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Functional niche partitioning in herbivorous coral reef fishes

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Chapter 2:

- Simon Brandl: concept of study, data collection, writing of manuscript
- David Bellwood: concept of study, writing of manuscript

Chapter 3:

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Abstract

Ecological niche theory predicts that the diversity of life hinges on differences in the ways in which species exploit available resources, i.e. their ecological niche. An organism's niche can be divided into the fundamental and the realized niche. The fundamental niche refers to a species' inherent potential capabilities (based on, for instance, its morphology), while the realized niche represents a species' behaviour when it can interact with the biotic and abiotic components of its environment. Tropical coral reefs stand out as one of the most diverse ecosystems on Earth, but patterns of niche partitioning among coral reef organisms are poorly understood. Herbivorous coral reef fishes are frequently considered to perform one of the most critical ecosystem processes on coral reefs, the removal of algal and detrital material from the reef substratum. However, while several classification schemes have previously been employed to characterize the functional role of different herbivores, detailed holistic investigations of niche differences among herbivore species are rare. Therefore, in this thesis, I use social, morphological, behavioural, and environmental factors to disentangle the functional niches of herbivorous fishes on coral reefs.

One of the most prominent social systems in animals is the association between two individuals, commonly termed a 'pair'. However, given that sexual reproduction in higher animals commonly requires the association between two partners, reproductive connotations frequently override the social-ecological benefits that a partner can provide and thus, the potential effects of pairing on an animal's functional niche. In teleost fishes, pairing is common but little is known about the potential drivers and consequences of this behaviour. My first objective, therefore, was to quantify the extent of pair-formation in coral reef fishes and to examine potential ecological/reproductive correlates of pair-formation. Of a total of 1,981 species of Indo-Pacific reef fishes, 341 (17.2%) are reported to form pairs, with pair-forming species being particularly common (more than 50% of species) in five families. Pair-

forming species had few commonalities with regards to their reproductive strategies. Instead, two ecological traits appear to be prevalent in pairing species: 1) the consumption of small, benthic, and relatively immobile prey items, and 2) the maintenance of permanent burrows. Based on these results, I conclude that pairing may have important ecological benefits in coral reef fishes.

To further explore this hypothesis, I performed an ecomorphological assessment of pair-forming fishes, evaluating whether pairing fishes are also morphologically similar. Using a suite of six morphological traits, predominantly describing the cranial region and overall body shape of reef fishes, I demonstrate that morphology can accurately predict the prevalence of pairing behaviour in 47 species of benthos-feeding, reef fishes and that there is a strong relationship between morphology and pairing behaviour in three common families of reef fishes, the Acanthuridae, Chaetodontidae, and Siganidae. Basically, pair-forming fishes are characterized by concave foreheads, pointed snouts, deep bodies, and large eyes, attributes that relate to the feeding on small prey in topographically complex environments.

I then sought to examine specific benefits of pair-forming behaviour using four species of pairing rabbitfishes as model organisms. In doing so, I revealed evidence for a reciprocal cooperative system in rabbitfishes. In all four species, vigilance was strongly coordinated between pair members, with one individual assuming a head-up position elevated vertically above the substratum, while the partner was feeding, often in small cracks and crevices. Pair members altered their positions more often than one fish feeding continuously. Furthermore, compared to individual fishes, fishes in pairs exhibited longer vigilance bouts, more bites per foray, and deeper penetration of the substratum. By evaluating these findings against a set of six requirements for reciprocal cooperation, I show that the observed behaviour in rabbitfishes may be based on the reciprocal exchange of food and safety between pair members and that the presence of a partner permits the foraging in concealed microhabitats, unavailable for solitary fishes.

Based on these findings, I examined the fine-scale utilization of foraging microhabitats in herbivorous coral reef fishes. To do so, I introduced a novel individual-based analysis of functional niche overlap in animal communities, which uses convex hull volumes in order to assess niche breadth, overlap, and turnover vs. nestedness in multiple dimensions. Using this analysis on *in situ* behavioural data of the foraging behaviour of 21 species of herbivorous reef fishes, I show that there is limited functional redundancy among reef fish species, with an average niche overlap of only 15.2%. I further reveal a clear distinction between species that utilize predominantly flat, exposed surfaces of sand or bare rock, and species that feed on a wide range of different microhabitats, including cracks and crevices in dead corals and other complex substrata. Thus, the utilization of foraging microhabitats appears to represent an important axis of niche partitioning in herbivorous coral reef fishes.

Using the family Acanthuridae as a study subject, I then quantitatively explored ecological specialization in reef fishes with regards to both fundamental and realized niches. Specifically, I examined ecological specialization in ten surgeonfish species with regards to morphology and two realized niche axes associated with diet and foraging microhabitat utilization, and investigated the relationships between morphological and behavioural specialization. These relationships differed markedly from the traditional ecomorphological paradigm. While morphological specialization showed no relationship with dietary specialization, it exhibited a strong relationship with foraging microhabitat specialization. However, this relationship was inverted: species with specialized morphologies were microhabitat generalists while generalized morphotypes were microhabitat specialists. Thus, I highlight the potential importance of including niche axes beyond dietary specialization into ecomorphological frameworks and suggest that, on coral reefs, morphotypes commonly perceived as most generalized may, in fact, be specialized in exploiting flat and easily accessible microhabitats.

To investigate the role of concealed microhabitats for benthic organisms, I then performed an observational study on the distribution patterns of juvenile corals and early life-stage macroalgae. Specifically, I examined the microhabitat occupation of juvenile acroporid and pocilloporid corals and early life-stages of the macroalgae *Turbinaria ornata*, revealing that both corals and macroalgae were more prevalent in concealed microhabitats when compared to open or semi-concealed microhabitats. Corals were more common on the reef crest, while macroalgae were more abundant on the reef flat. The distribution patterns of herbivorous fishes also showed a distinct difference between the flat and crest, with species utilizing concealed microhabitats being more common on the crest. In particular, high abundance of pairing rabbitfishes and surgeonfishes of the genus *Zebrasoma* were positively related to high numbers of juvenile corals. Overall, this study suggested that coral reef crevices might be an important microhabitat for corals and algae alike and that the feeding activity of herbivorous fishes capable of feeding in crevices may influence this relationship.

Finally, I experimentally investigated the effects of micro-topographic refuges on grazing dynamics on coral reefs. Micro-topographic refuges decreased overall grazing pressure more than ten-fold and permitted access to only few species of cropping herbivores. In contrast, grazing pressure from detritivorous fishes was virtually absent, therefore precluding an entire ecosystem-process, the removal of particulates. As a consequence, benthic communities differed markedly between microhabitats, with micro-topographic refuges exhibiting longer algal filaments and a more diverse community, including scleractinian corals, which were completely absent from exposed microhabitats. Thus, although occurring on the scale of a few centimetres, micro-topographic refuges appear to generate fundamentally different dynamics between grazing fishes and the benthos.

Overall, the results of this thesis demonstrate that herbivory on coral reefs is not a uniform process, but a multifaceted interplay between morphological, behavioural, social, and environmental factors. This thesis has begun to disentangle the complex differences among herbivorous fish species, their drivers, and the consequences of their feeding behaviour for coral reefs. However, the results of this work suggest that micro-topographical complexity on the scale of a few centimetres represents an important ecological axis, along which fishes appear to partition their functional niches. Future research may focus on examining foraging micro-habitat utilization in reef fishes with an even higher resolution, the effects of reducing the grazing pressure exerted by crevice-feeding fishes, and the long-term consequences of the loss of functional diversity in herbivorous fishes on diversity patterns in the coral reef benthos.

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Chapter 1: General Introduction

In the middle of the 20th century, Hutchinson (1957) asked why there are so many species inhabiting planet Earth. This question has reverberated through the field of ecology throughout the second half of the century (Paine 1966; Whittaker et al. 1973; Brown 1981), and up until now, questions concerning the diversity of organismal communities have a firm hold in the ecological literature (Brown 2014; Laliberté et al. 2014; Stork et al. 2015). Perhaps the most important legacy of Hutchinson's seminal assay was the notion that one can portray a species' ecological niche as an abstract volume in a synthetic niche space, in which the axes consist of biotic and abiotic factors that affect the species' survival (Grinnell 1917; Hutchinson 1957). Due to incongruence between the space over which a species can theoretically persist, and the realized distribution patterns of a given species, Hutchinson (1957; 1959) suggested a distinction between a species' fundamental niche (the space over which it can possibly persist), and its realized niche (the space over which a species occurs once all biotic and abiotic interactions are accounted for). This concept has been a cornerstone of niche theory throughout its existence (Whittaker et al. 1973; Holt 2009), and with the rise of environmental niche modelling, as a function of the accessibility of global environmental data, research on species' environmental, or Grinnellian, niches across the globe has flourished (Guisan & Thuiller 2005; Warren et al. 2008).

While Hutchinson proposed his niche concept in the context of a Grinnellian niche (i.e. a species' niche defined as its tolerance to a set of environmental factors), ecologists have also adapted his ideas and applied them in an Eltonian niche framework (i.e. a species' niche defined by its functional interactions with biotic and abiotic ecosystem components; Elton 1927; Leibold 1996). Hutchinson's ideas of fundamental and realized niche spaces apply to the Eltonian niche, enabling distinctions between the functional niche space a species could theoretically occupy vs. its functional niche space in real life (Whittaker et al.

1973; Chase & Leibold 2003). Yet, due to the often laborious and field-intensive methods necessary to collect locality-specific data, and the intricate interrelationships between axes in a multidimensional Eltonian niche space, realized Eltonian niches and their relationships on a community scale are often difficult to examine (Araujo & Guisan 2006; Soberon 2007; Devictor et al. 2010).

Meanwhile, however, the increasing human-mediated pressure on biodiversity has positioned species' functional niches on the centre stage of ecological research (Tilman et al. 2014). Towards the end of the 20th century, a clear consensus emerged among ecologists that a diversity of species and their functional niches is crucial for the maintenance of ecosystem functioning (Naeem et al. 1994; Loreau et al. 2001). The establishment of this paradigm was largely due to long-term experiments conducted in relatively low-diversity grassland ecosystems (Tilman & Downing 1996; Tilman et al. 1997; Diaz & Cabido 2001) in which the functional diversity of communities, measured as differences in ecological traits, is easily manipulable and ecosystem responses (by means of, for instance, primary production) are distinctly measurable. Following this, trait-based assessments of functional diversity have spread beyond grassland communities, leading to the establishment of a wide range of literature across ecosystems (Zak et al. 2003; Duffy et al. 2003; Slade et al. 2007; Flynn et al. 2009; reviewed in Hooper et al. 2005; Lefcheck et al. 2015). This has contributed to a deeper understanding of the effects of human activities on entire ecosystems and has resulted in a strong call for the conservation of diversity in the interest of humanity and the biosphere (Hooper et al. 2012; Cardinale et al. 2012; Tilman et al. 2014). However, trait-based studies rarely acknowledge that only species' fundamental niches are considered. This is problematic, given the explicit Hutchinsonian theory that a species' realized niche can be distinctly different from its fundamental niche. While recent years have seen calls for a stronger consideration of realized functional niches (Schleuter et al. 2010), this is difficult to achieve due to the obstacles imposed by fine-scale variability in the factors governing a species functional niche, and the limits to empirical observations.

