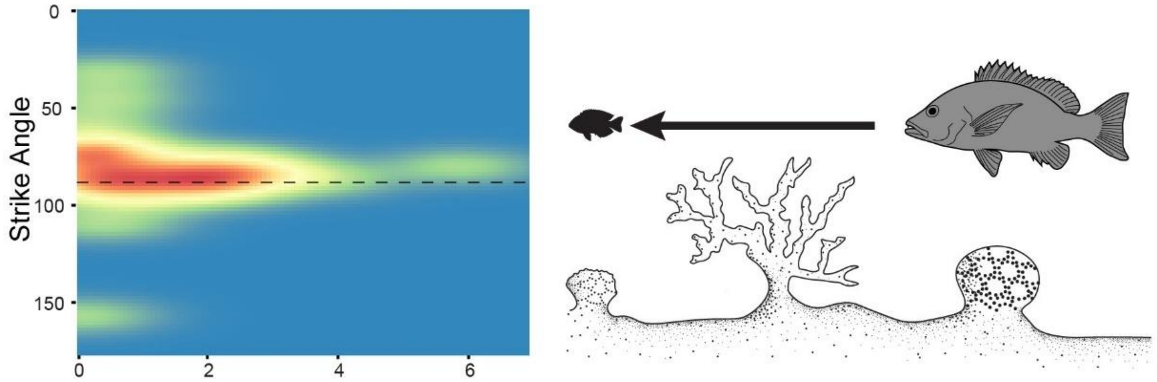


*Figure 4.1* The three morphotypes investigated in this study. (a) macrodont, (b) villiform, (c) edentulate, following Chapter 3. Illustrations show the myology of each morphotype, with macrodonts having distinct adductor mandibulae (AM) subdivisions, attaching to different parts of the maxilla-mandibular ligament. Villiform and edentulate engulfers displayed fused AM subdivisions, with muscle fibres attaching along the length of the maxillo-mandibular ligament. (d) macrodont morphotypes had a larger AM muscle mass than edentulate morphotypes (significance level indicated by asterisks). Edentulate morphotypes had higher jaw protrusion than macrodont morphotypes. Plots show mean predicted values for each group (± 95% Confidence Intervals). Photos by Salvatore Di Lauro and Victor Huertas.

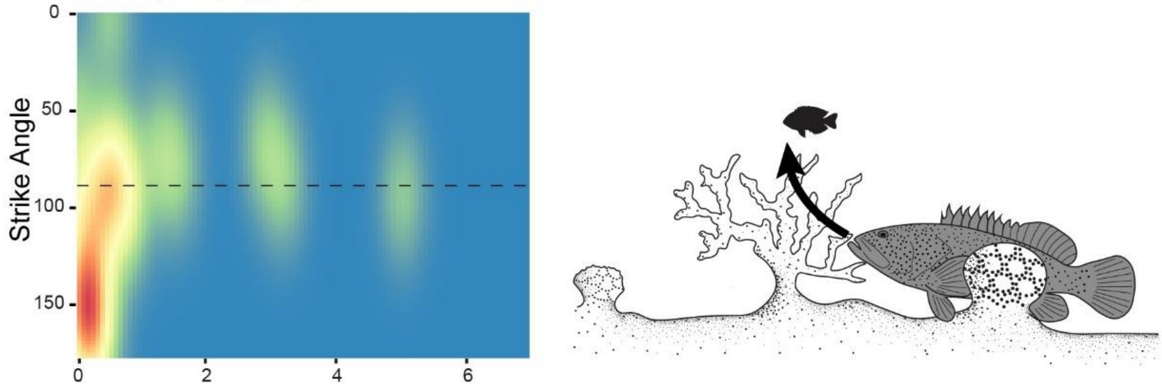
#### *4.3.2 Performance-based experiments*

Both strike angle and strike distance differed significantly among piscivorous fish morphotypes (Figure 4.2). Villiforms were found to strike from significantly different angles compared to edentulate morphotypes (GLMM; p<0.05, Appendix C Table 3), with villiforms striking from high angles below the prey, and edentulate morphotypes primarily striking from high angles above the prey (Figure 4.2). Basically, macrodonts strike from low (near horizontal) angles, whereas edentulate and villiform morphotypes strike from high angles. For strike distances, macrodont morphotype distances were significantly longer than either edentulate or villiform morphotypes (GLMM; p<0.01; Figure 4.2, Appendix C Table 3). Absolute standardised values of strike angle and strike distance showed a significant inverse relationship (GLM; p<0.01, Appendix C Figure 4). Overall, macrodont piscivores struck from low angles (approximately horizontal to the prey) from longer distances (>1 body length); villiform piscivores struck both from high angles under the prey with the strike directed upwards, from a relatively short distance (usually less than 1 body length), and from low (horizontal) angles from a longer distance; edentulate piscivores struck from high angles above the prey, with the strike directed downwards, and from a relatively short distance (<1 body length) (Fig. 4.2).

(a) Macrodont (n=28; spp.=8)



(b) Villiform (n=27; spp=6)



(c) Edentulate (n=29; spp=5)

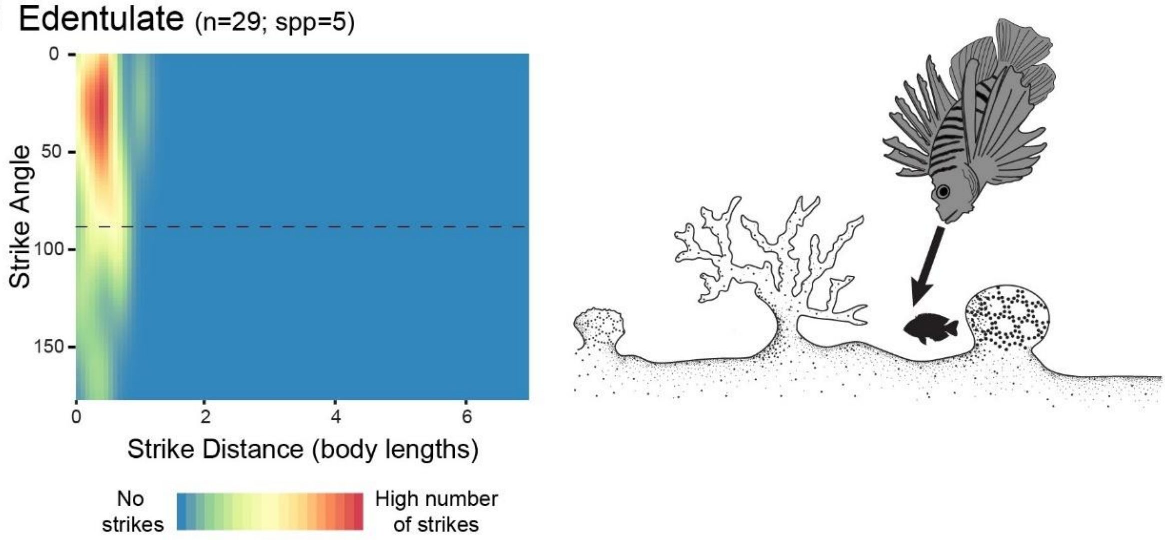


*Figure 4.2* Heat maps showing the strike angle and strike distance of piscivorous coral reef fishes: (a) macrodont, (b) villiform, and (c) edentulate morphotypes. Macrodont piscivores are characterised by near horizontal, long-distance strikes; villiform piscivores strike predominantly from below and close

to their prey; edentulate piscivores strike primarily from short distances, from high angles above their prey. Illustrations highlight likely strike patterns on the reef.

Capture modes also differ between morphotypes with macrodonts differing significantly from both villiform and edentulate morphotypes (GLMM, p<0.001, Figure 4.3). Macrodont piscivores primarily grabbed prey (83% of strikes; of these 84% were tail-first and 16% body-first) (Figure 4.3), whereas edentulate and villiform piscivores used engulfing as the primary capture mode (97% and 80% of strikes respectively) (Figure 4.3). For villiform morphotype grabbing strikes (34% of all villiform strikes), 43% were head-first whereas 57% were tail-first. In essence, macrodont piscivores primarily feed by grabbing their prey tail-first; edentulate and villiform piscivores primarily feed by engulfing their prey.

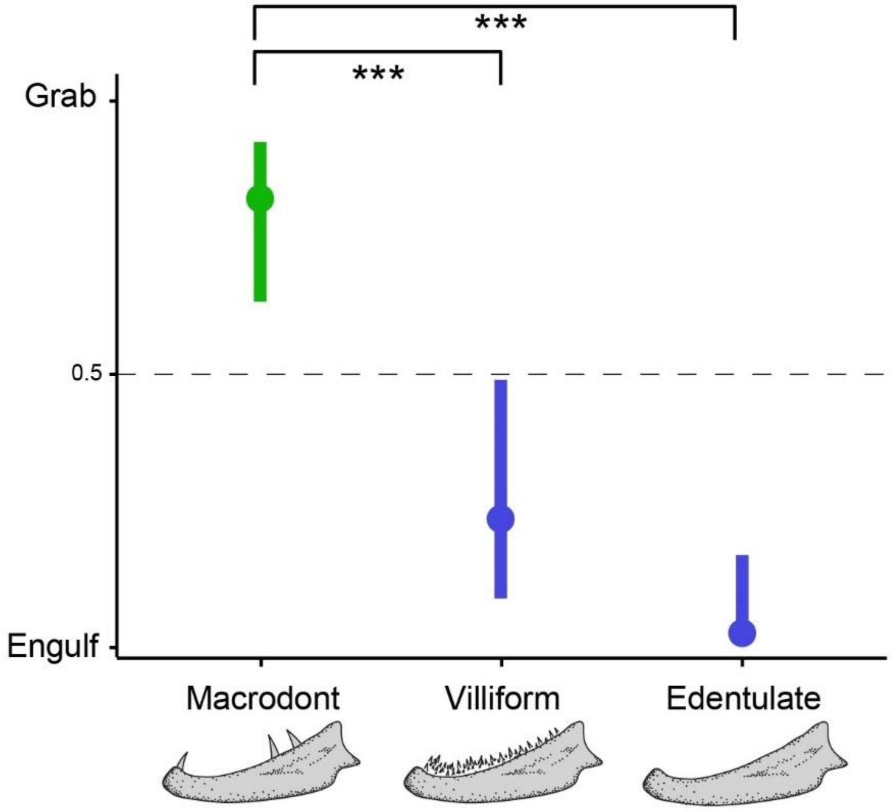


*Figure 4.3* Capture behaviour of piscivorous fishes. Macrodont piscivores predominantly capture their prey by grabbing (green colour); villiform and edentulate piscivores capture their prey by

engulfing (blue colour). Plot shows mean predicted values for each group (± 95% Confidence Intervals). The horizontal dashed line represents the threshold between grabbing and engulfing. Significance level indicated by asterisks.

Of all grabbing strikes, only macrodont fishes followed with head shaking behaviour, or hitting their prey against the base of the aquarium, resulting in prey laceration. After this behaviour, they usually spat the prey out and re-grabbed it head-first before swallowing it. This behaviour was also observed on the reef, in the macrodont *Oxycheilinus digramma* (Appendix C Figure 5). Essentially, villiform dentitions were only observed to be used for capturing, whereas macrodont dentitions were used for both capture and post-capture processing.

Based on the morphological and behavioural results described above, two functional groups of piscivorous fishes can be identified: grabbers and engulfers. Grabbers encompass macrodont morphotypes, while engulfers encompass edentulate and villiform morphotypes.

### *4.3.3 Realised niche axis and ecosystem-level implications: a meta-analysis*

We found clear evidence of resource partitioning in piscivorous fishes, along a relative prey size axis (Figure 4.4), with grabbing yielding larger relative prey (mean predator-prey size ratio: 0.42 with 0.40-0.43 95% CI), when compared to engulfing (mean predator-prey size ratio: 0.37 with 0.36-0.39 95% CI) (Figure 4.4) (see also Appendix C Table 3 for model results). However, there appear to be ontogenetic changes for grabbers, with relative prey size decreasing as predator body size increases; for engulfers this relationship does not appear to change with ontogeny (Figure 4.4, Appendix C Table 3).

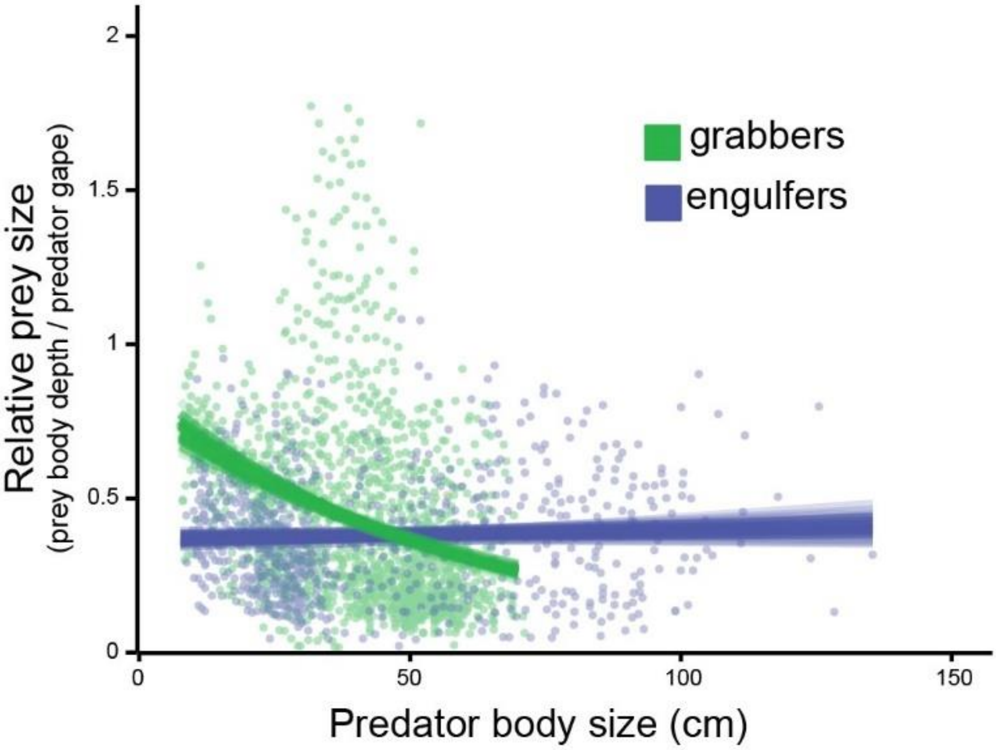


*Figure 4.4* A meta-analysis of trophic interactions in aquatic (marine and freshwater) ecosystems. Relative prey size (prey body depth/predator gape size) of piscivorous fishes vs. predator body size for both grabbers (green) and engulfers (blue). Blue and green lines show randomly selected model fits selected from the posterior distribution for each functional group.

### 4.4 Discussion

We found fundamental differences in the functional morphology, feeding behaviour, and feeding niches of piscivorous fishes. These differences characterise two distinct functional groups: grabbers and engulfers (Figure 4.5). I identify two distinct aspects of feeding: (1) based on how piscivores strike, capture, and process their prey, with clear evidence of resource partitioning, and (2) more extensive behavioural variation based on how predators behave prior to the strike. The functional groups identified herein, complement previous terminologies, and highlight the mechanistic basis of variation in the feeding behaviour of piscivorous fishes.

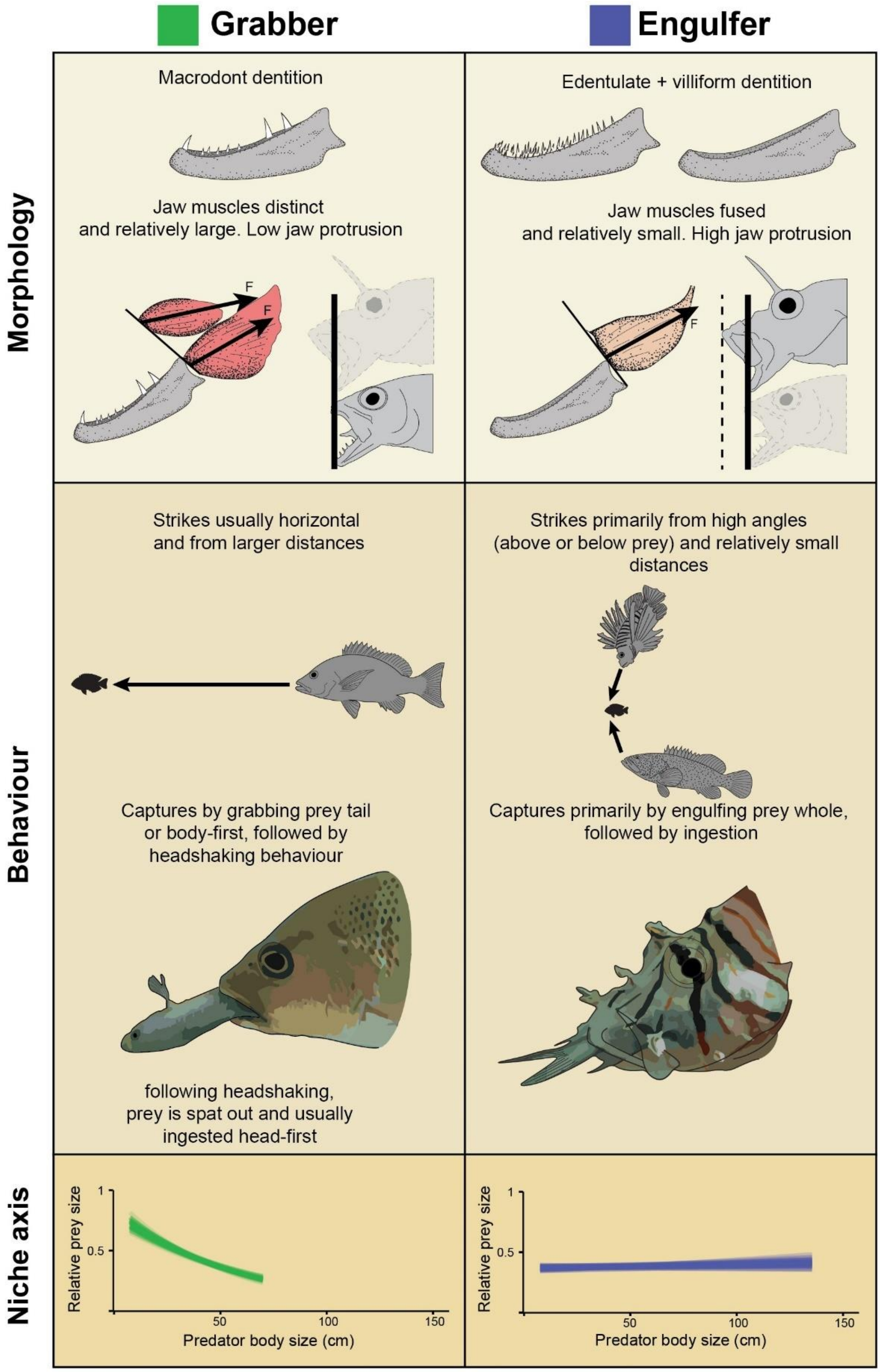

🟩 Grabber
🟦 Engulfer
Morphology
Macrodont dentition
Jaw muscles distinct and relatively large. Low jaw protrusion
F
F
Edentulate + villiform dentition
Jaw muscles fused and relatively small. High jaw protrusion
F
Behaviour
Strikes usually horizontal and from larger distances
Captures by grabbing prey tail or body-first, followed by headshaking behaviour
following headshaking, prey is spat out and usually ingested head-first
Strikes primarily from high angles (above or below prey) and relatively small distances
Captures primarily by engulfing prey whole, followed by ingestion
Niche axis
Relative prey size
1
0.5
50
100
150
Predator body size (cm)
Relative prey size
1
0.5
50
100
150
Predator body size (cm)

*Figure 4.5* Summary of the morphology, behaviour, and realised niche axis of grabbers and engulfers.

### *4.4.1 Functional groups: grabbers*

There is a clear axis of variation in piscivores. On one extreme, grabbers (primarily macrodont morphotypes) are characterised by longer strike distances from a horizontal position (Figure 4.2), with captures being primarily tail-first. Previous work has found piscivores to be striking at the centre of mass of prey fishes (Webb & Skadsen 1980; Webb 1986). The difference in capture location may be linked with the body shape of the prey. Moody et al. (1983) found the freshwater piscivore *Esox*, to be grabbing shallow-bodied prey primarily mid-body or tail-first (49% and 37% respectively), whereas deep-bodied prey was captured primarily tail-first (63%). Such results have been attributed to deep-bodied bluegills (*Lepomis macrochirus*) being more difficult to capture, as opposed to shallow-bodied fathead minnows (*Pimephales promelas*) (Gillen et al. 1981; Wahl & Stein 1988). These differences in capture location on the prey's body (and ultimately the strike outcome), may also be reflected in the wild, where prey availability consists of both deep-bodied and shallow bodied prey fish.

Furthermore, the location of capture along the preys' body, may be related to the predators' jaw morphology. Jaw elongation in aquatic predators, creates a velocity advantage at the tip of the jaw. Such increased velocity, may, however, decrease the accuracy of the strike, thus resulting in the predator striking at the body part suggested to move least in fast escape response (Weihs 1973; Webb & Skadsen 1980). Indeed, most studies which mention prey being captured at the centre of mass appear to be predominantly conducted with piscivores that have elongated jaw morphologies (e.g. *Lepisosteus*) (Webb & Skadsen 1980; Porter & Motta 2004), and feed by positioning themselves next to the prey, and conducting a high-speed lateral head movement (Porter & Motta 2004). This was also found in one of the most extreme cases of jaw elongation and feeding through lateral head movement in sailfish and marlins (Domenici et al. 2014; Hansen et al. 2020)(Supplemental video of their study showing sailfish capturing prey at centre of mass). Interestingly, jaw length has been found throughout multiple major taxa to be a primary axis of morphological variation (Martinez et al. 2018; Price et al. 2019; Arbour et al. 2020; Martinez et al. 2021). Such patterns of jaw elongation and dentition have also been found in other vertebrate taxa, such as crocodylomorphs (Stubbs et al. 2013).

Tail-first captures could also be a product of the prey noticing the predator, and initiating an escape response before capture, given that grabbers were found striking from relatively longer distances. It is reported that schooling fishes have a 'slower' response to predator strikes when compared to solitary fishes (Domenici & Batty 1997). Given that grabbers may strike from longer distances, and that schooling fishes (on reefs) are found further away from the benthos (Hobson 1965) suggests that grabbers may be more successful at feeding on schooling fishes in the water column.

Essentially, grabbers, because of their capacity to strike from a longer distance, may have an advantage when targeting schooling fishes as they may have a performance-based competitive advantage over engulfers that strike from close distances. This scenario is consistent with field evidence. On the reef, the grabber *Plectropomus leopardus* has been found to be feeding predominantly on pomacentrids and other social fishes in the water column (St. John et al. 2001; Matley et al. 2018). Benthic taxa such as gobies and blennies, which are also highly abundant on coral reefs were almost absent from their diet. These observations, along with the difficulties associated with a body ram-strike towards the benthos, strongly suggest that macrodont grabbers are better suited for feeding on prey swimming in the water column.

### *4.4.2 Functional groups: engulfers*

At the other extreme, engulfers (edentulate and villiform morphotypes) were found to strike from short distances, at high angles from above or below, and primarily engulf their prey. This relationship between strike distance and angle, appears to be strongly linked (Appendix C Figure 4). This suggests that a grabbing strike may require more space relative to an engulfing strike. Indeed, grabbing strikes are often observed in open pelagic waters, whereas engulfing strikes are primarily observed in benthic associated predators.

Morphological specialisations associated with this feeding mode, such as jaw protrusion, have been found to enhance the suction ability of fishes (Holzman et al. 2008; Staab et al. 2012b). The combination of high jaw protrusion and enhanced suction abilities appears to have evolved for feeding on elusive prey, especially those associated with the benthos (Higham et al. 2006; Bellwood et al. 2015). The inertia associated with long-distance high-velocity strikes (Wainwright et al. 2001; Tran et al. 2010), may result in the predator injuring its jaws and/or teeth against the substratum if a body-ram strike is used on a benthic prey fish (e.g. gobies). Furthermore, prey that are strongly associated with the benthos may constrain the potential success of grabbing predators because of the need to identify the precise location for a grabbing bite. When using jaw protrusion and suction, there are fixed biomechanical limitations on jaw excursion i.e., in the extent to which the jaw can extend. Furthermore, the predators' body, will act as an anchor in stopping the predator from moving post-capture, following jaw protrusion. Thus, strike distance can be carefully controlled. This feeding behaviour closely matches field observations, i.e. strikes from close-range using jaw protrusion to engulf prey (see the engulfer *Pterois volitans,* Appendix C Figure 5)(see also Collins & Motta 2017; Green et al. 2019). Essentially, these traits (jaw protrusion and enhanced suction) may provide engulfers with distinct advantages in reef environments, as they appear to be exceptionally well suited for accessing prey that are closely associated with the substratum.

### *4.4.3 Linking functional groups to previous terminology*

Classifications of piscivorous fish groups are widespread in the literature, and incorporate terms such as ambush vs. pursuit, transient vs. resident, ram vs. suction etc. When reviewing the literature, I found 11 different terms describing different types of feeding behaviours in predatory fishes (Figure 4.6). Furthermore, I found the term ‘ambush’ to be used for multiple types of piscivorous fishes with different feeding morphologies. For example, *Pterois volitans, Epinephelus maculatus*, and *Plectropomus leopardus* are all termed ambush predators. However, these species display highly differentiated functional feeding traits, having fundamentally different dentitions (respectively edentulate, villiform, and macrodont) (sensu Chapter 3). I also found the same species to be classified with different terms in different studies. For example, I found the grabber *Pseudochromis fuscus* to be classified as both an ambush and pursuit predator (see Appendix C Table 1). Such inconsistencies likely arise by classifying predators based on different aspects either related to morphology (i.e., biters, suction-feeders) or behaviour. Within behaviour, classifications have been further divided based on different aspects, such as striking behaviour (i.e., ambush, pursuit) or spatial behaviour (i.e., resident, transient).

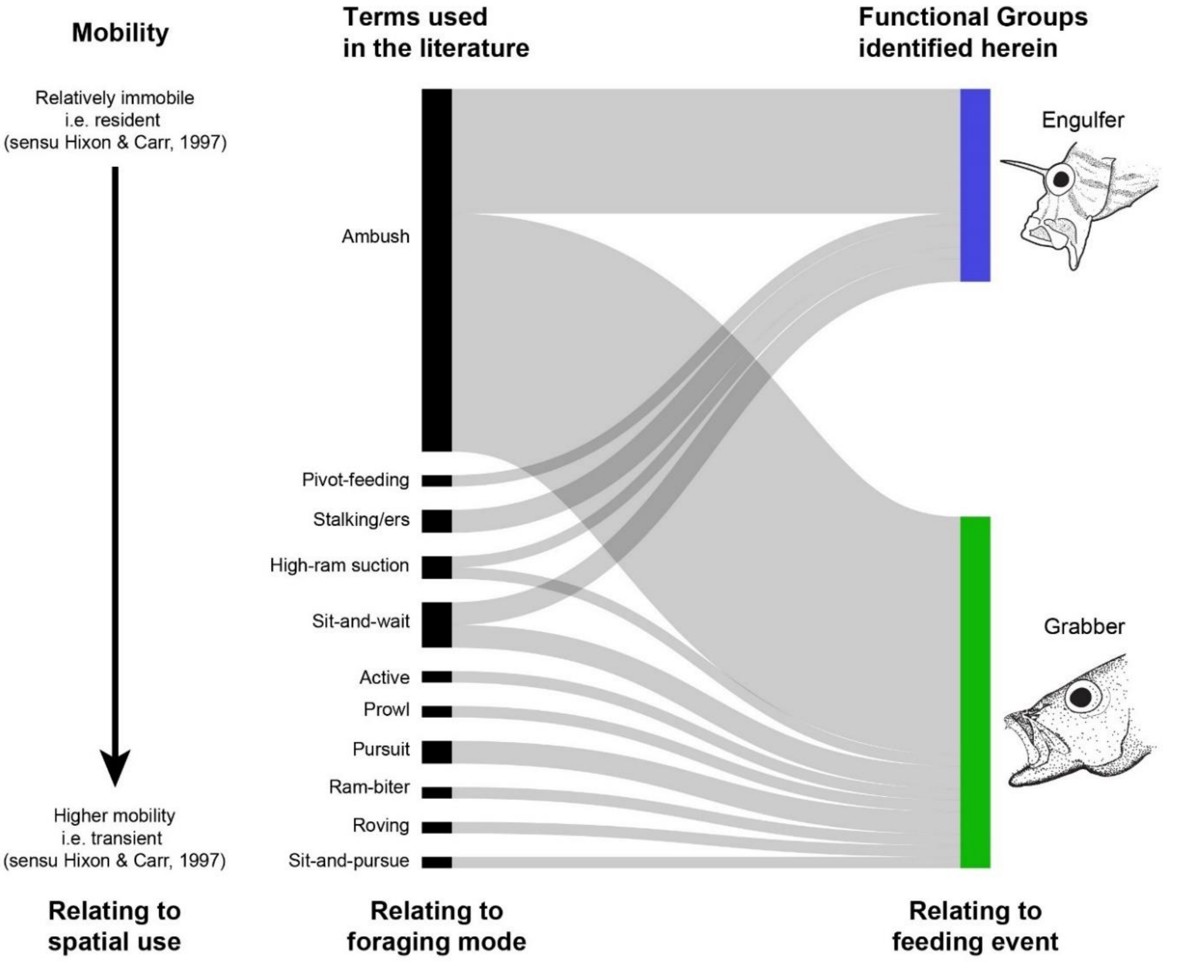


*Figure 4.6* Classification of predatory/piscivorous fishes. The figure relates classification terms used in the literature, to the functional groups identified herein. The 'Mobility' column highlights an axis of low-to-high activity, reflecting the resident vs. transient distinction of Hixon and Carr (1997). While previous terms used in the literature refer primarily to the predators' foraging mode (i.e., activity leading up to the feeding event), or an aspect of its hunting behaviour (e.g., pursuit), the functional groups identified herein relate directly to the feeding event (timeframe of few seconds), and link the functional feeding morphology of the predator to its striking, capturing, and processing behaviour.

The classifications identified in the current study are based on principles denoting functional morphology (or ecomorphology) (Wainwright & Reilly 1994; Wainwright & Bellwood 2002). Following principles of this field, morphological attributes (i.e., traits) are tested in an experimental, performance-based context (testing their maximal abilities), to inform how organisms are able to use these tools (i.e., morphology) to carry out different tasks (i.e., behaviour). Performance experiments help to distinguish between spurious correlations, and morphological attributes used by the organism in these tasks. As a result, such studies have been able to link functional morphology, to performance, to behaviour, and finally, to realised niches (Wainwright 1987; Wainwright 1988; Fulton et al. 2017; Huertas & Bellwood 2017).

In this context, the groups identified herein, relate to the final moment of the strike. However, there is a much broader array of classifications which relate to different aspects of the feeding strategies of these fishes and how this leads to the capture of prey (Figure 4.6). Such classifications may extend to aspects relating to the entire lifestyle of the predator (i.e., ambush), the approaching technique it utilises (i.e., stalking), or the strike initiation (i.e., pursuit). The functional groups identified herein relate to the few seconds/minutes between strike initiation and prey ingestion, and encompass morphology and behaviours related to striking, capturing, and processing.

### ***4.4.4 Ecological implications***

Most studies, when quantifying predator-prey size relationships, tend to quantify predator vs. prey relationships as a Standard Length vs. Standard Length relationship (Scharf et al. 2000; Gaeta et al. 2018). However, body depth is arguably the major axis of variation in fishes (Claverie & Wainwright 2014; Friedman et al. 2019), as well as being the limiting factor in gape limitation for piscivorous fishes (Wainwright & Richard 1995; Nilsson & Brönmark 2000; Mihalitsis & Bellwood 2017). While SL vs. SL relationships may be beneficial for studies focusing on population structure, they may mask the mechanistic basis of functional relationships between predators and prey. These results suggest that shifting this relationship to a predator gape size vs. prey body depth relationship, and incorporating their functional signature, may provide a mechanistic, causal, link between the functional morphology or behaviour, and functional role of piscivorous fishes in ecosystems (Figure 4.4)(e.g. Dörner & Wagner 2003). For example, results from the current study suggest that piscivory (i.e., prey removal) may be separated into the piscivores that predominantly remove relatively large prey vs. small prey (Figure 4.4), and that the 'who' removes large vs. small prey, changes with increasing body size.

Differences in the composition of piscivores, therefore, may influence the size structure of prey fish communities. Juveniles of a certain species (and therefore smaller body size) focus on growth, while larger individuals focus more on reproduction (Roff 1983; Barneche et al. 2018; Morais & Bellwood 2020). By feeding on 'growth-focused' individuals vs. 'reproduction-focused' individuals, piscivores may disproportionately influence the productivity potential of a fish community. By quantifying predator body size (that can then be transformed to gape size) and incorporating piscivore functional groups when surveying the piscivorous fish community on a coral reef, may provide critical insights to the potential predation pressure, and its size specificity.

### *4.4.5 Evolutionary implications*

Macrodont fishes appear to be the first recorded piscivorous morphotype in the evolution of bony fishes (Osteichthyes)(Figure 4.7). To my knowledge, the first evidence of macrodont dentition directly associated with piscivory, is in the Late Devonian sarcopterygian *Onychodus* (Long 1991; Andrews et al. 2005). Furthermore, Long (1991) described a fossil of an *Onychodus* having captured and ingested a placoderm (Placodermi). In keeping with my results, Long (1991) suggests that the predator captured the prey fish tail-first. This evidence, along with results herein, suggests that 'grabbing' as a means of capturing elusive prey, already existed in the Devonian (419.2-358.9 Mya). Grabbing (and by association body-ram striking) as a means of prey capture, may therefore have arisen before engulfing (and by association jaw-ram striking), which requires further morphological modifications (Figure 4.7).

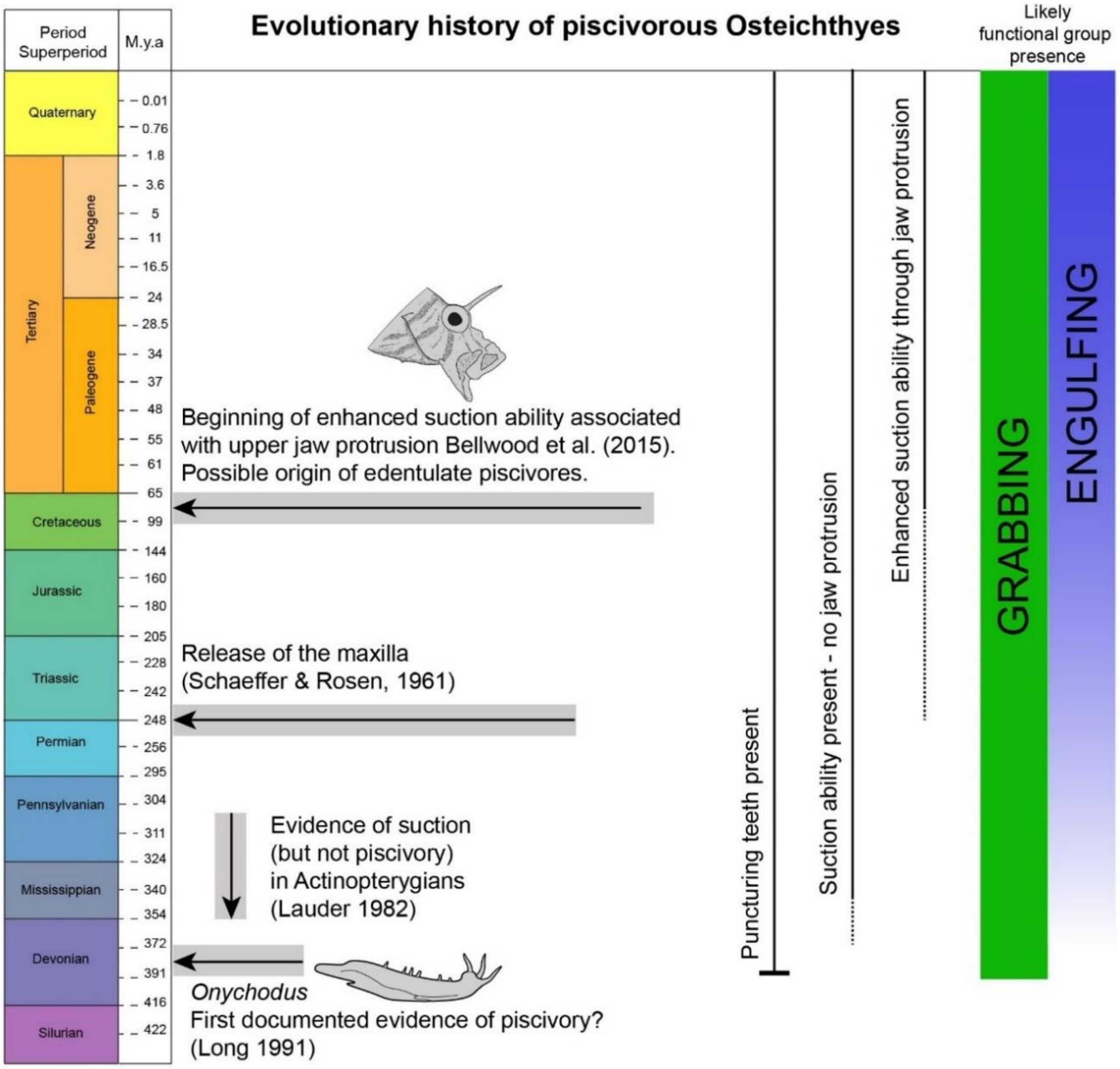


*Figure 4.7* Evolutionary history of piscivorous Osteichthyes. Evidence of grabbing within the Osteichthyes has been found dating back to the Devonian, with the sarcopterygian *Onychodus*. Early

actinopterygians have been shown to be able to use suction (Lauder 1982), yet, how much this contributes to prey capture relative to body and jaw ram (jaw protrusion) remains unknown, and there is currently no direct link to piscivory. Increased jaw protrusion (Bellwood et al. 2015), leading to enhanced suction abilities (Staab et al. 2012b), is only seen more recently in the Late Cretaceous and is a common feature of many extant piscivores.