In marine ecosystems, these problems are further exacerbated by the nature of aquatic environments, which often preclude sustained observation periods and continuous measurement of abiotic and biotic variables influencing a species functional niche (Hooper et al. 2005). In this context, coral reefs are particularly challenging. In these extremely diverse environments (Connell 1978), there are countless biotic and abiotic interactions (Huston 1985), ranging from associational refuges among primary producers (Hay 1991; Pfister & Hay 1988; Roff et al. 2015), to symbioses between fishes and crustaceans (Karplus 1987; Thompson 2005) or collaborative interspecific foraging benefits for herbivores and carnivores alike (Robertson et al. 1976; Bshary et al. 2006; Vail et al. 2013). Nevertheless, the steep decline of coral reef systems due to anthropogenic disturbances has necessitated the investigation of the relationship between biodiversity and ecosystem functioning, for which researchers relied predominantly on trait-based classifications of species' fundamental functional niches (Bellwood et al. 2003; Mouillot et al. 2013; D'Agata et al. 2013; Mouillot et al. 2014). Although the results of these studies are already sobering, with dramatic declines in ecosystem functioning following moderate decreases in species diversity (Burkepile & Hay 2008; 2010; Bellwood et al. 2012; Rasher et al. 2013), there is good evidence that current trait-based classifications used to identify species' fundamental niches are insufficient (Biro et al. 2010; Fox & Bellwood 2011; Brandl & Bellwood 2014a).

One group of coral reef organisms that has received particular attention throughout the last two decades are nominally herbivorous fishes (*sensu* Choat et al. 2002). Herbivorous fishes exert intense grazing pressure on the coral reef benthos (Poore et al. 2012), and therefore strongly affect patterns of primary production, species diversity, succession, and community composition (Hixon & Brostoff 1996). As a consequence, severe reductions in the grazing pressure of herbivorous fishes have resulted in catastrophic shifts in the benthic communities on coral reefs worldwide (Hughes 1994; Ledlie et al. 2007; Cheal et al. 2010), with dramatic implications for coral reef ecosystems (Jackson et al. 2001; Bellwood et al. 2004; Graham et al. 2006; Hughes et al. 2010; Graham et al. 2015). Due to the critical importance of herbivorous reef fishes in these ecosystem shifts, a focus has been placed on the functional categorization of herbivorous fishes (Bellwood & Choat 1990; Bellwood et al. 2004; Nyström 2006; Green & Bellwood 2009; Burkepile & Hay 2008; 2010; Rasher et al. 2013), resulting in several complementary schemes to classify the impact of herbivorous fishes on the benthos. Yet, aside from coarse divisions of fishes based on their feeding mechanics and targeted prey, variation in species' functional niches has been given little consideration, and realized niches are rarely quantified.

Two recent observations have provided an additional impetus to re-consider the functional niches of herbivorous fishes and their relationships. The first observation relates to the social systems found in herbivorous fishes, and, in particular, the formation of pairs. Brandl & Bellwood (2013b) investigated the nature of pairs in the herbivorous rabbitfish *Siganus doliatus*, one of the dominant herbivore species on the inner Great Barrier Reef (Fox & Bellwood 2007; Bennett & Bellwood 2011; Loffler et al. 2015). The prevalence of pairs in this species increased with size, and pair members maintained a tight association over extended periods of time, thus corroborating previous observations of monogamy in reef fish species (Whiteman & Côté 2003, 2004). However, 25% of all pairs in this species were found to be same-sex pairs, suggesting that pair-formation in *S. doliatus*, and possibly other pairing herbivorous reef fishes, may have other, non-reproductive, ecological benefits (Brandl & Bellwood 2013b). The second observation relates to the importance of micro-topographic complexity for the foraging of herbivorous fishes. While recognized early as a potentially important ecological axis (Robertson et al. 1979; Robertson & Gaines 1986; Choat &

Bellwood 1985; Bellwood & Choat 1990), a recent study by Fox & Bellwood (2013) emphasized the importance of micro-topographic complexity for herbivorous fishes. Interestingly, Fox & Bellwood (2013) identified three species of pairing rabbitfishes that exploited micro-topographically complex microhabitats (i.e. cracks and crevices on the reef) more often than most other herbivorous species, suggesting that foraging microhabitat utilization patterns (i.e. the ability to exploit micro-topographically complex environments) may be an important axis of niche partitioning in herbivorous reef fish communities on the Great Barrier Reef.

1.1 Thesis aim and outline

The primary aim of this thesis, therefore, was to investigate the potential of microhabitat utilization as an axis of niche partitioning in herbivorous coral reef fish communities and to explore social, morphological, behavioural, and environmental factors that drive foraging microhabitat utilization. To do so, I considered both the fundamental and realized niches of herbivorous fish species and employed a wide range of different techniques.

In **Chapter 2**, I examine the literature on pair-formation in coral reef fishes, in order to assess the likelihood of pairing as an indicator of distinct functional niches. In **Chapter 3**, I expand on these results by performing an ecomorphological study on a large community of benthic-feeding coral reef fishes and relating species’ morphologies to their social system.

In **Chapter 4**, I focus on the realized benefits of pair-formation in four species of rabbitfishes and present evidence for a reciprocal cooperative system between pair members, in which partners coordinate their foraging and vigilance behaviour. In **Chapter 5**, I present a community-scale analysis of the realized niches of 21 herbivorous fish species. By introducing a novel, individual-based analysis of functional niche overlap, I present an analytical framework for the investigation of realized niche overlap in diverse communities.

In **Chapter 6**, I use this knowledge to examine ecological specialization in surgeonfishes (f. Acanthuridae).

In **Chapter 7**, I evaluate the significance of micro-topographic complexity for benthic organisms, focusing on juvenile corals and macroalgae as two of the most strongly affected organismal groups. Finally, in **Chapter 8**, I support these conclusions through an experimental assessment of the effects of micro-topographic refuges on the dynamics between grazing fishes and the coral reef benthos.

Chapter 2: Pair-formation in coral reef fishes: an ecological perspective

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2.1 Introduction

Of all the ecosystems on the planet, coral reefs are among the most diverse. Providing structural complexity and heterogeneous habitats for countless organisms, coral reefs harbour approximately 5,000 species of fishes (Bellwood et al. 2012), 1,400 species of corals (Baird et al. 2009) and at least 165,000 species of reef-associated invertebrates (Stella et al. 2011). This exceptional diversity is matched by a comparable variety of behavioural traits and almost every known social interaction can be observed in reef-dwelling organisms.

Although social and reproductive behaviours have elicited intensive theoretical and empirical examination, they are inherently difficult to study. As opposed to morphological characteristics, which are usually conspicuous in a species' external appearance and relatively consistent among individuals, social and reproductive traits are more variable and responsive to localized environmental factors (Yahner 1979). These traits thus exhibit the potential for extremely high plasticity within narrow taxonomic units such as species or families (e.g., Colin & Bell 1991; Morgan & Kramer 2004; Wong et al. 2005). Nevertheless, social and reproductive behaviour are important determinants of an organisms' ecology and a sound understanding of these traits, including their underlying environmental drivers and functional consequences, is crucial for organismic and community ecology (Orians 1961). Meaningful evaluations of social and reproductive behaviours, however, are often stymied by the close relationship between social organizations and reproduction, and the resulting ambiguity of the terms 'social system' and 'mating system' (Emlen & Oring 1977; Robertson

& Hoffmann 1977; Neudecker & Lobel 1982; Hourigan 1989; Reynolds 1996). Social groupings commonly pave the way for reproductive activity throughout the animal kingdom (e.g., Fricke 1980; Getz & Hofmann 1986). Yet, there are well-known examples in which social associations appear to be unrelated to reproductive behaviour, and instead appear to be linked to ecological benefits such as increased safety or foraging success (e.g., Robertson et al. 1976; Parrish & Edelstein-Keshet 1999; Morgan & Kramer 2004). Although invariably interrelated, this review will distinguish between ecological factors (i.e. factors related to survival and energy intake) and reproductive factors (i.e. factors enhancing reproductive output, fertilization rate or ensuring mate availability).

The distinction between social and mating systems is particularly unclear in cases where the social unit is a pair, i.e. two individuals of the same species. Sexual reproduction, by default, requires two individuals, and many animals form transient breeding pairs whose sole purpose is reproduction (e.g., Liske & Davis 1987). It may be for this reason that, in the current literature, pair-formation (i.e. the prolonged association with only one other conspecific) is, with few exceptions (e.g. Gwinner et al. 1994; Pratchett et al. 2006; Young et al. 2008; Brandl & Bellwood 2013a), predominantly linked to a monogamous mating system and circumstances that led to the evolution of monogamy (Emlen & Oring 1977; Wittenberger & Tison 1980; Barlow 1984; Fricke 1986; Reavis & Barlow 1998; Whiteman & Côté 2003, 2004; Reavis & Copus 2011). The social or ecological aspects of pair-formation, the environmental circumstances that have led to the formation of a pair, and the evolutionary factors underpinning pairing behaviour are often not considered.

Pair-formation is described in many taxa, ranging from unicellular organisms to higher vertebrate species. However, understanding of the significance of pairing varies markedly among taxa (**Table 2.1**). Pairing has been extensively studied in birds where the manifest link between pairing and monogamous mating is well established (Orians 1969;

Wittenberger & Tilson 1980; Black 2001; but see Westneat & Stewart 2003). The significance of prolonged pairing beyond the act of reproduction in birds is easily explained by biparental care (e.g. Wittenberger & Tilson 1980; Reynolds 1996; Adkins Regan 2002). In contrast, most marine fishes display virtually no characteristics commonly associated with monogamous mating (Wittenberger & Tilson 1980; Reynolds 1996) and evidence for "genetic monogamy" (i.e. exclusive reproduction with only one mate) is rare. A comprehensive review of monogamy in marine fishes (Whiteman & Côté 2004) found evidence for "genetic monogamy" in only 14.6% of the 164 species of marine fishes that were described as monogamous in the literature, while the majority (64%) display "social monogamy", described as "a social coalition with no implications for exclusive mating" (Whiteman & Côté 2004). While this definition suggests that these pairs are a 'social coalition' rather than a mating pair, environmental factors leading to the formation of social pairs and the possible ecological consequences beyond reproductive advantages or constraints are largely unexplored. This is particularly intriguing, as pair-formation appears to be a common social system in marine fishes, especially on tropical coral reefs (Randall et al. 1997; Allen et al. 2003; Froese & Pauly 2012).

Table 2.1: Pair-formation in animals. Pair-formation is a common behaviour from protists to mammals.

Kingdom	Phylum	Class	Order	Example	Source
Protista	Ciliophora	Ciliatea	Peniculida	*Paramecium primaurelia*	Corrado et al. 1997
		Oligohymenophorea	Hymenostomatida	*Tetrahymena pyriformis*	Bruns and Brussard 1973
Animalia	Acanthocephala	Eoacanthocephala	Neoechynorhynchida	*Neoechynorhynchus pseudomydis*	Cable and Hopp 1954
	Platyhelminthes	Trematoda	Strigeidida	*Schistosoma spp.*	Beltran and Boissier 2008
	Annelida	Polychaeta	Phyllodocida	*Harmothoë imbricata*	Daly 1973
	Arthropoda	Merostomata	Xiphosura	*Limulus polyphemus*	Botton and Loveland 1992
		Crustacea	Malacostraca	*Homarus americanus*	Atema et al. 1979
		Insecta	Mecoptera	*Panorpa spp.*	Thornhill 1979
	Mollusca	Gastropoda	-	*Ovula ovum*	Kei 2010
	Chordata	Chondrichthyes	Carcharhiniformes	*Carcharhinus melanopterus*	Johnson and Nelson 1978
		Actinopterygii	Perciformes	*Amatitliana nigrofasciata*	Mackereth and Keenleyside 1992
		Amphibia	*Anura*	*Rana sylvatica*	*Howard and Kluge 1985*
		Reptilia	*Squamata*	*Tiliqua rugosa*	*Leu et al. 2011*
		Aves	*Passeriforma*	*Taeniopygia guttata*	*Adkins-Regan 2002*
		Mammalia	*Rodentia*	*Galea monasteriensis*	*Adrian et al. 2008*

The formation of long-term pairs in coral reef fishes has been a widely studied phenomenon. The majority of studies examining reef fish pairs are case studies that seek explanations as to why species that lack bi-parental care and exhibit potential for polygamous mating restrict themselves to a single reproductive partner (e.g., Fricke & Fricke 1977; Gore 1983; Fricke 1986; Barlow 1987; Donaldson 1989; Herold & Clark 1993; Kuwamura et al. 1993; Reavis 1997a,b; Reavis & Barlow 1998; Takegaki 2000; Harding et al. 2003; Whiteman & Côté 2003; Pratchett et al. 2006; Sogabe et al. 2007; Reavis & Copus 2011). The most commonly cited reasons for the evolution of monogamy are: 1) environmental factors that prevent the sequestration of multiple mates; 2) paternal egg tending leading to mutual mate guarding; and 3) sparse populations. In contrast, few studies examine possible ecological correlates of pairing as a social system (Robertson et al. 1979; Hourigan 1989; Pratchett et al. 2006; Brandl & Bellwood 2013a,b). These studies suggest increased feeding efficiency, benefits for territorial defence, and increased vigilance, as possible ecological benefits of pair-formation. However, no holistic approach to examine common ecological traits among pairing species has been made to date. Yet, such an approach may enable inferences about environmental determinants of pair-formation to be made and will provide more detailed insights into the functional ecology of pairing species. This review, therefore, aims to provide an overview of pairing in coral reef fishes following a social-ecological definition of the term pair-formation. To do so, 1) an ecologically orientated definition of the term ‘pair-formation’ is offered, and 2) a meta-analysis of pair-formation, ecological traits, and reproductive modes in coral reef fishes of the Indo-Pacific is conducted to identify common characteristics of pairing species. These characteristics are then discussed from an ecological perspective.

2.2 The definition of ‘pair-formation’

Initially, the definition of the term ‘pair-formation’ appears to be simple, describing an association between two individuals. In its simplicity, this is only appropriate for molecular pair bonds. However, this definition fails when projected on animals, as every interaction between two individuals would be considered pair-formation. To identify the most common use of the term ‘pair-formation’ in the literature, a basic meta-analysis was performed, searching for studies with the term ‘pair-formation’ in the title. The search was specified by the word ‘animals’ in the topic to exclude a large body of literature about pair-formation in molecules. Using the ISI Web of Knowledge database, a total of 168 studies were found (from 1969 to 2012), with 67 being off-topic or duplicates. The remaining 101 studies were divided into four different categories: 1) articles, describing copulation or spawning and associated courtship or pre-mating behaviours, 2) articles, describing pair-formation beyond copulation or courtship, including post-mating behaviour or the function of long-term pairs, 3) articles about the conjugation of unicellular organisms, including all studies on unicellular eukaryotes and their form of ‘mating’, and 4) articles, describing pairs without any reproductive background.

Of the 101 studies, half (50.5%) were restricted to the process of copulation or spawning as well as courtship or pre-copulatory mate guarding. Another 33.7% described reproductive pairs, but examined post-copulatory behaviour or long-term pair-formation (where the pair bond is maintained over more than one reproductive season). A further 11.9% of articles described conjugation of unicellular organisms and just 4% of all 101 studies described cooperative ‘pairs’, without a clear reproductive purpose (**Figure 2.1**). Because more than half of the studies on pair-formation described only copulation or pre-copulatory behaviour, referring to a ‘mating system’ rather than a ‘social system’, a more precise definition of pair-formation is needed that incorporates both ecological and reproductive components. Pair-formation must be distinguished from pure mating and pre-mating behaviour such as courtship or pre-copulatory mate guarding (Kortlandt 1995), as the latter only pave the way for copulation (e.g. Johnson & Nelson 1978; Hartnoll & Smith 1978; Burpee & Sakaluk 1993). As an example, in spawning aggregations of numerous families of reef fishes (e.g. Mullidae, Serranidae, Siganidae), actual spawning occurs between members of a pair, temporarily separating from the aggregation (Johannes 1981; Samoilys & Squire 1994; Domeier & Colin 1997). Likewise, many other species (e.g. Acanthuridae) spawn in pairs but remain solitary throughout their lives within their own individual feeding territories (Robertson et al. 1979; Robertson 1984). These ‘pairs’ are therefore restricted to brief encounters that only serve to fertilize eggs and have no implications for daily survival.

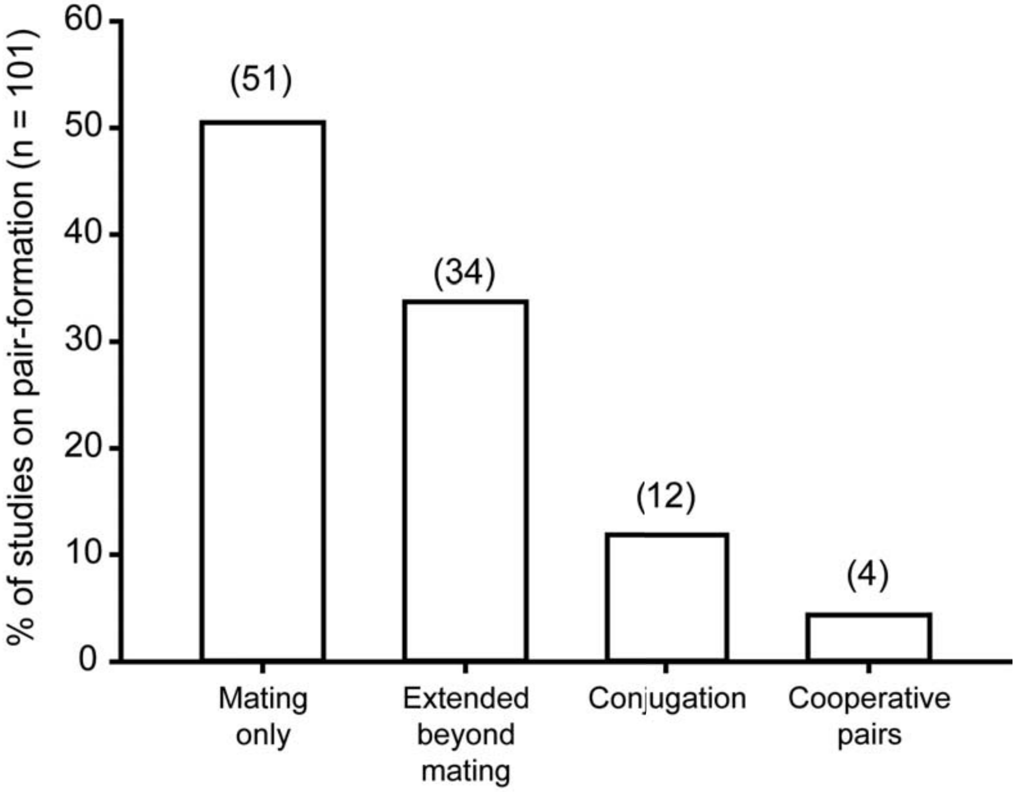

Figure 2.1: Proportions of studies investigating 'pair-formation' in animals. Papers are assigned to different categories, reflecting the use of the word pair-formation. Numbers are based on the ISI Web of Knowledge database in November 2011.

With few exceptions (see Ahlgren et al. 2011), there are no clear ecological implications of these transient pairing associations. Hence, if the formation of a pair is restricted to copulation only, the term ‘pair-formation’ may be misleading, as it does not describe a social system but simply the process of reproduction, i.e. a mating system. Therefore, I suggest that the term ‘pair-formation’ be limited to associations that are maintained beyond the process of reproduction, such as 1) cooperation in rearing offspring (e.g. Robertson 1973; Cox et al 1993; Adrian et al. 2008; Young et al. 2008), 2) mutual maintenance of a dwelling or territory (e.g. Linsenmaier and Linsenmaier 1971; Fricke 1986; Mathews 2002), 3) increased predator avoidance through shared vigilance (Gwinner et al. 1994; Pratchett et al. 2006) or 4) improved feeding efficiency (e.g. Robertson et al. 1979; Hourigan 1989; Gwinner et al. 1994). In contrast, pairing for copulation alone is perhaps more appropriately termed a ‘mating-pair’.

An apparent issue arises for pairs in which mate-guarding occurs after reproducing, as it initially appears to solely benefit the guarding individual in terms of its reproductive success. However, pair-formation in these species can be ecologically meaningful. For example, female lobsters (*Homarus americanus*) experience lower predation rates after moulting for reproduction (Atema et al. 1979) and female water-striders (*Gerris remigis*) exhibit higher foraging rates when guarded by males after copulation (Wilcox 1984). Both of these benefits are seen in the Australian sleepy lizard, *Tiliqua rugosa*, where the female can dedicate more time to foraging efforts and predation risk is reduced through increased vigilance of the male (Bull and Pamula 1998; Leu et al. 2011). Thus, in order to address ecological implications of associating with a single individual, I suggest that pair-formation be defined as ‘an association between two conspecific individuals, maintained beyond the time required for reproductive activity leading to fertilization’. With this definition of pair-formation as a social system, one can begin to explore the role of this behaviour in coral reef fishes.

2.3 Pair-formation in coral reef fishes

To explore pair-formation in reef fishes in greater detail, the Indo-Pacific coral reef fish fauna was examined. The primary goal was to understand the basis of pair-formation in fishes. As a first step, I sought to identify ecological traits that are shared by pair-forming species. Often, ecological traits are correlated and, if evolutionary successful, they occur repeatedly among distantly related taxonomic groups (Westneat et al. 2005). For example, foraging in large aggregations appears to be a beneficial trait for species that feed on pelagic zooplankton. As such, aggregations frequently occur in distantly related taxa such as the Caesionidae, Labridae, Pomacentridae or Serranidae (e.g., Hamner et al. 1988; Hobson 1991). Similarly, cryptobenthic fishes are almost exclusively known to spawn adhesive, demersal eggs that are deposited in a cave, burrow or nesting site (e.g. Fishelson 1976; Thresher 1984; Hernaman & Munday 2007). I therefore reviewed a comprehensive set of traits among Indo-Pacific reef fishes (extracted from Randall et al. 1997; Allen et al. 2003; Randall 2005). The traits encompassed social systems, trophic affiliation, strategies to avoid predators and reproductive characteristics (**Appendix C**). Specifically, each species was classified as either pairing or non-pairing, assigned to a trophic category and classified with regards to other ecological characteristics (maximum size, maintenance of burrows, nocturnal or diurnal activity). In addition, reproductive characteristics such as the spawning mode (pair or group spawning), the nature of gamete release (broadcast, demersal, pouchbrooding, mouthbroding, egg-scattering, gelatinous egg-mass spawning), and the mating system were recorded.