Within Actinopterygians, however, it is still unclear which of the two feeding behaviours arose first. Lauder (1985) suggested that suction feeding was a basal trait in the Osteichthyes, and Lauder (1980) demonstrated the ability of the primitive actinopterygian *Amia calva*, to use suction as a means of feeding. Indeed, *A.calva* shows reduced, curved, and compact dentition, more aligned with villiform dentition, primarily used for holding as opposed to puncturing flesh during a grabbing strike (Chapter 3). Furthermore, it is not clear to what extent the origin of suction was associated with piscivory, and the contribution of suction relative to other mechanisms (e.g., jaw and body ram) in the early actinopterygian fishes has, to my knowledge, yet to be quantified. The distinction of whether fishes are able to use suction vs. how much suction contributes to prey capture, is an important distinction, as noted by Longo et al. (2016).

Engulfing involves, and probably requires, some degree of jaw protrusion and suction, and it therefore requires specific modifications of the cranial morphology. Jaw protrusion in actinopterygians was triggered by the release of the maxilla from the preopercular and infraorbital bones, at some point during the Late Permian (256-248 Mya) (Schaeffer & Rosen 1961). Subsequent expansion and specialisation of this trait, has been identified as a major modification facilitating the capture of elusive prey by fishes (Bellwood et al. 2015). Engulfing via jaw protrusion thus appears to be a relatively recent feeding mode, when compared to grabbing (Figure 4.7). Although the fish investigated herein are coral reef fishes, the functional groups identified in my study, are likely to apply to fishes from any aquatic environment (Camp et al. 2015; Arbour et al. 2020; Keppeler et al. 2020; Weller et al. 2020).

### *4.4.6 Future Implications*

Piscivorous fishes are primary targets in many coral reef fisheries (e.g. Dulvy et al. 2004a; Graham et al. 2005; Cinner et al. 2009; Madin et al. 2016; Valdivia, Cox & Bruno 2017). The implications of this removal on ecological functions remains unknown. Most coral reef fisheries catch-data are analysed from a taxonomic, trophic guild or trait-based approach (Russ & Alcala 1989; Cinner et al. 2009). Such studies have been useful in shifting the focus from a biodiversity-based perspective, to a more mechanistic or functional perspective (Bellwood et al. 2004). However, to date, functional evaluations of coral reefs have focused predominantly on herbivores (Bellwood et al. 2012; Robinson et al. 2020). My work suggests that future studies may also need to incorporate different functional groups of piscivorous fishes. Fisheries may be removing different functional groups of piscivorous fishes disproportionately, changing both the composition of piscivorous fishes and their functional role in reef ecosystems. The ecological implications of the removal of functional groups within piscivorous coral reef fishes are unknown, but given the overwhelming importance of piscivory in energetic and nutrient flows, their role may be an important one.

Furthermore, my observations suggest that fishes along the grabbers to engulfers axis may also differ in their dependency on structural complexity. It is well documented, that coral reefs in the Anthropocene are losing topographic complexity, and that they are turning into more flattened, less structurally complex environments (Hughes et al. 2017a; Zawada et al. 2019). Getting close to potential prey for a short distance strike may therefore become more challenging in the future. Piscivorous fishes may thus be subject to both direct and indirect human disturbance.

Overall, I show that piscivores are not a uniform group, but a spectrum of different functions and modes. Specifically, there are two different functional groups of benthic piscivorous fishes, based on their functional morphology, striking, capturing, and processing behaviour. I identify a major axis of variation in the feeding behaviour of piscivorous fishes, grabbing vs. engulfing. These results suggest that a separation of piscivorous fishes into functional groups may be valuable in future studies, as different groups are likely to have significant implications for both functional and community ecology.

# Chapter 5. The role of fishes as food: A functional perspective on predator-prey interactions

Published as: The role of fishes as food: A functional perspective on predator-prey interactions (2021), *Functional Ecology*, 35(5), 1109-1119.

## 5.1 Introduction

In nature, animal mortality often occurs due to predation by another animal (Sinclair et al. 2003; Chesson & Kuang 2008). Predator–prey interactions are therefore pivotal in maintaining the flow of energy and material within ecosystems. Studies have investigated the ecological implications of mortality in both terrestrial and aquatic ecosystems for decades, and have shown how important this process is for structuring both animal communities and the environment (Estes & Palmisano 1974; Pace et al. 1999; Ripple et al. 2001). This also applies to coral reefs, an iconic ecosystem with remarkable species diversity and habitat complexity. On reefs, key interactions and processes, essential for ecosystem functioning, are primarily mediated by fishes (Bellwood et al. 2019). Within coral reefs, the main driver of mortality in fish communities is piscivory, with up to 53% of fishes on a coral reef contributing to this ecosystem function (Randall 1967a; Hixon 1991). Mortality in coral reef fish, therefore, is directly tied to piscivory.

To date, piscivory on coral reefs has been studied largely from the perspective of the predator. For predators, studies have investigated the functional morphology (Ferguson et al. 2015; McGee et al. 2015; Muruga et al. 2022) and behaviour of piscivorous fishes (Hobson 1965; Hobson 1968; Sweatman 1984; Grubich, Rice & Westneat 2008; Holmes & McCormick 2010), along with their ability to influence reef fish population dynamics (Hixon 1991; Almany & Webster 2004; Albins & Hixon 2008; Stier et al. 2014). Understanding prey selectivity by piscivorous coral reef fishes has been pursued for decades in the literature. However, this has been undertaken primarily from a taxonomic perspective (e.g. what species has the predator fed on) (Randall 1967a; Kingsford 1992).

Furthermore, this relationship has primarily been assessed from the perspective of predator-based control of fish populations (Hixon & Webster 2002; Hixon 2015). If we are to understand the mechanisms regulating predator-prey interactions at a community level, we may also need to consider factors other than prey species identity and abundance. It may be important to not only look at the predators' ability to select and capture prey, but also, the ability of prey fish to influence their relative catchability by different predators. In other words, we should ask not only `what can the predator do to the prey?`, but also, `what can the prey do to influence the predator?`.

Previous studies focusing on fishes as prey, have investigated both their morphology (Hambright 1991; Price et al. 2015) and behaviour (Nilsson & Brönmark 2000; Scharf et al. 2003; Herbert-Read et al. 2017), linking such traits to anti-predator mechanisms. Indeed, there have been several reviews linking these components to predation (Domenici & Blake 1997; Blake 2004; Langerhans & Reznick 2010). Fish-based studies have linked morphological traits such as body size (Hambright 1991; Scharf et al. 2003; Goatley & Bellwood 2016), the body depth of fishes (Brönmark & Miner 1992; Domenici et al. 2008; Price, Friedman & Wainwright 2015; Mihalitsis & Bellwood 2017), and behaviours, such as schooling (Magurran 1990; Krause & Godin 1995; Ioannou et al. 2012), to predation risk. Schooling behaviour has also been investigated on coral reefs (Major 1978; Parrish 1993), along with boldness (McCormick et al. 2018), and predator recognition in the context of predation (Coates 1980; Rizzari et al. 2014; Catano et al. 2016; Lester et al. 2020b). This work has been crucial in identifying the morphologies and behaviours that may be shaping predator-prey interactions. However, there is still a need to assess such established morphological and behavioural traits in-situ, and in a community-wide context.

Quantifying functional traits at a community level is crucial if we are to understand ecological processes within complex ecosystems (McGill et al. 2006; Martini et al. 2020). Recent work conducted from a trait-based perspective, has shown great promise in being able to predict predator-prey interactions in situ (Green & Côté 2014; Green et al. 2019). By moving away from a taxonomic perspective, to a functional-trait based approach, allows us to elucidate the underlying mechanics of ecosystem processes, as well as to better predict the uncertain future of such ecosystems (Bellwood et al. 2019). When considering functional traits in predator-prey interactions, a significant amount of work has been undertaken in experimental aquaria, often focusing on a single, or few species (Webb & Skadsen 1980; Hoyle & Keast 1987; Domenici et al. 2008; Mihalitsis & Bellwood 2017; McCormick et al. 2019). This is understandable, as piscivory is highly uncertain, making it difficult to quantify in situ. Thus, while there is significant evidence of how prey fishes respond to predators, and how specific morphological and behavioural traits may influence the interaction between the predator and the prey, there is still a need to quantify these traits at a community-wide scale, and directly on the reef (i.e. in situ).

In the current study, therefore, I look at the nature of prey species and ask: which anti-predator traits are most prevalent in coral reef fish communities, and to what extent may fishes influence their catchability as prey? Specifically, I quantify morphological, behavioural and demographic traits among individuals in coral reef fish communities, identifying distinct functional groups of potential prey. I then explore patterns of mortality in these functional groups, based on a meta-analysis of published mortality rates of coral reef fishes. In essence, I provide a quantitative community-level evaluation of the ecosystem function of prey fishes: food provision for piscivores.

## 5.2 Materials & Methods

Reef fishes experience their highest mortality rates between settlement and approximately 43 mm total length (TL) (Goatley & Bellwood 2016). I therefore focus on this vulnerable period to investigate four traits that may work synergistically in influencing predation risk in coral reef fishes. These traits include a) distance from the benthos (as a proxy for distance from closest shelter), b) body size (Total Length: TL), c) absolute body depth (BD), and d) social behaviour (solitary/social). Distance from benthos is a proxy for distance from shelter (i.e. predation) (Motro et al. 2005; Lester et al. 2020b), increasing body size reduces mortality rates (Goatley & Bellwood 2016), increased absolute body depth imposes a constraint on gape limited predators (Mihalitsis & Bellwood 2017), while social behaviour (e.g. schooling) has anti-predator benefits (Krause & Godin 1995; Domenici & Batty 1997). Although not directly linked to predation, I also assessed the data in terms of fineness ratio as this trait is functionally relevant to the swimming abilities of fishes (Blake 1983; Blake 2004; Walker et al. 2013). I used BD as a proxy for body cross-sectional diameter to measure fineness ratio (TL/BD).

### ***5.2.1 Sampling***

The four traits were quantified using a quadrat-based method, modified after (Wismer et al. 2019) (see also Appendix D Figure 1), examining the entire fish community <100mm (TL). Sampling was conducted between 2018 and 2020, at two locations on the Great Barrier Reef, Australia: Lizard Island (n= 3 sites) and Orpheus Island (n= 2 sites) (James Cook University Animal Ethics A2529) (see Appendix D Figure 2 for maps). An array of locations from lagoon to crest were sampled.

Visual censusing methods often underestimate fish abundances, especially small-bodied fishes (Ackerman & Bellwood 2000), which in the context of fish as prey are the most important size class (Goatley & Bellwood 2016). I therefore developed a methodology which censuses both fishes swimming in the water column, as well as fishes living within the reef complexity, over a known area of reef. Fishes swimming in the water column, were visually censused using photographs following Wismer et al. (2019), photographing fish from >2m away with minimal disturbance. The small-bodied fishes in the water column, remained in the position first seen, and did not appear to be affected by the presence of divers from >2m away. Images were taken within seconds of arrival at each location. A second diver, swimming behind the first, subsequently placed a 1x1m quadrat on the photographed area, for scaling and reference points. A second photograph was then taken from the same position as the first photograph with the quadrat in the photograph. A total of 51 such quadrats were quantified, resulting in 374 observations of coral reef fish positions in the water column.

Fish sizes, relative body depth (RBD) and distance from benthos were quantified using the software ImageJ (Rasband 1997). Photographs were scaled based on the quadrat, and traits were quantified in the original image where fishes were in their undisturbed positions. Distance from the benthos was measured as the distance between the eye of the fish, and the closest reef structure (coral, rubble, etc.). Body length was measured as Standard Length (SL) and Total Length (TL), RBD was measured as the largest vertical measure on the fish (excluding fins) (BD), divided by SL. I only quantified traits on fishes that were perpendicular to the camera, with their position clearly delineated relative to the benthos, however, if one of the measurements (TL, BD) was not clearly visible, it was calculated from published morphometric relationships (Froese & Pauly 2014).

For a subset of the quadrats (23 out of 51), I also sampled the cryptobenthic fish community using enclosed clove oil stations (modified after Depczynski and Bellwood (2004)). At each site, 4-5 clove oil stations were deployed. This resulted in the collection of 238 fish specimens. After the second photograph was taken, a 1 $m^2$ fine-mesh (1mm) net was laid along the perimeter of the quadrat, was then closed at the top (see Appendix D Figure 1), and secured to the benthos using a chain (sewed into the net) which also sealed off any gaps. The two divers then used a mix of clove oil and ethanol (25% and 75% respectively), which was sprayed under the net using spray bottles. The entire area under the net was sprayed. After approximately 5mins, the divers removed the net from small areas of the quadrat, and began collecting fishes using a set of tweezers. Divers continued uncovering the netted area, until the entire area was examined, and no new fish were found after 3-5 mins. Rocks and rubble were carefully uncovered to ensure that all fauna was collected, and no live fishes were detected in the area. Specimens were transferred to the laboratory where body size (SL and TL) and BD were measured. Specimens collected from clove oil stations which are known, from the literature or previous photographic evidence, not to be substratum associated were removed from the analysis, as distance from the benthos/shelter was not quantifiable for those specimens. Traits from the observations and the lab-based measurements were then used to characterise three major functional groups, with regards to predation avoidance traits.

Finally, I conducted a meta-analysis of published experimental mortality rates of coral reef fishes (modified after Goatley & Bellwood 2016), to investigate whether the functional groups identified herein, may influence relative rates of predation and thus the ecosystem process of piscivory. Mortality rates within this dataset contain both naïve and experienced individuals (sensu Goatley & Bellwood 2016). For studies based on experimental assessments of mortality rates on recently settled/juvenile fishes, I used the mean body size of the cohort examined, or mean size at settlement for the analyses. For studies investigating mortality rates on adult fishes, the mean asymptotic size (*Linf*) was used. As studies have indicated a <1yr lifespan for cryptobenthic fishes, and thus multiple cohorts within a year (Lefèvre et al. 2016; Brandl et al. 2019), studies estimating mortality rates for such species as a yearly estimate, were excluded. If body size data were provided as Standard Length (SL) they were transformed to TL based on published species-specific relationships (Froese & Pauly 2014). Daily mortality rates were calculated by dividing overall mortality by the days over which the experiments were conducted.

### *5.2.2 Analyses*

I classified species as solitary or social based on observations in the field. For species not observed in the study (e.g. those in the mortality dataset) classifications of this behaviour were based on the literature (e.g. Randall 2005; Froese & Pauly 2014). Some species are social as juveniles, and more solitary as adults (e.g. *Thalassoma hardwicke* (Lecchini et al. 2007)), whereas other species are initially solitary and become social at later life stages (e.g. some siganids and chaetodontids) (Pratchett et al. 2006; Mirbach & Brandl 2016). If both juveniles and adults were recorded, they were classified separately. Pairing fishes were considered social as this behaviour has been associated with anti-predator benefits (Brandl & Bellwood 2015). Social species in this study therefore refers to the presence of two or more individuals found in close proximity; it includes pairing, loose aggregations and coordinated schools.

For modelling purposes, fishes known to be substratum-associated (e.g. Blenniidae) were assigned a value of zero in terms of 'distance from benthos' since they primarily reside directly on the substratum. Nocturnal schooling fishes (e.g. Apogonidae) are known to be closely associated with the benthos during the daytime and to feed in the water column at night (Marnane & Bellwood 2002). To avoid such nocturnal species influencing the results, I removed them from the analysis. To examine where different types of potential prey can be found on the reef, I analysed the data with a Generalised Linear Model (GLM) with distance from benthos as the response variable, and body size, BD, RBD, and social behaviour as explanatory variables. Distance from the benthos followed a Gamma distribution; I therefore modeled only non-zero values. As such, for this analysis specifically, I excluded specimens with a zero value for distance from benthos, i.e. cryptobenthic species 'sitting on the benthos'. I used a log link function for the GLM. To avoid issues with pseudoreplication (multiple individuals within the same school), I used a mean value of the distance from benthos for each species for each quadrat. For sample sizes used in each model, see Appendix D Table 1. I investigated different models, incorporating interaction terms between variables; the best model was chosen based on the Akaike Information Criterion (AIC). The Variance Inflation Factor (VIF) was also assessed for the models. If a variable was found to have a VIF over three, it was removed from the model following Zuur et al. (2013). Model validation (residual plots, Cooks' distance etc.) follows Zuur et al. (2013); only suitable models were considered. See also power analyses of the models in Appendix D Table 1. All models were analysed in the software R (R Core Team 2017), using the packages *effects* (Fox & Weisberg 2019), *emmeans* (Lenth 2019), *car* (Fox & Weisberg 2019), *ggplot2* (Wickham 2016), and *stats* (R Core Team 2017).

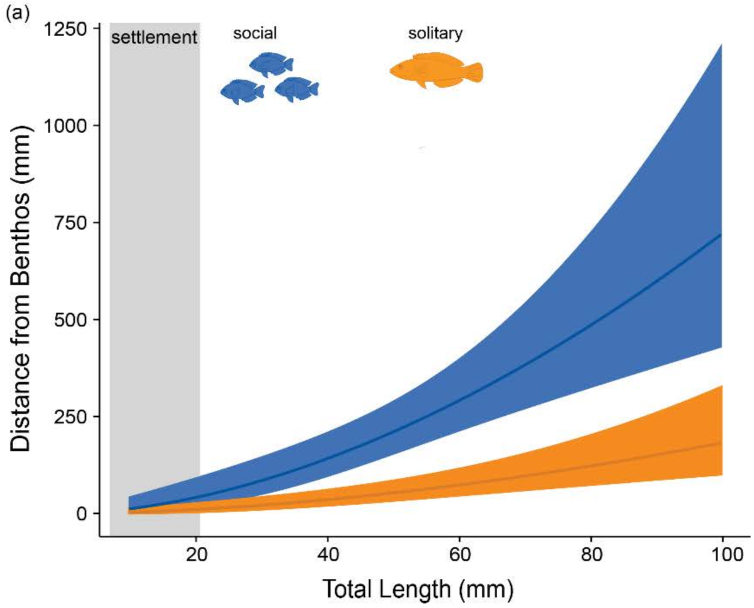
As the primary model did not allow for the incorporation of zeros (and therefore species in contact with the benthos), I conducted a second analysis, where solitary species were modelled separately, using a segmented GLM in the R package *segmented* (Muggeo & Muggeo 2017). Significance between the slopes of the segmented relationship were tested using the Davies test (k=20).

Mortality was modelled using a beta regression, where daily proportional mortality was the response variable, and body size within the three prey functional groups (as classified herein) the explanatory variables. I tested the models with and without an interaction term, and chose the best model using the AIC.

Finally, I also tested for the phylogenetic non-independence of RBD and body size (TL) (independent variables) vs. distance from benthos (dependent variable). A phylogenetic tree was downloaded from (Siqueira et al. 2020), which was then pruned to represent the species in my analysis, using the *ape* package (Paradis & Schliep 2019). Branch lengths were computed using the Grafen method. The phylogenetic tree used for the analysis can be found in Appendix D Figure 6. Phylogenetic Generalized Least Squares (PGLS) analyses were fit using the *nlme* package (Pinheiro et al. 2014). Models of both Brownian and Pagels' correlation were run, and the best model fit was chosen based on AIC. The initial λ (lambda) value was set to 1 and was non-fixed. Both models were estimated using maximum likelihood.

## 5.3 Results

### *5.3.1 Distance from benthos*



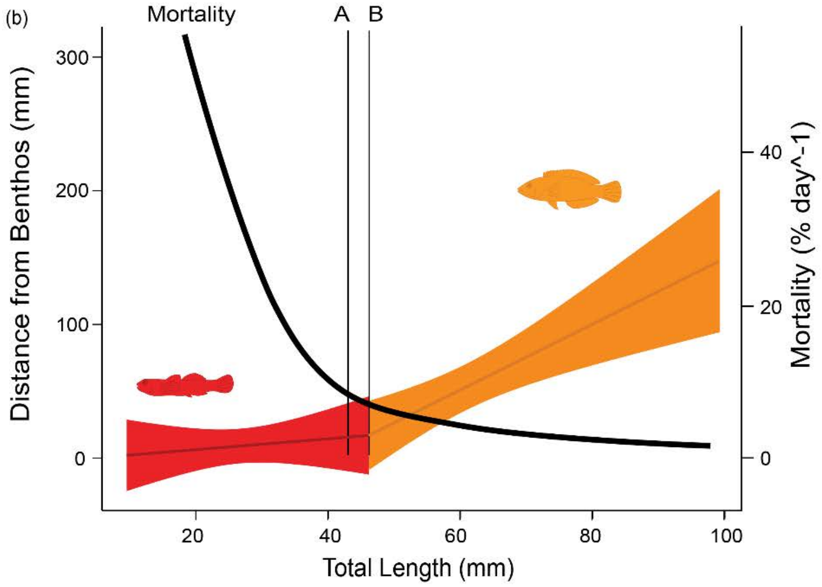


*Figure 5.1* (a) Distance from benthos vs. body size in coral reef fishes. Blue colour represents social fishes, orange represents solitary species. (b) Distance from benthos vs. body size for solitary species only. Note the difference in the y-axes between (a) and (b). Red colour represents the first linear regression of the segmented linear regression, and the functional group of cryptobenthic substratum dwelling species. Orange represents the second part of the segmented linear regression, and the functional group of solitary epibenthic species. The vertical line denoted 'A' represents the point at which mortality in coral reef fishes decreases significantly, based on Goatley and Bellwood (2016),

whereas vertical line 'B' represents the point at which the segmented linear regression found a significant change in behaviour for solitary species (based on the distance from the benthos).

In the models herein, distance from the benthos in coral reef fishes was significantly influenced by both body size and social behaviour (Gamma GLM; $p<0.01$; Appendix D Table 1; Figure 5.1). The best model found that a 1 mm increase in Total Length (TL), resulted in a 2 mm increase in average distance from the benthos (Appendix D Table 1). Social fishes occurred predominantly in the water column (Figure 5.1a). This behaviour appears to be primarily associated with planktivorous schooling species, especially pomacentrids (Appendix D Figure 3). By contrast, I found solitary species to be strongly associated with the substratum (Figure 5.1a). Similar results as above were also found when distance from benthos was modelled against BD (Figure 5.2c).

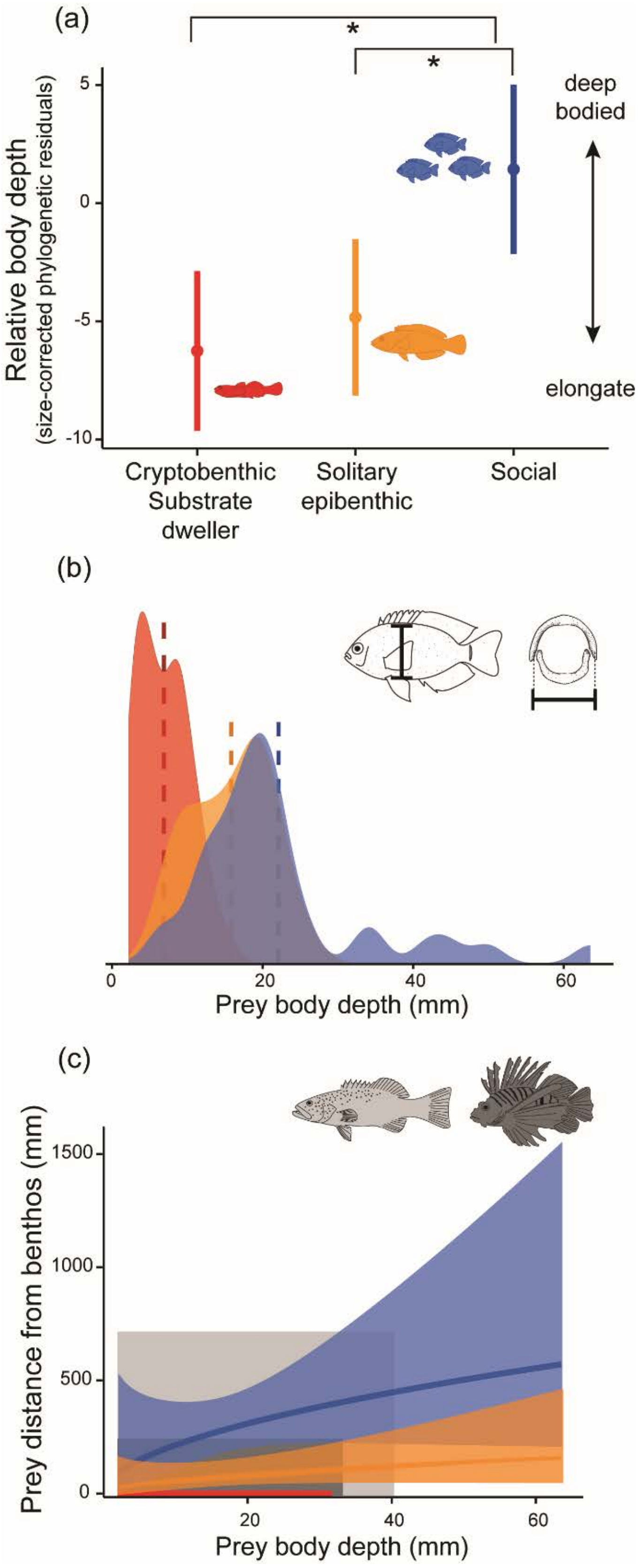


*Figure 5.2* Body depth of coral reef fishes. (a) Relative body depth (RBD) (size-corrected phylogenetic residuals) of coral reef fishes among the three prey functional groups (mean with 95% Confidence

Intervals): cryptobenthic substratum dwellers (red), solitary epibenthic (orange), and social (blue) fishes. b) Raw values of body depth (BD) of the three functional groups. BD values of prey fish relate to the gape size required by a piscivore to be able to capture and ingest them (Mihalitsis & Bellwood 2017). Dashed lines represent mean values for each functional group. (c) BD vs. prey distance from the benthos (mm). Prey distance from benthos relates to the minimum strike distance required by an ambush predator, to have a high probability of successfully capturing the prey. Two examples of estimated niche space are presented for two piscivores of the same body size; of an engulfing piscivore (e.g. *Pterois volitans*), which has a gape size of 32.2mm and a strike distance of 238mm, and a grabbing piscivore (e.g. *Plectropomus leopardus*), which has a gape size of 40.7mm and a strike distance of 714mm (Chapter 4). Note that distances from benthos for prey fishes are during the day.

When solitary species were modelled separately, a segmented GLM analysis split solitary species at a body size of 46.1 mm TL (+/- 9.3 S.E) (Figure 5.1b), with a significant difference between the slopes of the segmented regressions (Davies test; $k=20$, $p<0.05$, Figure 5.1b). For the first segment of the regression, the model found that a 1 mm increase in body length (TL), resulted in an increase of 0.41 mm in the distance from benthos (Figure 5.1b). For the second segment, this value increased to 2.1 mm in distance from benthos for a 1 mm increase in TL (Figure 5.1b). In essence, solitary fishes below approximately 50 mm, were strongly associated with the substratum, whereas solitary fishes over approximately 50 mm were found in the water column above the substratum (Figure 5.1b).

### *5.3.2 Establishing functional groups*

Based on model results, I was able to classify three distinct functional groups of prey fishes on coral reefs. These groups are: cryptobenthic substratum dwellers, solitary epibenthics, and social fishes. Cryptobenthic substratum dwellers are fishes closely associated with the benthos (i.e. some part of their body touches the substratum most of the time). They are primarily cryptobenthic reef fishes which remain small bodied (< 50 mm) throughout their lives (note this group does not include Apogonidae, Pseudochromidae and other non-substratum associated cryptobenthics) (Figure 5.1b, Appendix D Table 1). Solitary epibenthic species are fishes predominantly swimming above, within or around the substratum, however, they usually stay within close proximity to the benthos (Figure 5.1a, Appendix D Table 1). They are primarily juveniles of species that attain a larger body size in adulthood (e.g. *Halichoeres hortulanus*). Social species are fishes known to school, pair, or form aggregations, and primarily feed in the water column (Figure 5.1a). They are primarily planktivores and pairing non-planktivores (Appendix D Figure 3). With prey functional groups established, I further tested if the proportional abundance per square meter of reef, differed between functional groups. A GLM model found significant differences between the proportional abundance per square meter of reef for the three functional groups (GLM, p<0.001; Appendix D Figure 5a). This was 54.5% (+/- 4.1% S.E) for cryptobenthic substratum dwellers, 26.7% (+/- 5.8 S.E) for social fishes, and 18.8% (+/- 5.8 S.E) for solitary mobile fishes (Appendix D Figure 5a). I note that while these groups may not be mutually exclusive, they encapsulate the majority of the most abundant coral reef fish species.

### *5.3.3 Body depth*

I found significant differences between the relative body depths (RBD) of the three functional groups (GLM; p<0.01, Figure 5.2). Cryptobenthic substratum dwellers and solitary epibenthic were highly elongate, while social fishes had a larger RBD than either of the two other groups (Figure 5.2). When raw body depth values (BD) were compared among functional groups, I also found significant differences between all three functional groups (GLM; p<0.01; Figure 5.2b). Cryptobenthic substratum dwellers had a mean BD of 6.8mm (+/- 1.8 S.E); solitary epibenthic fishes had a mean BD of 16.4mm (+/- 2.2 S.E) (142% larger than cryptobenthic substrate dwellers); social fishes had a mean BD of 26.3mm (+/- 2 S.E) (60.4% larger than solitary epibenthics) (Figure 5.2b). When displayed in terms of fineness ratio, I found that all three functional groups appear to have body shapes associated with a low pressure drag coefficient, and reflect optimal fineness ratios for water column swimming (social, solitary epibenthic) or burst-and-coast swimming (cryptobenthic substrate dwellers) (Appendix D Figure 8).

### *5.3.4 Mortality*

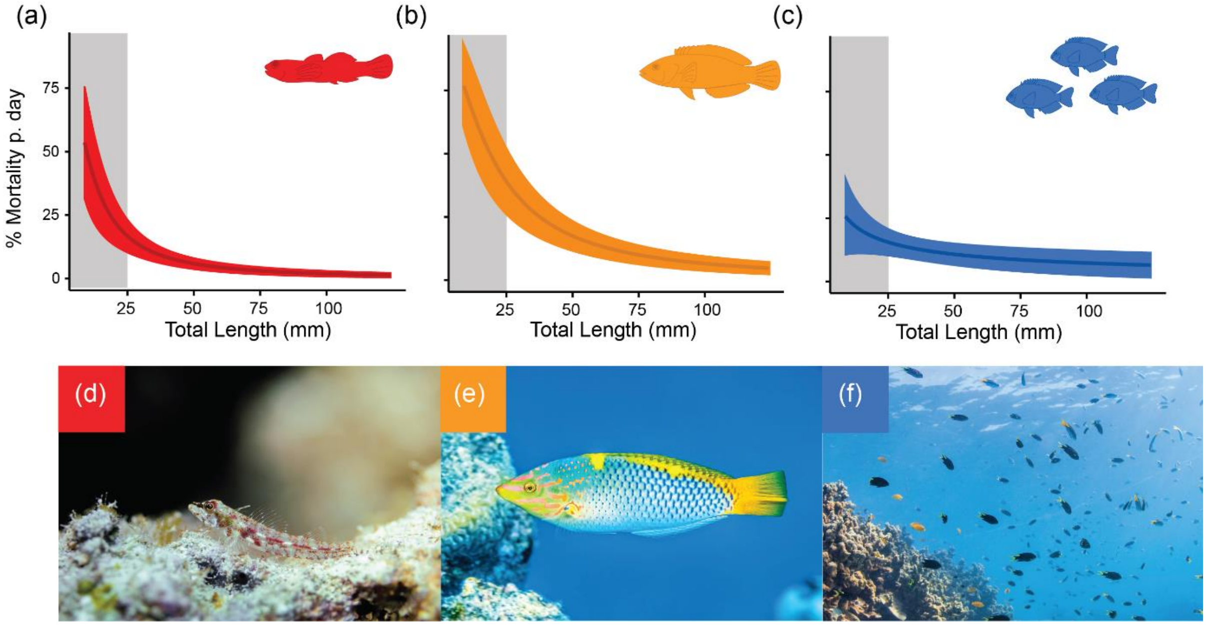


*Figure 5.3* Daily mortality rates vs. body size in mm Total Length (TL)(mean with 95% Confidence Intervals) for the three prey functional groups: (a) cryptobenthic substratum dwellers (red), (b) solitary epibenthic (orange), and (c) social (blue) fishes. Gray areas represent settlement on the reef, and thus encompasses naïve individuals. Photographs represent each functional group: (d) cryptobenthic substratum dweller *Ucla xenogrammus* (e) solitary epibenthic *Halichoeres hortulanus*, and (f) schooling *Neopomacentrus sp*. Photos: Victor Huertas.

Given the three distinct functional groups based on size, behaviour, and morphology, I explored the combined effect they may have on mortality rates. I found that the three prey functional groups classified herein (cryptobenthic substratum dwellers, solitary epibenthics, and social fishes) displayed different patterns of mortality (beta regression; $p<0.01$; Appendix D Table 1; Figure 5.3). The best model based on the AIC was found to be with an interaction term between TL and functional group, and had an $R^2$ value of 0.74. Mortality rate decreased significantly with increasing body size (Appendix D Table 1; Figure 5.3), and was highest for all three functional groups upon settlement. However, among groups the highest mortality rate was in solitary epibenthic species (21.6 %), followed by social fishes (11.6 %), followed by cryptobenthic substratum dwellers (9.7 %) (Appendix D Figure 4).

## 5.4 Discussion

A combination of morphological and behavioural traits distinguished three distinct functional groups of fishes as potential prey for piscivores on coral reefs. The properties of each functional group reflect differences in where they are typically found on the reef, what gape sizes are required to feed on them (based on prey fish absolute body depth), and from which directions piscivores can strike at them. These morphological and behavioural traits suggest that even though all types of prey fishes may be abundant on coral reefs, they may differ in their relative availability for different piscivore types. The characteristics of each functional group may therefore influence predator-prey dynamics on coral reefs, and coral reef trophodynamics, as reflected in my results on varying mortality rates. The established functional groups may be unequally accessible to different types of predators, suggesting that piscivory is not only reliant on predator selectivity, but also, how prey influence their relative catchability.

The first functional group is the cryptobenthic substratum dwellers. This tight association with the substratum may be a behavioural defence mechanism against predation. By being substratum associated, these fishes may potentially reduce the dimensionality, and thus, the angles from which a predator can strike at them (see also Pawar et al. 2012). Furthermore, a predation strike that is predominantly based on body ram, requires the predators' body to travel beyond the point of prey capture, due to inertia. Therefore, striking towards the substratum at a high-speed, from a high angle, may result in the predator colliding with the substratum, potentially injuring its jaws and/or anteriormost teeth (Figure 5.4c). Jaw ram or protrusion is a feeding adaptation associated with high precision and a strictly limited maximum excursion (i.e. a point that the jaws cannot pass, regardless of inertia) (Ferry-Graham et al. 2001; Ferry-Graham et al. 2002; Staab et al. 2012a; Staab et al. 2012b) (see also Figure 5.4c). Furthermore, protrusion increases the force exerted on prey through suction feeding (Holzman et al. 2008; Staab et al. 2012b). Cryptobenthic substratum dwellers may therefore be primarily accessible to fishes that have a high degree of jaw protrusion (Figure 5.4c). This suggests that the predator must get relatively close (limited strike distance) to their prey before initiating a strike. Cryptobenthic substratum dwellers may therefore be more likely to rely on crypsis, rather than a fast escape response, when first sighting a predator. In essence, this functional group of fishes, may require their potential predators to have an increased degree of jaw protrusion and some mechanism which allows the predator to get close to the prey (e.g. crypsis, elongated head, or decreased body width). Furthermore, by requiring these traits from their potential predators, cryptobenthic substratum dwellers may be less accessible to predominantly body-ram predators (e.g. *Lutjanus*).

The second functional group is solitary epibenthic fishes. Such species may also be highly substratum associated upon settlement (Bellwood 1988) or stay hidden within the structural complexity of the reef (Lecchini 2005). In my study, I found that these fishes appear to become markedly less dependent on the benthos after 49.8mm TL (Figure 5.1b). This value is strikingly close to the size at which Goatley and Bellwood (2016) found a significant decrease in the mortality rate of coral reef fishes (approximately 43 mm TL). Furthermore, this body size (> 48 mm) has also been shown to be the point at which, the presence of antipredatory colouration such as an ocellus in small reef fishes is most prevalent (Hemingson et al. 2020). This similarity between the three values suggests that there may be a causal relationship between the size at which mortality decreases significantly in coral reef fish communities, and the point at which many coral reef fishes change their ecology, and become more exploratory or bold. By not 'sitting' on the benthos a majority of the time, solitary epibenthic prey fish are more mobile than cryptobenthic substratum dwellers. This increased prey mobility, may reduce the strike success of a high-precision strike (e.g. a jaw protrusion-based strike) (Ferry-Graham et al. 2001; Ferry-Graham et al. 2002). Their catchability, therefore, may require piscivores to utilise a more pursuit-based strike, or a strike which is more 'responsive' to swift avoidance movements from the prey. Such predators may therefore require teeth that function for grabbing highly mobile prey (sensu Chapter 3). By having a significantly higher body depth (BD) than cryptobenthic substratum dwellers (Figure 5.2), and being more mobile, a prolific predator on these fishes may need increased gape sizes (sensu Mihalitsis & Bellwood 2017) and dentition functionally equipped for grabbing (Chapter 3).

The third functional group is social species. These species are predominantly found in the water column (Figure 5.1), and are therefore highly exposed to predation (Motro, Ayalon & Genin 2005). Furthermore, predators are able to strike at them from all directions (Figure 5.4). By feeding in the water column, these fishes dictate that the piscivore must be fast and able to strike from a long distance, as getting close to the prey is not likely as an option (Figure 5.4). Therefore, ram and pursuit strikes are likely to be the primary traits required by a piscivore to capture such prey, whereas jaw protrusion strikes are unlikely to be as effective. There may, however, be two windows of opportunity throughout a day when piscivores which use predominantly jaw protrusion or engulfing may be able to increase the probability of capturing these fishes: at dawn and dusk (see Appendix D Figure 7).

Social fishes, and more specifically, schooling fishes have a circadian behaviour of moving up and down the water column (Hobson 1965; Hobson 1972). A large distance from the benthos for some schooling fishes, may limit their availability to be highly benthic-associated predators during the daytime (see also Hixon & Carr 1997). However, during crepuscular hours, these fishes are either seeking or leaving shelter on/in the substratum. Essentially, diurnal schooling fishes are more likely to be close to the benthos during crepuscular hours, increasing their vulnerability to benthic or engulfing predators for a short time (see Appendix D Figure 7 for graphical illustration of this concept) (Hobson 1965; Hobson 1972). In this context, it is interesting to note that Sweatman (1984) noticed crepuscular feeding in lizardfishes primarily targeted schooling fishes, whereas diurnal feeding was mostly associated with non-schooling fishes. In essence, the behaviour of schooling fishes feeding in the water column by day, and going within the reef at night, may be limiting both when they are available as prey and which predators can capture and ingest them. This behaviour may therefore exclude benthic associated piscivores (striking from below) during diurnal hours (Appendix D Figure 7) or limit the relative prey sizes available to them.

Previous work suggests that upon settlement, schooling species seek conspecifics on the reef (Sweatman 1988; Booth 1995; Booth 2002). Schooling may also reduce the time required by naive individuals to become experienced in avoiding predation (Booth 2002; McCormick, Fakan & Allan 2018). This appears to be reflected in a lower mortality rate of social species during early post-settlement life (Figure 5.3). Indeed, there is a large amount of literature on the benefits of schooling as an anti-predatory mechanism (reviewed in Pitcher & Parrish 1993). Unfortunately, there is limited information on when schooling starts in coral reef fishes (before or after settlement), yet this information may be crucial in the population dynamics of these species.

Quantifying these anti-predatory traits in a community-wide context, provides an additional facet to the quantification of the niches of piscivorous fishes, which may be based not only on the predators but on their prey as well (Figure 5.2c). The gape size of most piscivorous fishes dictates the maximum prey size they can feed on (Wainwright & Richard 1995; Mihalitsis & Bellwood 2017). They are also likely to have a specific strike distance from which they can ambush their prey, after which they would have to initiate a pursuit behaviour to catch their prey (Figure 5.2c). The predators' strike distance may therefore need to be smaller than the preys' distance from the benthos (i.e. shelter), if the predator is to successfully capture its prey without initiating pursuit behaviour. If so, we can begin asking questions on the relative predation risk probabilities, that different types of predators exert on different types of prey, at specific points in time (Figure 5.2c). By incorporating such probabilities, along with the relative abundance of different prey types, we can begin to address the mechanistic basis of piscivory on coral reefs.

This study provides a step towards an understanding of predator-prey interactions in a community-wide context. McGill et al. (2006) highlight the need to establish and better understand functional traits, as opposed to focusing on pairwise species interactions. By changing the wording of 'a *Plectropomus* fed on a *Halichoeres*' to 'a body-ram feeding piscivore fed on a solitary epibenthic fish' may help reveal the functional mechanisms underpinning these intricate interactions. Furthermore, this approach may provide a better understanding of energetic and nutrient pathways, essential for understanding trophodynamics on coral reefs.

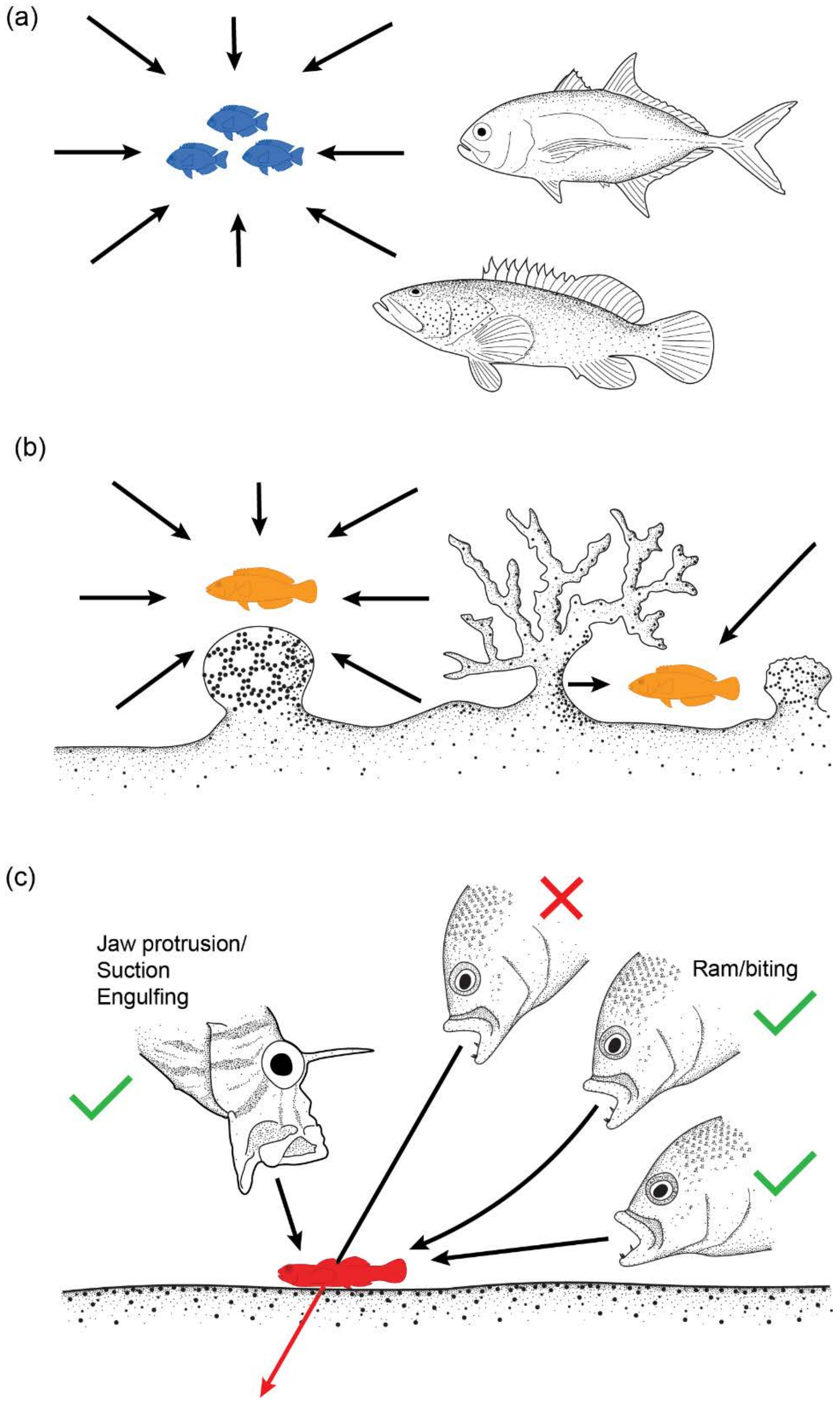


*Figure 5.4* Graphical illustration representing the relative catchability of the three prey functional groups. Arrows represent the directions from which strikes from predators are likely to occur. (a) Social/schooling fishes can be attacked from every direction. (b) Catchability/availability of solitary epibenthic fishes is highly context dependent, with the nature of the substratum being likely to

influence the strike outcome. (c) Cryptobenthic substratum dwellers are likely to be primarily accessible to piscivores with some degree of jaw protrusion, whereas predators using ram/biting as their striking mode, may have problems capturing this prey type. Black arrows indicate predator strikes, whereas the red arrow indicates the unlikely strike direction.

In conclusion, my study suggests that the nature of predation as an ecosystem function on coral reefs may not only be influenced by what the predators do to the prey, but also, how prey influence their potential catchability to different types of predators. Indeed, I identify three functional groups of prey which appear to shape 1) their potential for predation (catchability), 2) the mode of predation to which they are most vulnerable, and 3) location-specific mortality rates. In essence, prey fishes appear to influence where, when, and how they can be caught. This may suggest that even though prey fishes are abundant on a reef, they may not be equally available to all types of predators. If so, we may need to re-think how we evaluate such energy transactions through predation. We may have to include functional traits of both predators and prey.

# Chapter 6. A new world of predation on coral reefs: Quantifying fish predation at a community level

## 6.1 Introduction

For many animals in high diversity systems, such as coral reefs, population dynamics are driven by early life stage mortality (a type 3 survivorship curve), with recruitment functioning as a population bottleneck (Hixon 1991; Harms et al. 2000; Nathan & Muller-Landau 2000). Indeed, predation-based mortality is widely regarded as one of the most important processes determining fish population structures on coral reefs (Sale 1993; Hixon & Carr 1997; Doherty et al. 2004). On reefs, many, if not most fishes, are eaten by other fishes (Randall 1967a). While the consequences of high mortality in these ecosystems is well documented (Almany & Webster 2006; Goatley & Bellwood 2016), the predators that drive this process are largely unknown.

In the last few years, the main focus of fish predation studies on coral reefs, has been on trophic cascades or indirect effects on behaviour. Although, predation does not appear to elicit trophic cascades on coral reefs (Rizzari, Bergseth & Frisch 2015; Roff et al. 2016; Casey et al. 2017; Desbiens et al. 2021), recent studies have suggested that the functional importance of these predators is not restricted to consumption, but may also include non-consumptive 'fear-effects' (Madin et al. 2016; Rasher et al. 2017; Lester et al. 2020a; Mitchell & Harborne 2020). However, the fish predators investigated in these fields were primarily sharks and other mesopredators. Yet, other recent work, has highlighted the trophic importance of small-bodied coral reef fishes (Goatley et al. 2017; Brandl et al. 2019). This raises questions over the identity and size of fish predators from an ecosystem function perspective. Basically, big questions still remain: Who are the main predators of fishes on coral reefs? At which size does most predation happen? And, while all individuals in a community go through the predation gauntlet, how does this process scale at a community level?

We address these questions by implementing a functional group approach (McGill et al. 2006; Bellwood et al. 2019) and applying it to coral reef fishes, with a particular focus on the process of predation on fishes, by fishes. We first surveyed a coral reef fish community and constructed an algorithm to model predator-prey interactions based on the functional constraints imposed by both predators and prey (following Chapters 4,5). Predators were classified by their functional group (grabbers vs. engulfers) and size, while prey were classified by body depth (which determines the size of predators able to feed on them) and prey functional group (cryptobenthic, epibenthic, social)(Chapter 5). This produced a modelled community of 32,218 fish which were simulated one million times to produce 349,000 potential predation events (functionally viable events). These results were then compared to the documented consumption of reef fish prey by fish predators, based on a metanalysis of gut content data (n=1,677 predation events) across Indo-Pacific coral reef ecosystems.

## 6.2 Materials & Methods

Quantifying ecosystem processes at a community level is a logistically difficult and time-consuming process. Usually, processes are inferred based on collected empirical data, most often recorded as presence/absence or abundance data, or through simulation-based approaches. Here we compare and contrast these two.

### *6.2.1 Quantifying predator abundance and prey availability at a community level*

We first surveyed a coral reef fish community at Lizard Island, a marine reserve with no fishing, located on the Great Barrier Reef, Australia, following (Morais & Bellwood 2019). Fish surveys were conducted in all traditionally recognised reef zones (back, flat, crest, slope). Both underwater visual surveys and enclosed clove oil stations were used to maximise the proportion of the fish community surveyed. The two approaches were chosen for different groups of fishes, based on their body sizes and behaviours (Ackerman & Bellwood 2000). Visual surveys were done with a diver initially conducting a 50x5m transect tape survey to count large (>25cm TL), water column-positioned or fast swimming fishes likely to be scared away by the diver. Upon return along the tape, the same diver conducted a 30x5m survey targeting smaller-bodied fishes that are less mobile. The diver then conducted another 30x5m survey over the same area to count small-bodied, non-cryptic fishes usually found just above the reef benthos. Finally, the diver conducted a last 30x1m survey to count cryptic individuals (e.g., within or under crevices) which would not have been surveyed using traditional visual surveying techniques (Morais & Bellwood 2019). In addition, to provide more accurate abundance estimates of cryptobenthic reef fishes, a set of eight enclosed clove oil stations (following Ackerman & Bellwood 2000) were deployed in each habitat. A total of three sets of visual surveys and eight clove oil stations were conducted in each reef zone at each of the sites (n=3 sites). For more detailed information on sampling methods, see (Morais & Bellwood 2019).

To account for the different spatial extents of the different surveying methods, a resampling algorithm was constructed. This allowed scaling the observed fish abundance to a standardised common area among surveys. This procedure generated one standard, 1,200m$^2$ community, which can be interpreted as a reef section spanning the different reef zones, and with equal area in each of these zones. This 'multihabitat' coral reef fish community had 32,235 fish individuals from 266 species. We then assigned all fishes to their respective prey functional group (based on their functional traits, see Appendix E Table 1) following Chapter 5.

Our quantification of potential predation events at a community level, started with a community dataset including fish species and body size. Based on body size and previously published relationships between body size and functional traits of both predator and prey fishes (Chapters 4,5), we converted body sizes to functional trait values directly related to predator-prey interactions (i.e., prey body depth, predator gape size). We then conducted repeated simulations of potential predation events by sampling individuals (one predator and one prey at a time) within the community. Only realistic interactions, based on the functional trait relationships, were considered (e.g., if the prey could fit in the predators' gape. More details below). Following simulations, we compared our results of potential predation, to observed consumption patterns, based on a metanalysis of the gut contents of coral reef fish predators.

Individual fishes were assigned as predators if that species has been found to feed on elusive prey in the literature, or other online sources (e.g. Froese & Pauly 2014). All fishes were considered as potential prey. Prey body size was then transformed to body depth based on the functional group of the species following Chapter 5:

$$D_{f,i} = a_f + b_f * \log(L_{f,i})$$

with $a_f$ and $b_f$ representing the y-intercept and slope, *f* one of the three functional groups, and *i* an index denoting an individual fish, $a_f = (-1.58, -0.78, -0.9), b_f = (1.04, 0.74, 0.95)$, for $f = (cryptobenthic,\ epibenthic,\ social)$ respectively. L is the total length of an individual fish. Predator body sizes were then transformed to gape sizes following relationships obtained from coral reef fish specimens (Chapters 2,3), based on the functional group to which the surveyed predator belonged to:

$$G_{f,i} = a_f + b_f * L_{f,i}$$

where *f* is one of the two functional groups, and *i* an index denoting an individual fish,

$a_f = (0.93, 0.04)$, $b_f = (0.17, 0.17)$, for $f = (engulfers, grabbers)$ respectively. L is the total length of an individual fish.

We then conducted a series of simulations, whereby an individual predator from the community (along with its respective functional trait values) was randomly matched against an individual prey fish (along with its respective functional trait values). Each simulation consisted of 10,000 potential piscivory events, and the simulation was conducted 100 times with replacement. We then calculated the relationship between predator gape size and prey body depth, for each potential predation event (following Mihalitsis & Bellwood 2017), by dividing prey body depth to predator gape size. We only kept instances in which the obtained ratios were within the range of 0.14 – 0.7, as this has been found to be the relative prey size within which 95% of predation occurs (Chapter 4), and eliminated any other instances. Next, we binned these events into respective size bins of predators (from 5 to 50cm, at 5cm intervals), and calculated the relative contribution of each prey functional group to the overall prey availability for each predator size bin:

$$C_{f,b} = \frac{A_{f,b}}{\sum_{f=1}^{n} A_{f,b}}$$

Where C is the relative contribution of available prey of a specific functional group *f* at a specific size bin *b*, *A* is the abundance of individuals of the specific prey functional group, for the given size bin, and the denominator is the summation of the abundances of all *n* functional groups for the given size bin. These contributions were then compared to the observed consumption of each prey functional group, based on the metanalysis of gut content data (see below).

### *6.2.2 Observed diet of predators (metanalysis)*

Diet information was collected from published literature on the gut contents of piscivorous coral reef teleost fishes in the Indo-Pacific realm (Appendix E Figure 1). Information extracted from the literature was: range of predator body sizes sampled from each study, predator species, prey species, and number of occurrences that the prey species was found in predator guts. Prey species were then classified into functional groups (as above). We removed pelagic predators as they likely operate at a broader spatial scale than more benthic associated predators.

Individual body sizes were not available, as only size ranges were reported in the literature. Therefore, for every predation event recorded from the literature, we drew individual body sizes from a uniform distribution delimited by the range of sizes provided by the respective study. This process was done for each predation event recorded (n=1,224), and was simulated 1000 times with replacement. In some instances, the exact size of the predator was recorded, and was therefore used as the only potential body size for the given predation events, throughout the simulations. These observed predation events were compared to our simulated predation events, based on the overlap coefficient from the R-package 'bayestestR' (Makowski et al. 2020). These predation events were then assigned into the same body size bins as the ones used in our community survey (see above). We then summarised the relative contribution of each prey functional group to each predator body size bin (as above).

## 6.3 Results

We found that fish predation on coral reefs is overwhelmingly dominated by small, diminutive predators. The average fish predator that feeds on other fish on reefs is just 3.6 cm, and the average prey just 1.5 cm. By combining surveys at different spatial scales, to generate as complete a census as possible, our modelled fish community contained 32,218 fishes from 266 species. Simulating one million potential predator-prey interactions (i.e., predation events) within this community, by applying size-based functional constraints (prey body depth/predator gape size, we obtained 349,081 potential (i.e., functionally feasible) predation events. In this extensive pool of potential events, the median size of a predator fish was just 3.65 cm (95% CI: 2.38 – 15) Total Length (TL) (mean: 5.6 cm) (Figure 6.1a). Essentially, 95% of potential predation events involve predators less than 15 cm. When simulated predation events from our modelled community were compared to a literature-based dataset of 1,677 observed predation events, by size, there was only 8% overlap (Figure 6.1b). In essence, the vast majority of studies have exclusively quantified predation by exceptionally large predators; most predation events go unobserved and unrecorded. Our results suggest there is a need for a paradigm shift in the way we consider fish predation, and the role of trophic interactions in shaping the species, and functional, composition of coral reef fish communities. Furthermore, based on abundance-based encounter likelihoods, these predators are unlikely to be juveniles of 'large' reef fish predators; the predators driving the process are predominantly cryptopredators (Figure 6.1c), defined herein as carnivorous fishes below 10 cm.

The same patterns apply to prey fish. The estimated median size of prey fish was just 1.5 cm TL (95% CI: 0.8-3.65) (mean: 1.75 cm) (Figure 6.2a); 95% of potential predation events involve prey sizes less than 3.65 cm. Functionally feasible predation events were simulated based on prey body depth vs. gape size relationships. These simulations resulted in 349,081 functionally feasible predation events. Of these events, the prey involved were: 90.4% cryptobenthic prey, 8.4% social prey, and 1.2% epibenthic prey (Figure 6.2b). When these predation events are compared to values of published reef fish mortality rates, their distribution matches closely (Figure 6.2).

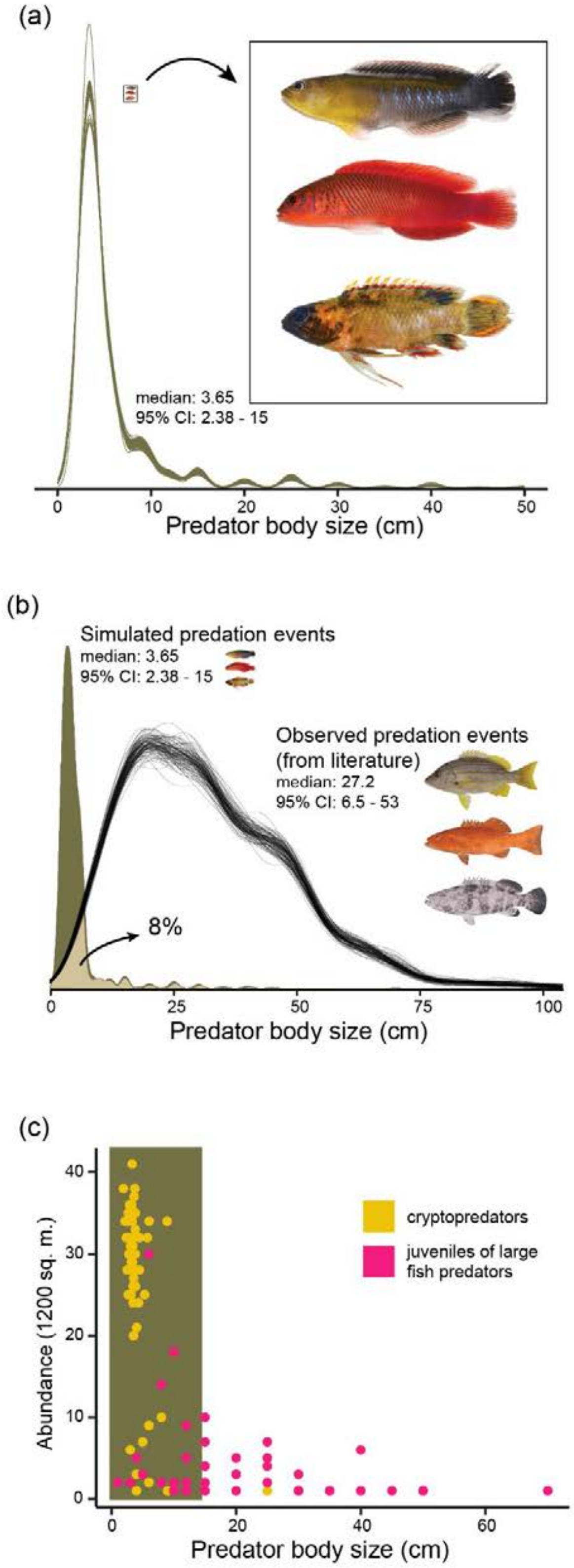


*Figure 6.1* (a) Community level predation of coral reef fishes, along a predator size gradient, based on simulations from reef surveys. Examples of cryptopredators, that shape community composition

in coral reef ecosystems, top to bottom: *Pseudochromis cyanotaenia*, *Cypho purpurascens, Plesiops sp*.. (b) Predation events simulated from our surveyed community (same as (a)) vs. observed predation events (metanalysis of literature). Multiple lines in observed predation events reflect draws from a distribution (see Methods). (c) Abundance estimates of cryptopredator species, relative to juveniles of 'large' reef fish predator species (sensu Brandl et al. 2019). The coloured box represents the size range within which most predation events occur. Photographs C. R. Hemingson, with permission.

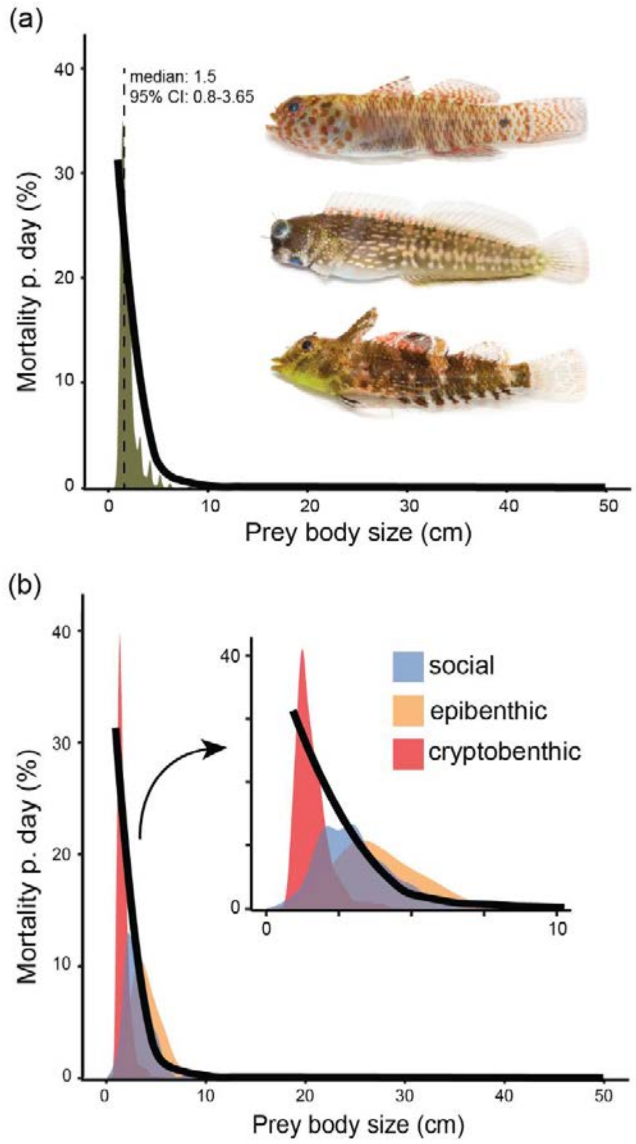


*Figure 6.2* (a) Community level predation simulated in our study along a prey size gradient (brown), mirrors the exponentially declining line which represents observed reef fish mortality rates from an independent metanalysis on reef fish mortality (Goatley & Bellwood 2016). Examples of primary contributors to this density distribution, from top to bottom: *Eviota queenslandica*, *Salarias guttatus*, *Enneapterygius tutuilae*. (b) The same density curve, in 6.2a, split according to prey functional groups, namely: cryptobenthic = red, epibenthic = yellow, social = blue. Photographs C. R. Hemingson, with permission.

### *6.3.1 Functional group contributions*

When the 32,218 fishes in our community were classified into prey functional groups, 59% were cryptobenthic substratum dwellers (referred to hereafter as cryptobenthic), 7 % were solitary epibenthic forms (referred to as epibenthic), and 34 % were social (for details on functional groups, see Appendix E Table 1). Furthermore, of the 32,218 fishes in our community, 1,726 (5.4%) were considered potential fish predators (based on their trophic status from the literature, see Methods). The functional groups of these predators were 85% grabbers and 15% engulfers.

### *6.3.2 Comparing size-specific simulated predation to observed predation events at a community level*

The distribution of potential predation events among different size classes of predators in our simulated community was found to closely reflect the distributions in our metanalysis. This applied to both predator functional groups (grabbers and engulfers) (Figure 6.3a,b) and all three prey functional groups (Figure 6.3c-e), except for small predator body sizes. In essence, for small predators (i.e., ≤ 20-25 cm), cryptobenthic prey are under-represented (Figure 6.3e), while epibenthic and social prey are over-represented (Figure 6.3c-e). This may be linked to the functional traits of these prey groups, and the predators involved in this predation.

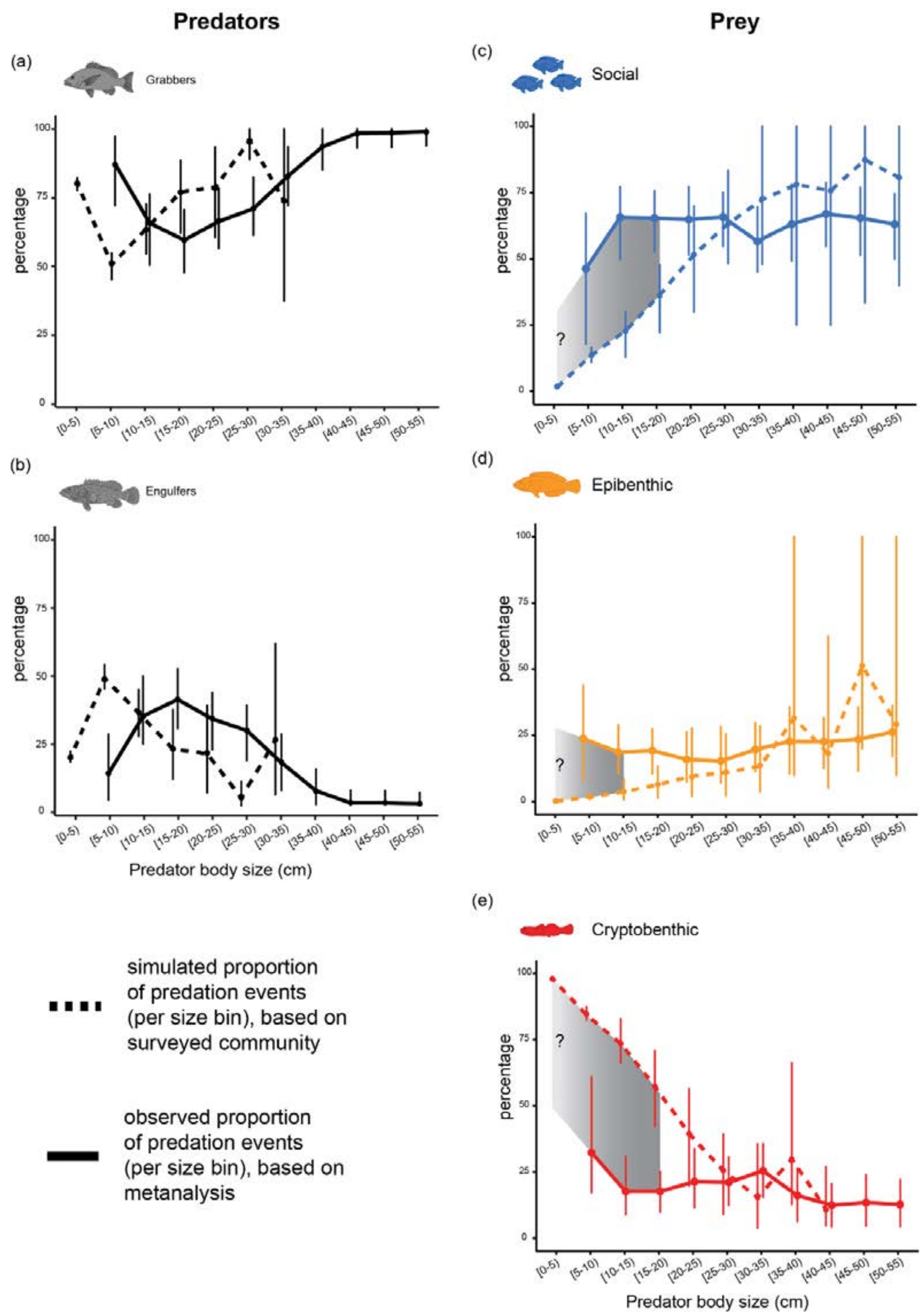


*Figure 6.3* Simulated vs. observed relative contributions to the process of piscivory on reefs, based on predator functional groups (a, b) and prey functional groups (c-e). Overall, the trajectories of simulated contributions (dashed lines) and observed contributions (solid lines) were in agreement for predator and prey functional groups. Disparity was only found between the two estimates for small predator sizes, when results are based on prey functional groups: Social and epibenthic prey were

overrepresented in the diet of small predators, whereas cryptobenthic prey were underrepresented. Filled circles indicate means, whereas vertical bars indicate the range of values (minimum, maximum) for a specific size bin. Grey zones indicate size bins where a difference between predicted and observed relative contribution was found to be significant.

## 6.4 Discussion

Cryptopredators have only recently been identified as significant fish consumers (Goatley, González-Cabello & Bellwood 2017). Their overwhelming abundance (relative to juveniles of large reef fish predators), along with our results of simulated community-level predation, highlight the potential of these previously overlooked cryptopredators to be the primary contributors to the process of fish predation in coral reef ecosystems. Common examples of cryptopredators (cryptobenthic reef fishes sensu Brandl et al. (2018) which are carnivorous) include the Pseudochromidae, Plesiopidae, Gobiidae, and Apogonidae. Most of the species within these families remain under 15 cm throughout their lives (Brandl et al. 2018).

The fishes consumed by cryptopredators, based on our simulations, are overwhelmingly cryptobenthic (approx. 90% of predation events) (Figure 6.2). Our results mirror previous empirical studies showing a high consumption of, and high turnover in, cryptobenthic fishes; a 'crypto-pump', fuelling coral reef ecosystems (Brandl et al. 2019). In essence, our results illuminate the 'dark-productivity' (sensu Brandl et al. 2019) that fuels coral reefs, by identifying their most likely predators. These fishes sustain some of the most important trophic pathways on coral reefs (e.g., the detrital and piscivory-cryptobenthic pump). This may add to the variety of mechanisms of energy recycling, which appear to be an essential attribute of oligotrophic ecosystems with high species diversity and biomass (Wild et al. 2004; De Goeij et al. 2013). We show that one of the key pathways that links these fishes to the rest of the food-chain, is through cryptopredators.

Although the underestimation of cryptobenthic prey in the diet of predators may be associated with methodological challenges (Brandl et al. 2019), we suggest that there may also be underlying reasons associated with the specific features of this prey functional group (cryptobenthic prey). There is overwhelming evidence from multiple ecosystems, that most mortality in animals is during the early life stages at small body sizes, and that this is due to predation (Harms et al. 2000; Nathan & Muller-Landau 2000; Doherty et al. 2004; Goatley & Bellwood 2016). This is completely at odds with the life history of cryptobenthic fishes. How can cryptobenthic fishes, the shortest living vertebrates (Depczynski & Bellwood 2005; Robitzch Sierra et al. 2021), with extremely small body sizes and extremely high mortality rates, maintain viable populations? Sustained temporal reproduction (Lefèvre et al. 2016), fast growth (Gillooly et al. 2001), and abundant larvae (Brandl et al. 2019) may all help to facilitate the extreme cryptobenthic lifestyle. However, our data strongly suggest that their success may also be dependent on their ability to reduce relative predation risk. By reducing predation, they would be better able to spread predation-based mortality throughout their life on the reef, sustaining a higher number of reproducing individuals during this vulnerable period (Appendix E Figure 3). These benefits may be directly related to the characteristics of the cryptobenthic functional prey group.

Cryptobenthic prey consist of small-bodied, elongate fishes that 'sit' on the benthos, move through 'burst-and-coast' swimming (Chapter 5), and have cryptic colouration (Hemingson 2021; Hemingson et al. 2022). The drab colouration and 'sitting still' may indeed be a highly successful anti-predatory strategy. This pattern is also followed by some juvenile 'large' reef fishes after settlement (Bellwood 1985). This sit and hide strategy (crypsis) agrees with experiments by Cook and Streams (1984) showing that smaller body size, lighter colouration, and remaining motionless on the benthos, can make aquatic insects in streams less vulnerable to insectivorous fish predators. Similarly on reefs, cryptobenthic prey must balance high mortality rates with the need to maintain populations for long enough to ensure reproduction. In this respect, the ability of cryptobenthic prey to sustain predation below expected, based on their abundance, provides a strong indication that despite high absolute mortality, relative mortality is less than expected, given their size and abundance. Ultimately, it may be that it is their relatively low, not high, mortality that distinguishes cryptobenthic fishes from other reef fishes.

The results discussed above, only became evident when investigating the community from a functional group perspective. Indeed, we show that the functional group approach is a powerful tool in elucidating the complexities of hyperdiverse systems such as coral reefs (see also Thibaut et al. 2012; McLean et al. 2021; Pozas-Schacre et al. 2021). This functional approach may indeed, explain how cryptobenthic prey are able to exist at all.

In 1988 the term 'wall of mouths' was put forward (Hamner et al. 1988), to illustrate how the high abundance of planktivorous fishes operates as a highly effective process for biomass accumulation on reefs by using external subsidies (Morais et al. 2021; Skinner et al. 2021). Our results suggests that the process of piscivory, may operate in a similar manner, where, upon arrival to the reef, early-life stage fishes are confronted with a high abundance of cryptopredator mouths within which they fit (see also Almany and Webster (2006)). Cryptopredators may therefore, function as a 'matrix of mouths', enveloping coral reefs in a reefscape of potential predation events, transferring energy and nutrients of small-bodied, post-settlement fishes, up the benthic food chain.

Overall, we show that the vast majority of fish predation events on coral reefs is likely to involve predators below 15 cm. The vast majority of prey in these predation events is below 5cm. 'Typical' predators on reefs, such as jacks, barracudas and groupers, are not the ones carrying out most predation on reefs. Most fish are eaten by cryptopredators in a 'matrix of mouths' on the reef. We highlight the overwhelming importance of cryptopredators as drivers of predation at a community level. Furthermore, our data suggests that, contrary to expectations, a small body size may indeed function as an anti-predatory mechanism, especially when 'sitting' on the benthos; our functional groups approach revealed that predation events are also governed by prey functional traits. Overall, predation on coral reefs is a game of small fishes, and cryptobenthic prey fishes appear to be winning the game.

# Chapter 7. General Discussion

This thesis followed the conceptual framework of Wainwright and Reilly (1994) regarding functional morphology, and its association with performance and behaviour, and ultimately, ecological patterns. This framework was followed within a context of predator-prey interactions between coral reef fishes. Specifically, I investigated the functional ecology of piscivorous fishes (fish that eat fish). I identified who the main piscivores on a reef are, what they look like, what they can do (i.e., feeding abilities), as well as how they do it. I also identified their most likely prey, as well as how different prey fishes avoid being eaten. Finally, I applied these results to a reef fish community, to assess predation as a process at a community scale.

## 7.1 Predators

In this thesis I first identified the main ecomorphotypes of piscivorous fishes on coral reefs (Chapter 2), namely, diurnal benthic, nocturnal, and pelagic. These groups display distinct morphological traits, which are directly linked to different habitats and life histories. While these ecomorphotypes were separated along a secondary axis of variation related to fin shape, the main axis of variation, and thus, the one explaining most morphological variation, was mostly associated with feeding related traits (e.g., gape size). Indeed, I found high variation in the gape size of piscivorous fishes, from all ecomorphotypes, with the highest variation being found in diurnal benthic piscivores. In essence, this first data Chapter provided clues that this high diversity of piscivorous fishes on coral reefs, is most likely linked to feeding related morphologies, thus calling for more focus on their feeding related functional morphology. At this point, the gape size of predatory fishes had been studied extensively (Staab et al. 2012b; Luiz et al. 2019; Keppeler, Montaña & Winemiller 2020), however, there was one aspect directly linked to fish feeding, the functional implications of which, remained largely unstudied: teeth.

In the next Chapter (Chapter 3), I therefore investigated the functional morphology of teeth in piscivorous fishes. I found three morphologically distinct morphotypes, namely edentulate villiform, and macrodont. My analyses suggested, that based on the functional traits, there are two major groups of piscivorous fishes, that feed in different ways. This Chapter also provided a framework to assess fish dentitions as a whole, as opposed to quantifying the morphology of single teeth. Fish teeth function as a whole (i.e., dentition), they do not function individually, and these dentitions differ in the functions they are able to carry out. These results agree with other recent work, showing that similar-looking teeth along the jaw, can apply different levels of stress onto their prey, while different-looking teeth may apply similar levels of stress (Cohen et al. 2020a; Cohen et al. 2020b). This work builds onto previous studies showing that these systems need to be assessed as a whole (i.e. myology, dentitions, osteology), rather than separate (Motta 1988; Wainwright & Richard 1995; Konow et al. 2008). Ultimately, the integration of these traits into analyses can provide information to not only what fishes feed on, but also, how they feed (Motta 1988; Westneat 1994; Ferguson et al. 2015). Based on Chapters two and three, there were clues indicating that piscivorous fishes strike at, capture, and process their prey in fundamentally different ways.