2.3.1 The prevalence of pairing behaviour in reef fishes

Of 1,981 species of coral reef fishes in 79 families, 341 species are reported to form pairs, while 1,561 species have no records of pair-formation. No information was available for 79 species, which are predominantly small, cryptbenthic species. An average of 18.7% ± 0.3 (mean ± SE) of species within a family are reported to form pairs, ranging from 100% in the Malacanthidae, Microdesmidae, Monocentridae, Pegasidae, Solenostomidae and Zanclidae to 0% in 42 families (**Figure 2.2**). To account for extreme proportions in families with low numbers of species, families with less than five species were not considered subsequently.

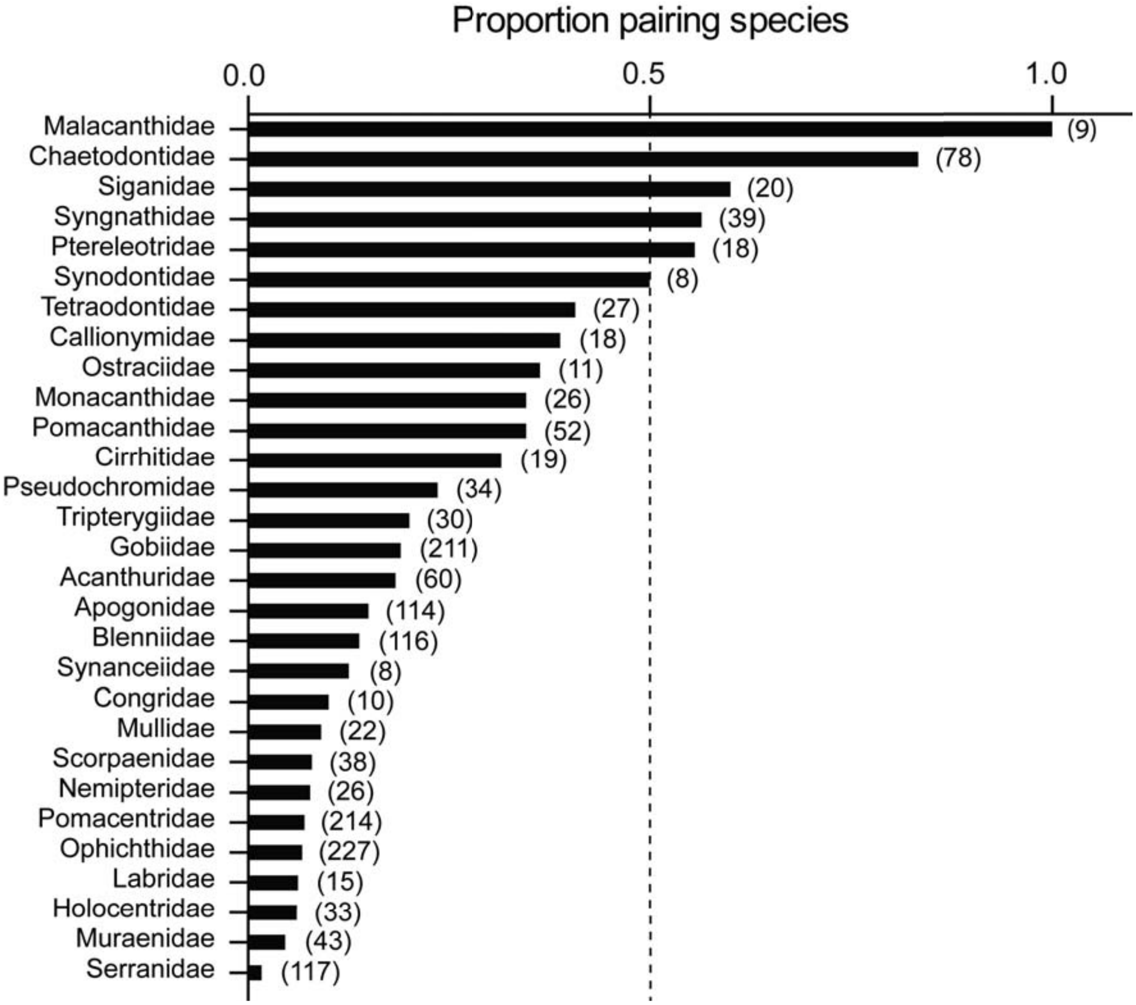

Figure 2.2: The prevalence of pair-formation in coral reef fish families. Only families with more than five species are considered. Dashed line marks the 50% mark. The number of species in each family is given in parentheses.

Five families of reef fishes contain more than 50% of the total pair-forming species. Belonging to two different orders (Perciformes and Syngnathiformes), these include tilefishes (Malacanthidae, 100% of the examined species in pairs), butterflyfishes (Chaetodontidae, 83.3% pairs), rabbitfishes (Siganidae, 60.0%), seahorses and pipefishes (Syngnathidae, 56.4%) and dartfishes (Ptereleotridae, 55.5%) (**Figure 2.3**). The two following families, lizardfishes (Synodontidae, 50.0%) and pufferfishes (Tetraodontidae, 40.7%), belong to different orders, the Aulopiformes and Tetraodontiformes, respectively. Given that the seven families with the highest proportions of pairing species belong to four different orders, the tendency to arrange in pairs appears to have evolved independently across several phylogenetically distinct lineages. Furthermore, there are major differences between families within the same order. For example: triggerfishes (Balistidae) and porcupinefishes (Diodontidae) do not comprise any pairing species (0%), whereas pair-formation is relatively common in pufferfishes (Tetraodontidaem 40.7%), box- and cowfishes (Ostraciidae, 36.3%) and filefishes (Monacanthidae, 34.6%). All these families belong to a single order, the Tetraodontiformes. A similar situation occurs in the Syngnathiformes, where seahorses and pipefishes (56.4%) are in marked contrast to trumpet- (Aulostomidae, 0%) and cornetfishes (Fistulariidae, 0%). Overall, based on the most recently assembled phylogeny of fishes (Near et al. 2012), pairing appears to have arisen at least 13 times among reef fishes.

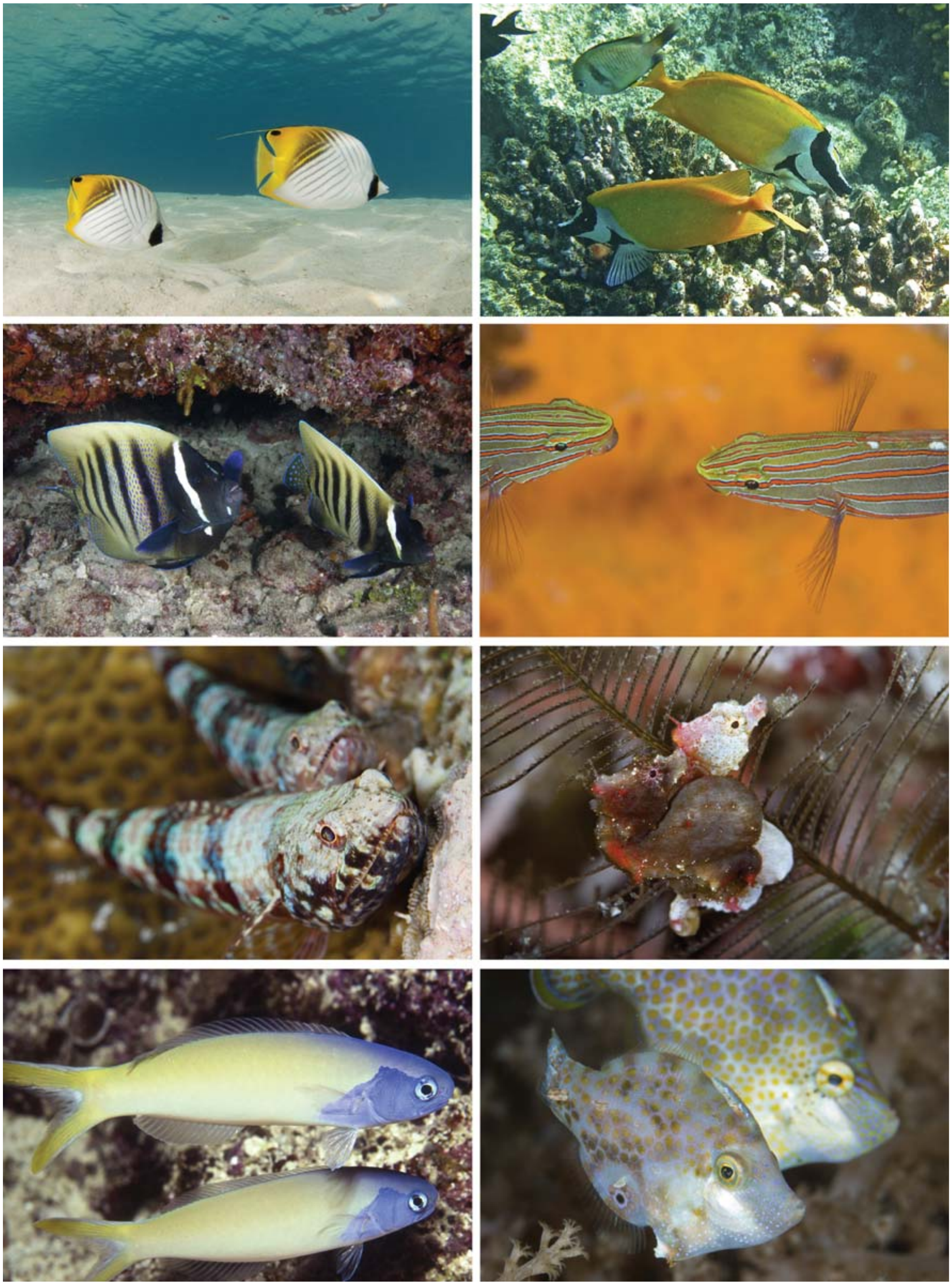

Figure 2.3: Examples of pair forming species in the Chaetodontidae, Siganidae, Pomacanthidae, Gobiidae, Synodontidae, Syngnathidae, Malacanthidae and Monacanthidae. Photographs by J.P. Krajewski, B. Halstead and S.J. Brandl.