These hypotheses were investigated in Chapter four, through aquarium-based performance experiments. In this Chapter I found evidence that agreed with the inferences from Chapter two, showing the presence of two distinct functional groups: grabbers and engulfers. Grabbers and engulfers strike at, capture, and process their prey in fundamentally different ways. Furthermore, a metanalysis revealed that generally, these groups feed on different prey sizes. This Chapter builds on a plethora of studies (Wainwright 1988; Fulton 2007; Konow et al. 2008; Huertas & Bellwood 2017) which have utilised the tool of functional morphology following the framework of Wainwright and Reilly (1994) (i.e., morphological assessment → performance experiments to causally link to behaviour → ecological fitness). Basically, the identification of these functional groups through this framework, has opened up new avenues regarding the questions that can be asked in the field of piscivory on coral reefs.

By identifying the causal and mechanistic links between how and why an organism feeds, provides us with clues as to which realised niche axes they may differ across. For example, while acanthurids are broadly considered herbivores (what they feed on), an evaluation of their functional morphology and how they feed (e.g. Tebbett et al. 2017; Tebbett et al. 2018), has revealed differences in the microhabitats these fishes feed on (Brandl et al. 2015). In essence, by identifying 'how' fishes feed, provides us with a more nuanced 'what' when compared to broad trophic categories (planktivore, herbivore etc.). By identifying how piscivores feed, we can now begin to ask questions regarding potential ecological differences grounded in the different 'hows'.

Piscivorous coral reef fishes provide a perfect example for this. To date, piscivory on reefs has been quantified (through gut content analyses) primarily from a taxonomic perspective (Almany & Webster 2004; Albins & Hixon 2008), asking 'what species of prey has predator x fed on?'. By identifying functional groups of piscivores through aquarium-based experiments (i.e. identifying how), I found that the relative prey size, not the taxonomic identity of the prey, is an axis along which piscivores are separated. Previous work has demonstrated the importance of linking morphology, not only to what they feed on, but also how (Motta 1988; Brandl, Robbins & Bellwood 2015). This thesis, therefore, suggests that when conducting gut content analyses on piscivores, the relative prey size, not the prey identity, may be of greater importance.

This result led to the realisation, that the outcome of a predation event, may indeed be influenced by aspects of the prey as well, not only the predator. There was therefore a need to investigate the role of fishes as prey as well in these interactions.

### 7.2 Prey – not a reef full of fish flesh

Piscivory is a highly dynamic process, where the outcome of a piscivores' strike is highly uncertain, and primarily associated to the preys' ability to escape (Holmes & McCormick 2009; Holmes & McCormick 2010; Feeney et al. 2012). This appears to be related to the functional traits linked to the predator avoidance strategies of reef fishes. While reefs are teeming with small fishes, they may not all be equally available to all piscivores. Piscivory cannot be viewed as functionally the same between events (Chapter 5). It is highly context dependent, and depends on multiple factors such as the functional group of both the predator and prey involved, as well as the relative size of each individual.

Interestingly, the highest functional group diversity for prey groups was found for small-bodied reef fishes, with three functional groups found for reef fishes up to 50mm, and only two groups (social and epibenthic) found for prey fishes above 50mm (Chapter 5). Indeed, relatively few species with 'larger' maximum body sizes are found to be substratum dwellers (e.g. Synodontidae, Pinguipedidae, Platycephalidae). Substratum dwelling, thus, appears to be a strategy primarily associated with small body sizes for coral reef fishes. Small-bodied reef fishes have recently gained significant traction in the literature, through their identification as significant contributors in both biodiversity, ecological function, and being ideal aquatic organisms in testing ecological theories (Brandl et al. 2018; Huie et al. 2020; Doll et al. 2021; Majoris et al. 2021). As the majority of these species follow a substratum dwelling strategy, it seems pertinent to ask the question of how much this may have contributed to the establishment of these species on coral reefs. Fish lineages respond to predation through changes in both morphology (Brönmark & Miner 1992; Langerhans et al. 2004; Hemingson, Cowman & Bellwood 2020), and behaviour (Holmes & McCormick 2011; McCormick, Fakan & Allan 2018). It is therefore likely that by combining the morphology of a small body size and the behaviour of benthic 'sitting', may have sparked the evolutionary diversification of benthic substratum dwellers on coral reefs.

At this point of the thesis, we have functional groups of fishes within both predators and prey. The delineation of these groups allows a more nuanced perspective into the nature of predation, as well as how predation may be occurring on a coral reef. However, while the delineation of functional groups elucidates how predation occurs between a single predator and prey, it does not tell us how the process of predation occurs at a community level.

## 7.3 Piscivory on reefs – a community perspective

In my last data Chapter (Chapter 6), I investigated the process of piscivory at a community level. Due to the nature of piscivory, and the uncertainty of when and where it will occur, a new approach was required to investigate the dynamics of this process at such a scale. I therefore implemented principles from functional morphology which provide information as to what the animals are able to do (performance). By combining these, with community data and simulation-based approaches, I built a stepwise approach which incorporates functional morphology, performance, and behavioural traits at a community level.

New results have arisen from this thesis regarding the functional importance of small-bodied predators on coral reefs. 'Larger-bodied' piscivores are likely not required to perform to their maximal abilities as often, as there is a broad range of relatively smaller prey sizes on the reef for them to feed on with greater ease (Kingsford 1992; Ackerman & Bellwood 2000). Indeed, multiple studies have found that large predators continue feeding on relatively small prey sizes, even as 'large' individuals (Kingsford 1992; St. John 1999). However, cryptopredators may not necessarily have this option when feeding on fish, as there is a much narrower range of prey sizes they can feed on, given that their minimum prey size will be approaching the settlement size of fishes (Grutter et al. 2017), and thus, the smallest prey sizes available on the reef. Therefore, such predation events are more likely to be close to the maximal feeding capabilities of the cryptopredators (sensu Mihalitsis & Bellwood 2017), thus requiring them to perform feeding behaviours directly related to their maximal feeding abilities, and therefore directly linked to the functional group they belong to (Chapter 4). Functional groups of piscivorous fishes, may therefore be significantly more delineated, if this framework is to be investigated specifically for cryptopredators.

Basically, the process of piscivory on coral reefs, while studied for decades, is only now emerging as a process for which we have limited knowledge, in how it operates in such hyperdiverse ecosystems. The forces governing the composition and structuring of coral reef fish communities, have been studied for decades (Hamner et al. 1988; Sale 1993; Thibaut, Connolly & Sweatman 2012; Lefcheck et al. 2021). While fish predation has received significant attention in how it may influence biomass-related processes (Dulvy et al. 2004a; Graham et al. 2005; Sandin et al. 2008), its potential impacts on numerical-based processes (e.g. abundance) has received less attention. This thesis reveals that when investigated from a numerical approach, predation may operate in a different way than previously considered.

### 7.4 Piscivory in the future-the predation of tomorrow

This thesis also highlighted on how predator presence may be linked to other factors influencing community structure, such as abiotic environmental factors. For example, it is known that certain habitats (i.e., reef flat) on a reef are available to only certain fish morphotypes (Fulton, Bellwood & Wainwright 2005; Bellwood et al. 2018). These assemblages, dominated by fishes with high pectoral fin aspect ratios (functionally linked to swimming abilities), belong to the group of epibenthic fishes as prey. Other habitats, which may be dominated by a high number of schooling, reef-associated planktivores (e.g., crest or lagoon) belong to the social group of prey fishes. Therefore, due to environmental factors, the distribution of different sizes and types of prey fishes available, may not be homogeneous across a coral reef. This is likely to influence whether predators can be found at specific areas of the reef at specific times of the day (i.e., their spatial ecology). Also, depending on the different prey sizes available at each reef location, may determine where these predators need to be, at a given point in time, to find available food.

Fishing is one of the last remaining resources for which humans utilize hunting techniques in the wild. Despite this, however, technological advancements have tilted the scales of this human-nature interaction, resulting in massively overfished stocks worldwide. Indeed, research suggests that only 10% of pre-industrial stocks worldwide, still remain (Myers & Worm 2003). A common trait, for both coastal and oceanic fisheries worldwide, is the prioritization of large predatory fishes as a target, often resulting in local extinctions of this trophic level (Dulvy et al. 2004b; Valdivia, Cox & Bruno 2017), often termed 'fishing down the food chain' (Pauly et al. 1998). In this thesis I demonstrate that the 'typical' predators, which are the ones mostly studied and caught through fisheries, are not the ones carrying out most of the process (Chapter 6). In essence, the predators carrying out most piscivory on coral reefs, are significantly different from the ones caught through fisheries. Piscivory, as a process on coral reefs, may thus be at low risk regarding the disturbance of fisheries.

Lastly, structural complexity is decreasing on coral reefs, due to anthropogenic climate change (Hughes et al. 2017a; Hughes et al. 2017b; Zawada et al. 2019). Through the identification of functional groups of both predators and prey of coral reef fishes, this thesis allows us to investigate how this reduction of complexity may influence both predators and prey. For example, the relative strike distance of predators, as well as the distance of prey fishes from shelter, may both be dependent on, and thus altered, with a decrease of structural complexity.

This thesis also reveals a significant knowledge gap, as the fishes contributing mostly, to the main process of energy and nutrient transfer between fishes, are also the fishes we know least about (i.e. cryptobenthic fishes). Recent work has begun disentangling the life history of these fishes at the individual level (Brandl et al. 2020; Huie, Thacker & Tornabene 2020; Nickles et al. 2020; Majoris et al. 2021), as well as their role in large-scale coral reef processes (Brandl et al. 2018; Brandl et al. 2019). However, there is still a need to better understand the trophic ecology of cryptobenthic fishes, specifically the drivers governing their diet, as they may not be the same as those of larger coral reef fishes.

## 7.5 Conclusion

Overall, this thesis shines light on the direct interaction between coral reef predatory fishes and prey fishes. It answers the questions of 'who are the predators on a reef?', 'who do they feed on?', and 'how do they do it?'. By answering these fundamental questions, this thesis provides causal, mechanistic, links between the morphology and feeding behaviour of fish predators on coral reefs, a detailed quantification of the prey types they feed on, as well as a fundamentally different view of how this process operates on coral reef ecosystems. At the start of this thesis, a typical piscivore was a 30 cm serranid or lutjanid, considered to be feeding in broadly similar modes as any other fish – at the end, it is a 4 cm pseudochromid that grabs gobies. The predator size has shrunk, but the scope has expanded. I hope others share this enthusiasm of the world of fish with me, and that this thesis may help provide a foundation for future exciting work on reef fish predation.

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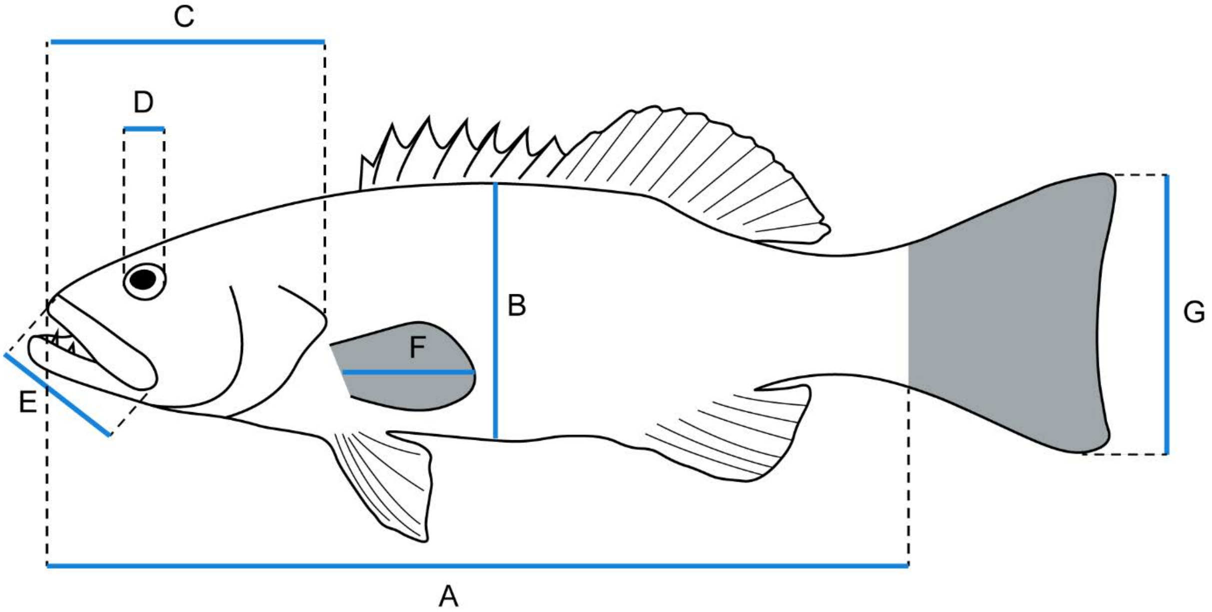
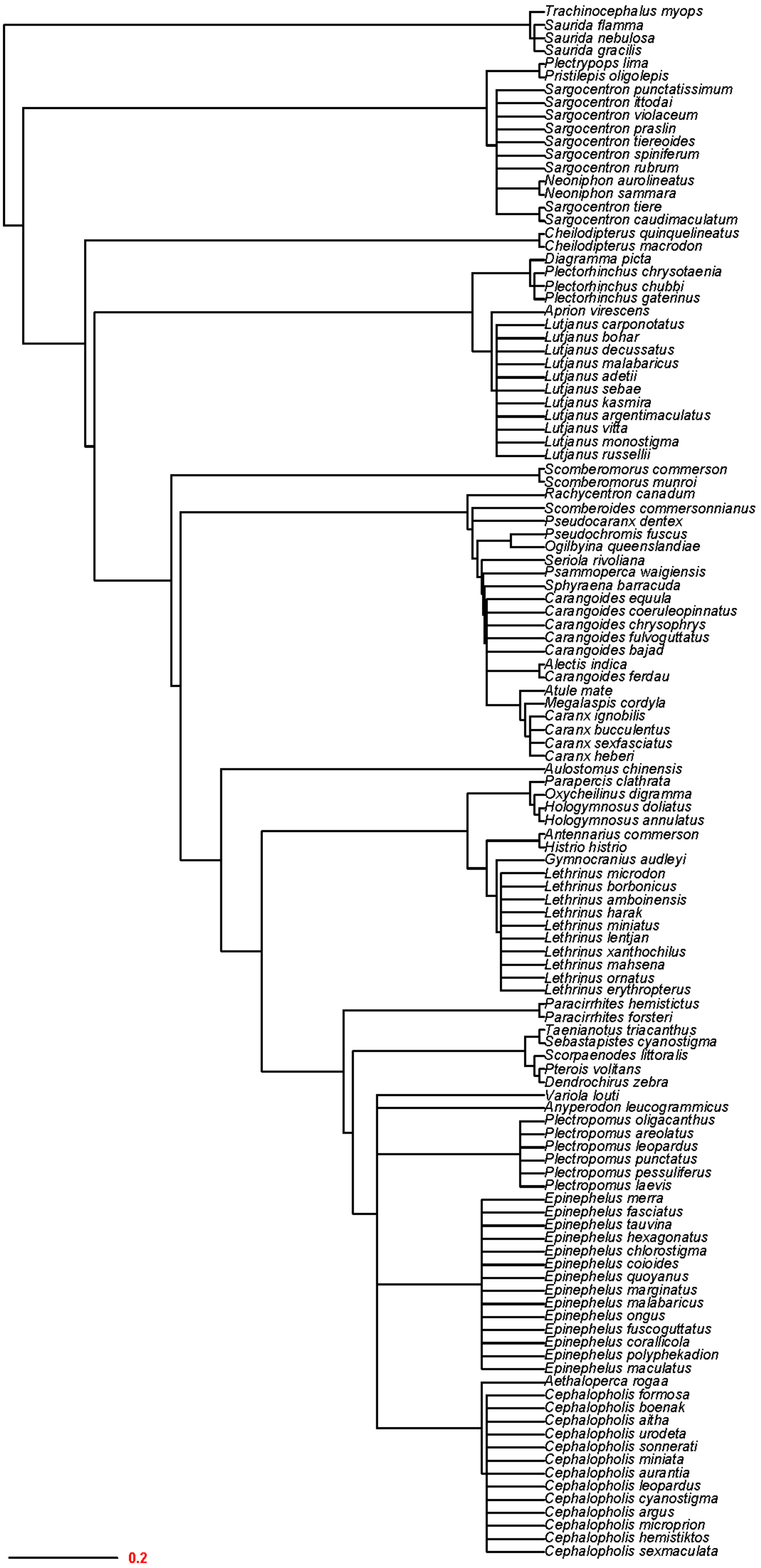
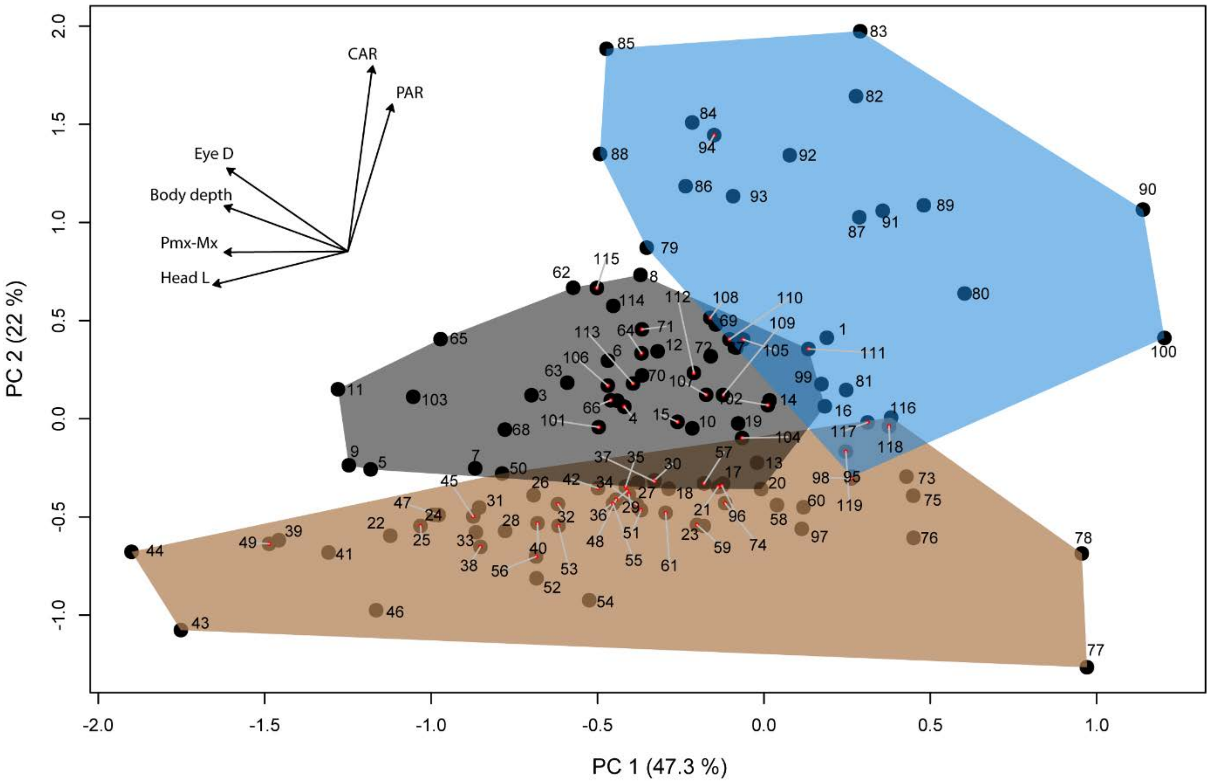
## Appendix A (Supplemental material for Chapter 2)



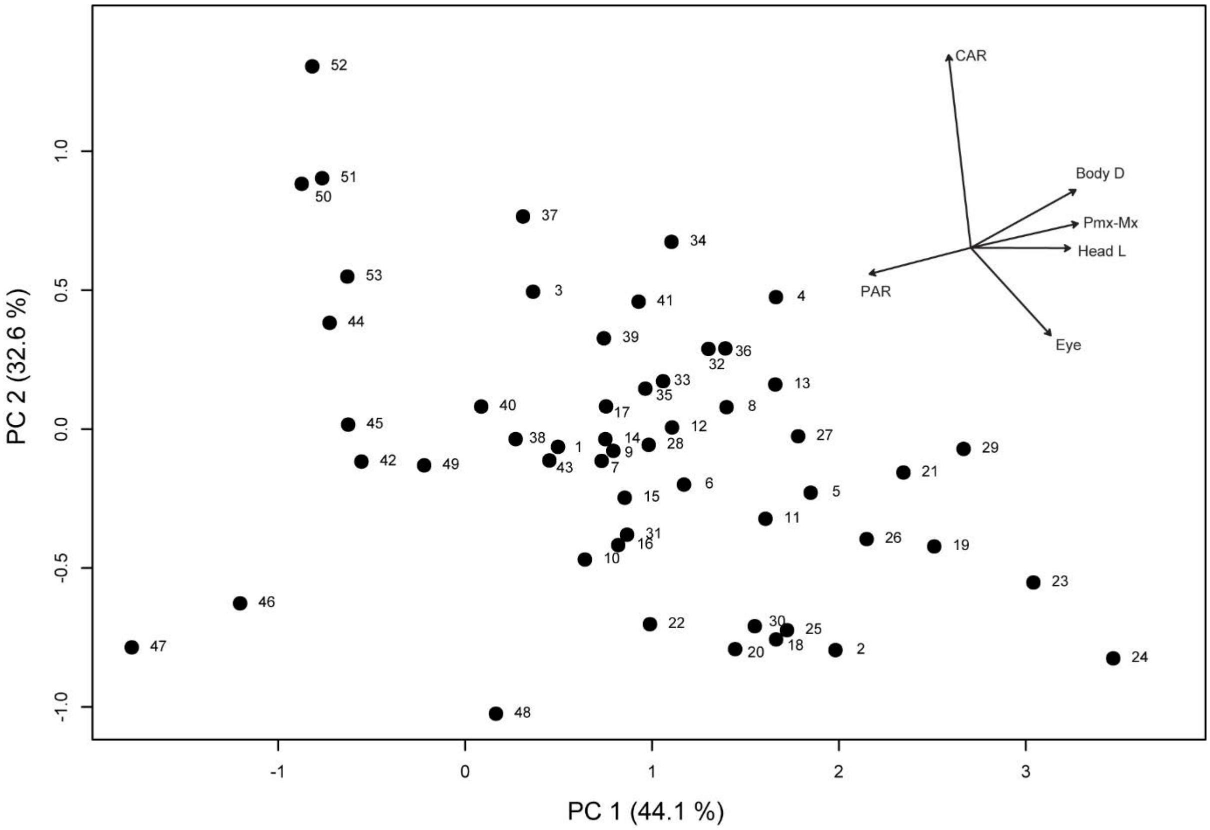
**Appendix A Fig. 1**. Morphological traits measured in my analysis: A) Standard length, B) Body depth, C) Head length, D) Eye diameter, E) Premaxilla-Maxilla length, F) Pectoral fin aspect ratio (fin length squared, divided by fin area), G) Caudal fin aspect ratio (fin height squared, divided by fin area).


Trachinocephalus myops
Saurida flamma
Saurida nebulosa
Saurida gracilis
Plectrypops lima
Pristilepis oligolepis
Sargocentron punctatissimum
Sargocentron ittodai
Sargocentron violaceum
Sargocentron praslin
Sargocentron tiereoides
Sargocentron spiniferum
Sargocentron rubrum
Neoniphon aurolineatus
Neoniphon sammara
Sargocentron tiere
Sargocentron caudimaculatum
Cheilodipterus quinquelineatus
Cheilodipterus macrodon
Diagramma picta
Plectorhinchus chrysotaenia
Plectorhinchus chubbi
Plectorhinchus gaterinus
Aprion virescens
Lutjanus carponotatus
Lutjanus bohar
Lutjanus decussatus
Lutjanus malabaricus
Lutjanus adetii
Lutjanus sebae
Lutjanus kasmira
Lutjanus argentimaculatus
Lutjanus vitta
Lutjanus monostigma
Lutjanus russellii
Scomberomorus commerson
Scomberomorus munroi
Rachycentron canadum
Scomberoides commersonnianus
Pseudocaranx dentex
Pseudochromis fuscus
Ogilbyina queenslandiae
Seriola rivoliana
Psammoperca waigiensis
Sphyraena barracuda
Carangoides equula
Carangoides coeruleopinnatus
Carangoides chrysophrys
Carangoides fulvoguttatus
Carangoides bajad
Alectis indica
Carangoides ferdau
Atule mate
Megalaspis cordyla
Caranx ignobilis
Caranx bucculentus
Caranx sexfasciatus
Caranx heberi
Aulostomus chinensis
Parapercis clathrata
Oxycheilinus digramma
Hologymnosus doliatus
Hologymnosus annulatus
Antennarius commerson
Histrio histrio
Gymnocranius audleyi
Lethrinus microdon
Lethrinus borbonicus
Lethrinus amboinensis
Lethrinus harak
Lethrinus miniatus
Lethrinus lentjan
Lethrinus xanthochilus
Lethrinus mahsena
Lethrinus ornatus
Lethrinus erythropterus
Paracirrhites hemistictus
Paracirrhites forsteri
Taenianotus triacanthus
Sebastapistes cyanostigma
Scorpaenodes littoralis
Pterois volitans
Dendrochirus zebra
Variola louti
Anyperodon leucogrammicus
Plectropomus oligacanthus
Plectropomus areolatus
Plectropomus leopardus
Plectropomus punctatus
Plectropomus pessuliferus
Plectropomus laevis
Epinephelus merra
Epinephelus fasciatus
Epinephelus tauvina
Epinephelus hexagonatus
Epinephelus chlorostigma
Epinephelus coioides
Epinephelus quoyanus
Epinephelus marginatus
Epinephelus malabaricus
Epinephelus ongus
Epinephelus fuscoguttatus
Epinephelus corallicola
Epinephelus polyphekadion
Epinephelus maculatus
Aethaloperca rogaa
Cephalopholis formosa
Cephalopholis boenak
Cephalopholis aitha
Cephalopholis urodeta
Cephalopholis sonnerati
Cephalopholis miniata
Cephalopholis aurantia
Cephalopholis leopardus
Cephalopholis cyanostigma
Cephalopholis argus
Cephalopholis microprion
Cephalopholis hemistiktos
Cephalopholis sexmaculata
0.2

**Appendix A Fig. 2**. Phylogenetic tree used in my analysis.



**Appendix A Fig. 3.** Ecomorphotype Phylogenetic Principal Component Analysis (PPCA), with numbered data points. Numbers represent following species: *[1]Aprion virescens, [2]Lutjanus russellii, [3]Lutjanus monostigma, [4]Lutjanus vitta, [5]Lutjanus argentimaculatus, [6]Lutjanus kasmira, [7]Lutjanus sebae, [8]Lutjanus adetii, [9]Lutjanus malabaricus, [10]Lutjanus decussatus, [11]Lutjanus bohar, [12]Lutjanus carponotatus, [13]Diagramma picta, [14]Plectorhinchus gaterinus, [15]Plectorhinchus chubby, [16]Plectorhinchus chrysotaenia, [17]Scorpaenodes littoralis, [18]Dendrochirus zebra, [19]Pterois volitans, [20]Sebastapistes cyanostigma, [21]Taenianotus triacanthus, [22]Anyperodon leucogrammicus, [23]Variola louti, [24]Aethaloperca rogaa, [25]Cephalopholis sexmaculata, [26]Cephalopholis hemistiktos, [27]Cephalopholis microprion, [28]Cephalopholis argus, [29]Cephalopholis cyanostigma, [30]Cephalopholis leopardus, [31]Cephalopholis aurantia, [32]Cephalopholis miniate, [33]Cephalopholis sonnerati, [34]Cephalopholis urodeta, [35]Cephalopholis aitha, [36]Cephalopholis boenak, [37]Cephalopholis formosa, [38]Epinephelus maculatus, [39]Epinephelus polyphekadion, [40]Epinephelus corallicola, [41]Epinephelus fuscoguttatus, [42]Epinephelus ongus, [43]Epinephelus malabaricus, [44]Epinephelus marginatus, [45]Epinephelus quoyanus, [46]Epinephelus coioides, [47]Epinephelus chlorostigma, [48]Epinephelus hexagonatus, [49]Epinephelus tauvina, [50]Epinephelus fasciatus, [51]Epinephelus* *merra, [52]Plectropomus laevis, [53]Plectropomus pessuliferus, [54]Plectropomus punctatus, [55]Plectropomus leopardus, [56]Plectropomus areolatus, [57]Plectropomus oligacanthus, [58]Paracirrhites forsteri, [59]Paracirrhites hemistictus, [60]Histrio histrio, [61]Antennarius commerson, [62]Gymnocranius audleyi, [63]Lethrinus erythropterus, [64]Lethrinus ornatus, [65]Lethrinus mahsena, [66]Lethrinus xanthochilus, [67]Lethrinus lentjan, [68]Lethrinus miniatus, [69]Lethrinus harak, [70]Lethrinus amboinensis, [71]Lethrinus borbonicus, [72]Lethrinus microdon, [73]Parapercis clathrate, [74]Oxycheilinus digramma, [75]Hologymnosus annulatus, [76]Hologymnosus doliatus, [77]Aulostomus chinensis, [78]Rachycentron canadum, [79]Pseudocaranx dentex, [80]Scomberoides commersonnianus, [81]Seriola rivoliana, [82]Carangoides bajad, [83]Carangoides fulvoguttatus, [84]Carangoides chrysophrys, [85]Carangoides coeruleopinnatus, [86]Carangoides equula, [87]Carangoides ferdau, [88]Alectis indica, [89]Atule mate, [90]Megalaspis cordyla, [91]Caranx heberi, [92]Caranx sexfasciatus, [93]Caranx bucculentus, [94]Caranx ignobilis, [95]Sphyraena barracuda", [96]Psammoperca waigiensis, [97]Ogilbyina queenslandiae, [98]Pseudochromis fuscus, [99]Scomberomorus munroi, [100]Scomberomorus commerson, [101]Cheilodipterus macrodon, [102]Cheilodipterus quinquelineatus, [103]Pristilepis oligolepis, [104]Plectrypops lima, [105]Sargocentron rubrum, [106]Sargocentron spiniferum, [107]Sargocentron tiereoides, [108]Sargocentron Praslin, [109]Sargocentron violaceum, [110]Sargocentron ittodai, [111]Sargocentron punctatissimum, [112]Sargocentron caudimaculatum, [113]Sargocentron tiere, [114]Neoniphon samara, [115]Neoniphon aurolineatus, [116]Trachinocephalus myops, [117]Saurida gracilis, Saurida nebulosi, [119]Saurida flamma.*



**Appendix A Fig. 4.** Benthic piscivores Phylogenetic Principal Component Analysis (PPCA), with numbered data point. Numbers represent following species: *[1]Taenianotus triacanthus, [2]Anyperodon leucogrammicus, [3]Variola louti, [4]Aethaloperca rogaa, [5]Cephalopholis sexmaculata, Cephalopholis hemistiktos, [7]Cephalopholis microprion, [8]Cephalopholis argus, [9]Cephalopholis cyanostigma, [10]Cephalopholis leopardus, [11]Cephalopholis aurantia, [12]Cephalopholis miniate, [13]Cephalopholis sonnerati, [14]Cephalopholis urodeta, [15]Cephalopholis aitha, Cephalopholis boenak, [17]Cephalopholis formosa, [18]Epinephelus maculatus, [19]Epinephelus polyphekadion, [20]Epinephelus corallicola, [21]Epinephelus fuscoguttatus, [22]Epinephelus ongus, [23]Epinephelus malabaricus, [24]Epinephelus marginatus, [26]Epinephelus quoyanus, [27]Epinephelus coioides, [27]Epinephelus chlorostigma, [28]Epinephelus hexagonatus, [29]Epinephelus tauvina, [30]Epinephelus fasciatus, [31]Epinephelus merra, [32]Plectropomus laevis, [33]Plectropomus pessuliferus, [34]Plectropomus punctatus, [35]Plectropomus leopardus, [36]Plectropomus areolatus, [37]Plectropomus oligacanthus, [38]Paracirrhites forsteri, [39]Paracirrhites hemistictus, [40]Histrio histrio, [41]Antennarius commerson, [42]Parapercis clathrata, [43]Oxycheilinus digramma, [44]Hologymnosus annulatus, [45]Hologymnosus doliatus, [46]Aulostomus chinensis, [47]Rachycentron canadum, [48]Ogilbyina queenslandiae, [49]Pseudochromis fuscus, [50]Trachinocephalus myops, [51]Saurida gracilis, [52]Saurida nebulosa, [53]Saurida flamma*.