Narrowing the taxonomic scale reveals that there is also significant variation within families. In some cases, entire lineages are pair-forming and there are clear distinctions between genera. In the Malacanthidae, for example, pairing is restricted to highly reef-associated, tropical Indo-Pacific species in the genera *Hoplolatilus* and *Malacanthus* (Clark & Pohle 1992; Clark et al. 1998); temperate and Atlantic species of the genera *Branchiostegus*, *Caulolatilus*, *Lopholatilus* and *Malacanthus* are solitarily or live in colonies (Able et al. 1982; Ross 1982; Baird & Baird 1992; Mitamura et al. 2005). In the Tetraodontidae, pairing is restricted to the genus *Canthigaster* (Kobayashi 1986; Sikkel 1990), the smallest genus in the family. In other families, the prevalence of pairing behaviour varies within genera. For example, there is a clear dichotomy in *Siganus*, the single genus of the Siganidae, with pair-formation being reported only for reef-associated, colourful tropical species, while drab-coloured, mangrove-associated, estuarine and subtropical species form schools (Woodland 1990; Borsa et al. 2007; Brandl & Bellwood 2013b). Likewise, in the Chaetodontidae, there are pairing and non-pairing species in the dominant genus *Chaetodon*, regardless of their phylogenetic relationships (Hourigan 1989; Roberts & Ormond 1992; Kelley et al. 2013). In the Syngnathidae, both pipefishes (genera *Corythoichthys*, *Dunckerocampus*, *Doryrhamphus*) and sea horses (genus *Hippocampus*) comprise several species that form pairs, while others live solitarily or in groups (Allen et al. 2003; Foster & Vincent 2004; Sogabe & Yanagisawa 2008). Given the occurrence of pairing behaviour in a diverse array of orders and families and the high variation within closely related taxa, it appears that pair-formation has arisen repeatedly over many millions of years. With such diverse groups involved, there is ample opportunity for a critical evaluation of the ecological and reproductive role of pair-formation in coral reef fishes.

In ecology, the three main drivers of social behaviour are associated with feeding, predation avoidance and reproduction. To identify ecological and reproductive traits that are associated with pair-formation in reef fishes, I will explore each of these components separately.

2.3.2 Trophic ecology of pair forming fishes

The acquisition of food is a crucial process in the life history of animals and their prey. Consequently, species are often classified within certain trophic groups (e.g. Williams & Hatcher 1983; Green & Bellwood 2009; Cheal et al. 2012), where species with similar foraging strategies are grouped based on their major prey items. Interestingly, there is a clear pattern with regards to the prevalence of pairing species within trophic groups (**Figure 2.4**). In three trophic groups, spongivores, corallivores and micro-invertevores, more than half of the species form pairs. This is a remarkable proportion considering the relatively small number of pairing species (341) compared to non-pairing species (1,640, i.e. 17.2% pairing species). Two additional groups, omnivores and herbivores, also had relatively high proportions of pairing species (> 25%), while the proportion of pairing species is low in planktivores, macro-invertevores, piscivores, carnivores and detritivores.

The major pattern that emerges from these results is the link between small and / or immobile, sedentary prey items and pairing behaviour (**Figure 2.4**), as all trophic groups that forage on such prey have high proportions of pairing species. Their prey includes coral (polyps, mucus), micro-invertebrates (e.g., harpacticoid copepods, amphipods, small polychaetes, molluscs), filamentous or fleshy algae, sponges, or all of the above (omnivores). All these prey items require relatively high visual acuity and are located in topographically complex microhabitats on the coral reef benthos. Consequently, the majority of pairing species are also reported to be diurnal (96.4%) and are, on average, smaller than non-pairing species (mean maximum total length ± SE: 162.6 ± 6.4mm vs. 278.0 ± 8.6mm, respectively). Likewise, in 19 of 29 families that contain both pairing and non-pairing species, pairing species were on average smaller than their non-pairing counterparts, suggesting that size differences are not solely due to phylogenetic effects.

The relationship between pair-formation and selected trophic groups may be due to the relatively immobile nature and distribution of prey. Although benthic micro-invertebrates are sometimes motile, their movements are restricted to small scales, making these organisms a largely stationary food source on a whole-reef scale (Klumpp et al. 1988; Kramer et al. 2012). Widely distributed prey has been associated with the evolution of monogamous mating systems in animals, as such prey prevents the monopolization of multiple mates (Emlen & Oring 1977; Whiteman & Côté 2004; Reavis & Copus 2011). Such a relationship has been proposed for butterflyfishes, distinguishing between mobile, planktivorous schooling species and benthos-associated, corallivorous species that occur predominantly in pairs (Reese 1975; Fricke 1986), leading to the assumption that environmental factors, food availability in particular, can predict the social system in this family (Hourigan 1989). Several studies argue that evenly distributed, stationary and predictable food sources promote pairing behaviour in butterflyfishes, as males are not able to sequester more than one female (e.g., Hourigan 1989; Reavis & Copus 2011). This is in accordance with theoretical expectations based on the evolution of monogamy (e.g. Emlen & Oring 1977) and is consistent with the high proportion of corallivores that occur in pairs (**Figure 2.4**).

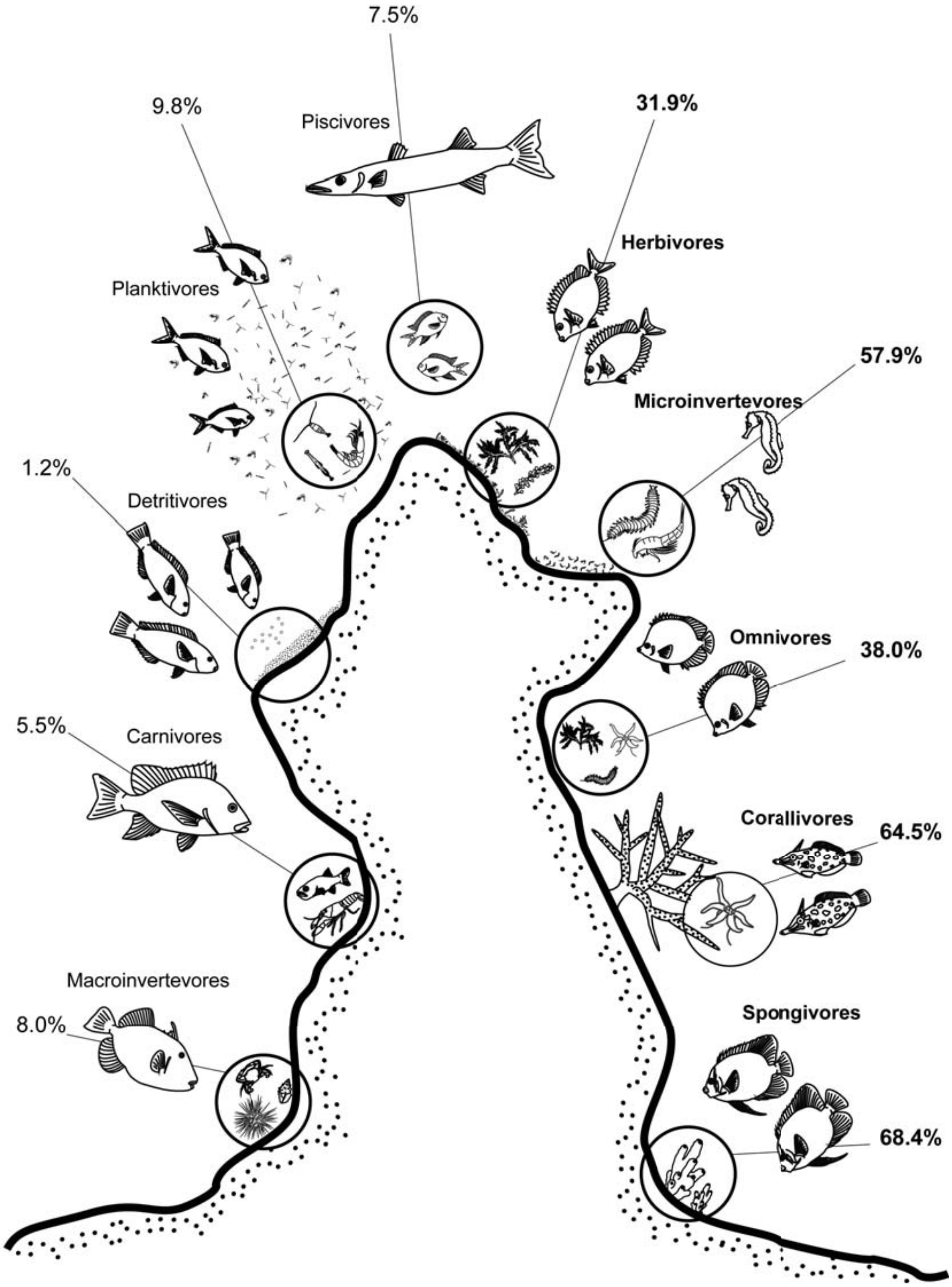

Figure 2.4: The prevalence of pair-formation in major trophic groups of coral reef fishes. Percentages indicate the proportion of pair-forming species within each

trophic group. Groups with more than 25% pairing species are marked are in bold. Black circles indicate prey items.

However, there are other factors that may also favour the formation of pairs in these trophic groups. One key aspect may be the size and benthic nature of prey items. With the exception of some large species of algae or sponges, the majority of organisms preyed on by pair-rich trophic groups are relatively small (e.g., coral polyps, filamentous algae, harpacticoid copepods) and are located in a micro-topographically highly complex and heterogeneous environment (Mundy 2000). Therefore, species foraging on these items may require highly dexterous movements and fine-scale interactions with the substratum to obtain their prey. This has been documented in several pair-forming groups such as butterflyfishes or rabbitfishes (Motta 1988; Ferry-Graham et al. 2001; Fox & Bellwood 2013) and other studies have highlighted the ability of some species to exploit complex microhabitats (Hobson 1975; Robertson & Gaines 1986; Motta 1988; Montgomery et al. 1989; Ferry-Graham et al. 2001; Fox & Bellwood 2013). Interestingly, many of the latter species are known to form pairs. This may be due to rapid decreases in the feeding efficiency of larger groups (White & Warner 2007a). A loss of foraging efficiency may be exacerbated by increases in the inaccessibility of prey or increased handling time of small, benthic prey (Pratchett et al. 2006; Fox & Bellwood 2013; Brandl & Bellwood 2013a,b). In such circumstances, one would anticipate selection against large groups and more frequent pair-formation (Ford & Swearer 2013b).

Another specialized trophic mode that appears to be related to pair-formation is the maintenance of cleaning stations. Several species of reef fishes clean clients and perform their cleaning tasks as cooperative pairs (Bshary et al. 2008). Besides the most widely known species in the labrid genus *Labroides*, which commonly live in harems or pairs (Allen et al. 2003), there are species within the Gobiidae (e.g. *Elacatinus evelynae*) and Syngnathidae (e.g. *Dunckerocampus pessuliferus*), which are commonly found in pairs and maintain cleaning stations (Harding et al. 2002; Whiteman & Côté 2003; Allen et al. 2003). In most of these species, it appears that the cleaning service provided by a pair is superior to cleaning by solitary individuals (Whiteman & Côté 2003; Bshary et al. 2008). This benefits both individuals in a simple way, as clients are more likely to visit high quality cleaner stations (Whiteman & Côté 2003). While this has well known ramifications for the mating system and the reproductive success (Bshary et al. 2008), it also provides a good example of cooperative, social pairing that ecologically benefits both pair members.