**Appendix A Table 1**. All Phylogenetic Least Squares (PGLS) models conducted.

| **Variable** | **Level** | **Model** | **lambda** | **AIC** | **Estimate** | **St. Error** | **t-value** | **p-value** |
|---|---|---|---|---|---|---|---|---|
| pmx-mx | Benthic (Intercept) | Brownian | | 757.903 | 0.167 | 7.934 | 0.021 | 0.983 |
| | Nocturnal | | | | -0.121 | 1.919 | -0.063 | 0.949 |
| | Pelagic | | | | -0.788 | 3.393 | -0.232 | 0.816 |
| pmx-mx | Benthic (Intercept) | Pagels' | 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) | Brownian | | 921.301 | 0.458 | 15.763 | 0.029 | 0.976 |
| | Nocturnal | | | | 0.254 | 3.813 | 0.066 | 0.947 |
| | Pelagic | | | | -4.221 | 6.742 | -0.626 | 0.532 |
| head length | Benthic (Intercept) | Pagels' | 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) | Brownian | | 215.699 | -0.411 | 0.813 | -0.506 | 0.614 |
| | Nocturnal | | | | 0.179 | 0.196 | 0.913 | 0.363 |
| | Pelagic | | | | 2.357 | 0.347 | 6.779 | <0.001 |
| caudal AR | Benthic (Intercept) | Pagels' | 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) | Brownian | | 413.311 | -0.465 | 1.865 | -0.249 | 0.803 |
| | Nocturnal | | | | 0.393 | 0.451 | 0.872 | 0.384 |
| | Pelagic | | | | 1.999 | 0.797 | 2.506 | 0.014 |
| pectoral AR | Benthic (Intercept) | Pagels' | 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) | Brownian | | 1081.163 | 0.741 | 30.857 | 0.024 | 0.981 |
| | Nocturnal | | | | -2.634 | 7.465 | -0.353 | 0.725 |
| | Pelagic | | | | 3.848 | 13.199 | 0.291 | 0.771 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| body depth | Benthic (Intercept) | Pagels' | 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) | Brownian | | 639.247 | -1.623 | 4.819 | -0.337 | 0.737 |
| | Nocturnal | | | | 2.578 | 1.165 | 2.212 | 0.029 |
| | Pelagic | | | | 2.752 | 2.06 | 1.335 | 0.184 |
| eye size | Benthic (Intercept) | Pagels' | 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 |

**Appendix A Table 2**. Ecomorphotype classifications for each species used in my analysis

| **Species** | **Ecomorphotype** |
|---|---|
| *Aethaloperca rogaa* | Benthic |
| *Alectis indica* | Pelagic |
| *Antennarius commerson* | Benthic |
| *Anyperodon leucogrammicus* | Benthic |
| *Aprion virescens* | Pelagic |
| *Atule mate* | Pelagic |
| *Aulostomus chinensis* | Benthic |
| *Carangoides bajad* | Pelagic |
| *Carangoides coeruleopinnatus* | Pelagic |
| *Carangoides chrysophrys* | Pelagic |
| *Carangoides equula* | Pelagic |
| *Carangoides ferdau* | Pelagic |
| *Carangoides fulvoguttatus* | Pelagic |
| *Caranx bucculentus* | Pelagic |
| *Caranx heberi* | Pelagic |
| *Caranx ignobilis* | Pelagic |
| *Caranx sexfasciatus* | Pelagic |
| *Cephalopholis aitha* | Benthic |
| *Cephalopholis argus* | Benthic |
| *Cephalopholis aurantia* | Benthic |

| | |
|---|---|
| *Cephalopholis boenak* | Benthic |
| *Cephalopholis cyanostigma* | Benthic |
| *Cephalopholis formosa* | Benthic |
| *Cephalopholis hemistiktos* | Benthic |
| *Cephalopholis leopardus* | Benthic |
| *Cephalopholis microprion* | Benthic |
| *Cephalopholis miniata* | Benthic |
| *Cephalopholis sexmaculata* | Benthic |
| *Cephalopholis sonnerati* | Benthic |
| *Cephalopholis urodeta* | Benthic |
| *Cheilodipterus macrodon* | Nocturnal |
| *Cheilodipterus quinquelineatus* | Nocturnal |
| *Dendrochirus zebra* | Nocturnal |
| *Diagramma picta* | Nocturnal |
| *Epinephelus chlorostigma* | Benthic |
| *Epinephelus coioides* | Benthic |
| *Epinephelus corallicola* | Benthic |
| *Epinephelus fasciatus* | Benthic |
| *Epinephelus fuscoguttatus* | Benthic |
| *Epinephelus hexagonatus* | Benthic |
| *Epinephelus maculatus* | Benthic |
| *Epinephelus malabaricus* | Benthic |
| *Epinephelus marginatus* | Benthic |
| *Epinephelus merra* | Benthic |
| *Epinephelus ongus* | Benthic |
| *Epinephelus polyphekadion* | Benthic |
| *Epinephelus quoyanus* | Benthic |
| *Epinephelus tauvina* | Benthic |
| *Gymnocranius audleyi* | Nocturnal |
| *Histrio histrio* | Benthic |
| *Hologymnosus annulatus* | Benthic |
| *Hologymnosus doliatus* | Benthic |
| *Lethrinus amboinensis* | Nocturnal |
| *Lethrinus borbonicus* | Nocturnal |

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|---|---|
| *Lethrinus erythropterus* | Nocturnal |
| *Lethrinus harak* | Nocturnal |
| *Lethrinus lentjan* | Nocturnal |
| *Lethrinus mahsena* | Nocturnal |
| *Lethrinus microdon* | Nocturnal |
| *Lethrinus miniatus* | Nocturnal |
| *Lethrinus ornatus* | Nocturnal |
| *Lethrinus xanthochilus* | Nocturnal |
| *Lutjanus adetii* | Nocturnal |
| *Lutjanus argentimaculatus* | Nocturnal |
| *Lutjanus bohar* | Nocturnal |
| *Lutjanus carponotatus* | Nocturnal |
| *Lutjanus decussatus* | Nocturnal |
| *Lutjanus kasmira* | Nocturnal |
| *Lutjanus malabaricus* | Nocturnal |
| *Lutjanus monostigma* | Nocturnal |
| *Lutjanus russellii* | Nocturnal |
| *Lutjanus sebae* | Nocturnal |
| *Lutjanus vitta* | Nocturnal |
| *Megalaspis cordyla* | Pelagic |
| *Neoniphon aurolineatus* | Nocturnal |
| *Neoniphon sammara* | Nocturnal |
| *Ogilbyina queenslandiae* | Benthic |
| *Oxycheilinus digramma* | Benthic |
| *Paracirrhites forsteri* | Benthic |
| *Paracirrhites hemistictus* | Benthic |
| *Parapercis clathrata* | Benthic |
| *Plectorhinchus chrysotaenia* | Nocturnal |
| *Plectorhinchus chubbi* | Nocturnal |
| *Plectorhinchus gaterinus* | Nocturnal |
| *Plectropomus areolatus* | Benthic |
| *Plectropomus laevis* | Benthic |
| *Plectropomus leopardus* | Benthic |
| *Plectropomus oligacanthus* | Benthic |

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|---|---|
| *Plectropomus pessuliferus* | Benthic |
| *Plectropomus punctatus* | Benthic |
| *Plectrypops lima* | Nocturnal |
| *Pristilepis oligolepis* | Nocturnal |
| *Psammoperca waigiensis* | Nocturnal |
| *Pseudocaranx dentex* | Pelagic |
| *Pseudochromis fuscus* | Benthic |
| *Pterois volitans* | Nocturnal |
| *Rachycentron canadum* | Benthic |
| *Sargocentron caudimaculatum* | Nocturnal |
| *Sargocentron ittodai* | Nocturnal |
| *Sargocentron praslin* | Nocturnal |
| *Sargocentron punctatissimum* | Nocturnal |
| *Sargocentron rubrum* | Nocturnal |
| *Sargocentron spiniferum* | Nocturnal |
| *Sargocentron tiere* | Nocturnal |
| *Sargocentron tiereoides* | Nocturnal |
| *Sargocentron violaceum* | Nocturnal |
| *Saurida flamma* | Benthic |
| *Saurida gracilis* | Benthic |
| *Saurida nebulosa* | Benthic |
| *Scomberoides commersonnianus* | Pelagic |
| *Scomberomorus commerson* | Pelagic |
| *Scomberomorus munroi* | Pelagic |
| *Scorpaenodes littoralis* | Nocturnal |
| *Sebastapistes cyanostigma* | Nocturnal |
| *Seriola rivoliana* | Pelagic |
| *Sphyraena barracuda* | Pelagic |
| *Taenianotus triacanthus* | Benthic |
| *Trachinocephalus myops* | Benthic |
| *Variola louti* | Benthic |

**Appendix A Table 3**. Raw data of species used in my analysis. Standard Length (SL), Dody depth, eye diameter (eye D), Premaxilla-Maxilla length (Pmx-Mx), and head length (head L), are presented in millimetres (mm).

| **Species** | **SL** | **Body depth** | **caudal AR** | **eye D** | **Pmx-Mx** | **head L** | **pectoral AR** |
|---|---|---|---|---|---|---|---|
| *Aethaloperca rogaa* | 276 | 120.506 | 1.693 | 12.497 | 47.31 | 91.408 | 2.311 |
| *Aethaloperca rogaa* | 295 | 124.555 | 1.908 | 13.144 | 50.762 | 102.862 | 2.230 |
| *Alectis indicus* | 256 | 161.032 | 3.854 | 20.854 | 29.096 | 74.934 | 7.932 |
| *Alectis indicus* | 173 | 117.534 | 3.107 | 13.213 | 20.163 | 53.045 | 5.396 |
| *Alectis indicus* | 245 | 145.7 | 4.826 | 17.564 | 24.825 | 74.581 | 7.862 |
| *Antennarius commerson* | 62 | 44.366 | 1.329 | 3.474 | 9.047 | 18.84 | 0.888 |
| *Antennarius commerson* | 86 | 52.986 | 1.359 | 4.74 | 7.793 | 24.834 | 0.706 |
| *Antennarius commerson* | 89 | 56.582 | 1.641 | 4.537 | 16.485 | 27.753 | 0.751 |
| *Antennarius commerson* | 135 | 95 | 1.377 | 3.18 | 21.427 | 47.456 | 0.635 |
| *Antennarius commerson* | 154 | 120.229 | 1.592 | 9.037 | 27.38 | 58.01 | 0.891 |
| *Anyperodon leucogrammicus* | 242 | 70.986 | 1.368 | 15.411 | 43.657 | 91.765 | 2.441 |
| *Anyperodon leucogrammicus* | 305 | 87.831 | 1.476 | 19.836 | 51.705 | 119.391 | 1.996 |
| *Aprion virescens* | 339 | 84.093 | 4.486 | 16.86 | 35.775 | 94.229 | 2.884 |
| *Atule mate* | 183.5 | 54.552 | 3.644 | 11.966 | 19.845 | 47.089 | 9.122 |
| *Atule mate* | 211.8 | 62.054 | 3.732 | 12.356 | 22.055 | 56.348 | 8.588 |
| *Atule mate* | 220.8 | 61.079 | 3.288 | 11.638 | 19.776 | 58.596 | 6.519 |
| *Aulostomus chinensis* | 165 | 10.529 | 1.107 | 5.518 | 6.552 | 56.488 | 1.511 |
| *Aulostomus chinensis* | 375 | 31.513 | 1.768 | 9.968 | 17.997 | 118.347 | 1.052 |
| *Aulostomus chinensis* | 440 | 37.069 | 1.294 | 11.899 | 24.183 | 144.158 | 1.184 |
| *Carangoides bajad* | 196 | 70.875 | 4.378 | 10.52 | 21.793 | 54.25 | 5.945 |
| *Carangoides bajad* | 234 | 84.862 | 6.161 | 15.149 | 24.763 | 72.511 | 10.283 |
| *Carangoides bajad* | 358 | 128.671 | 5.005 | 17.278 | 34.654 | 98.207 | 9.352 |
| *Carangoides caeruleopinnatus* | 203.7 | 95.627 | 5.526 | 20.695 | 27.842 | 64.225 | 7.144 |
| *Carangoides caeruleopinnatus* | 261.9 | 118.496 | 5.756 | 21.47 | 32.83 | 82.326 | 7.978 |
| *Carangoides caeruleopinnatus* | 255.3 | 121.113 | 4.517 | 20.155 | 32.025 | 78.264 | 8.643 |
| *Carangoides chrysophrys* | 234 | 89.704 | 3.646 | 17.97 | 28.32 | 73.48 | 8.612 |
| *Carangoides chrysophrys* | 247 | 104.713 | 5.363 | 17.968 | 29.645 | 75.312 | 7.320 |
| *Carangoides equula* | 412 | 137.673 | 4.846 | 23.061 | 45.651 | 117.61 | 7.027 |
| *Carangoides equula* | 430 | 141.538 | 5.303 | 24.578 | 45.937 | 127.778 | 6.498 |
| *Carangoides ferdau* | 199.8 | 85.193 | 3.789 | 5.277 | 21.091 | 56.103 | 7.855 |
| *Carangoides ferdau* | 214.3 | 96.752 | 3.507 | 14.51 | 18.904 | 52.818 | 7.730 |
| *Carangoides ferdau* | 187.6 | 80.558 | 3.165 | 11.8711 | 19.373 | 53.484 | 6.881 |
| *Carangoides fulvoguttatus* | 310 | 104.486 | 5.326 | 18.734 | 33.295 | 91.823 | 8.165 |
| *Carangoides fulvoguttatus* | 345.3 | 116.188 | 7.050 | 23.194 | 35.236 | 99.176 | 9.751 |
| *Carangoides fulvoguttatus* | 505 | 148.424 | 6.343 | 21.26 | 47.43 | 126.081 | 10.362 |

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|---|---|---|---|---|---|---|---|
| *Caranx bucculentus* | 120 | 53.7 | 3.193 | 11.057 | 20.058 | 41.099 | 6.608 |
| *Caranx bucculentus* | 132 | 59.123 | 5.881 | 11.291 | 17.092 | 43.11 | 5.931 |
| *Caranx bucculentus* | 133 | 59.111 | 2.977 | 10.826 | 17.966 | 40.923 | 5.481 |
| *Caranx bucculentus* | 150 | 67.621 | 4.563 | 12.822 | 20.742 | 46.578 | 5.178 |
| *Caranx bucculentus* | 159 | 68.565 | 3.180 | 14.189 | 22.999 | 49.355 | 6.088 |
| *Caranx heberi* | 330.9 | 112.7 | 3.747 | 15.734 | 35.146 | 89.132 | 9.009 |
| *Caranx heberi* | 564.8 | 160.852 | 4.091 | 24.082 | 55.833 | 150.253 | 11.092 |
| *Caranx ignobilis* | 244 | 111.599 | 4.792 | 14.455 | 30.952 | 70.598 | 7.499 |
| *Caranx ignobilis* | 253 | 95.126 | 4.088 | 17.426 | 33.383 | 74.341 | 8.670 |
| *Caranx sexfasciatus* | 195.2 | 70.399 | 4.013 | 15.16 | 26.567 | 56.277 | 8.423 |
| *Caranx sexfasciatus* | 358 | 109.45 | 3.812 | 22.523 | 38.42 | 90.493 | 9.206 |
| *Cephalopholis aitha* | 86 | 28.921 | 1.496 | 7.563 | 16.51 | 35.693 | 2.278 |
| *Cephalopholis aitha* | 141 | 47.408 | 1.407 | 10.573 | 27.449 | 57.951 | 1.799 |
| *Cephalopholis argus* | 212 | 61.624 | 1.755 | 10.835 | 37.729 | 80.895 | 1.753 |
| *Cephalopholis argus* | 232 | 76.235 | 1.555 | 11.779 | 42.819 | 91.721 | 2.066 |
| *Cephalopholis aurantia* | 190 | 73.268 | 1.417 | 13.054 | 34.755 | 74.904 | 2.200 |
| *Cephalopholis aurantia* | 199 | 79.862 | 1.322 | 12.861 | 32.209 | 78.948 | 2.207 |
| *Cephalopholis aurantia* | 222 | 79.793 | 1.663 | 14.67 | 36.139 | 83.61 | 1.821 |
| *Cephalopholis aurantia* | 235 | 85.865 | 1.697 | 15.233 | 37.998 | 86.141 | 1.642 |
| *Cephalopholis boenak* | 117 | 39.252 | 1.207 | 8.713 | 20.541 | 41.541 | 2.648 |
| *Cephalopholis boenak* | 129 | 45.748 | 1.237 | 8.406 | 22.634 | 47.808 | 2.544 |
| *Cephalopholis boenak* | 137 | 47.729 | 1.465 | 11.084 | 24.642 | 50.823 | 2.135 |
| *Cephalopholis boenak* | 165 | 63.666 | 1.504 | 11.72 | 28.034 | 62.01 | 1.665 |
| *Cephalopholis cyanostigma* | 165 | 59.172 | 1.283 | 9.822 | 30.955 | 62.567 | 2.360 |
| *Cephalopholis cyanostigma* | 93 | 31.808 | 1.488 | 6.426 | 17.349 | 34.798 | 2.050 |
| *Cephalopholis cyanostigma* | 100 | 32.226 | 1.664 | 7.756 | 18.017 | 38.87 | 2.383 |
| *Cephalopholis cyanostigma* | 140 | 53.586 | 1.444 | 8.334 | 25.44 | 52.74 | 2.174 |
| *Cephalopholis cyanostigma* | 206 | 76.374 | 1.587 | 11.406 | 35.954 | 74.466 | 1.715 |
| *Cephalopholis formosa* | 108 | 37.818 | 1.581 | 7.85 | 17.907 | 41.818 | 1.847 |
| *Cephalopholis formosa* | 135 | 49.968 | 1.721 | 9.801 | 23.16 | 52.159 | 1.800 |
| *Cephalopholis hemistiktos* | 120 | 39.351 | 1.455 | 9.383 | 21.433 | 45.195 | 2.803 |
| *Cephalopholis hemistiktos* | 263 | 97.344 | 1.597 | 13.9 | 47.704 | 99.052 | 2.270 |
| *Cephalopholis leopardus* | 87 | 30.789 | 1.459 | 7.084 | 15.841 | 35.026 | 2.007 |
| *Cephalopholis leopardus* | 92 | 34.007 | 1.068 | 8.102 | 16.843 | 36.436 | 2.341 |
| *Cephalopholis leopardus* | 110 | 39.515 | 1.310 | 8.807 | 20.229 | 44.854 | 2.346 |
| *Cephalopholis leopardus* | 120 | 42.745 | 1.327 | 10.294 | 24.037 | 50.196 | 3.102 |
| *Cephalopholis microprion* | 93 | 33.759 | 1.502 | 7.127 | 17.259 | 37.51 | 2.311 |
| *Cephalopholis microprion* | 123 | 46.506 | 1.562 | 8.84 | 22.063 | 46.976 | 1.851 |
| *Cephalopholis microprion* | 147 | 54.048 | 1.407 | 9.462 | 27.623 | 59.517 | 2.651 |
| *Cephalopholis miniata* | 106 | 37.681 | 1.488 | 8.518 | 19.749 | 43.316 | 2.849 |
| *Cephalopholis miniata* | 165 | 56.803 | 1.703 | 10.406 | 27.468 | 62.213 | 2.321 |
| *Cephalopholis miniata* | 204 | 73.629 | 1.461 | 13.577 | 35.106 | 79.709 | 2.246 |

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|---|---|---|---|---|---|---|---|
| *Cephalopholis miniata* | 212 | 73.385 | 1.721 | 10.283 | 38.915 | 85.615 | 2.068 |
| *Cephalopholis miniata* | 254 | 93.717 | 1.639 | 9.986 | 39.608 | 92.841 | 1.681 |
| *Cephalopholis sexmaculata* | 200 | 75 | 1.564 | 12.29 | 34.868 | 77.632 | 2.005 |
| *Cephalopholis sexmaculata* | 256 | 93.836 | 1.558 | 14.831 | 52.208 | 105.68 | 1.796 |
| *Cephalopholis sexmaculata* | 263 | 94.611 | 1.455 | 14.781 | 41.988 | 94.611 | 2.138 |
| *Cephalopholis sonnerati* | 208 | 81.569 | 1.635 | 14.339 | 37.503 | 77.49 | 1.488 |
| *Cephalopholis sonnerati* | 215 | 92.54 | 1.759 | 10.644 | 41.193 | 79.32 | 1.369 |
| *Cephalopholis sonnerati* | 233 | 83.85 | 1.538 | 11.351 | 38.335 | 77.172 | 1.857 |
| *Cephalopholis sonnerati* | 280 | 111.821 | 1.425 | 13.626 | 39.402 | 91.246 | 1.685 |
| *Cephalopholis sonnerati* | 330 | 137.143 | 1.888 | 13.97 | 56.145 | 112.5 | 1.321 |
| *Cephalopholis urodeta* | 129 | 42.88 | 1.409 | 10.153 | 23.391 | 51.484 | 2.192 |
| *Cephalopholis urodeta* | 130 | 45.59 | 1.290 | 7.482 | 22.626 | 48.299 | 2.139 |
| *Cephalopholis urodeta* | 139 | 46.609 | 1.498 | 7.88 | 23.504 | 50.287 | 2.111 |
| *Cephalopholis urodeta* | 153 | 50.605 | 1.470 | 8.192 | 26.229 | 53.49 | 2.179 |
| *Cephalopholis urodeta* | 223 | 78.931 | 1.844 | 9.242 | 38.086 | 82.31 | 1.896 |
| *Cheilodipterus macrodon* | 113 | 33.25 | 1.756 | 11.538 | 17.684 | 38.562 | 2.075 |
| *Cheilodipterus macrodon* | 133 | 40.427 | 2.181 | 13.647 | 24.276 | 46.382 | 2.312 |
| *Cheilodipterus macrodon* | 159 | 48.058 | 2.098 | 17.417 | 29.804 | 60.233 | 1.946 |
| *Cheilodipterus quinquelineatus* | 55 | 14.838 | 1.816 | 6.532 | 9.54 | 20.971 | 3.182 |
| *Cheilodipterus quinquelineatus* | 74 | 21.065 | 1.880 | 9.21 | 14.032 | 25.077 | 3.103 |
| *Dendrochirus zebra* | 99 | 34.21 | 1.132 | 10.179 | 15.19 | 35.851 | 2.079 |
| *Dendrochirus zebra* | 110 | 41.095 | 1.199 | 10.413 | 16.897 | 42.574 | 1.963 |
| *Diagramma pictum* | 194 | 74.014 | 2.185 | 12.593 | 15.198 | 52.372 | 2.189 |
| *Diagramma pictum* | 210 | 81.144 | 1.852 | 14.842 | 15.203 | 60.915 | 1.994 |
| *Diagramma pictum* | 242 | 91.2 | 2.195 | 14.943 | 17.292 | 62.133 | 2.617 |
| *Diagramma pictum* | 352 | 135.978 | 2.170 | 19.233 | 26.672 | 94.628 | 2.907 |
| *Diagramma pictum* | 504 | 180.024 | 2.446 | 25.068 | 39.748 | 149.095 | 2.042 |
| *Epinephelus chlorostigma* | 290 | 96.99 | 1.922 | 15.549 | 42.51 | 100.87 | 1.784 |
| *Epinephelus chlorostigma* | 327 | 108.344 | 1.916 | 20.329 | 50.309 | 118.943 | 2.205 |
| *Epinephelus coioides* | 175 | 54.725 | 1.383 | 9.021 | 31.19 | 67.354 | 1.525 |
| *Epinephelus coioides* | 196 | 56.551 | 1.702 | 9.725 | 28.918 | 71.331 | 1.169 |
| *Epinephelus coioides* | 323 | 88.957 | 1.422 | 16.745 | 50.855 | 124.964 | 1.301 |
| *Epinephelus coioides* | 330 | 98.571 | 1.123 | 17.96 | 55.56 | 136.071 | 1.716 |
| *Epinephelus coioides* | 688 | 213.118 | 1.502 | 24.761 | 105.68 | 266.397 | 1.676 |
| *Epinephelus corallicola* | 147 | 48.349 | 1.446 | 9.767 | 21.422 | 52.744 | 1.675 |
| *Epinephelus corallicola* | 197 | 66.736 | 1.148 | 14.015 | 28.503 | 71.87 | 1.809 |
| *Epinephelus corallicola* | 201 | 64.752 | 1.266 | 15.082 | 28.972 | 79.591 | 1.655 |
| *Epinephelus corallicola* | 235 | 83.929 | 1.288 | 18.384 | 36.111 | 94.32 | 1.566 |
| *Epinephelus fasciatus* | 153 | 47.264 | 1.638 | 15.478 | 22.881 | 56.035 | 2.482 |
| *Epinephelus fasciatus* | 155 | 49 | 1.614 | 13.124 | 25.715 | 58 | 2.372 |
| *Epinephelus fasciatus* | 183 | 57 | 1.570 | 19.433 | 30.364 | 78.6 | 1.714 |
| *Epinephelus fasciatus* | 213 | 70.754 | 1.442 | 18.791 | 32.737 | 84.021 | 1.879 |

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|---|---|---|---|---|---|---|---|
| *Epinephelus fasciatus* | 218 | 74.351 | 1.636 | 17.828 | 33.307 | 81.57 | 1.848 |
| *Epinephelus fuscoguttatus* | 90 | 31.711 | 1.367 | 6.672 | 17.941 | 37.752 | 2.199 |
| *Epinephelus fuscoguttatus* | 121 | 44.83 | 1.308 | 7.703 | 24.359 | 49.59 | 1.384 |
| *Epinephelus fuscoguttatus* | 551 | 219.33 | 1.695 | 26.509 | 103.424 | 226.463 | 1.323 |
| *Epinephelus hexagonatus* | 156 | 49.84 | 1.734 | 10.407 | 25.143 | 56.319 | 1.359 |
| *Epinephelus hexagonatus* | 160 | 50.301 | 1.535 | 11.032 | 27.625 | 60.468 | 1.941 |
| *Epinephelus maculatus* | 224 | 74.186 | 1.393 | 15.194 | 33.974 | 81.389 | 2.212 |
| *Epinephelus maculatus* | 263 | 92.933 | 1.172 | 15.728 | 40.949 | 96.578 | 1.812 |
| *Epinephelus maculatus* | 291 | 99.527 | 1.324 | 16.042 | 37.895 | 112.925 | 1.543 |
| *Epinephelus malabaricus* | 309 | 104.236 | 1.145 | 15.464 | 47.67 | 117.521 | 2.059 |
| *Epinephelus malabaricus* | 317 | 101.198 | 1.334 | 13.238 | 51.363 | 125.138 | 1.381 |
| *Epinephelus malabaricus* | 328 | 98.716 | 1.495 | 16.264 | 56.345 | 133.509 | 1.712 |
| *Epinephelus malabaricus* | 510 | 150.16 | 1.464 | 26.723 | 97.064 | 220.15 | 1.461 |
| *Epinephelus malabaricus* | 584 | 179.211 | 1.627 | 24.553 | 95.676 | 233.259 | 1.767 |
| *Epinephelus marginatus* | 208 | 76.408 | 1.476 | 15.533 | 34.297 | 81.714 | 1.623 |
| *Epinephelus marginatus* | 340 | 121.03 | 1.491 | 23.901 | 58.317 | 138.548 | 1.414 |
| *Epinephelus marginatus* | 383 | 130.348 | 1.765 | 23.185 | 58.962 | 146.988 | 1.182 |
| *Epinephelus marginatus* | 404 | 167.387 | 1.269 | 29.206 | 79.911 | 187.473 | 1.539 |
| *Epinephelus merra* | 93 | 30.919 | 1.204 | 7.731 | 15.956 | 36.112 | 1.876 |
| *Epinephelus merra* | 176 | 57.533 | 1.482 | 11.194 | 29.816 | 64.839 | 1.555 |
| *Epinephelus ongus* | 94 | 30.571 | 1.197 | 8.33 | 16.178 | 38.552 | 2.393 |
| *Epinephelus ongus* | 114 | 38.234 | 1.231 | 10.541 | 20.047 | 44.8 | 2.341 |
| *Epinephelus ongus* | 222 | 75.803 | 1.481 | 17.1 | 34.77 | 83.235 | 2.171 |
| *Epinephelus polyphekadion* | 250 | 84.126 | 1.480 | 18.609 | 43.088 | 94.024 | 2.228 |
| *Epinephelus polyphekadion* | 408 | 145 | 1.764 | 19.716 | 68.306 | 162.4 | 2.169 |
| *Epinephelus quoyannus* | 181 | 58.152 | 1.323 | 14.903 | 27.234 | 72.126 | 1.904 |
| *Epinephelus quoyannus* | 192 | 63.684 | 1.426 | 15.257 | 31.137 | 76.911 | 1.895 |
| *Epinephelus quoyannus* | 225 | 76.628 | 1.411 | 15.271 | 35.828 | 84.175 | 1.657 |
| *Epinephelus quoyannus* | 255 | 89.059 | 1.448 | 17.734 | 40.738 | 101.022 | 1.714 |
| *Epinephelus tauvina* | 182 | 62.228 | 1.510 | 11.764 | 36.63 | 81.445 | 1.527 |
| *Epinephelus tauvina* | 192 | 63.634 | 1.793 | 12.191 | 35.405 | 79.667 | 1.645 |
| *Epinephelus tauvina* | 252 | 78.146 | 1.661 | 15.977 | 46.235 | 100.75 | 1.281 |
| *Epinephelus tauvina* | 310 | 104.219 | 1.690 | 19.386 | 67.527 | 140.236 | 1.415 |
| *Epinephelus tauvina* | 407 | 128.481 | 2.049 | 22.271 | 79.809 | 174.296 | 1.356 |
| *Gymnocranius audleyi* | 193 | 80.199 | 3.258 | 18.605 | 19.308 | 57.813 | 3.598 |
| *Gymnocranius audleyi* | 262 | 109.13 | 3.456 | 25.532 | 30.583 | 83.651 | 3.385 |
| *Histrio histrio* | 46 | 26.535 | 1.369 | 1.844 | 5.743 | 15.572 | 1.597 |
| *Histrio histrio* | 49 | 28.923 | 1.321 | 2.167 | 5.986 | 16.49 | 0.883 |
| *Histrio histrio* | 62 | 39.625 | 1.043 | 2.585 | 12.261 | 24.083 | 2.005 |
| *Hologymnosus annulatus* | 95 | 18.881 | 1.471 | 4.287 | 7.286 | 30.235 | 2.414 |
| *Hologymnosus annulatus* | 197 | 49.328 | 2.026 | 7.626 | 14.846 | 63.909 | 2.746 |
| *Hologymnosus annulatus* | 247 | 59.814 | 2.037 | 7.375 | 18.492 | 75.16 | 2.877 |

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|---|---|---|---|---|---|---|---|
| *Hologymnosus doliatus* | 192 | 44.52 | 1.643 | 6.558 | 14.847 | 60.751 | 1.811 |
| *Hologymnosus doliatus* | 214 | 45.47 | 1.247 | 7.238 | 15.02 | 67.123 | 2.927 |
| *Hologymnosus doliatus* | 230 | 54.375 | 1.668 | 7.847 | 17.371 | 72.939 | 2.887 |
| *Hologymnosus doliatus* | 241 | 49.411 | 1.722 | 9.079 | 17.401 | 74.304 | 1.815 |
| *Hologymnosus doliatus* | 242 | 59.834 | 1.904 | 8.689 | 16.573 | 76.564 | 2.353 |
| *Lethrinus amboinensis* | 236 | 72.245 | 2.563 | 15.706 | 21.993 | 74.252 | 3.130 |
| *Lethrinus amboinensis* | 260 | 86.812 | 3.024 | 22.371 | 28.137 | 93.356 | 3.548 |
| *Lethrinus borbonicus* | 182 | 80.351 | 2.580 | 15.067 | 15.904 | 61.742 | 3.138 |
| *Lethrinus borbonicus* | 251 | 100.315 | 3.099 | 19.092 | 28.244 | 82.75 | 5.363 |
| *Lethrinus erythropterus* | 212 | 89.759 | 2.403 | 17.218 | 22.279 | 66.883 | 3.102 |
| *Lethrinus erythropterus* | 238 | 100.064 | 2.018 | 21.137 | 29.023 | 80.729 | 3.885 |
| *Lethrinus harak* | 207 | 71.039 | 2.907 | 15.921 | 20.135 | 62.882 | 4.134 |
| *Lethrinus harak* | 239 | 88.397 | 3.281 | 18.036 | 23.863 | 71.823 | 3.879 |
| *Lethrinus lentjan* | 88 | 35.993 | 2.622 | 9.269 | 10.822 | 31.341 | 3.427 |
| *Lethrinus lentjan* | 140 | 52.232 | 2.564 | 12.148 | 16.185 | 51.198 | 4.008 |
| *Lethrinus mahsena* | 252 | 109.714 | 2.796 | 21.083 | 30.505 | 86.143 | 4.811 |
| *Lethrinus mahsena* | 310 | 132.422 | 2.159 | 20.353 | 40.317 | 102.995 | 5.083 |
| *Lethrinus mahsena* | 320 | 133.677 | 2.923 | 24.737 | 47.588 | 112 | 4.763 |
| *Lethrinus microdon* | 230 | 71.419 | 3.045 | 14.863 | 23.983 | 76.027 | 3.695 |
| *Lethrinus microdon* | 259 | 76.076 | 3.176 | 17.403 | 25.075 | 89.111 | 4.118 |
| *Lethrinus miniatus* | 325 | 122.171 | 2.037 | 21.683 | 34.305 | 110.638 | 3.633 |
| *Lethrinus miniatus* | 350 | 121.724 | 2.632 | 21.614 | 44.745 | 117.097 | 3.530 |
| *Lethrinus ornatus* | 156 | 62.614 | 2.373 | 14.68 | 16.131 | 52.803 | 3.031 |
| *Lethrinus ornatus* | 204 | 82.693 | 3.254 | 18.345 | 21.618 | 69.025 | 2.769 |
| *Lethrinus xanthochilus* | 313 | 93.213 | 3.234 | 21.245 | 33.763 | 101.799 | 3.432 |
| *Lethrinus xanthochilus* | 395 | 118.998 | 2.608 | 24.647 | 39.227 | 127.098 | 3.646 |
| *Lutjanus adetii* | 170 | 63.283 | 2.698 | 12.382 | 19.046 | 53.79 | 7.186 |
| *Lutjanus adetii* | 238 | 91.481 | 2.801 | 18.282 | 29.638 | 78.094 | 7.242 |
| *Lutjanus adetii* | 245 | 90.875 | 3.086 | 18.916 | 29.026 | 80.334 | 6.659 |
| *Lutjanus adetii* | 250 | 96.99 | 3.180 | 18.213 | 30.69 | 83.194 | 5.219 |
| *Lutjanus adetii* | 247 | 94.397 | 2.457 | 20.179 | 32.36 | 86.189 | 6.555 |
| *Lutjanus argentimaculatus* | 258 | 89.544 | 2.252 | 14.456 | 34.564 | 87.908 | 4.677 |
| *Lutjanus argentimaculatus* | 447 | 153.726 | 1.857 | 23.64 | 55.748 | 157.209 | 4.537 |
| *Lutjanus argentimaculatus* | 509 | 169.667 | 1.994 | 31.175 | 71.748 | 195.449 | 3.983 |
| *Lutjanus bohar* | 263 | 92.259 | 3.037 | 19.625 | 40.094 | 95.181 | 4.951 |
| *Lutjanus bohar* | 520 | 194.684 | 2.589 | 27.812 | 72.861 | 182.885 | 4.512 |
| *Lutjanus carponotatus* | 87 | 33.858 | 2.557 | 6.773 | 11.5 | 28.951 | 3.302 |
| *Lutjanus carponotatus* | 131 | 47.695 | 2.763 | 10.81 | 19.022 | 45.753 | 4.472 |
| *Lutjanus carponotatus* | 173 | 71.889 | 2.603 | 11.996 | 24.965 | 61.076 | 3.147 |
| *Lutjanus carponotatus* | 215 | 81.938 | 2.603 | 13.311 | 25.408 | 71.083 | 5.133 |
| *Lutjanus carponotatus* | 245.9 | 101.096 | 2.639 | 19.007 | 38.076 | 93.495 | 5.147 |
| *Lutjanus decussatus* | 162 | 57.192 | 2.045 | 10.613 | 22.99 | 54.345 | 3.115 |

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|---|---|---|---|---|---|---|---|
| *Lutjanus kasmira* | 221 | 81.145 | 2.592 | 16.728 | 25.884 | 79.292 | 3.859 |
| *Lutjanus kasmira* | 227 | 88.814 | 2.702 | 16.406 | 27.526 | 77.35 | 4.331 |
| *Lutjanus malabaricus* | 202 | 81.865 | 1.751 | 13.819 | 26.203 | 70.778 | 3.222 |
| *Lutjanus malabaricus* | 325 | 122.631 | 2.071 | 20.69 | 40.369 | 114.382 | 5.195 |
| *Lutjanus malabaricus* | 373 | 136.705 | 1.634 | 20.245 | 50.917 | 134.024 | 4.570 |
| *Lutjanus malabaricus* | 434 | 178.346 | 1.833 | 24.542 | 59.301 | 161.251 | 4.647 |
| *Lutjanus malabaricus* | 570 | 233.92 | 1.868 | 31.248 | 75.956 | 210.05 | 4.067 |
| *Lutjanus monostigma* | 249 | 83 | 2.597 | 17.707 | 36.015 | 88.257 | 3.473 |
| *Lutjanus russellii* | 141 | 48.653 | 2.380 | 11.376 | 19.436 | 50.779 | 2.877 |
| *Lutjanus russellii* | 219 | 80.061 | 2.246 | 15.587 | 28.426 | 74 | 3.102 |
| *Lutjanus russellii* | 223 | 80.722 | 2.767 | 14.817 | 30.596 | 74.456 | 3.118 |
| *Lutjanus russellii* | 232 | 85.184 | 2.503 | 15.39 | 32.655 | 82.044 | 3.564 |
| *Lutjanus sebae* | 188 | 83.917 | 1.714 | 12.794 | 24.099 | 68.088 | 4.303 |
| *Lutjanus sebae* | 287 | 122.047 | 2.081 | 16.222 | 35.842 | 104.248 | 4.716 |
| *Lutjanus sebae* | 618.4 | 232.617 | 1.633 | 28.637 | 73.807 | 199.188 | 3.877 |
| *Lutjanus vitta* | 154 | 50.103 | 2.548 | 11.873 | 20.643 | 53.861 | 4.995 |
| *Lutjanus vitta* | 190 | 64.077 | 1.916 | 14.453 | 24.993 | 62.908 | 2.514 |
| *Lutjanus vitta* | 225 | 75.13 | 1.805 | 18.183 | 33.121 | 81.488 | 3.296 |
| *Megalaspis cordyla* | 133 | 35.589 | 2.447 | 7.322 | 14.069 | 33.352 | 8.371 |
| *Megalaspis cordyla* | 425 | 103.165 | 3.671 | 18.642 | 36.634 | 95.359 | 10.936 |
| *Megalaspis cordyla* | 471 | 113.194 | 4.254 | 16.363 | 33.357 | 92.232 | 11.609 |
| *Neoniphon aurolineatus* | 152 | 49.269 | 2.455 | 17.895 | 21.698 | 50.186 | 4.078 |
| *Neoniphon aurolineatus* | 158 | 50.08 | 3.689 | 18.161 | 23.093 | 52.241 | 4.284 |
| *Neoniphon aurolineatus* | 179 | 61.117 | 3.214 | 21.292 | 26.54 | 62.304 | 3.298 |
| *Neoniphon sammara* | 160 | 47.568 | 2.866 | 19.737 | 22.025 | 52.703 | 3.710 |
| *Ogilbyina queenslandiae* | 86 | 29.69 | 0.744 | 7.009 | 9.496 | 28.732 | 1.954 |
| *Ogilbyina queenslandiae* | 89 | 32.435 | 0.843 | 6.53 | 8.146 | 24.201 | 1.418 |
| *Oxycheilinus digrammus* | 108 | 37.583 | 1.322 | 7.735 | 12.618 | 38.974 | 1.616 |
| *Oxycheilinus digrammus* | 113 | 37.308 | 1.600 | 7.765 | 12.623 | 39.338 | 1.315 |
| *Oxycheilinus digrammus* | 117 | 36.996 | 1.211 | 7.713 | 15.013 | 45.42 | 1.817 |
| *Oxycheilinus digrammus* | 150 | 50.68 | 1.776 | 8.378 | 17.791 | 48.682 | 2.186 |
| *Oxycheilinus digrammus* | 217 | 77.879 | 1.637 | 11.58 | 26.235 | 79.03 | 1.925 |
| *Paracirrhites forsteri* | 67 | 23.14 | 1.482 | 4.866 | 8.542 | 22.185 | 1.478 |
| *Paracirrhites forsteri* | 75 | 25.714 | 1.341 | 5.39 | 9.84 | 24.102 | 1.246 |
| *Paracirrhites forsteri* | 105 | 37.405 | 1.370 | 6.998 | 13.463 | 35.205 | 1.371 |
| *Paracirrhites forsteri* | 116 | 43.603 | 1.764 | 6.71 | 14.621 | 34.592 | 1.403 |
| *Paracirrhites forsteri* | 156 | 59.158 | 1.219 | 8.283 | 18.577 | 49.249 | 1.494 |
| *Paracirrhites hemistictus* | 174 | 62.512 | 1.688 | 8.41 | 19.315 | 53.822 | 0.985 |
| *Paracirrhites hemistictus* | 192 | 74.915 | 1.761 | 9.993 | 24.861 | 67.081 | 0.960 |
| *Parapercis clathrata* | 84 | 15.291 | 1.617 | 5.526 | 6.356 | 23.544 | 2.186 |
| *Parapercis clathrata* | 119 | 20.286 | 1.504 | 7.51 | 9.85 | 30.429 | 2.400 |
| *Plectorhinchus chrysotaenia* | 148 | 50.749 | 1.735 | 11.862 | 10.937 | 39.432 | 3.849 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Plectorhinchus chrysotaenia* | 207 | 78.321 | 2.010 | 13.845 | 14.963 | 56.586 | 3.798 |
| *Plectorhinchus chubbi* | 205 | 93.767 | 2.009 | 14.162 | 15.816 | 61.592 | 2.428 |
| *Plectorhinchus chubbi* | 298 | 134.368 | 2.608 | 20.296 | 23.877 | 85.281 | 2.225 |
| *Plectorhinchus gaterinus* | 134 | 52.035 | 2.260 | 12.053 | 9.231 | 40.323 | 2.101 |
| *Plectorhinchus gaterinus* | 228 | 92.76 | 2.319 | 15.839 | 17.679 | 63.348 | 3.471 |
| *Plectropomus areolatus* | 316 | 89.802 | 1.743 | 15.08 | 43.214 | 99.78 | 1.828 |
| *Plectropomus areolatus* | 350 | 109.672 | 1.753 | 16.206 | 46.719 | 114.166 | 1.117 |
| *Plectropomus areolatus* | 374 | 122.211 | 2.441 | 17.05 | 55.83 | 124.907 | 1.279 |
| *Plectropomus laevis* | 108 | 30.958 | 1.854 | 7.811 | 16.365 | 36.587 | 1.677 |
| *Plectropomus laevis* | 175 | 53.463 | 1.652 | 10.955 | 25.311 | 58.994 | 2.102 |
| *Plectropomus laevis* | 475 | 142.557 | 2.005 | 19.661 | 74.03 | 171.33 | 1.711 |
| *Plectropomus laevis* | 534 | 152.392 | 2.038 | 21.558 | 75.451 | 167.505 | 1.450 |
| *Plectropomus laevis* | 597 | 185.476 | 2.010 | 17.628 | 76.264 | 182.578 | 1.335 |
| *Plectropomus leopardus* | 208 | 65.824 | 1.803 | 12.037 | 32.35 | 69.797 | 1.726 |
| *Plectropomus oligacanthus* | 241 | 73.594 | 2.202 | 10.766 | 31.389 | 77.96 | 2.444 |
| *Plectropomus pessuliferus* | 117 | 39.402 | 1.809 | 8.748 | 19.441 | 42.736 | 2.857 |
| *Plectropomus pessuliferus* | 480 | 165.818 | 1.747 | 18.33 | 68.446 | 152.658 | 1.922 |
| *Plectropomus punctatus* | 446 | 147.66 | 2.018 | 15.579 | 59.709 | 128.4 | 1.304 |
| *Plectrypops lima* | 50 | 19.167 | 1.591 | 5.786 | 9.429 | 18.222 | 2.546 |
| *Plectrypops lima* | 78 | 31.021 | 2.093 | 8.078 | 14.786 | 28.681 | 1.480 |
| *Pristilepis oligolepis* | 149 | 61.84 | 2.707 | 14.506 | 28.497 | 55.185 | 2.022 |
| *Pristilepis oligolepis* | 180 | 74.513 | 2.435 | 17.232 | 35.068 | 65.844 | 2.481 |
| *Pristilepis oligolepis* | 212 | 87.58 | 2.680 | 21.362 | 39.725 | 73.679 | 1.798 |
| *Pristilepis oligolepis* | 231 | 87.75 | 2.093 | 20.887 | 44.414 | 85.25 | 2.101 |
| *Psammoperca vaigiensis* | 187 | 63.181 | 1.701 | 13.274 | 22.947 | 64.007 | 2.225 |
| *Psammoperca vaigiensis* | 63.6 | 19.738 | 0.987 | 5.357 | 10.246 | 22.906 | 2.426 |
| *Pseudocaranx dentex* | 368.3 | 131.769 | 4.410 | 25.016 | 43.93 | 128.575 | 5.893 |
| *Pseudocaranx dentex* | 442.697 | 145.022 | 4.649 | 21.11 | 51.315 | 136.88 | 8.034 |
| *Pseudocaranx dentex* | 151.582 | 55.34 | 3.806 | 10.723 | 17.709 | 50.438 | 5.234 |
| *Pseudocaranx dentex* | 414.7 | 144.878 | 3.912 | 20.767 | 46.254 | 125.466 | 5.927 |
| *Pseudochromis fuscus* | 46 | 14.627 | 1.223 | 3.989 | 4.738 | 13.815 | 1.615 |
| *Pseudochromis fuscus* | 52 | 19.422 | 1.498 | 4.372 | 5.396 | 15.642 | 2.114 |
| *Pseudochromis fuscus* | 52 | 17.879 | 1.333 | 4.412 | 5.644 | 16.194 | 2.197 |
| *Pterois volitans* | 106 | 35.646 | 1.259 | 8.98 | 17.063 | 36.31 | 4.491 |
| *Rachycentron canadum* | 265 | 41.992 | 1.290 | 10.322 | 22.736 | 67.488 | 3.631 |
| *Rachycentron canadum* | 256.5 | 42.942 | 1.200 | 9.664 | 21.863 | 63.283 | 4.279 |
| *Rachycentron canadum* | 496 | 88.146 | 1.609 | 14.198 | 37.926 | 112.032 | 4.026 |
| *Sargocentron caudimaculatum* | 89 | 32.694 | 2.149 | 10.737 | 9.349 | 26.849 | 2.946 |
| *Sargocentron caudimaculatum* | 114 | 40.78 | 2.273 | 14.348 | 13.214 | 41.151 | 2.108 |
| *Sargocentron caudimaculatum* | 174 | 66.614 | 3.207 | 16.263 | 19.533 | 59.34 | 2.222 |
| *Sargocentron ittodai* | 94 | 30.271 | 2.989 | 12.785 | 11.194 | 33.033 | 2.963 |
| *Sargocentron ittodai* | 111 | 35.652 | 2.330 | 13.694 | 13.364 | 35.285 | 2.252 |