Overall, although there may be benefits in pairing, it is not clear why all these species occur as pairs rather than in small groups. Perhaps there are other factors operating that limit social group sizes such as the suggestion that larger groups and shoaling behaviour may enhance the overall predation risk from different predator guilds (Ford & Swearer 2013a,b).

2.3.3 Predation avoidance in pair forming fishes

Mortality due to predation is another important force shaping species' behaviour, and is tightly linked to an animal's ecology (Holbrook & Schmitt 2004; Almany & Webster 2006; Holmes & McCormick 2011). Predation risk can influence behaviour in different ways, restricting the movement of prey fishes to small areas around shelter sites (Reavis 1997b; Welsh & Bellwood 2012a; Madin et al. 2012), away from unstable, complex habitats (Hoey & Bellwood 2011), or drive prey fishes to form large aggregations to avoid predation on the individual (Pitcher & Parrish 1993; White & Warner 2007b). Thus, the threat of predation, in synergy with the need to forage and reproduce, can either decrease (e.g., restriction of movements; Welsh & Bellwood 2012a) or increase (e.g., formation of large schools; Welsh & Bellwood 2012b) the size and movement of social groups. This raises the question: are there any circumstances, where a pair may be the preferred group size for avoiding predation?

Pair-formation in reef fishes has rarely been linked to anti-predatory strategies. However, several lines of evidence suggest that it may play a role. For mobile species, the individual risk of predation is likely to increase with decreasing group size (but see Ford & Swearer 2013a,b). In large groups, vigilance is shared between numerous individuals, providing security for each group member (Pitcher & Parrish 1986; White & Warner 2007b). Thus, in theory, in terms of overall predation risk, individuals in pairs should be more vulnerable than those in schools but less vulnerable than solitary individuals (Pratchett et al. 2006). One way that pairing fishes may compensate for the higher risk is with morphological and / or behavioural adaptations. It is striking that virtually all families of mobile (non-burrowing) reef fishes with high proportions of pairing species exhibit conspicuous physical adaptations to avoid predation. This includes large venomous spines (Siganidae, Pomacanthidae), exceptionally deep bodies and bright colouration (Chaetodontidae, Pomacanthidae) or body inflation, extremely tough skin or bony plates encasing the body and/or toxicity (Tetraodontidae, Ostraciidae, Monacanthidae) (Hixon 1991). Although some of these features are also found in solitary or schooling species (e.g., Acanthuridae, Balistidae), families with few pairing species often appear to have fewer morphological adaptations to avoid predation (e.g., Mullidae, Nemipteridae, Labridae, Caesionidae). In these predominantly schooling species, speed appears to be the major determinant of individual survival, as an individual often only needs to be faster than a single adjacent individual to avoid predation. Within families, there appears to be a similar trend. For example, within the Chaetodontidae, Acanthuridae and Siganidae, pairing species possess deeper bodies (Brandl & Bellwood 2013b) and may exhibit brighter coloration and more anti-predatory features, such as eye stripes, than non-pairing species (Kelley et al. 2013).

Behavioural adaptations offer an additional means of decreasing vulnerability to predation in pairs. Most mobile, pairing species are relatively slow swimmers (Fulton 2007), which makes predator avoidance through high-speed escape rather unlikely, although a deep body (Brandl & Bellwood 2013b) may make rapid direction changes a possible predator avoidance mechanism. The most commonly cited predation avoiding benefit of pair-formation in mobile reef fishes is to spawn with the respective partner. The permanent availability of a reproductive partner releases these species from the necessity to undertake dangerous, predation-prone ventures to spawning sites in search of a mate (Robertson et al. 1979; Herold & Clark 1993). However, many pairing species still migrate to spawning sites (e.g., *Siganus punctatus*, Johannes 1981; *Chaetodon lunulatus*, Yabuta 1997).

It has been suggested that the close association between pairing butterflyfishes and rabbitfishes and the reef matrix (i.e. swimming within the complex interstices of the reef) reduces vulnerability to predation (Hourigan 1989; Borsa et al. 2007). Although the mechanistic basis for this was not explored, recent observations provide an indication of the possible link between pairing, reef complexity and predation avoidance. A recent study of rabbitfishes raised the possibility of shared vigilance between pair-members while feeding, with one individual being observed ‘hanging’ tail-down vertically in the water column, scanning the environment (Fox & Bellwood 2013; Brandl & Bellwood 2013a) (**Figure 2.5a**). Interestingly, this exact same posture and behaviour have been described for pairing tilefishes, with one member of a pair hanging tail-down in the water column while the other one engages in other activities and escaping immediately prior to the arrival of a predator (Clark et al. 1998). The close resemblance of the shared vigilance behaviour observed in rabbitfishes and tilefishes suggests that it may be a common predator avoidance behaviour in pairing species. A similar type of shared vigilance (although lacking the tail-down posture), has been described in the gobies *Valenciennea helsdingenii* and *Valenciennea longipinnis*, in which pair members seem to alternate between vigilance and foraging (Takegaki & Nakazono 1999; Clark et al. 2000). This has also been suggested for the pairing butterflyfish

Chaetodon melannotus (Pratchett et al. 2006). In addition, several species of pair-forming rabbitfishes (*Siganus puellus*, *S. doliatus*, *S. punctatus*) have been observed swimming in a synchronized fashion, aligning their bodies in a manner that creates the illusion of one, significantly larger fish (also *S. stellatus*; Choat, pers. comm.) (**Figure 2.5b**). This is likely to decrease the risk of predation by smaller predators but needs to be explored in further detail. Thus, it appears that pairing reef fishes may escape predation through a range of behavioural responses that are tailored to their pairing social system.

Further support for a non-reproductive role for pair-formation is provided by the presence of homosexual and immature pairs in pairing reef fishes. Homosexual pairs have been found in the butterflyfishes *Chaetodon capistratus* (Gore 1983), *C. chrysurus* (Fricke 1986), *C. lunulatus* and *C. melannotus* (Pratchett et al. 2006), the surgeonfish *A. triostegus* (Robertson et al. 1979), the gobies *Valenciennea muralis* and *V. strigata* (Pratchett et al. 2006), and the rabbitfish *Siganus doliatus*, where 25% of pairs were homosexual (Brandl & Bellwood 2013a). This is also consistent with reports of non-reproductive, mixed-species pairs. Mixed species pairs have been reported in the blennies *Petroscirtes fallax* and *Meiacanthus lineatus* (Allen et al. 2003) and the tilefishes *Hoplolatilus cuniculus*, *H. chlupatyi*, *H. marcosi* and *H. purpureus* (Clark et al. 1998). All these examples question a purely reproductive function of pair-formation in the respective species and suggest a crucial role of pairing for daily survival. Mortality rates of paired vs. non-paired individuals have yet to be reported for any of these species but predation risk may be the most important driver of this behaviour (Reavis & Barlow 1998).

While anti-predatory behaviour in mobile pairing species is poorly understood, the relationship is much clearer in bottom-dwelling or burrowing species (Hixon 1991; Forrester & Steele 2004; Depczynski & Bellwood 2004; Hernaman & Munday 2005). Of the 102 species that inhabit and maintain permanent burrows, 50 commonly occur in pairs, with many of them being strongly paired and / or monogamous (Reavis 1997a,b; Reavis & Barlow 1998; Clark et al. 1998; Takegaki & Nakazono 1999; Clark et al. 2000; Pratchett et al. 2006; Hernaman & Munday 2007). While almost half of the burrowing species form pairs, it is noteworthy that 47 out of the remaining 52 species live in close association with shrimps of the family Alpheidae. In these latter, shrimp-associated species, there is a clear division of labour between the shrimp and the goby, where the shrimp is responsible for digging and maintaining the burrow (**Figure 2.5c**). Meanwhile, the goby acts as a sentinel, dedicating extensive time to vigilance and warning the shrimp through rapid tail flicks if a predator is approaching (Karplus 1987; Thompson 2004, 2005). This relationship is mutualistic and obligate. Solitary gobies experience rapid mortality through predation, and solitary shrimps exhibit slower growth rates due to decreasing foraging time (Karplus et al. 1972; Thompson 2004; 2005). While this relationship should be considered a symbiotic relationship rather than pair-formation, it demonstrates a key aspect of the ecology of burrowing species: the maintenance of a permanent burrow is greatly facilitated by the presence of a second individual. Overall, 95.1% of all fish species that maintain permanent burrows do so with a partner, be it fish or shrimp. Division of labour between pair members of burrowing fishes is well documented (Reavis and Barlow 1998; Clark et al. 1998; Takegaki & Nakazono 1999; Clark et al. 2000) and mainly involves the partitioning of circadian tasks (burrow maintenance, vigilance, foraging) (**Figure 2.5d**). Thus, for these species, the pair bond may be the essential feature for daily survival, suggesting a strong ecological basis for the establishment of pairs. This is further reinforced by the presence of non-reproductive pairs in burrowing gobies (Pratchett et al. 2006) and tilefishes (Clark et al. 1998). It is also seen in other organisms that maintain burrows as pairs, including shrimps of the genus *Lysiosquilla* (Christy & Salmon 1991).