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|---|---|---|---|---|---|---|---|
| *Sargocentron ittodai* | 132 | 41.583 | 3.580 | 14.701 | 13.742 | 39.237 | 2.237 |
| *Sargocentron ittodai* | 132 | 42.588 | 2.518 | 14.04 | 13.613 | 37.571 | 3.429 |
| *Sargocentron ittodai* | 165 | 54.283 | 2.922 | 17.229 | 17.495 | 49.581 | 2.823 |
| *Sargocentron praslin* | 115 | 40.202 | 2.687 | 12.512 | 13.441 | 33.727 | 3.808 |
| *Sargocentron praslin* | 135 | 49.251 | 2.779 | 15.398 | 16.182 | 42.215 | 3.215 |
| *Sargocentron praslin* | 157 | 58.263 | 2.893 | 17.324 | 18.882 | 46.818 | 4.005 |
| *Sargocentron punctatissimum* | 76 | 26.429 | 2.854 | 8.981 | 9.191 | 24.09 | 3.659 |
| *Sargocentron punctatissimum* | 89 | 31.075 | 2.437 | 10.404 | 9.217 | 25.933 | 3.157 |
| *Sargocentron punctatissimum* | 96 | 30.874 | 2.342 | 9.895 | 9.266 | 27.899 | 3.242 |
| *Sargocentron rubrum* | 114 | 3.733 | 2.924 | 14.937 | 14.007 | 34.163 | 3.218 |
| *Sargocentron rubrum* | 156 | 57.624 | 2.667 | 16.519 | 18.417 | 43.737 | 2.775 |
| *Sargocentron spiniferum* | 100 | 36.672 | 2.451 | 10.608 | 12.657 | 32.484 | 2.556 |
| *Sargocentron spiniferum* | 246 | 93.733 | 2.660 | 17.448 | 29.626 | 80.682 | 2.882 |
| *Sargocentron spiniferum* | 355 | 152.222 | 2.705 | 24.558 | 38.94 | 107.222 | 3.346 |
| *Sargocentron tiere* | 150 | 52.736 | 2.458 | 17.525 | 23.675 | 50.58 | 3.572 |
| *Sargocentron tiere* | 157 | 51.99 | 2.351 | 13.702 | 21.424 | 49.674 | 2.354 |
| *Sargocentron tiere* | 183 | 65.357 | 2.766 | 14.619 | 24.507 | 58.163 | 2.585 |
| *Sargocentron tiere* | 209 | 71.865 | 2.574 | 15.519 | 28.589 | 68.394 | 2.505 |
| *Sargocentron tiereoides* | 88 | 29.932 | 2.087 | 11.615 | 11.817 | 28.81 | 2.810 |
| *Sargocentron tiereoides* | 110 | 39.578 | 2.266 | 13.061 | 14.63 | 35.18 | 2.408 |
| *Sargocentron tiereoides* | 110 | 39.916 | 2.023 | 12.627 | 14.647 | 36.237 | 2.202 |
| *Sargocentron violaceum* | 82 | 31.071 | 2.050 | 11.058 | 10.668 | 28.842 | 2.419 |
| *Sargocentron violaceum* | 112 | 43.794 | 2.110 | 12.057 | 12.609 | 36.246 | 2.821 |
| *Saurida flamma* | 109 | 17.709 | 1.824 | 5.577 | 16.968 | 22.199 | 2.434 |
| *Saurida flamma* | 137 | 22.78 | 1.735 | 6.926 | 26.288 | 34.972 | 3.576 |
| *Saurida flamma* | 263 | 44.627 | 2.493 | 9.539 | 48.708 | 57.717 | 3.887 |
| *Saurida gracilis* | 99 | 14.545 | 1.862 | 5.416 | 18.25 | 23.929 | 3.278 |
| *Saurida gracilis* | 113 | 21.155 | 2.221 | 4.672 | 20.199 | 24.767 | 2.992 |
| *Saurida gracilis* | 146 | 23.559 | 2.262 | 6.339 | 27.912 | 35.173 | 3.914 |
| *Saurida gracilis* | 147 | 22.221 | 2.497 | 5.852 | 26.935 | 32.819 | 3.344 |
| *Saurida nebulosa* | 153 | 24.411 | 2.488 | 5.885 | 26.501 | 33.351 | 3.007 |
| *Scomberoides commersonnianus* | 612.4 | 155.577 | 4.582 | 19.172 | 65.972 | 125.38 | 4.246 |
| *Scomberoides commersonnianus* | 105 | 39.81 | 3.253 | 6.974 | 16.054 | 25.419 | 2.334 |
| *Scomberoides commersonnianus* | 300 | 98.828 | 6.037 | 14.482 | 35.336 | 59.162 | 4.794 |
| *Scomberoides commersonnianus* | 464 | 126.303 | 5.786 | 14.654 | 55.324 | 95.661 | 3.915 |
| *Scomberomorus commerson* | 418.8 | 75.189 | 6.394 | 12.698 | 44.692 | 95.175 | 6.092 |
| *Scomberomorus commerson* | 564 | 106.937 | 5.308 | 17.31 | 58.149 | 113.562 | 4.660 |
| *Scomberomorus commerson* | 691.5 | 114.196 | 4.372 | 22.43 | 87.348 | 144.331 | 4.266 |
| *Scomberomorus munroi* | 154 | 32.571 | 2.525 | 8.297 | 25.3 | 41.571 | 4.040 |
| *Scomberomorus munroi* | 211 | 45.409 | 3.074 | 11.538 | 30.199 | 53.15 | 3.105 |
| *Scorpaenodes littoralis* | 52 | 17.156 | 1.108 | 5.184 | 11.953 | 22.467 | 1.851 |
| *Scorpaenodes littoralis* | 56 | 20.953 | 1.240 | 6.726 | 13.536 | 23.302 | 2.540 |

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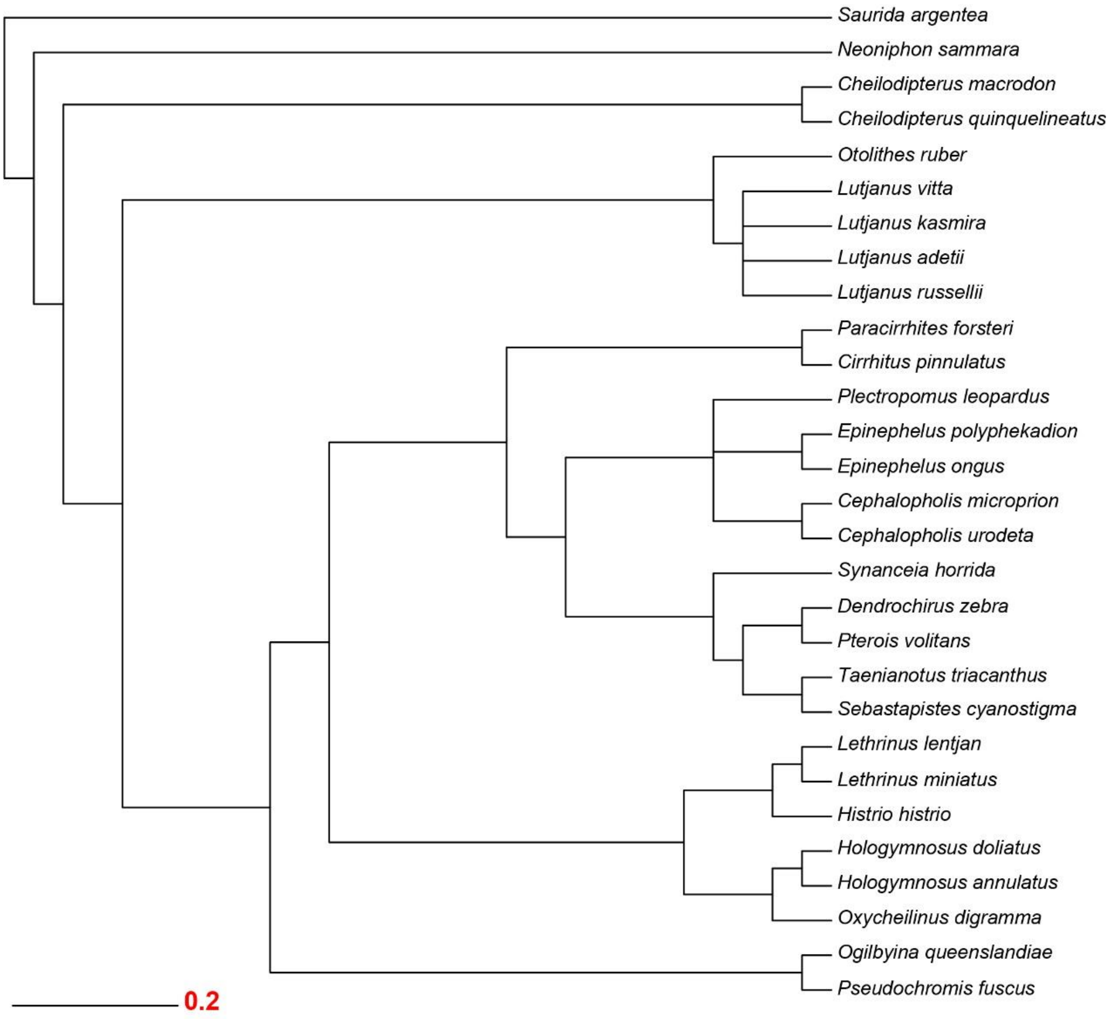
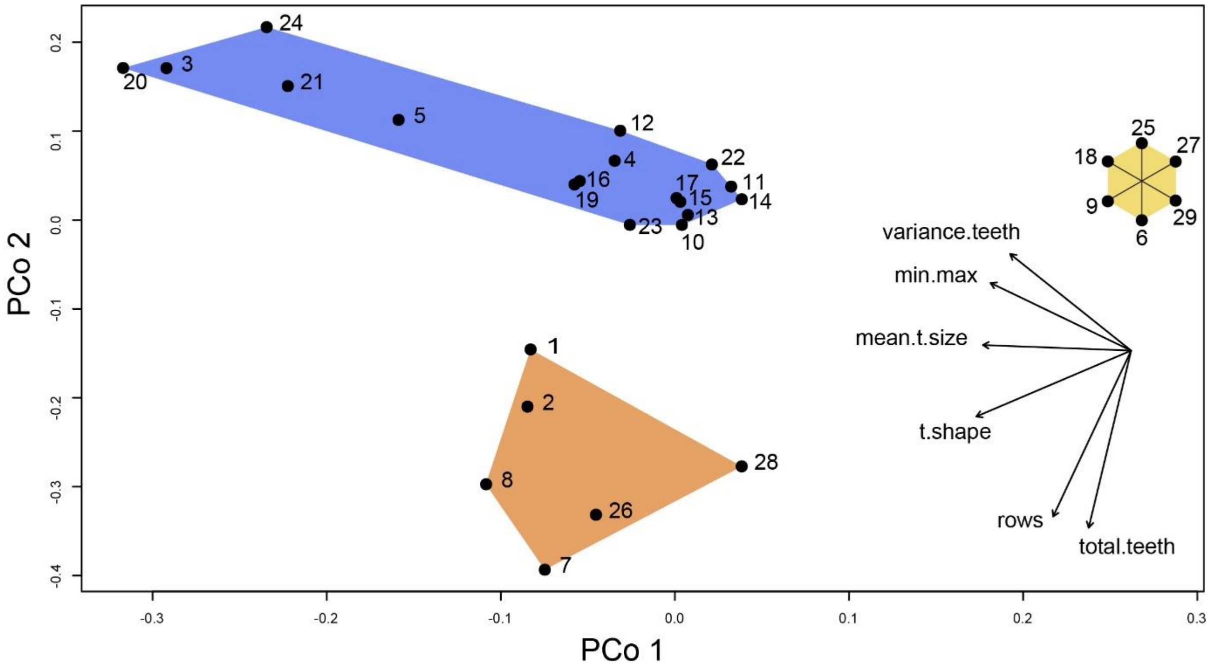
|---|---|---|---|---|---|---|---|
| *Scorpaenodes littoralis* | 80 | 28.696 | 1.358 | 6.943 | 15.193 | 29.826 | 1.775 |
| *Sebastapistes cyanostigma* | 30 | 11.57 | 1.132 | 4.599 | 6.163 | 11.724 | 1.354 |
| *Sebastapistes cyanostigma* | 45 | 18.312 | 1.349 | 5.605 | 9.48 | 19.512 | 1.125 |
| *Sebastapistes cyanostigma* | 47 | 17.553 | 1.436 | 6.714 | 7.788 | 20.147 | 1.437 |
| *Seriola rivoliana* | 385 | 123.022 | 4.374 | 17.593 | 35.444 | 101.562 | 2.965 |
| *Seriola rivoliana* | 538 | 155.544 | 4.051 | 20.386 | 49.66 | 135.415 | 2.948 |
| *Seriola rivoliana* | 620 | 171.751 | 4.561 | 25.974 | 66.337 | 163.373 | 4.357 |
| *Sphyraena barracuda* | 100 | 12.844 | 2.516 | 6.197 | 13.138 | 32.339 | 1.017 |
| *Sphyraena barracuda* | 187 | 27.553 | 2.692 | 10.477 | 24.761 | 60.978 | 3.150 |
| *Sphyraena barracuda* | 406 | 66.115 | 3.218 | 13.037 | 51.241 | 112.674 | 2.408 |
| *Sphyraena barracuda* | 434 | 60.418 | 2.636 | 16.111 | 55.748 | 118.821 | 3.844 |
| *Taenianotus triacanthus* | 53 | 27.312 | 1.330 | 4.635 | 9.729 | 21.455 | 1.838 |
| *Taenianotus triacanthus* | 53 | 26.087 | 1.372 | 5.04 | 10.633 | 22.807 | 1.430 |
| *Taenianotus triacanthus* | 85 | 45.291 | 1.382 | 6.812 | 15.025 | 35.491 | 1.648 |
| *Trachinocephalus myops* | 86 | 15.564 | 1.852 | 3.791 | 14.478 | 18.956 | 3.517 |
| *Trachinocephalus myops* | 112 | 21.508 | 1.636 | 4.836 | 16.789 | 26.754 | 2.535 |
| *Trachinocephalus myops* | 129 | 26.469 | 3.072 | 5.813 | 20.769 | 31.946 | 4.066 |
| *Trachinocephalus myops* | 152 | 29.521 | 2.211 | 6.76 | 22.426 | 36.549 | 3.751 |
| *Variola louti* | 273 | 85.358 | 1.923 | 10.536 | 34.017 | 87.566 | 2.250 |

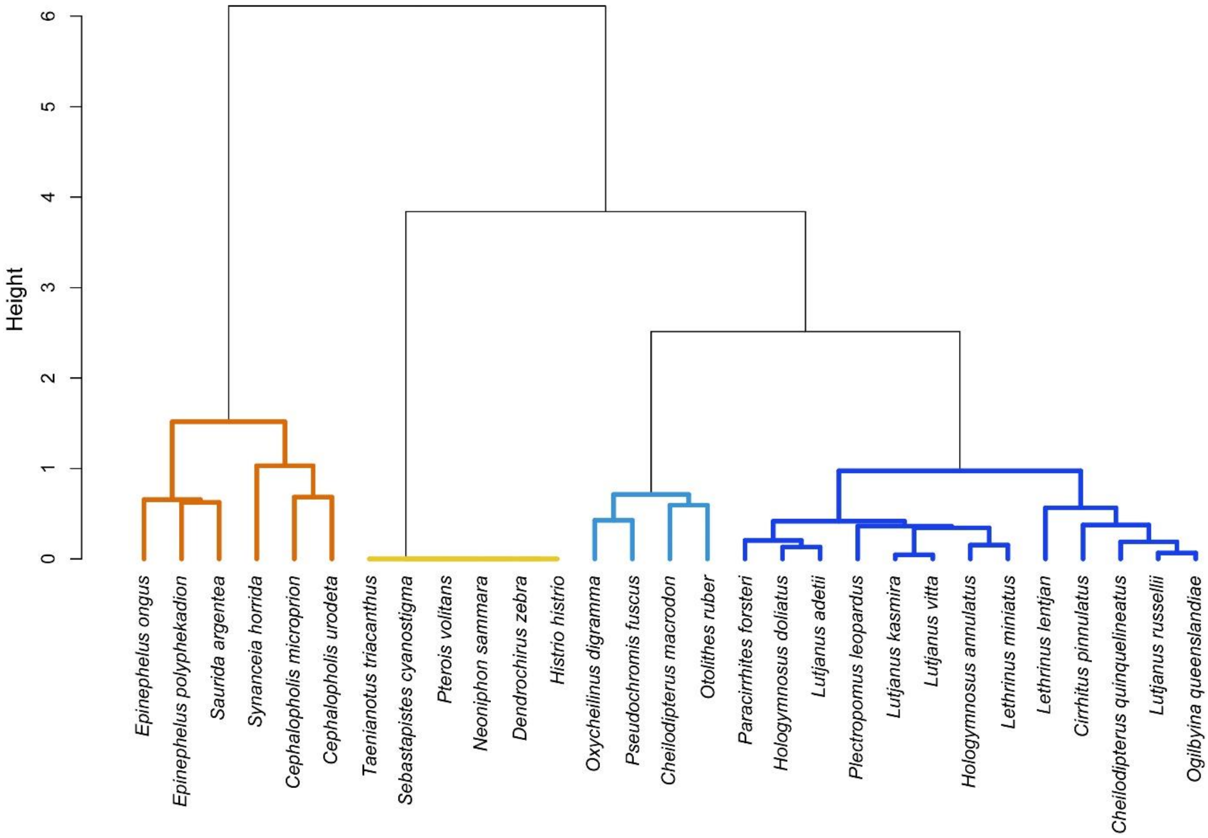
## Appendix B (Supplemental material for Chapter 3)



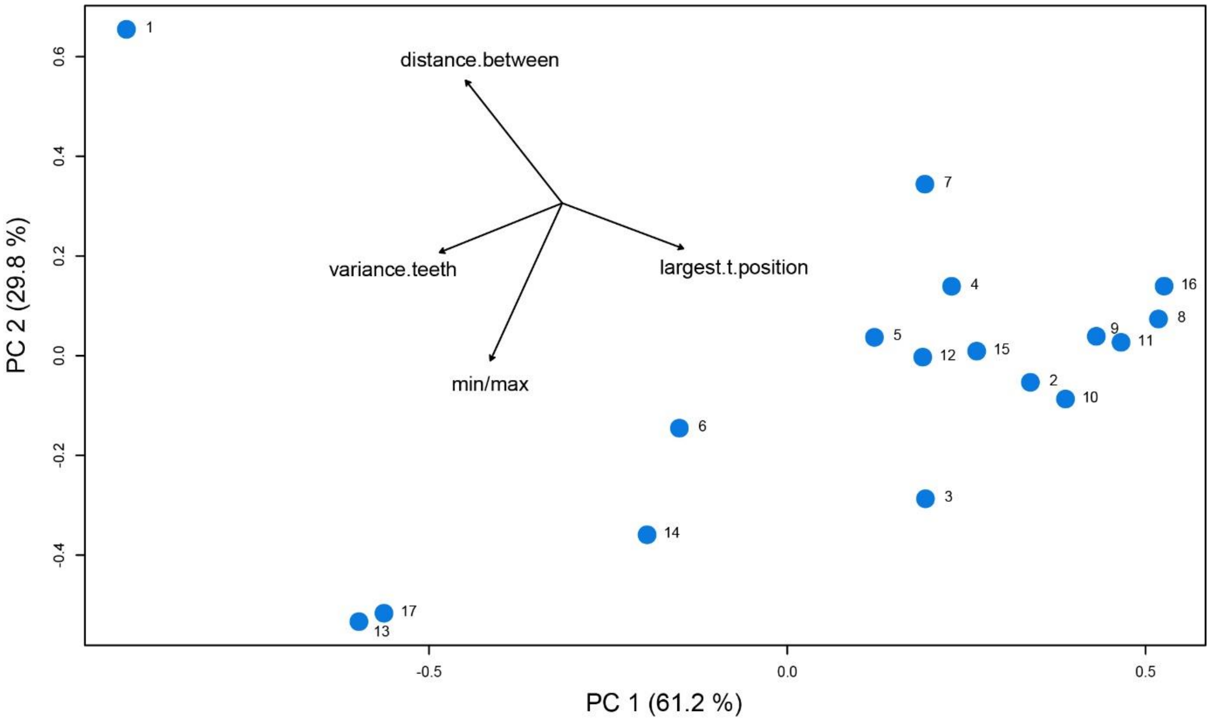
**Appendix B Fig. 1**. Phylogenetic tree used in my analyses



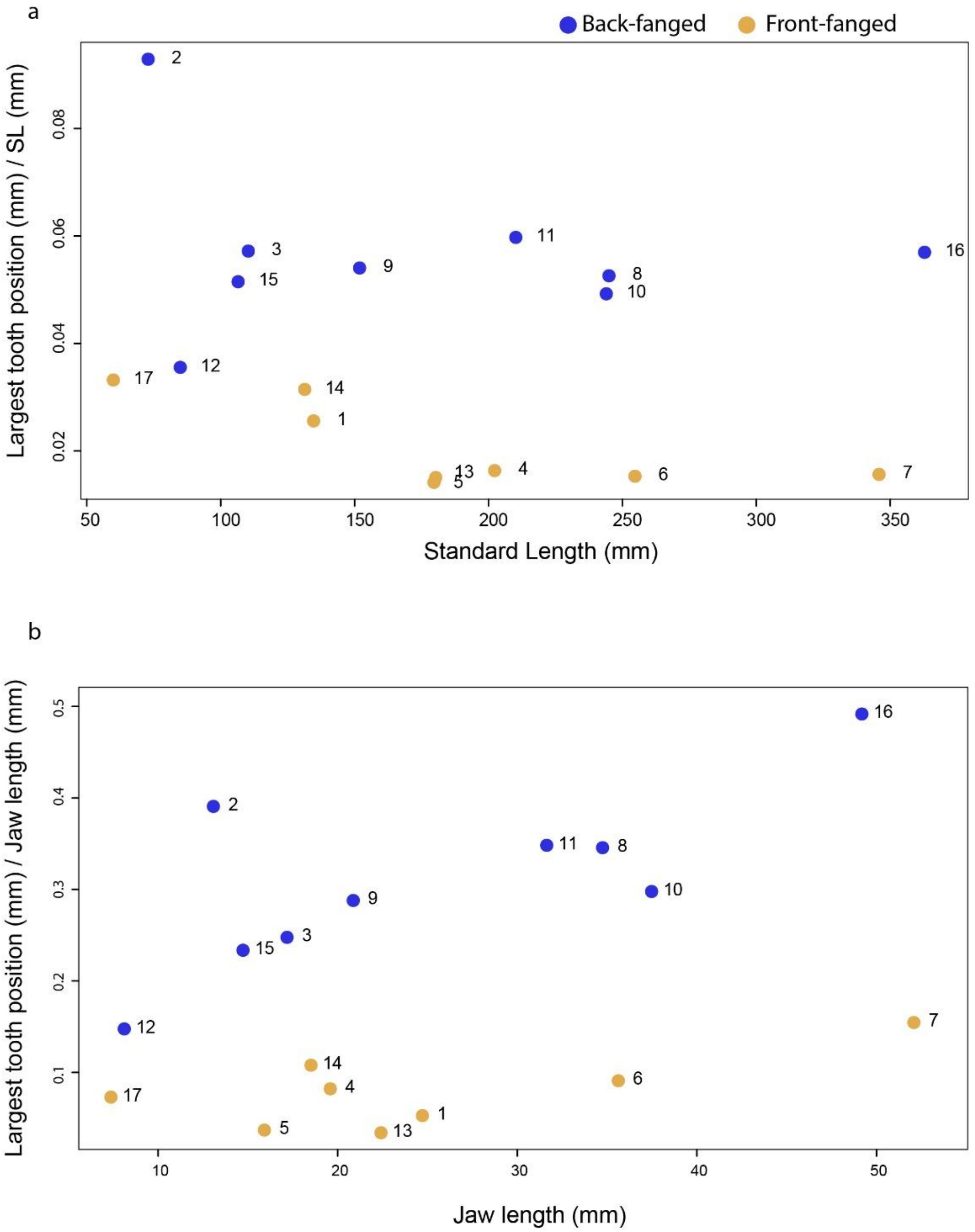
**Appendix B Fig. 2.** Principal Coordinate Analysis (PCoA). Species names: 1-*Cephalopholis microprion,* 2-*Cephalopholis urodeta,* 3-*Cheilodipterus macrodon,* 4-*Cheilodipterus quinquelineatus,* 5-*Cirrhitus pinnulatus,* 6-*Dendrochirus zebra,* 7-*Epinephelus ongus,* 8-*Epinephelus polyphekadion,* 9-*Histrio histrio,* 10-*Hologymnosus annulatus,* 11-*Hologymnosus doliatus,* 12-*Lethrinus lentjan,* 13-*Lethrinus miniatus,* 14-*Lutjanus adetii,* 15-*Lutjanus kasmira,* 16-*Lutjanus russellii,* 17-*Lutjanus vitta,* 18-*Neoniphon sammara,* 19-*Ogilbyina queenslandiae,* 20-*Otolithes ruber,* 21-*Oxycheilinus digramma,* 22-*Paracirrhites forsteri,* 23-*Plectropomus leopardus,* 24-*Pseudochromis fuscus,* 25-*Pterois volitans,* 26-*Saurida argentea,* 27-*Sebastapistes cyanostigma,* 28-*Synanceia horrida,* 29-*Taenianotus triacanthus.* For a detailed description of morphological traits, see Appendix B Table 1.



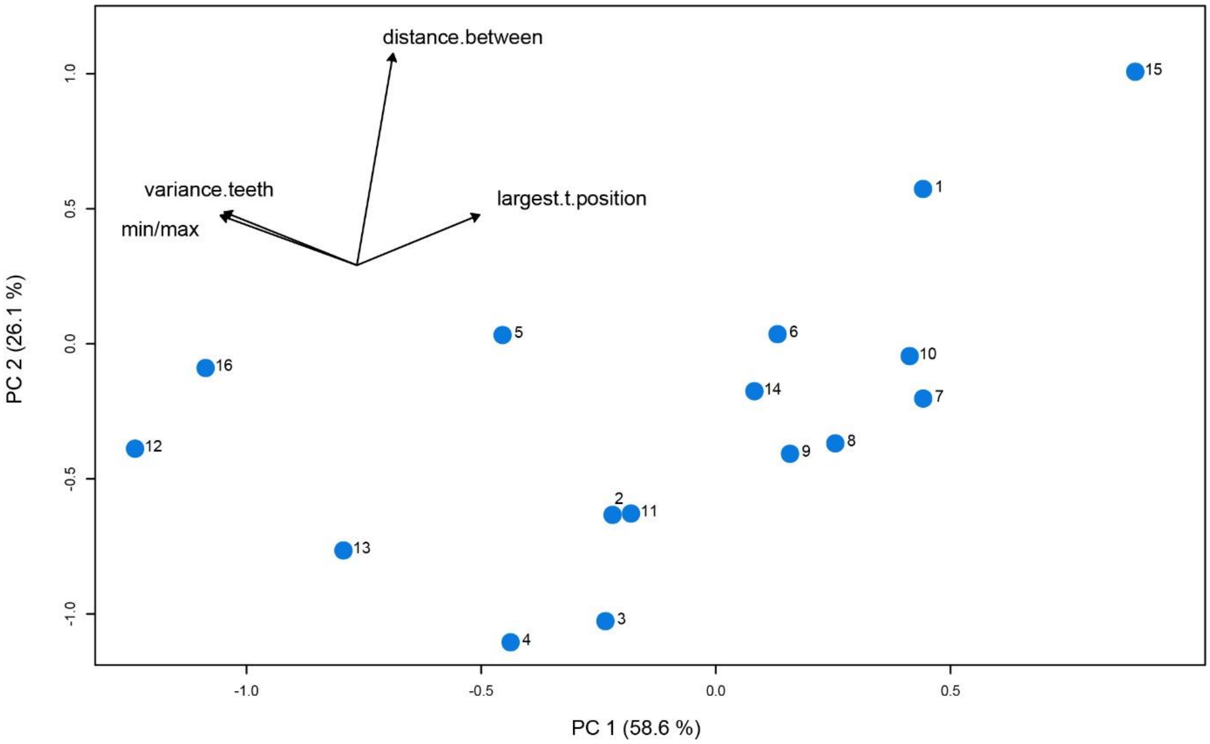
**Appendix B Fig. 3.** Hierarchical clustering analysis with SIMPROF analysis. Colours indicate significant clusters and are equivalent to colours used to indicate morphotypes in ordinations.



**Appendix B Fig. 4.** Macrodont-based Phylogenetic Principal Component Analysis (PPCA). Species names: 1-*Cheilodipterus macrodon,* 2-*Cheilodipterus quinquelineatus,* 3-*Cirrhitus pinnulatus,* 4-*Hologymnosus annulatus,* 5-*Hologymnosus doliatus,* 6-*Lethrinus lentjan,* 7-*Lethrinus miniatus,* 8-*Lutjanus adetii,* 9-*Lutjanus kasmira,* 10-*Lutjanus russellii,* 11-*Lutjanus vitta,* 12-*Ogilbyina queenslandiae,* 13-*Otolithes ruber,* 14-*Oxycheilinus digramma,* 15-*Paracirrhites forsteri,* 16-*Plectropomus leopardus,* 17-*Pseudochromis fuscus.* For a detailed description of traits used see Appendix B Table 1.



**Appendix B Fig. 5.** a) Position of largest tooth as distance from tip of the jaw, divided by body size (SL) to SL. b) Position of largest tooth as distance from tip of the jaw, divided by jaw length, to jaw length. Species names: 1-*Cheilodipterus macrodon,* 2-*Cheilodipterus quinquelineatus,* 3-*Cirrhitus pinnulatus,* 4-*Hologymnosus annulatus,* 5-*Hologymnosus doliatus,* 6-*Lethrinus lentjan,* 7-*Lethrinus miniatus,* 8-*Lutjanus adetii,* 9-*Lutjanus kasmira,* 10-*Lutjanus russellii,* 11-*Lutjanus vitta,* 12-*Ogilbyina queenslandiae,* 13-*Otolithes ruber,* 14-*Oxycheilinus digramma,* 15-*Paracirrhites forsteri,* 16-*Plectropomus leopardus,* 17-*Pseudochromis fuscus.* Colours represent respectively `back-fanged`(blue) and `front-fanged`(yellow) species.