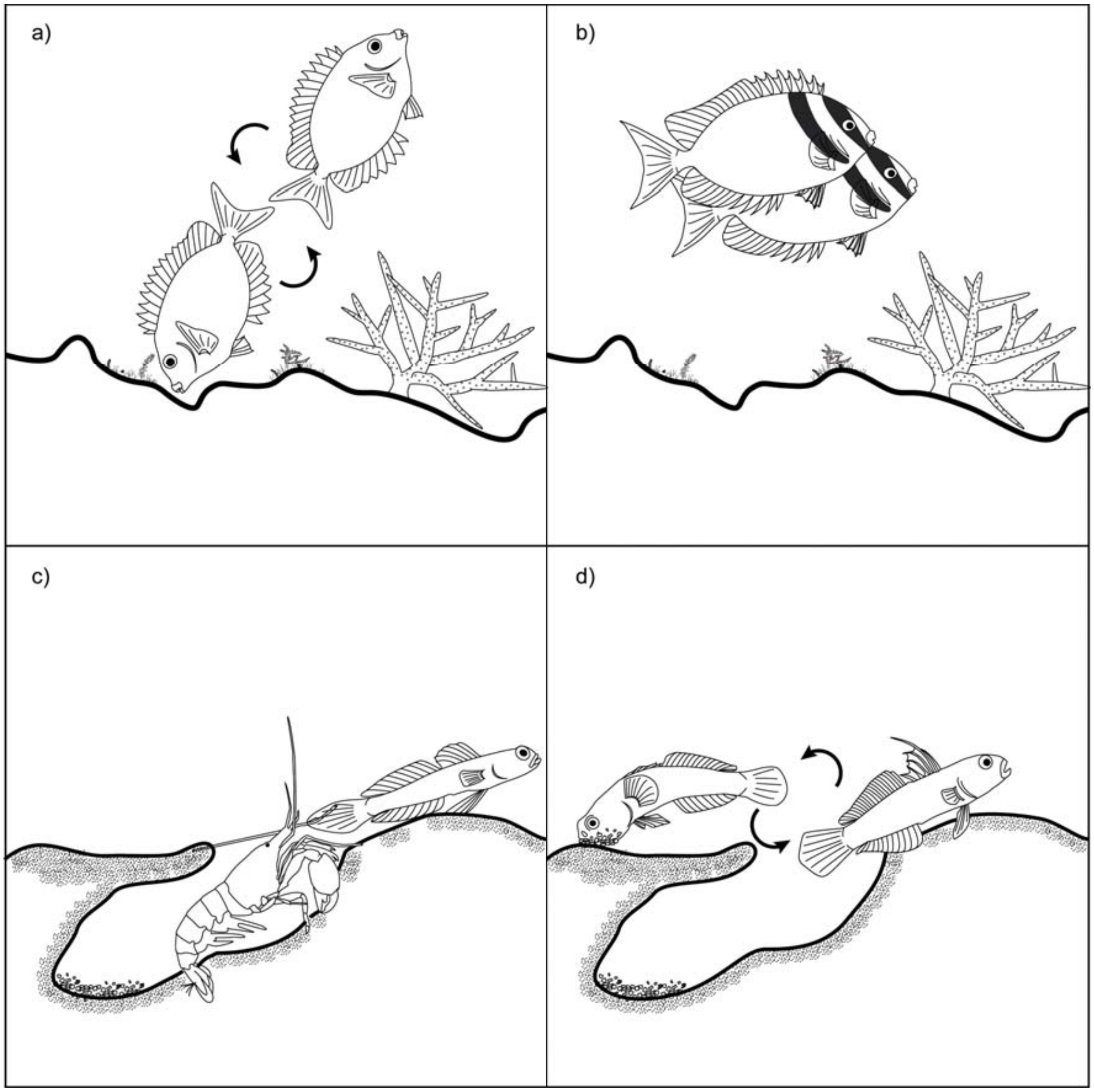

Figure 2.5: Observed behavioural adaptations of pair-forming species in mobile (a & b) and burrowing (c & d) species; a) shared vigilance in rabbitfishes. One individual is assuming a ‘tail-down’ position, scanning the environment, while the other individual is feeding; b) synchronized swimming in rabbitfishes. Individuals arrange in a manner that creates the illusion of a single, larger fish; c) shared labour in shrimp-associated, burrowing gobies. The fish is vigilant while the shrimp is performing maintenance of the burrow, maintaining contact with the goby through its antennae;

d) shared labour in burrowing gobies. One individual is remaining close to the burrow entrance, looking out for predators while the other individual is feeding further away from the burrow.

Thus, in summary, predation appears to be a significant factor that may influence the formation of pairs in numerous species and there appears to be a clear link between pairing and predation in species that maintain a permanent burrow. Although several behavioural traits also suggest anti-predatory benefits of pairing in free-living mobile species, the role of pairing behaviour for predator avoidance in these species is poorly understood.

2.3.4 Reproductive characteristics of pair forming fishes

Coral reef fishes exhibit virtually every form of mating system known in animals, from monogamous mating to mass spawning aggregations, where up to 100,000 individuals of a single species spawn simultaneously (Robertson 1983; Colin & Bell 1991; Sadovy de Mitcheson et al. 2008). Spawning modes include broadcast spawning, demersal clutch spawning, egg-scattering, pouchbrooding, mouthbrooding, the release of gelatinous floating egg rafts and even live bearing (Thresher 1984). If pairing behaviour were solely due to reproduction, one would expect to find several unifying reproductive traits among pairing species, resulting in the following three hypotheses: first, prolonged association with a single partner should result in a mating system restricted to pair members (i.e., pair-spawning), which, second, should lead to high proportion of monogamy in pairing species. Third, given the close link between parental care and pairing (Barlow 1981) and the advantages of aggregations for broadcast spawning (Thresher 1984; Sadovy de Mitcheson & Colin 2012), pairing species should predominantly spawn benthic, demersal eggs with a high incidence of prerequisites for parental investment.

Initially, it appears that these hypotheses are supported. Among pairing reef fishes, 284 out of 341 (83.3%) are reported to have a mating system based on pairs, i.e. courtship and fertilization occurs between two individuals, while the remaining 57 species spawn in groups or aggregations. However, the majority of non-pairing species (69.1%) also mate in pairs. Pairing species that are reported to spawn in aggregations rather than pairs are predominantly rabbitfishes, some surgeonfishes and few butterflyfishes. In surgeonfishes, this may be the result of relatively high plasticity in social and mating systems, observed throughout the family (Robertson et al. 1979; Robertson 1983). In butterflyfishes, pair spawning has been observed in *Chaetodon nippon* (Suzuki et al. 1980), *C. multicinctus* (Lobel 1989), *C. chrysurus* (Fricke 1986), *C. citrinellus, C. unimaculatus, C. ornatissimus* (Sancho et al. 2000), *Chaetodon lunulatus* (Yabuta 1997) and *Chaetodon rainfordi* (Thresher 1984), providing relatively good support for the hypothesis that permanently paired species should have a mating system based on pairs (Emlen and Oring 1977; Whiteman and Côté 2004). In contrast, anecdotal reports of spawning aggregations in several strongly paired species such as *C. ephippium, C. lunula* and *C. melannotus*, appear to be incongruous (Claydon 2004; Yabuta 2007). However, although these species may aggregate, they may ultimately spawn in pairs with numerous other pairs, utilizing a common location with favourable currents for egg dispersal (Bell & Colin 1986; Hixon 1991). In addition, the total fertilization rate of such pairs might be even higher in an aggregation (Petersen et al. 2001), particularly as interference in pair matings appears to be common in butterflyfishes (Suzuki et al. 1980; Neudecker & Lobel 1982; Lobel 1989).

Reliable records for rabbitfish spawning are not yet available (Woodland 1990). However, the few reports of spawning in rabbitfishes suggest that large spawning aggregations may be the common way of mating in this family (Johannes 1981; Hara et al. 1986; Domeier & Colin 1997; Hoque et al. 1999; Harahap et al. 2001; Sadovy de Mitcheson & Colin 2012). This is particularly surprising, because rabbitfishes are one of the most commonly and strongly paired families (Woodland 1990; Borsa et al. 2007; Brandl & Bellwood 2013a,b). As for butterflyfishes, it may be possible that siganid pairs also spawn in aggregations (Johannes 1981; Woodland 1990). However, there are no benefits in terms of egg dispersal, because rabbitfishes spawn negatively buoyant demersal eggs (Woodland 1990). Thus, given the reports of homosexual pairs (Brandl & Bellwood 2013a) and the suggested anti-predatory and feeding strategies of pairing rabbitfishes, reproductive factors may only play a partial role for pairing in this family.

Overall, most pairing species also reproduce in pairs. However, any links between reproduction and pairing may need to be interpreted with caution, given the few noteworthy exceptions as well as the general tendency of reef fishes to reproduce in pairs (69.1% of non-pairing species). Reproduction is probably an important factor of pairing in many species but it appears to be only one of a range of potential drivers.

The second hypothesis suggests that pairing leads to monogamy. However, only 25.2% of all species that are known to form pairs are monogamous. True genetic monogamy has rarely been reported in reef fishes (Barlow 1981; Whiteman & Côté 2004), although many studies infer exclusive mating with a single partner from field observations, replacement experiments or aquarium studies (e.g., Barlow 1987; Herold & Clark 1993; Hess 1993; Reavis & Barlow 1998; Whiteman & Côté 2003; Reavis & Copus 2011). Interestingly, some species, such as jawfishes of the genus *Opisthognathus* (Hess 1993) or the anemonefishes *Amphiprion clarkii*, *A. frenatus* and *A. perideraion* (Hirose 1995), appear to be monogamous but live either solitarily (jawfishes) or in groups (anemonefishes). These species are not pair forming *per se* and represent 15.2% of all monogamous species. Therefore, while monogamy appears to be a relatively good indicator of pair-formation, it is not an obligate requirement. In turn, pairing species are not necessarily monogamous, as the majority (74.8%) of pair forming species are not reported to be monogamous.

The third hypothesis predicts that pairing species should predominantly spawn demersal eggs, while spawning in aggregations should be the predominant spawning mode in non-pairing fishes. Guarding or breeding eggs requires high investments by the parents, and is usually rewarded by a stronger control of parentage and higher survival rates in offspring (Jones & Avise 1997). This high investment is regarded as a characteristic of pair mating, leading to the evolution of monogamy (Wittenberger & Tilson 1980). Thus, if pair-formation were driven by reproduction alone, one would expect all species with parental care to form pairs. Demersal clutch spawners have a high potential for parental care, as eggs are usually attached to the substratum within a restricted territory (e.g. Balistidae; Kawase 2002), cave (e.g. Blenniidae; Fishelson 1976) or burrow (e.g. Gobiidae; Reavis 1997a,b) and require intensive parental care (e.g. Hernaman & Munday 2007). Likewise, the specialized systems of mouthbrooding and pouchbrooding require high parental investment (e.g. Barlow 1981) and could therefore be assumed to have a high potential for pair-formation, while egg-scattering and broadcast spawning species appear to have a low capacity for pair-formation (Johannes 1981; Thresher 1984).

Surprisingly, the prevalence of pairing in the different spawning modes did not support the third hypothesis. Mouthbrooding had the lowest proportion of pairing species, followed by broadcast spawning and demersal clutch spawning. Pairing prevalence was highest in egg-scattering and pouchbrooding species (**Figure 2.6**). Mouthbrooding is largely restricted to cardinalfishes (f. Apogonidae) and few other lineages such as jawfishes (f. Opisthognathidae; Hess 1993). Most apogonid species live in aggregations, only forming 'transient' breeding pairs (Kuwamura 1985). In aggregating species (e.g. *Apogon notatus*, Allen et al. 2003), the females frequently desert the males after spawning, resulting in a solely courting and copulating pair, and hence a 'mating pair' (Kuwamura 1985). While in some pair-forming species, the female may engage in the defence of the eggs after spawning (e.g. *A. doederleini*, Kuwamura 1985), thus providing protection for the male, most pairs in cardinalfishes are probably 'mating pairs'. Similarly, in jawfishes, individuals are solitary and only pair for courtship and spawning, after which the solitary male orally incubates the eggs (Hess 1993). This is contrary to the suggestion that high parental investment will favour pair-formation. Similarly, the almost equal proportions of pairing and non-pairing species in broadcast and demersal spawning species, and the high prevalence of pairing in egg-scattering species, suggests that pairing is not significantly linked with parental investment. The two most commonly pairing families, tilefishes and butterflyfishes, are both broadcast spawn pelagic eggs (Thresher 1984; Clark et al. 1988), while egg-scattering is the most widespread spawning mode in rabbitfishes, the family with the third highest prevalence of pairing (Thresher 1984; Woodland 1990).