**Appendix B Fig. 6.** Macrodont Phylogenetic Principal Component Analysis (PPCA). Species names: 1-*Cheilodipterus quinquelineatus,* 2-*Cirrhitus pinnulatus,* 3-*Hologymnosus annulatus,* 4-*Hologymnosus doliatus,* 5-*Lethrinus lentjan,* 6-*Lethrinus miniatus,* 7-*Lutjanus adetii,* 8-*Lutjanus kasmira,* 9-*Lutjanus russellii,* 10-*Lutjanus vitta,* 11-*Ogilbyina queenslandiae,* 12-*Otolithes ruber,* 13-*Oxycheilinus digramma,* 14-*Paracirrhites forsteri,* 15-*Plectropomus leopardus,* 16-*Pseudochromis fuscus.*

**Appendix B Table 1.** Morphological traits used in my analyses. Analysis 1 indicates traits used in the morphotype analysis (Fig. 1), whereas Analysis 2 indicates traits used in the macrodont analysis (Fig. 3). Some of the morphological measurements were used to quantify some of the traits (e.g. jaw length used to quantify relative position of largest tooth).

| **Trait/Morphological meas.** | **Description** | **Analysis** |
|---|---|---|
| Jaw length | length from anterior tip of anteriormost tooth, to the midpoint of the articular-quadrate articulation | 2 |

| | | |
|---|---|---|
| tooth length (1-5) | tooth length from tip to the midpoint at the base | 1+2 |
| distance to jaw tip (1-5) | distance from midpoint at the base of tooth, to the anterior tip of the jaw. Used to calculate distance between teeth | 2 |
| largest tooth position | position of the largest tooth relative to jaw length (Out lever) | 2 |
| Variance in teeth size | variance in the tooth size of the 5 largest teeth of the left lower jaw. | 1+2 |
| Mean distance between teeth | Mean distance between the 5 largest teeth of the left lower jaw, relative to jaw length | 2 |
| tooth shape | maximum tooth width, measured at the base of the tooth. Used to calculate the ratio between tooth length / tooth width | 1 |
| min/max | ratio between the smallest (of the five largest teeth) and the largest tooth | 1+2 |
| total number of teeth | total number of teeth on left lower jaw | 1 |
| teeth rows | number of rows of teeth on left lower jaw | 1 |
| mean tooth size | mean length of the 5 largest teeth of the left lower jaw | 1 |

**Appendix B Table 2.** Functional feeding traits used in my analysis.

| **Trait** | **Description/Function** | **Refferences** |
|---|---|---|
| Jaw protrusion | Increases the speed and grasping range of the bite | [1, 2 ] |
| Gape size | Influences maximum ingestible prey size | [3, 4] |
| Distance between teeth | More distance between teeth increases the ability to puncture flesh | [5, 6] |
| mouth shape | Influences suction feeding. More round = more efficient suction | [7] |
| jaw lever | velocity vs. force potential | [8] |

| | | |
|---|---|---|
| ratios (Lo & Li) | | |

**Appendix B Table 3.** Vector loadings from Phylogenetic Principal Component Analysis (PPCA).

| **Morphotype PPCA** | **PC1** | **PC2** |
|---|---|---|
| variance teeth size | -0.6 | 0.664 |
| min/max | -0.457 | 0.304 |
| tooth shape | -0.913 | 0.109 |
| tooth abundance | -0.667 | -0.705 |
| rows | -0.715 | -0.664 |
| mean tooth size | -0.637 | 0.483 |
| **Functional PPCA** | **PC1** | **PC2** |
| Vert. Oral gape | -0.9 | 0.092 |
| Horiz. Oral gape | -0.874 | 0.453 |
| Protrusion | -0.256 | 0.181 |
| Mouth shape | 0.462 | -0.795 |
| Li/Lo | 0.816 | 0.546 |
| Lo/Li | -0.813 | -0.551 |
| **Macrodonts PPCA** | **PC1** | **PC2** |
| Largest tooth position | 0.819 | 0.224 |
| variance teeth size | -0.886 | 0.236 |
| min/max | -0.911 | -0.221 |
| distance between teeth | 0.242 | 0.942 |

**Appendix B Table 4.** Phylogenetic Least Squares (PGLS) models conducted on functional traits.

| **Trait (Response)** | **Morphotype (Explanatory)** | **AIC** | **BIC** | **logLik** | **Value** | **Std. Error** | **t-value** | **p-value** |
|---|---|---|---|---|---|---|---|---|
| **Horizontal gape** | | -66.69 | -61.22 | 37.345 | | | | |
| | **Edentulate (Intercept)** | | | | 0.378 | 0.075 | 5.075 | 0 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Villiform** | | | | -0.111 | 0.052 | -2.13 | 0.043 |
| | **Macrodont** | | | | -0.272 | 0.042 | -6.422 | 0 |
| | | | | | | | | |
| **Vertical gape** | | -97.338 | -91.869 | 52.669 | | | | |
| | **Edentulate (Intercept)** | | | | 0.324 | 0.044 | 7.384 | 0 |
| | **Villiform** | | | | -0.098 | 0.03 | -3.247 | 0.003 |
| | **Macrodont** | | | | -0.196 | 0.025 | -7.873 | 0 |
| | | | | | | | | |
| **Jaw Protrusion** | | 46.929 | 52.398 | -19.464 | | | | |
| | **Edentulate (Intercept)** | | | | 1.539 | 0.529 | 2.91 | 0.007 |
| | **Villiform** | | | | 0.464 | 0.366 | 1.265 | 0.217 |
| | **Macrodont** | | | | 0.092 | 0.3 | 0.307 | 0.761 |
| | | | | | | | | |
| **Mouth shape** | | 0.669 | 6.138 | 3.665 | | | | |
| | **Edentulate (Intercept)** | | | | 0.831 | 0.238 | 3.489 | 0.002 |
| | **Villiform** | | | | 0.057 | 0.165 | 0.349 | 0.73 |
| | **Macrodont** | | | | 0.221 | 0.135 | 1.634 | 0.114 |
| | | | | | | | | |
| **Li/Lo** | | -48.093 | -42.624 | 28.047 | | | | |
| | **Edentulate (Intercept)** | | | | 0.29 | 0.102 | 2.825 | 0.009 |
| | **Villiform** | | | | -0.016 | 0.071 | -0.221 | 0.826 |
| | **Macrodont** | | | | 0.12 | 0.058 | 2.056 | 0.05 |
| | | | | | | | | |
| **Lo/Li** | | 91.916 | 97.385 | -41.958 | | | | |
| | **Edentulate (Intercept)** | | | | 5.91 | 1.148 | 5.144 | 0 |
| | **Villiform** | | | | -0.417 | 0.796 | -0.524 | 0.604 |
| | **Macrodont** | | | | -2.622 | 0.653 | -4.013 | 0 |

## References

[1] Lauder, G.V. & Liem, K.F. 1981 Prey capture by Luciocephalus pulcher: implications for models of jaw protrusion in teleost fishes. *Environmental Biology of Fishes* **6**, 257-268.

[2] Liem, K.F. 1967 A morphological study of Luciocephalus pulcher, with notes on gular elements in other recent teleosts. *Journal of morphology* **121**, 103-133.

[3] Mihalitsis, M. & Bellwood, D.R. 2017 A morphological and functional basis for maximum prey size in piscivorous fishes. *PloS one* **12**, e0184679.

[4] Wainwright, P.C. & Richard, B.A. 1995 Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* **44**, 97-113.

[5] Vogel, S. 2013 *Comparative biomechanics: life's physical world*, Princeton University Press.

[6] Whitenack, L.B., Simkins Jr, D.C. & Motta, P.J. 2011 Biology meets engineering: the structural mechanics of fossil and extant shark teeth. *Journal of morphology* **272**, 169-179.

[7] Lauder, G.V. 1979 Feeding mechanics in primitive teleosts and in the halecomorph fish Amia calva. *Journal of Zoology* **187**, 543-578.

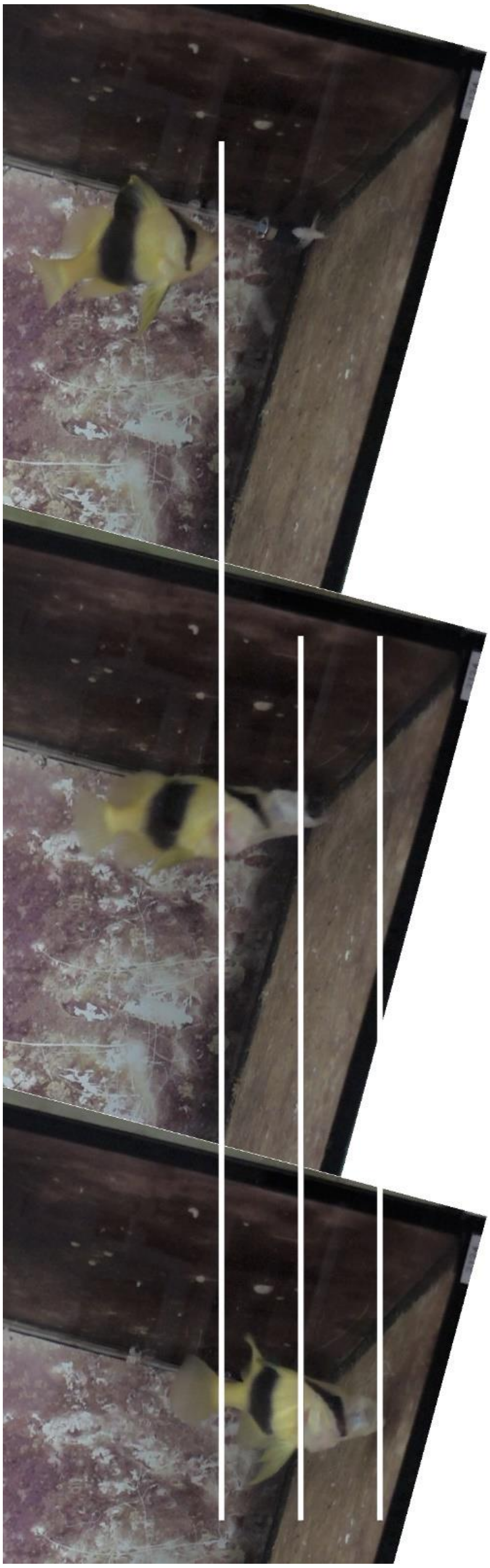
[8] Wainwright, P.C. & Bellwood, D. 2002 Ecomorphology of Feeding in Coral Reef Fishes. In *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. S. Peter), p. 33.

# Appendix C (Supplemental material for Chapter 4)

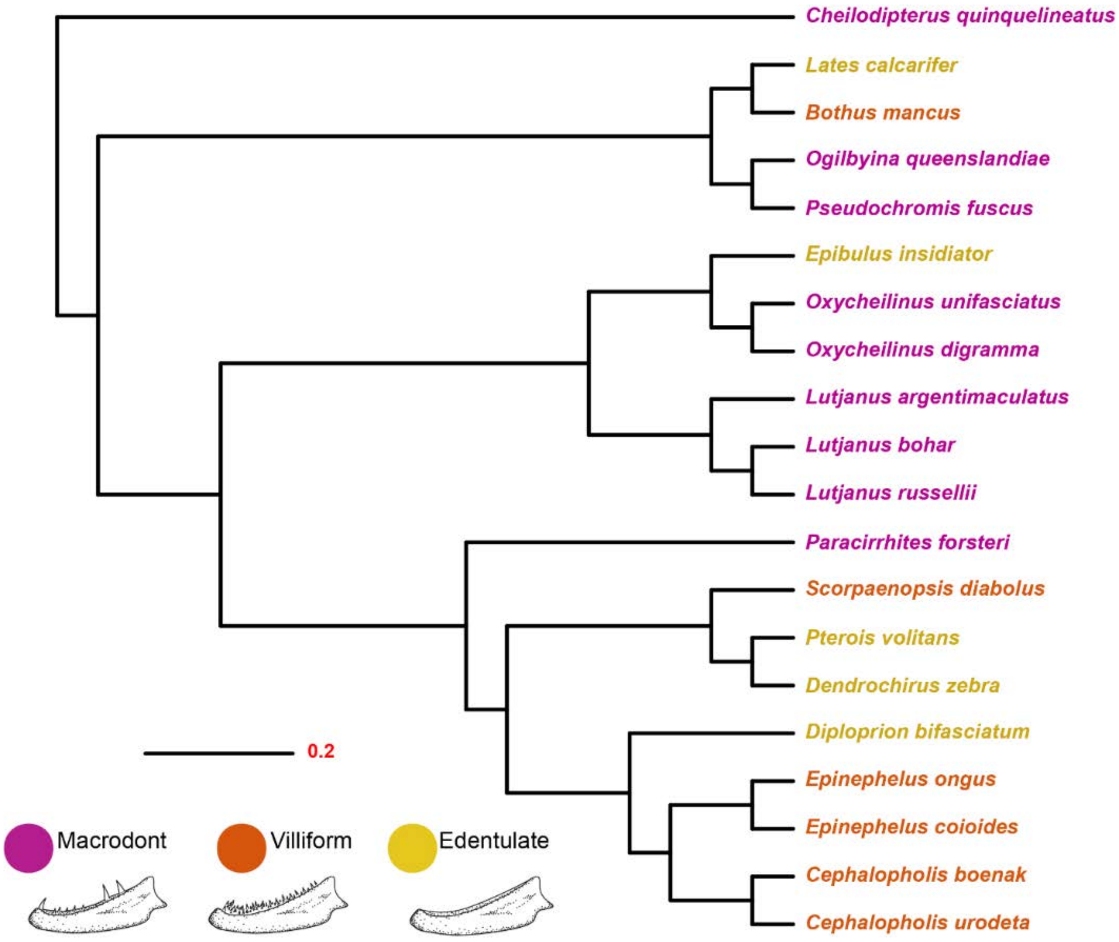
| **Term used in literature** | **Species** | **Morphotype** | **Functional Group** | **Reference** |
|---|---|---|---|---|
| Ambush | *Cephalopholis cruentata* | V | GR | Green et al. 2019 |
| Ambush | *Plectropomus leopardus* | M | GR | Wen et al. 2013, St. John 1995 |
| Ambush | *Pseudochromis fuscus* | M | GR | Wen et al. 2013, Feeney et al. 2012 |
| Ambush | *Epinephelus morio* | V | EN | Freitas et al. 2017 |
| Ambush | *Mycteroperca bonaci* | V | GR | Freitas et al. 2017 |
| Ambush | *Synanceia verrucosa* | V | EN | Grobecker 1983 |
| Ambush | *Cephalopholis cruentata* | V | GR | Almany 2004 |
| Ambush | *Cephalopholis fulva* | V | GR | Almany 2004 |
| Ambush | *Serranus tigrinus* | V | GR | Almany 2004 |
| Ambush | *Rypticus bistrispinus* | E | EN | Almany 2004 |
| Ambush | *Paracirrhites arcatus* | M | GR | DeMartini 1996, Hobson 1974, |
| Ambush | *Trachinocephalus uranoscopus* | V | GR | Kwik 2011 |
| Ambush | *Synodus intermedius* | V | GR | Rojas-Velez et al. 2019 |
| Ambush | *Sphyraena barracuda* | M | GR | Rojas-Velez et al. 2019 |
| Ambush | *Paracirrhites forsteri* | M | GR | Leray et al. 2012 |
| Ambush | *Paracirrhites hemistictus* | M | GR | Leray et al. 2012 |
| Ambush | *Epinephelus marginatus* | V | EN | Gerhardinger et al. 2006 |
| Ambush | *Synodus englemani* | V | GR | Sweatman 1984 |
| Ambush | *Synodus dermatogenys* | V | GR | McCormick et al. 2018 |
| Ambush | *Cephalopholis microprion* | V | GR | McCormick et al. 2018 |
| Ambush | *Pterois volitans* | E | EN | Morris, Akins 2009 |
| Ambush | *Cephalopholis boenak* | V | GR | Palacios et al. 2018 |
| Ambush | *Epinephelus maculatus* | V | EN | Palacios et al. 2018 |
| Ambush | *Synodus variegatus* | V | GR | Holmes McCormick 2006 |
| Ambush | *Epinephelus itajara* | V | EN | Collins Motta 2017 |
| Ambush | *Lates calcarifer* | E | EN | Norin and Clark 2017 |
| Ambush | *Trichiurus lepturus* | M | GR | Bemis et al. 2019 |

| | | | | |
|---|---|---|---|---|
| Ambush | *Dendrochirus zebra* | E | EN | Moyer and Zaiser 1981 |
| Ambush | *Aulostomus maculatus* | E | EN | Aronson 1983 |
| Ambush | *Antennarius hispidus* | E | EN | Longo et al. 2016 |
| Ambush | *Cephalopholis hemistiktos* | V | GR | Shpigel and Fishelson 1989 |
| Ambush | *Cephalopholis moiniata* | V | GR | Shpigel and Fishelson 1989 |
| Pursuit | *Pseudochromis fuscus* | M | GR | McCormick et al. 2018 |
| Pursuit | *Thalassoma lunare* | M | GR | McCormick et al. 2018 |
| Sit-and-wait | *Mycteroperca bonaci* | V | GR | Preisser et al. 2007, Parrish 1993, Catano et al. 2017 |
| Sit-and-wait | *Cephalopholis boenak* | V | GR | Palacios et al. 2018 |
| Sit-and-wait | *Epinephelus maculatus* | V | EN | Palacios et al. 2018 |
| Sit-and-wait | *Pterois volitans* | E | EN | Cure et al. 2012 |
| Sit-and-pursue | *Sphyraena barracuda* | M | GR | Preisser et al. 2007, Catano et al. 2017 |
| Stalking/ers | *Pterois volitans* | E | EN | Green et al. 2019, Cure et al. 2012 |
| Stalking/ers | *Dendrochirus zebra* | E | EN | Moyer and Zaiser 1981 |
| Active | *Pseudochromis fuscus* | M | GR | Preisser et al. 2007, Palacios et al. 2018 |
| Roving | *Lutjanus apodus* | M | GR | Green et al. 2019 |
| Prowl | *Plectropomus leopardus* | M | GR | St. John 1995 |
| Pivot-feeding | *Aulostomus maculatus* | E | EN | Longo et al. 2016 |
| High-ram suction | *Epinephelus ongus* | V | EN | Longo et al. 2016 |
| High-ram suction | *Caranx sexfasciatus* | E | GR | Longo et al. 2016 |
| Ram-biter | *Sphyraena barracuda* | M | GR | Longo et al. 2016 |

**Appendix C Table 1.** Data used for Figure 5 in the main text.



**Appendix C Figure 1**: Frames from videos used in my analyses. Vertical lines represent points from which strike distances, and distance travelled post captured were measured. Frames represent strike initiation, moment of capture, and frame at which strike is completed.



**Appendix C Figure 2**: Phylogenetic tree used in analyses.

**Appendix C Table 2**: Statistical models used to compare morphological variables between morphotypes, on body size and phylogenetic-corrected residuals.

*glm(Dependent ~ Morphotype)*

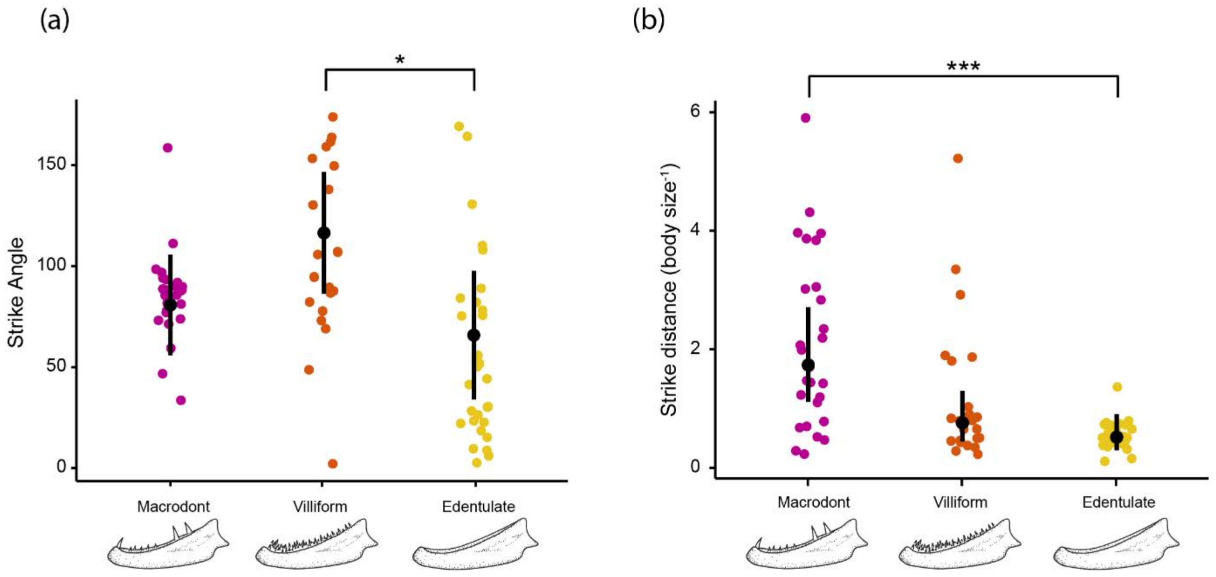
| Variable | Level | Estimate | St. Error | t-value | p-value |
|---|---|---|---|---|---|
| Protrusion | (Intercept) | 6.176 | 2.752 | 2.244 | 0.0384 |

| | | | | | |
|---|---|---|---|---|---|
| | Macrodont | -7.978 | 3.432 | -2.324 | **0.032** |
| | Villiform | -6.186 | 3.726 | -1.66 | 0.115 |
| Adductor Mandibulae | (Intercept) | -0.172 | 0.091 | -1.871 | 0.078 |
| | Macrodont | 0.339 | 0.114 | 2.96 | **<0.01** |
| | Villiform | 0.193 | 0.124 | 1.556 | 0.138 |
| Gape size | (Intercept) | -0.524 | 4.584 | -0.114 | 0.91 |
| | Macrodont | -0.9 | 5.717 | -0.158 | 0.877 |
| | Villiform | 8.86 | 6.207 | 1.427 | 0.172 |

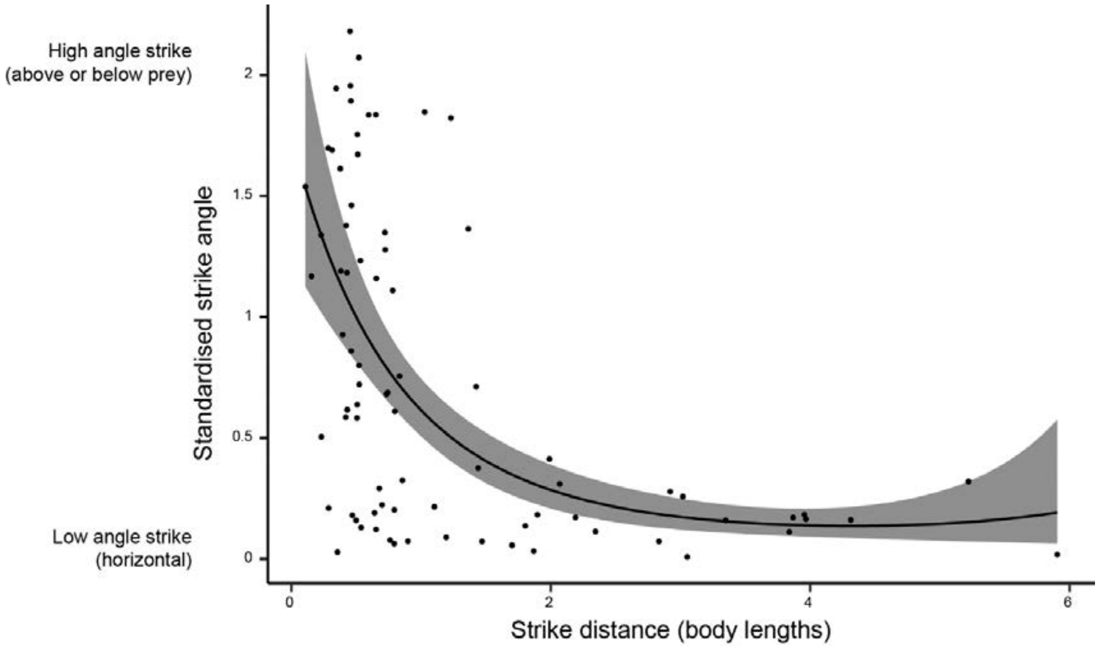
**Appendix C Table 3**: Statistical models used in behavioural analyses and metanalysis.

| **Strike behaviour** | **glmm(Angle ~ Morphotype + (1\|Species), REML = T)** | | **Estimate** | **Std. Error** | **z value** | **p-value** |
|---|---|---|---|---|---|---|
| | | (Intercept) | 65.86 | 16.47 | 3.999 | <0.001 |
| | | Macrodont | 13.53 | 21.43 | 0.632 | 0.5277 |
| | | Villiform | 50.65 | 22.65 | 2.236 | **0.0254** |
| | **glmm(Strike Distance ~ Morphotype + (1\|Species), family=Gamma(link='log'),REML=T)** | | **Estimate** | **Std. Error** | **z value** | **p-value** |
| | | (Intercept) | -0.6601 | 0.2826 | -2.336 | 0.0195 |
| | | Macrodont | 1.127 | 0.3696 | 3.049 | **0.0023** |
| | | Villiform | 0.3817 | 0.3915 | 0.975 | 0.3295 |
| | **glm(Angle ~ poly(Strike distance,2), family=Gamma(link='log'))** | | **Estimate** | **Std. Error** | **t value** | **p-value** |
| | | (Intercept) | 0.1191 | 0.138 | 0.863 | 0.391 |
| | | Strike distance | -0.486 | 0.089 | -5.465 | **<0.001** |
| **Capture behaviour** | **glmm(Capture ~ Morphotype+(1\|Species),family = binomial(link='logit'),REML=T)** | | **Estimate** | **Std. Error** | **z value** | **p-value** |
| | | (Intercept) | 0.0236 | 0.0252 | -3.51 | <0.001 |
| | | Macrodont | 175 | 209 | 4.32 | **<0.001** |
| | | Villiform | 7.44 | 9.07 | 1.65 | 0.09 |
| **Post-capture** | **glmm(Distance after strike ~ Morphotype + (1\|id/Species), family = 'Gamma'(link = 'log'), REML = T)** | | **Estimate** | **Std. Error** | **z value** | **Pr(>\|z\|)** |
| | | (Intercept) | 2.3394 | 0.2973 | 7.87 | <0.001 |
| | | Macrodont | 1.2822 | 0.3965 | 3.234 | **0.00122** |
| | | Villiform | 1.0031 | 0.4205 | 2.386 | **0.01705** |

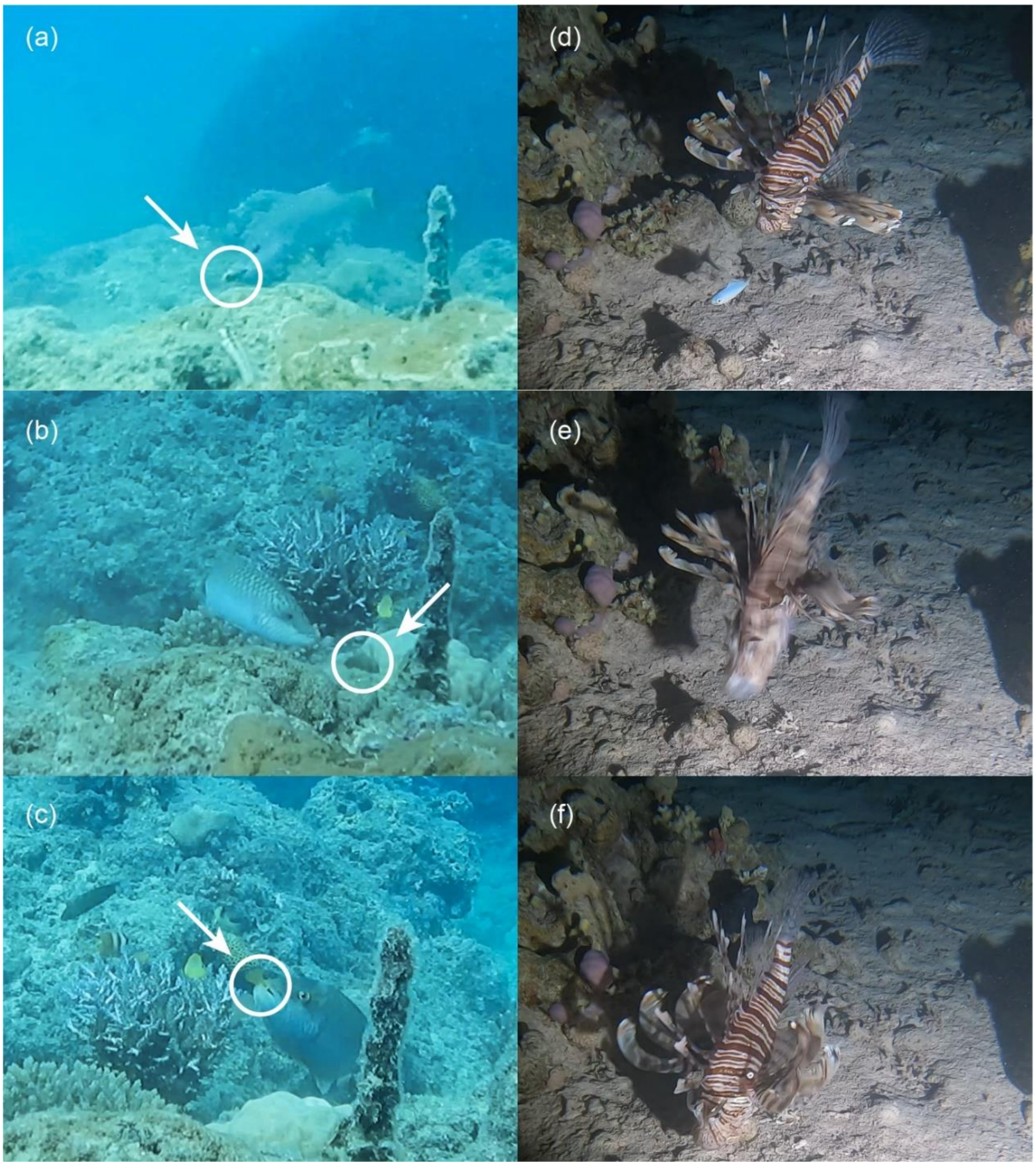
| **Metanalysis** | **stan_glm(prop_prey_size ~ FG2*pred_length, data=psdata, family=Gamma(link ='log'),refresh=0, chains=3,iter=5000,warmup=2000,thin=5, adapt_delta=0.99)** |  | **estimate** | **std.error** | **conf.low** | **conf.high** |
|---|---|---|---|---|---|---|
|  |  | (Intercept) | -1.02 | 0.04 | -1.09 | -0.934 |
|  |  | Functional group grab | 0.809 | 0.066 | 0.674 | 0.931 |
|  |  | pred_length | 0.0000771 | 0.0000791 | -0.0000796 | 0.000227 |
|  |  | Functional group grab:pred_length | -0.00169 | 0.000148 | -0.00199 | -0.00141 |
|  |  | shape | 2.76 | 0.0786 | 2.6 | 2.9 |
|  |  | mean_PPD | 0.412 | 0.00755 | 0.398 | 0.427 |
|  |  | log-posterior | 268 | 1.59 | 265 | 270 |
|  |  |  |  |  |  |  |



**Appendix C Figure 3.** (a) Strike angle and (b) distance of piscivorous fishes when striking at prey. Strike distance is shown relative to predators' body size (SL). Black bars represent means with 95% Confidence Intervals. Asterisks indicate level of significance between morphotypes.



**Appendix C Figure 4**: Relationship between strike distance and absolute values of centred strike angle data, showing a significant (GLM; p<0.01) inverse relationship.



**Appendix C Figure 5:** Field-based predation events observed for the grabber *Oxycheilinus unifasciatus* (a-c), and the engulfer *Pterois volitans* (d-f). Upon tail-first capture (a) *O.unifasciatus* was observed by one of the authors (MM) to conduct headshaking behaviour (not captured in video footage), followed by prey *Pomacentrus sp.* being spat out (b), and re-ingested head-first (c). *P.volitans* is observed conducting an engulfing strike and capture. Credits for *P.volitans* footage: Salvatore Di Lauro.

## References

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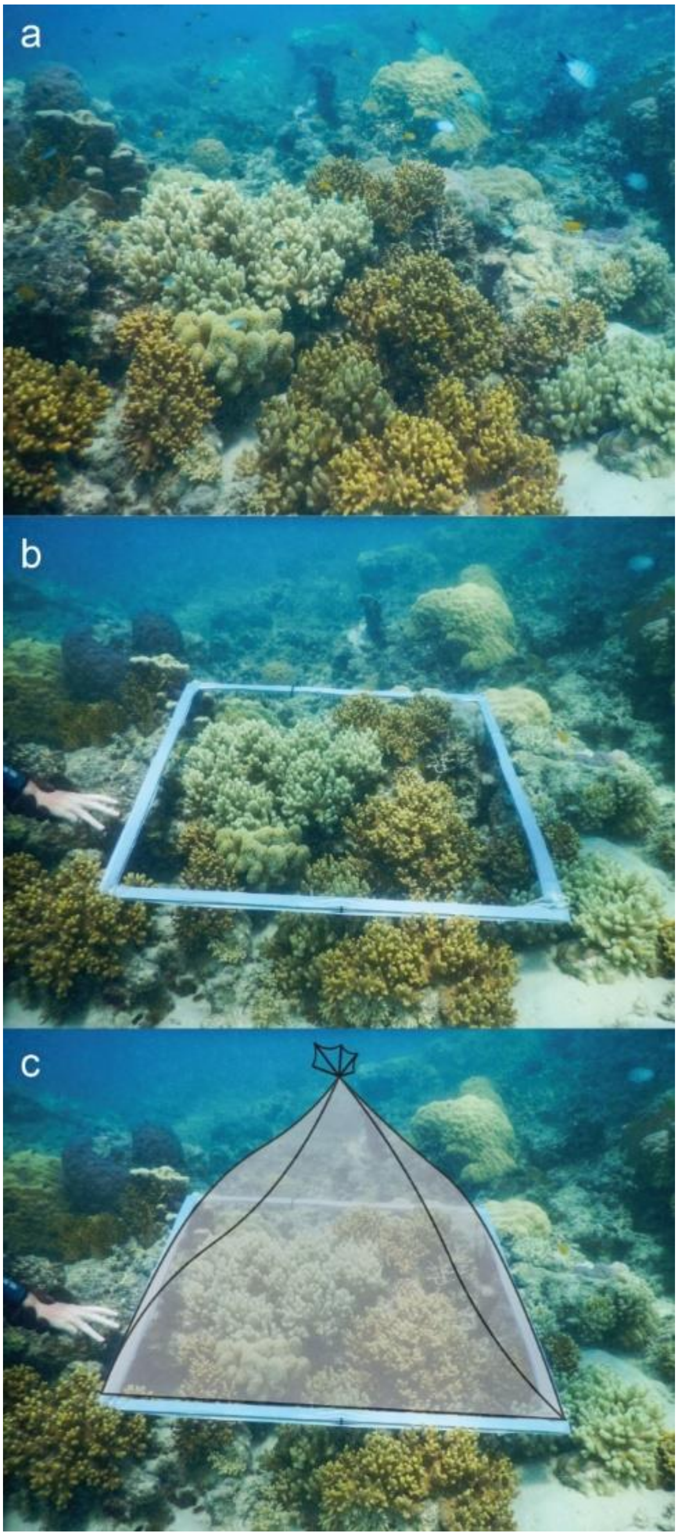
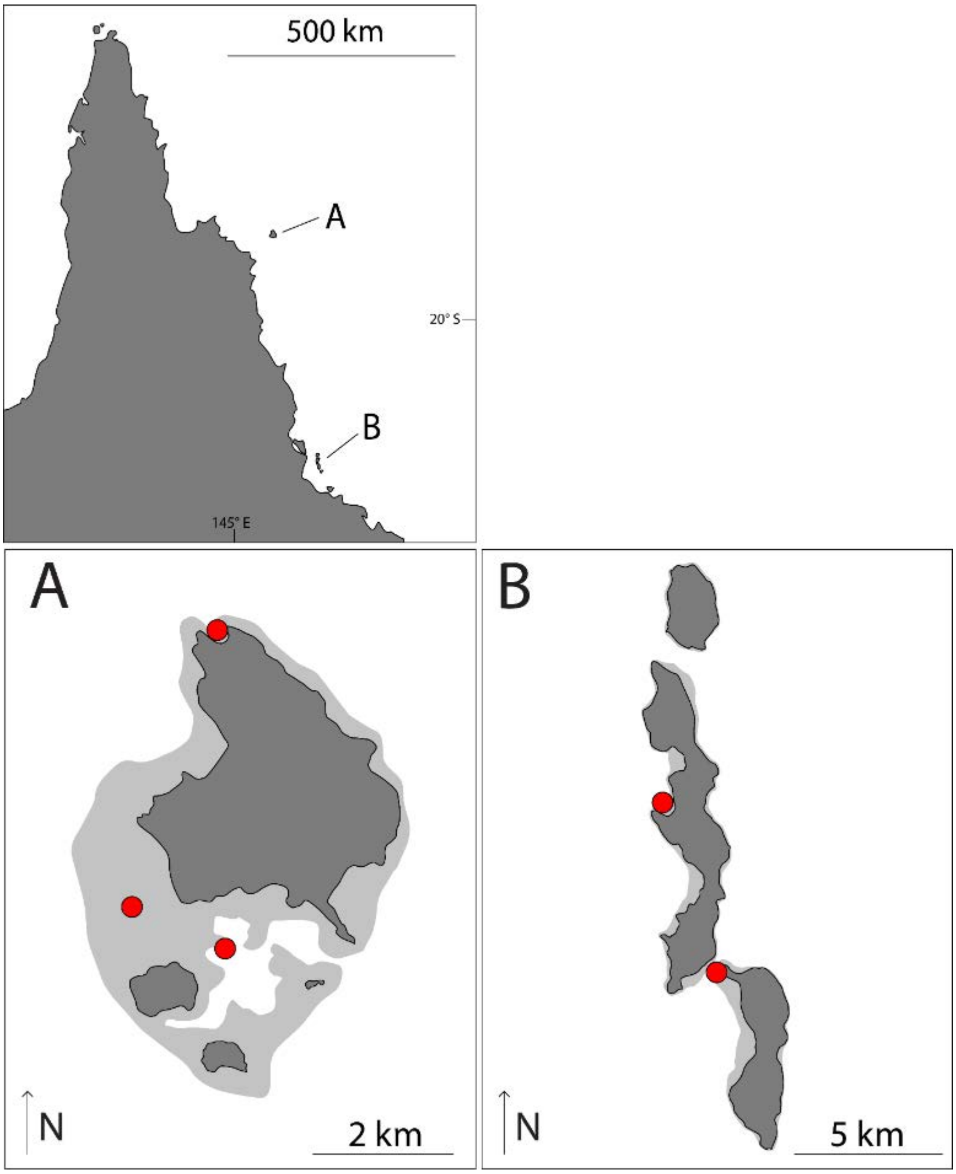
Long JA (1991) Arthrodire predation by Onychodus (Pisces, Crossopterygii) from the Late Devonian Gogo Formation, Western Australia. Western Australian Museum: Records 15:503-516

Schaeffer B, Rosen DE (1961) Major adaptive levels in the evolution of the actinopterygian feeding mechanism. American Zoologist:187-204

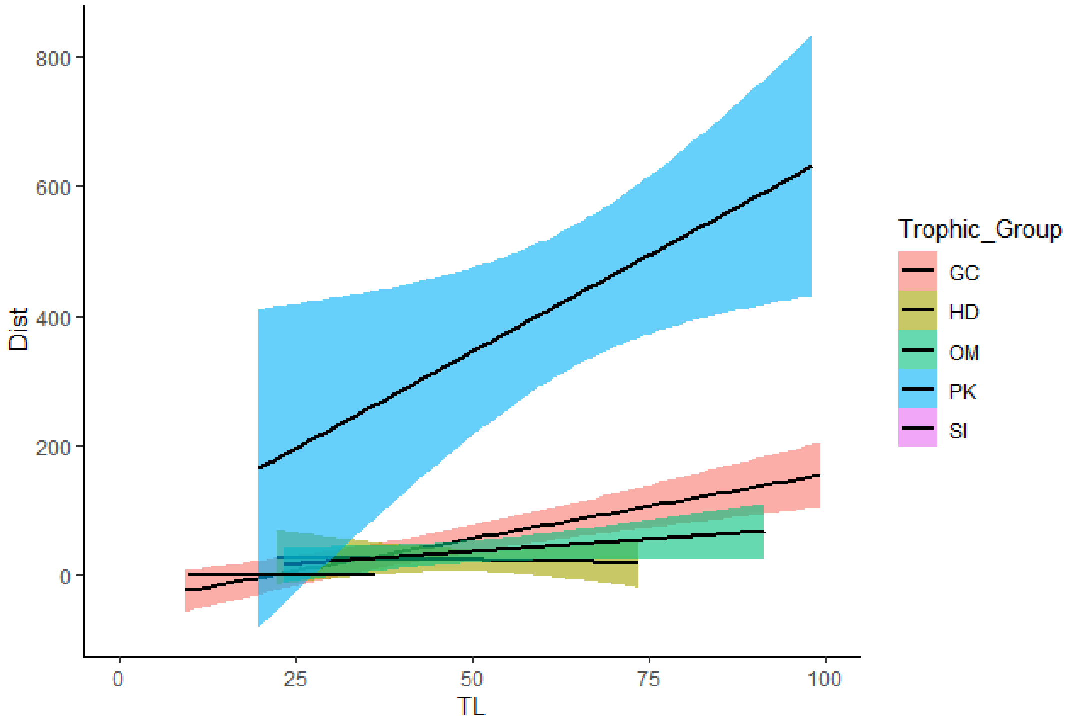
# Appendix D (Supplemental material for Chapter 5)



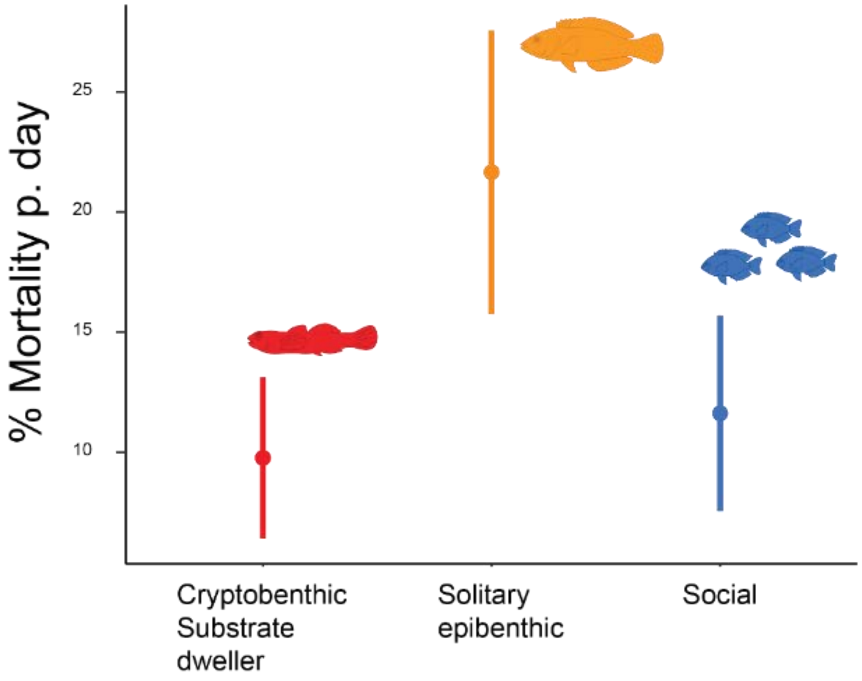
**Appendix D Figure 1.** Sampling quadrat methodology. (a) Haphazardly chosen location on the reef. (b) a 1sq.m quadrat overlaid in the desired location, used for scaling and delineation purposes. (c) A subset of the quadrats were also sampled as clove oil stations to sample cryptobenthic fish communities (sampling net drawn on this photo).



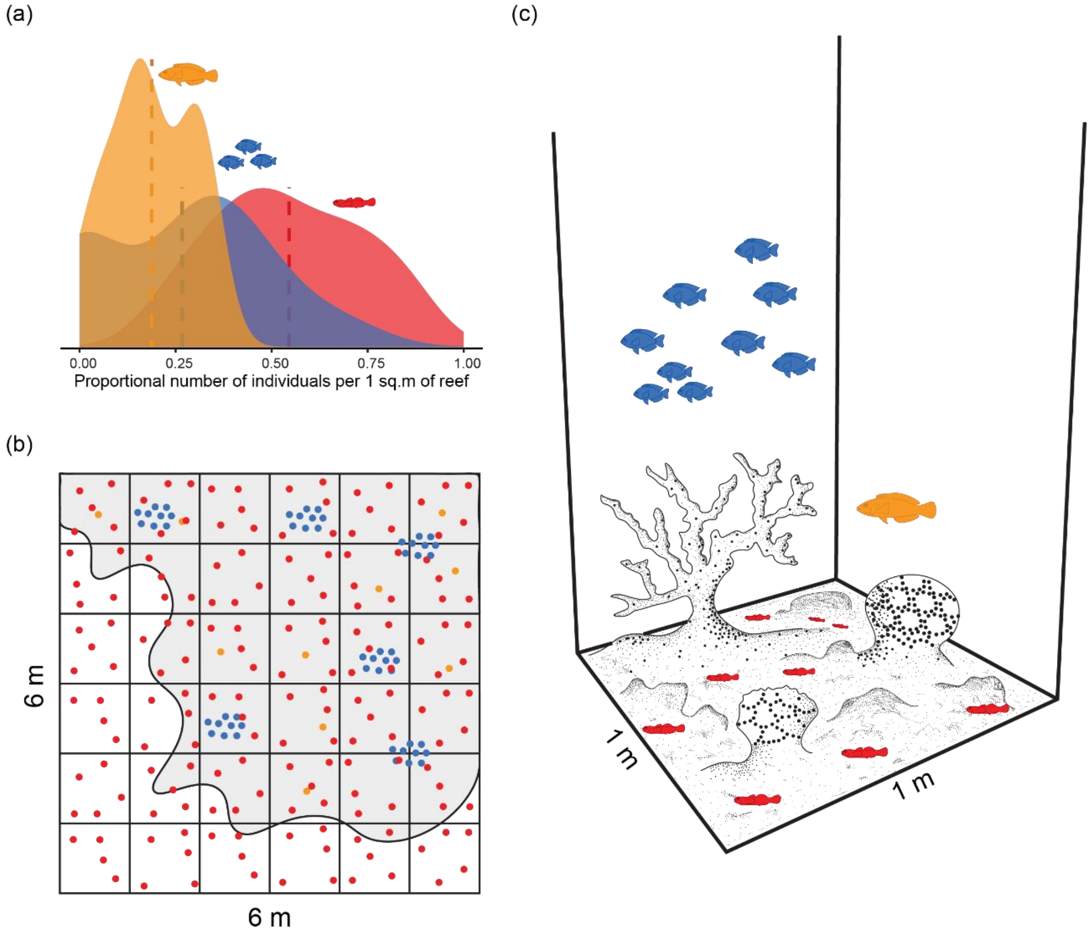
**Appendix D Figure 2.** Sites on Lizard Is. and Orpheus Is. where my study took place. Red dots indicate sampling sites.



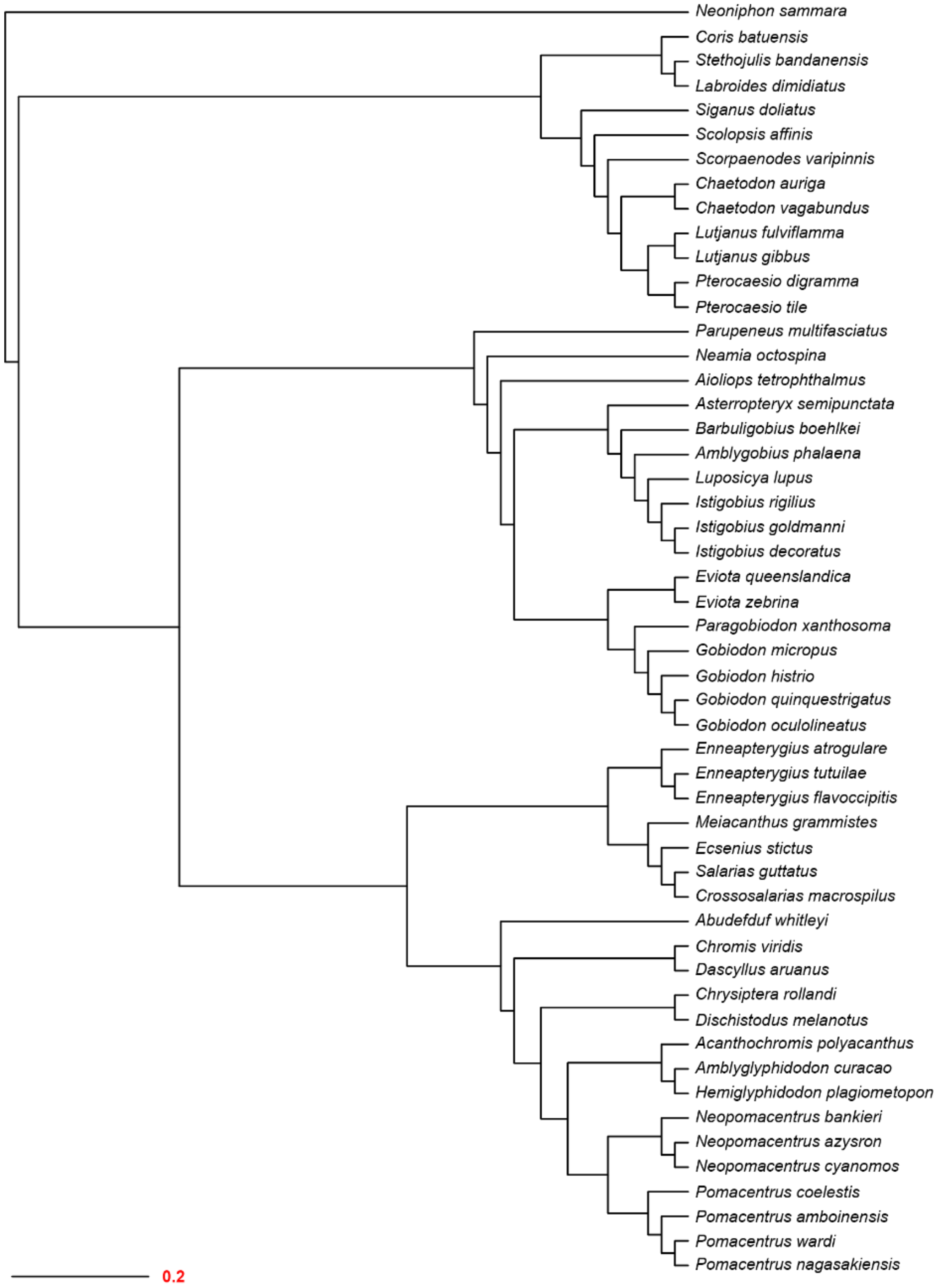
**Appendix D Figure 3.** Distance from benthos (Dist) vs. body size (Total Length) based on trophic groups of prey fishes. GC: Generalised carnivore, HD: Herbivore/Detritivore, OM: Omnivore, PK: Planktivore, SI: Sessile invertivore.



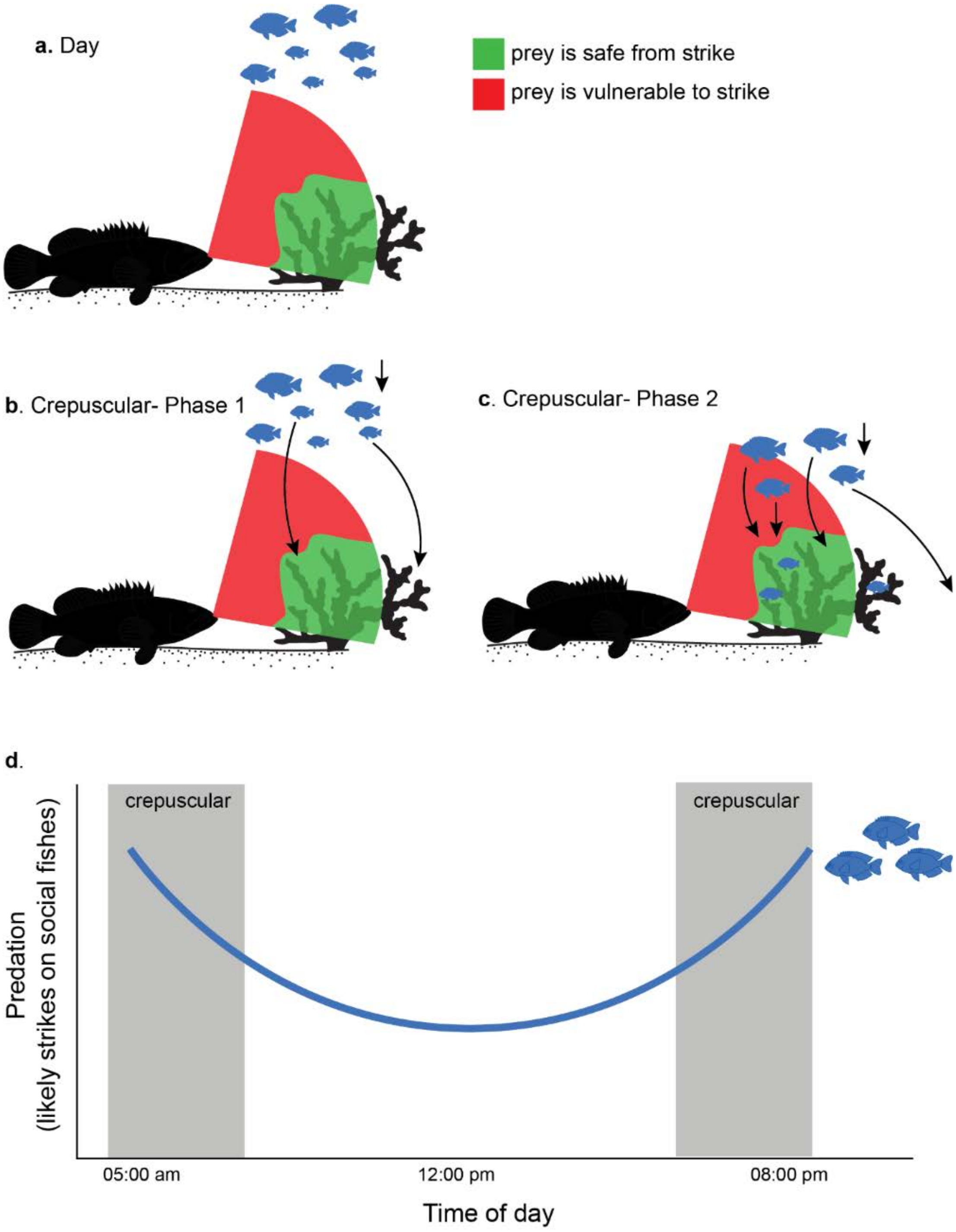
**Appendix D Figure 4**. Model output for mean mortality rates with 95% Confidence Intervals, between functional groups. I found the highest mortality rate to be for solitary epibenthic species (mean approx. 21.6% +/- 3 S.E mortality p. day), and cryptobenthic substratum dwellers (mean approx. 9.7% +/- 1.7 S.E mortality p. day) having highly similar rates with social (mean approx. 11.6% +/- 2 S.E mortality p. day) species. We note that the best fit model, was one with an interaction term between functional group and body size.



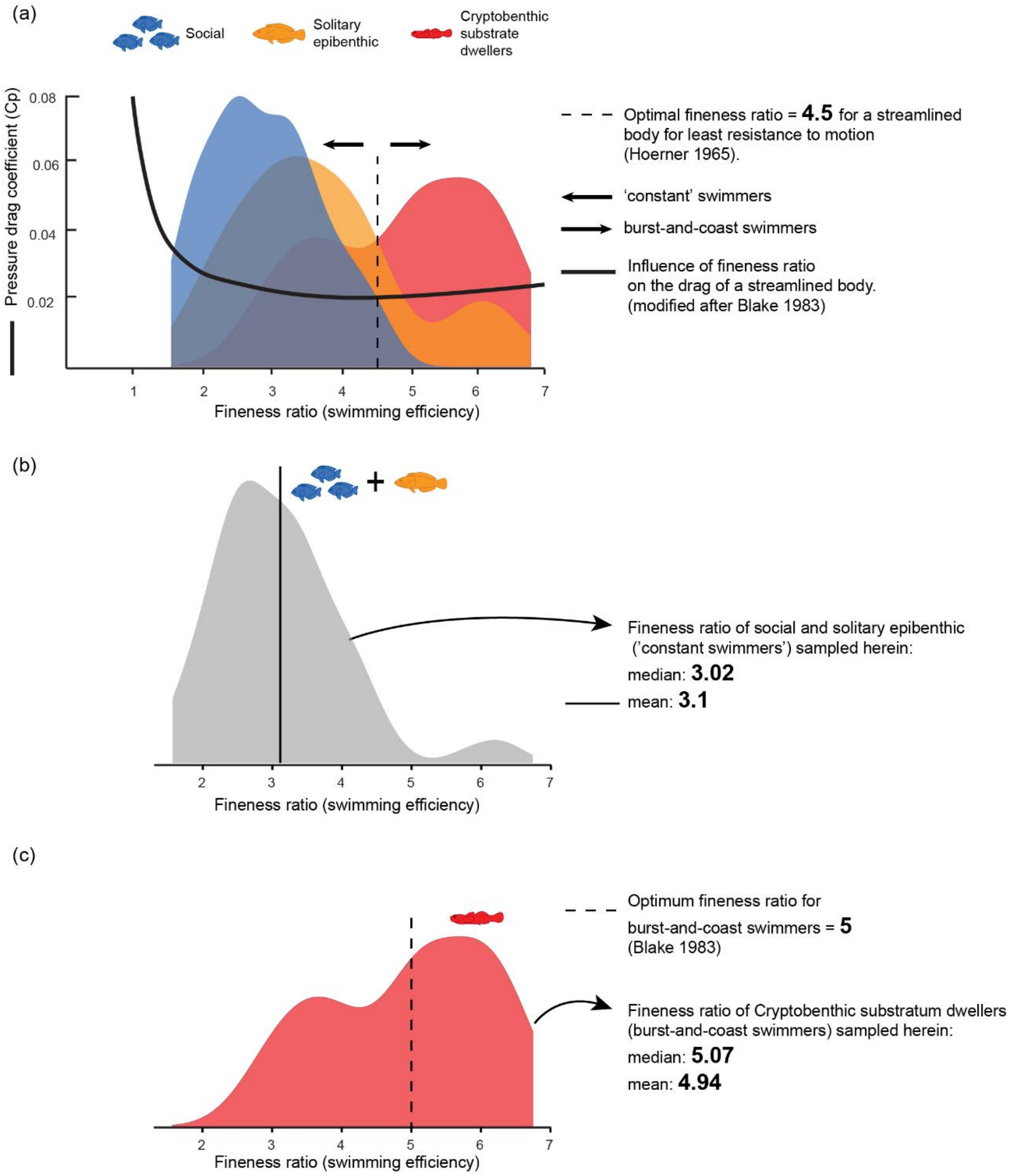
**Appendix D Figure 5**. Prey fish abundance in coral reef fishes. (a) Proportional number of individuals per 1 square meter of reef for the three established functional groups: cryptobenthic substratum dwellers (red), solitary epibenthic (orange), and social (blue) fishes. (b) graphical illustration of the relative abundance of each prey functional group at a larger scale (36 square meters) seen from above. (c) graphical illustration of each functional group relative to the reef benthos (at 1 square meter).



**Appendix D Figure 6**. Phylogenetic tree used in phylogenetically informed analyses.



**Appendix D Figure 7**. Graphical illustration of circadian behaviour of schooling fishes, and how this relates to predation risk by benthic associated predators. **a.** During daytime, schooling planktivorous fishes are found up in the water column. This behaviour may reflect a release from benthic/substratum-based predation. **b.** During the first phase of the crepuscular period, small-bodied schooling species, and smaller individuals within larger-bodied schools, individually carry out burst swims into hiding holes (reef crevices, branching corals etc.). Simultaneously, larger schooling species and larger individuals within a school, gradually swim closer towards the reef benthos (Hobson 1965; Hobson 1972). **c.** At the crepuscular phase 2, remaining larger individuals of the school, simultaneously swim into hiding areas on the reef (Hobson 1965; Hobson 1972). **d.** My results, along with previous observations suggest temporal variation of when different functional groups of prey are available to different types of predators. Furthermore, solitary fishes were among the first individuals to seek shelter during the crepuscular period, and therefore during high crepuscular piscivory peaks, solitary species were under cover (Hobson 1965; Hobson 1972).



**Appendix D Figure 8.** Fineness ratio of fish communities sampled herein, displayed in terms of fineness ratio (swimming efficiency). (a) Fineness ratio (Total Length/Body depth) of social (blue), solitary epibenthic (orange), and cryptobenthic substrate dwellers (red) relative to a pressure drag coefficient (Cp) (Blake 1983; Langerhans & Reznick 2010). Fish communities (of all functional groups) are primarily distributed over a fineness ratio of a low Cp values. Note that the density of such fishes increases significantly, as soon as Cp decreases significantly. (b) Density distribution of the fineness ratio of constantly swimming (social and solitary epibenthic) coral reef fishes (median:3.02, mean:3.1). These fishes appear to have a local drag minimum where Cp is still relatively low, while still maximising their body volume. Given that these fishes are active swimmers in the water column, and thus more visible on the reef, they are more exposed to gape-limited predators (Motro, Ayalon & Genin 2005). This value of Cp for this group of fishes appear to reflect a trade-off between swimming efficiency and avoiding predation. (c) Density distribution of the fineness ratio of cryptobenthic substrate dwellers (median:5.07, mean:4.94). Blake (1983) found the optimal fineness ratio in his experiments to be 5 for burst-and-coast swimmers, a value highly similar to the pattern reflected by cryptobenthic substrate dweller fishes in coral reef fish communities (which utilise this swimming behaviour).

**Appendix D Table 1**. Model summary outputs for analyses carried out throughout the manuscript. Adequate power (≥0.8) (di Stephano 2003) was found in all models.

| **Model** | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Distance from benthos ~ scale(log(TL))*Behaviour, family = 'Gamma'(link = 'log')** | | | | | | | | |
| **n=46** | **term** | **estimate** | **std.error** | **statistic** | **p.value** | **conf.low** | **conf.high** | **Power** |
| n=31 | (Intercept) | 263 | 0.157 | 35.5 | <0.01 | 196 | 365 | |
| | scale(log(TL)) | 1.89 | 0.131 | 4.89 | <0.01 | 1.48 | 2.41 | |
| n=15 | Behavioursolitary | 0.252 | 0.276 | -5.00 | <0.01 | 0.148 | 0.445 | |
| | | | | | | | | 0.91 |
| **glm(Dist~TL,seg.Z = ~TL)** | | | | | | | | |
| **n=46** | **term** | **Estimate** | **Std.Error** | **t value** | **Pr(>\|t\|)** | | | |
| | (Intercept) | -7.8892 | 19.6865 | -0.401 | 0.69 | | | |
| n=46 | TL | 0.4147 | 0.6927 | 0.599 | 0.551 | | | |
| | U1.TL | 2.0995 | 0.9576 | 2.192 | NA | | | |
| | | | | | | | | 0.99 |
| **glm(relative body depth phylogenetic residuals ~ Functional groups + Total Length)** | | | | | | | | |

| **n=50** | **term** | **estimate** | **std.error** | **statistic** | **p.value** | **conf.low** | **conf.high** | |
|---|---|---|---|---|---|---|---|---|
| n=20 | (Intercept) | -3.93 | 2.23 | -1.76 | 0.084 | -8.29 | 0.436 | |
| n=14 | FGSolitary_epibenthic | 1.42 | 2.57 | 0.553 | 0.583 | -3.61 | 6.45 | |
| n=16 | FGSocial | 7.69 | 2.89 | 2.66 | 0.01 | 2.02 | 13.4 | |
| | Total Length | -0.04 | 0.056 | -0.838 | 0.406 | -0.157 | 0.0630 | |
| | | | | | | | | 0.8 |
| Post-hoc analysis on body depth between functional groups (model summary above) | | | | | | | | |
| | contrast | estimate | SE | z.ratio | p.value | | | |
| | CryptoSub.Dwel - Solit.Epib | -1.42 | 2.57 | -0.553 | 0.845 | | | |
| | Crypto.Sub.Dwel - Social | -7.69 | 2.89 | -2.66 | 0.02 | | | |
| | Solit.Epib - Social | -6.27 | 2.34 | -2.675 | 0.02 | | | |
| | | | | | | | | NA |
| **betareg(Mortality ~ scale(log(Total Length))*Functional Group+0, link='logit')** | | | | | | | | |
| n=76 | **term** | **Estimate** | **Std.Error** | **z value** | **Pr(>\|z\|)** | | | |
| | scale(log(TL) | -1.47364 | 0.47432 | -3.107 | 0.00189 | | | |
| n=20 | FGCrypto.Sub.Dwel | -2.62936 | 0.32077 | -8.197 | 2.46E-16 | | | |
| n=26 | FGSocial | -2.09275 | 0.23226 | -9.01 | 2.00E-16 | | | |
| n=30 | FGSolit.Epib | -1.54462 | 0.19935 | -7.748 | 9.31E-15 | | | |
| | scale(log(TL):FGSocial | 0.87189 | 0.54545 | 1.598 | 0.10993 | | | |
| | scale(log(TL):FGSolit.Epib | -0.09269 | 0.50761 | -0.183 | 0.85511 | | | |
| | | | | | | | | 0.99 |

**Appendix D Table 2**. Classifications of Functional groups for prey species analysed herein. SOC=Social, SEP=Solitary Epibenthic, CSD=Cryptobenthic Substratum Dwellers.

| **Family** | **Genus** | **Species** | **Functional Group** |
|---|---|---|---|
| Pomacentridae | Abudefduf | whitleyi | SOC |
| Pomacentridae | Acanthochromis | polyacanthus | SOC |
| Gobiidae | Aioliops | tetrophthalmus | SEP |
| Pomacentridae | Amblyglyphidodon | curacao | SOC |
| Gobiidae | Amblygobius | phalaena | SEP |
| Gobiidae | Asterropteryx | semipunctata | CSD |
| Gobiidae | Barbuligobius | boehlkei | CSD |
| Gobiidae | Callogobius | cf. sclateri | CSD |

| | | | |
|---|---|---|---|
| Chaetodontidae | Chaetodon | auriga | SOC |
| Chaetodontidae | Chaetodon | vagabundus | SOC |
| Pomacentridae | Chromis | viridis | SOC |
| Pomacentridae | Chrysiptera | rollandi | SEP |
| Labridae | Coris | batuensis | SEP |
| Blenniidae | Crossosalarias | macrospilus | CSD |
| Pomacentridae | Dascyllus | aruanus | SOC |
| Pomacentridae | Dischistodus | melanotus | SEP |
| Pomacentridae | Dischistodus | perspicillatus | SOC |
| Blenniidae | Ecsenius | stictus | CSD |
| Tripterygiidae | Enneapterygius | atrogulare | CSD |
| Tripterygiidae | Enneapterygius | flavoccipitis | CSD |
| Tripterygiidae | Enneapterygius | tutuilae | CSD |
| Gobiidae | Eviota | queenslandica | CSD |
| Gobiidae | Eviota | zebrina | CSD |
| Apogonidae | Fowleria | sp. | SOC |
| Gobiidae | Gobiodon | histrio | CSD |
| Gobiidae | Gobiodon | micropus | CSD |
| Gobiidae | Gobiodon | oculolineatus | CSD |
| Gobiidae | Gobiodon | quinquestrigatus | CSD |
| Pomacentridae | Hemiglyphidodon | plagiometopon | SEP |
| Gobiidae | Istigobius | decoratus | CSD |
| Gobiidae | Istigobius | goldmanni | CSD |
| Gobiidae | Istigobius | nigrocellatus | CSD |
| Gobiidae | Istigobius | rigilius | CSD |
| Labridae | Labroides | dimidiatus | SEP |
| Gobiidae | Luposicya | lupus | CSD |
| Lutjanidae | Lutjanus | fulviflamma | SEP |
| Lutjanidae | Lutjanus | gibbus | SEP |
| Blenniidae | Meiacanthus | grammistes | SEP |
| Apogonidae | Neamia | octospina | SOC |

| | | | |
|---|---|---|---|
| Holocentridae | Neoniphon | sammara | SOC |
| Pomacentridae | Neopomacentrus | azysron | SOC |
| Pomacentridae | Neopomacentrus | bankieri | SOC |
| Pomacentridae | Neopomacentrus | cyanomos | SOC |
| Gobiidae | Paragobiodon | xanthosoma | CSD |
| Mullidae | Parupeneus | multifasciatus | CSD |
| Plesiopidae | Plesiops | sp. | SEP |
| Gobiidae | Pleurosicya | cf. labiata | CSD |
| Pomacentridae | Pomacentrus | amboinensis | SOC |
| Pomacentridae | Pomacentrus | coelestis | SOC |
| Pomacentridae | Pomacentrus | moluccensis | SOC |
| Pomacentridae | Pomacentrus | nagasakiensis | SOC |
| Pomacentridae | Pomacentrus | wardi | SEP |
| Caesionidae | Pterocaesio | digramma | SOC |
| Caesionidae | Pterocaesio | tile | SOC |
| Blenniidae | Salarias | guttatus | CSD |
| Nemipteridae | Scolopsis | affinis | SEP |
| Nemipteridae | Scolopsis | bilineatus | SEP |
| Scorpaenidae | Scorpaenodes | cf. guamensis | CSD |
| Scorpaenidae | Scorpaenodes | varipinnis | CSD |
| Siganidae | Siganus | doliatus | SEP |
| Labridae | Stethojulis | bandanensis | SEP |

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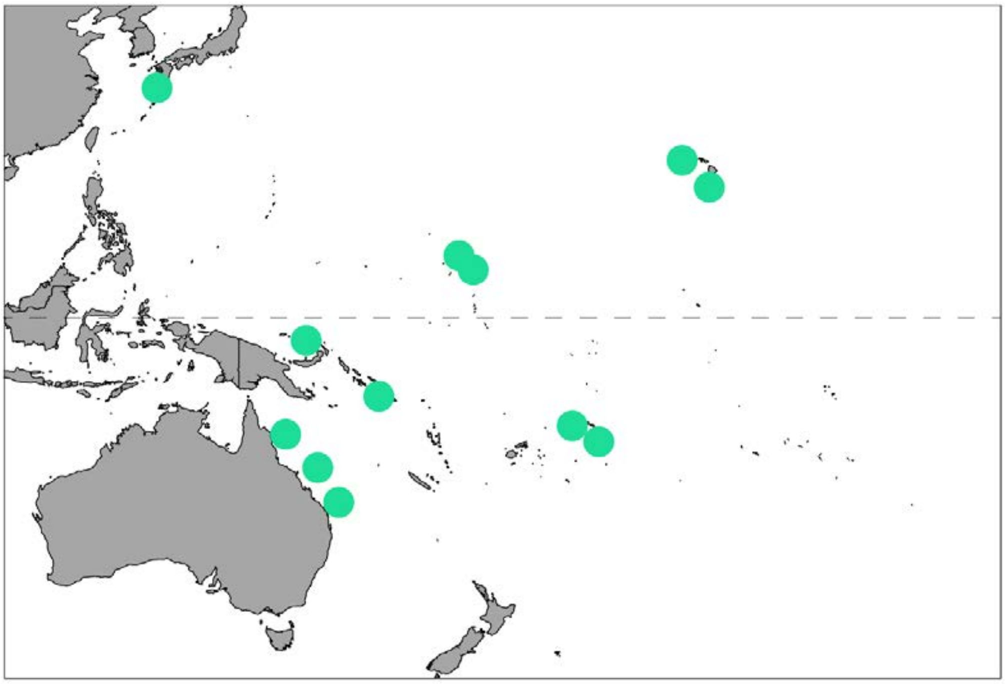
## Appendix E (Supplemental material for Chapter 6)

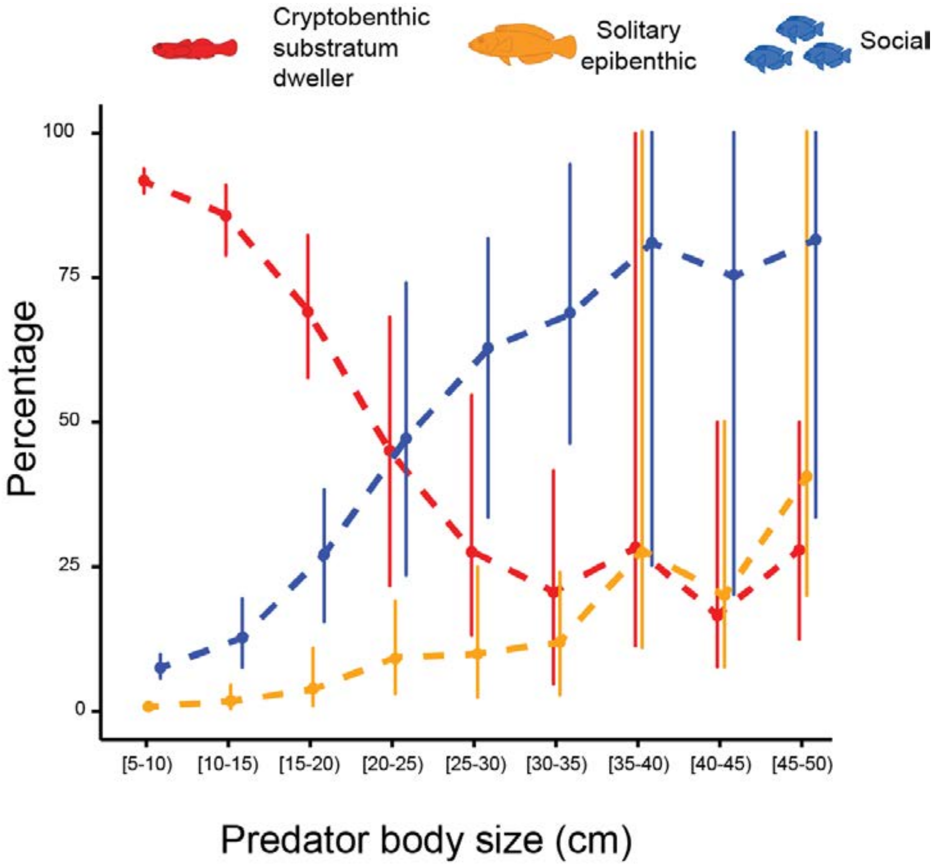


**Appendix E Figure 1**. Map showing the sites from which studies of our metanalysis conducted gut content analyses.

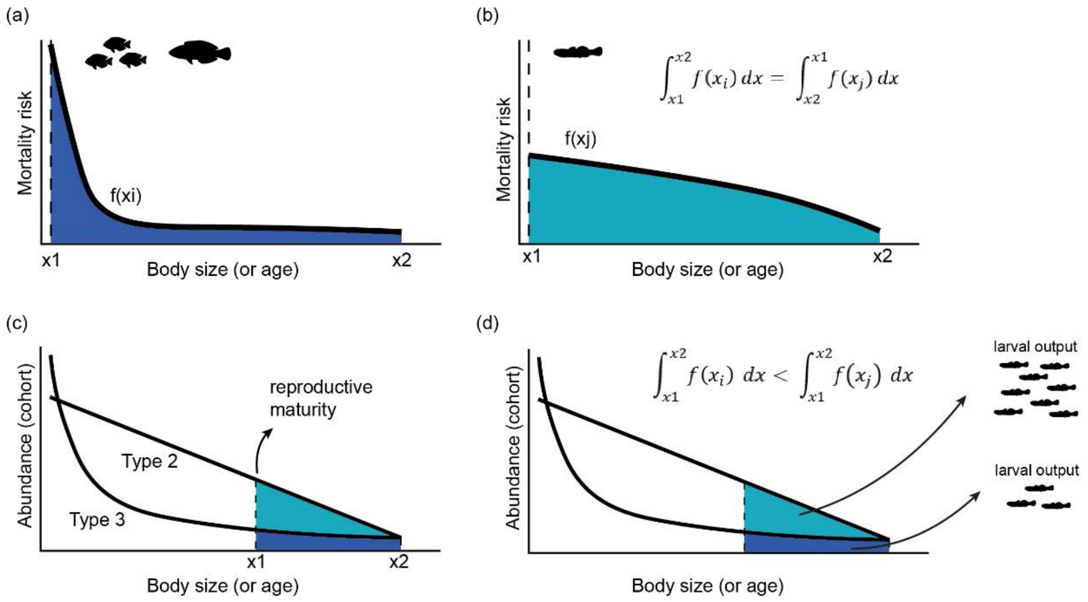
| | **Functional group** | **Description** |
|---|---|---|
| **Predator** | Grabber | macrodont dentition (sensu Chapter 3) with relatively large jaw musculature. Can strike from larger distances (>2 body lengths). Captures prey by grabbing it tail- or body-first, usually followed by headshaking behaviour. |
| | Engulfer | villiform or edentulate dentition (sensu Chapter 3) with relatively small jaw musculature. Strikes from high angles (above or below prey) and relatively small distances. Captures prey primarily by engulfing it whole. |
| **Prey** | Social | primarily deep bodied schooling planktivores swimming higher up in the water column. |

| | | |
|---|---|---|
| | Epibenthic | more elongate, solitary, and swimming above, but closer to the benthos |
| | Cryptobenthic | primarily elongate, solitary, and 'sitting' on the benthos |

**Appendix E Table 1**. Functional groups used in our study, along with a description of their functional traits directly related to predator-prey relationships. The implementation of a functional group approach (based on functional traits) has reduced the initial complexity of coral reef piscivores. This work has identified two functional groups of predators, grabbers and engulfers, which differ in their morphology, striking, capturing and prey processing behaviour (Chapter 4). Reef fish prey can also be divided into cryptobenthic substratum dwellers (referred to herein as 'cryptobenthic'), solitary epibenthic ('epibenthic' herein), and social fishes, which differ in anti-predatory morphological and behavioural traits, as well as in habitat use (e.g., position in water column) (Chapter 5). We note here that the term 'cryptobenthic' is slightly different than that of Brandl et al. (2018); For a detailed description of these functional groups, see Supplemental Table 1.



**Appendix E Figure 2**. For prey availability, we found distinct patterns between the different prey functional groups. We found that for small predator body sizes (< 15-20cm), the modelled availability of social and epibenthic prey contributed little to bin-specific predator diet. The vast majority of expected prey to be found in the guts of small-bodied predators, is crypto prey. This expected importance of cryptos as relative contribution to the potential diet of predators, decreased with increasing predator body size. As a consequence, epibenthic and social prey showed little predicted availability for small predator sizes, with increasing availability as predator sizes increased.



**Appendix E Figure 3**. (a) Current and (b) suggested models of body size vs. mortality relationships. While the overall mortality remains the same between the current and suggested model (area below curves), the shape of the suggested distribution (i.e., flattening the curve), results in different survivorship curves (Type 2 vs. Type 3) (c-d). These differences in survivorship curves may allow for a higher number of reproducing individuals, and provide a potential explanation for limited individual gamete output, resulting in high overall contribution to the larval pool near coral reefs (Brandl et al. 2019).