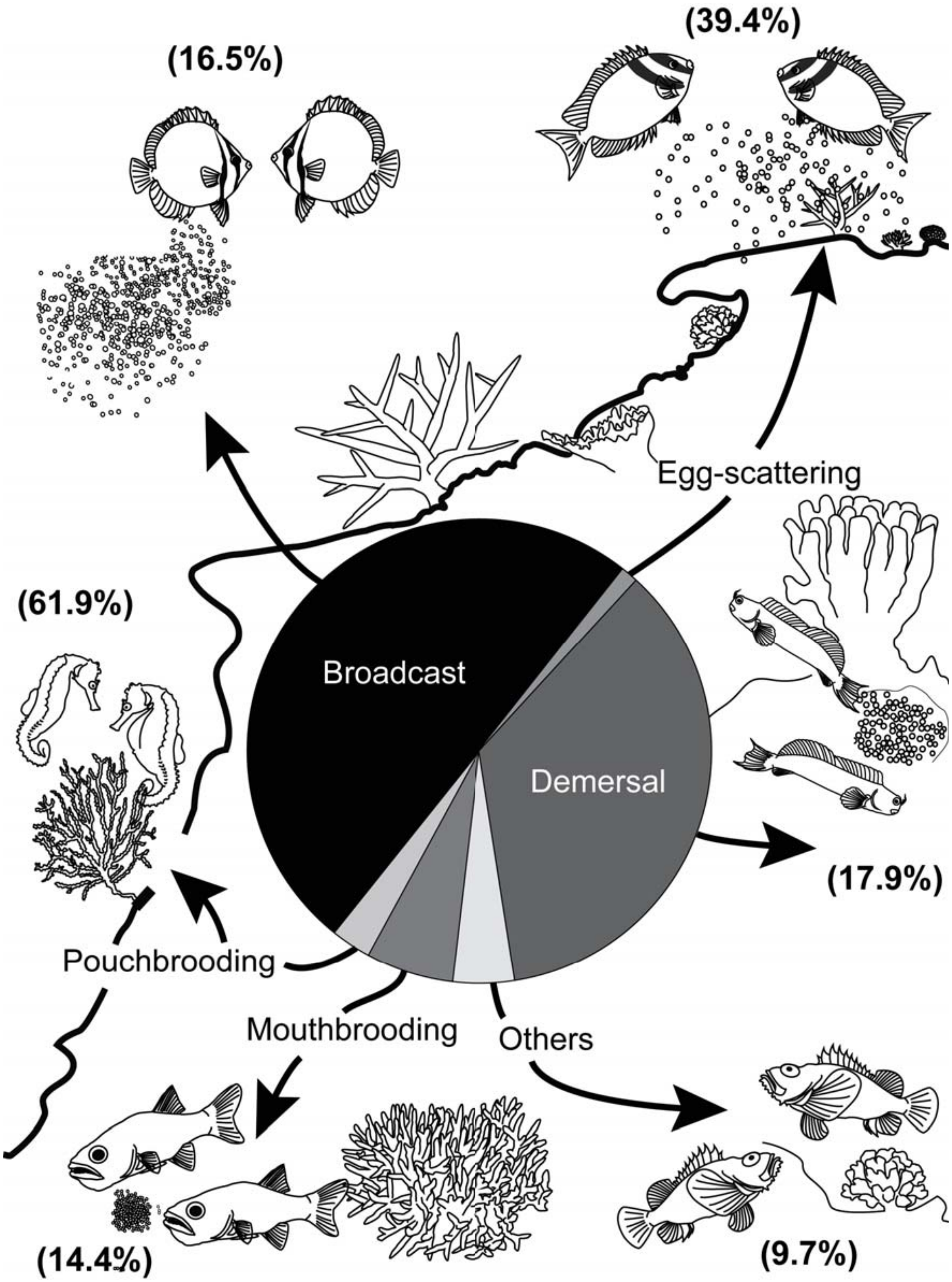

Figure 2.6: The prevalence of pair-formation in different spawning modes.

Proportions indicate the percentage of pair-forming species within each spawning mode. The pie chart indicates the contribution of each spawning mode to the overall species pool.

The only spawning mode that appears to support the hypothesis that high parental investment should lead to pairing and, subsequently, monogamy, is pouchbrooding, a specialized form of breeding in the Syngnathidae, where the male incubates egg clutches in a pouch located on its ventral surface (Vincent & Sadler 1995). Many syngnathids form pairs (Allen et al. 2003) and there is substantial evidence that numerous species are monogamous, maintaining their pair bond beyond the reproductive season (Vincent & Salder 1995; Jones et al. 1998; Kvarnemo et al. 2000; Sogabe & Yanagisawa 2008). However, overall, with the exception of the Syngnathidae, there is limited evidence in support of a direct correlation between pair-formation and the spawning mode of reef fishes.

2.4 Conclusion and future directions

The formation of pairs is a common social system for animals. Yet, the definition of pair-formation as a social system is ambiguous and often confused with reproduction between only two individuals, which may be more appropriately termed a ‘mating pair’. I therefore suggest restricting the term ‘pair-formation’ to ‘an association between two conspecific individuals, maintained beyond the time required for reproductive activity leading to fertilization’. Following this definition, pair-formation is identified as a common trait among coral reef fishes, occurring across a wide range of phylogenetic lineages. However, the processes that have led to the evolution of this social system are poorly understood. This is particularly true for ecological factors that may be correlated with pairing behaviour. Most research to date has focused on the evolution of monogamous mating (i.e. a specialized mating system) in pairing species rather than the implications of pair-formation for daily survival, including food acquisition or reducing predation risk. Furthermore, the majority of studies on pair-formation in reef fishes focus on three families, the Chaetodontidae, Gobiidae and Syngnathidae, while other families with a high proportion of pairing species such as the Malacanthidae, Siganidae, Ptereleotridae or Synodontidae are rarely investigated.

This review revealed several similarities in the ecology of pairing reef fishes, identifying two major traits. These appear to be common among pair forming species, regardless of phylogenetic relationships. First, pair-formation appears to be beneficial for species that forage on small, benthic, and relatively immobile prey, including coral polyps, sponges, filamentous algae or micro-invertebrates. This is consistent with the theoretical framework for the evolution of monogamous mating, explaining monogamy as a result of widely distributed resources and the inability of males to sequester multiple females. On reefs, the size and benthic nature of these resources may also influence the feeding efficiency of species that forage on such prey. As a consequence, associations with only one individual may be the preferred group size in these species. Second, the maintenance of permanent burrows appears to be almost exclusively restricted to species that live in association with a partner. While not all of these species can be considered to be pairing *per se*, these findings highlight the apparent necessity of a cooperative partner for the maintenance of permanent burrows. In both cases, the allocation of tasks between pair members appears to be important to avoid predation and maximize daily energy intake.

In contrast, there were few aspects of the reproductive biology of reef fishes that helped explain pairing species. Three hypotheses, based on the assumptions that pairing species should exhibit similarities in their reproductive behaviour, were not supported. While most pairing species also reproduce in pairs, there are some notable exceptions to this pattern and pair mating appears to be a common mating system among coral reef fishes in general. Thus, there is no clear link between pair-formation and reproduction in pairs. Monogamous mating, while being a good indicator for pair-formation, is reported in only a quarter of all pair-forming fishes. Finally, although parental investment appears to favour pairing in pouchbrooding species, there was no clear correlation between these two traits across a broad range of families.

Based on the finding of common ecological traits among pairing species and the unexpectedly weak correlations between pair-formation and reproductive traits, I suggest that pairing behaviour in reef fishes may be strongly linked to ecological factors, benefitting daily survival and food acquisition. However, as opposed to well-defined theories and numerous empirical studies investigating the reproductive biology of pairing species, the environmental circumstances and ecological benefits of pairing species remain poorly understood. Given the potential importance of these ecological aspects, this promises to be an interesting and exciting avenue for future research.

Chapter 3: Morphology, sociality, and ecology: can morphology predict pairing behaviour in coral reef fishes?

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3.1 Introduction

Few groups of animals exhibit the morphological diversity seen in coral reef fishes. To understand the ecological importance of different morphologies, many reef fish studies have used an ecomorphological framework, which seeks to predict an organism's performance of ecological tasks using morphological attributes (Motta 1988; Wainwright 1991; Dumay et al. 2004; Mouillot et al. 2007; Goatley & Bellwood 2009; Ferry-Graham & Konow 2010). Morphological attributes involved in prey acquisition have attracted much attention among ichthyologists and numerous reliable morphological predictors of foraging ecology have been identified. This includes dentition patterns (Motta 1989), jaw osteology or myology (Wainwright 1988; Alfaro et al 2001; Ferry-Graham et al. 2001a), bite kinematics (Ferry-Graham et al. 2002a; Konow & Bellwood 2005; Ferry-Graham & Konow 2010) and other associated functional complexes such as the visual sensory system (Job & Bellwood 1996; Goatley & Bellwood 2009; Schmitz & Wainwright 2011a) or the locomotory system (Bellwood & Wainwright 2001; Fulton & Bellwood 2002; Collar et al. 2008).

However, while morphological features can serve as proxies for the fundamental ecological niche (usually based on limits to mechanical performance; Hutchinson 1957), the realized ecological niche of a species or individual is determined by a variety of other biotic and abiotic factors (Hutchinson 1959; Ferry-Graham et al. 2002b), which restrict the realized niche that an organism can occupy. These factors can include prey availability (Beukers-Stewart & Jones 2004; Berumen et al. 2005), intra- and interspecific competition (Osenberg et al. 1992; Berumen & Pratchett 2006), predation pressure (Werner et al. 1983; Madin et al. 2010) and the quest for high reproductive success (Reese 1975; Sogabe et al. 2007; Reavis & Copus 2011). As a response, fishes display various behavioural traits, which further modify their ecological niches and thus their functional impact on the ecosystem (Ferry-Graham et al. 2002b). Behavioural traits commonly show relatively high plasticity (Mittelbach 1984; Robertson 1987; Gardiner & Jones 2010), exacerbating the difficulty of forecasting a realized ecological performance using morphology. Nevertheless, there are some clear examples of morphology predicting behavioural adaptations and thus allowing for an appraisal of realized ecological roles. For example, eye size has been used to make predictions about nocturnal or diurnal activity patterns of reef fishes (Goatley & Bellwood 2009; Schmitz and Wainwright 2011b), while fin aspect-ratios have been found to be strong predictors of habitat utilization behaviour in labrid fishes (Bellwood & Wainwright 2001; Fulton 2007) and good indicators of foraging behaviour in sunfishes (e.g., Robinson et al. 1993). This raises the question: can morphology predict other behavioural traits and therefore aid in understanding ecological performances of reef fishes?

One well-documented behavioural trait in coral reef fishes is the formation of social associations (for instance pairing behaviour or schooling) but to date, no study has examined a potential linkage between morphological attributes and different social associations. However, social systems are tightly linked to the life history of reef fishes, markedly influencing their realized ecological niche. The formation of inter- or intraspecific schools, for instance, has been shown to alter the range of exploitable resources, thereby modifying the realized niche of these schooling individuals (Robertson et al. 1976; Foster 1985; Welsh & Bellwood 2012). In contrast to schooling, pairing has rarely been linked to ecological factors and has largely been examined with regards to reproductive benefits or constraints, especially monogamous reproduction (Barlow 1987; Whiteman & Côté 2004; Reavis &

Copus 2011). Monogamous reproduction is arguably the most common underlying driver of pair-formation in reef fishes and there is strong evidence that the evolution of monogamy has involved changes in various behavioural traits (Emlen & Oring 1977). One trait includes the foraging ecology of species that regularly form pairs: it is argued that, in cases where biparental care is absent, monogamous reproduction arose as a response to feeding on dispersed, small prey items of high nutritional quality, which restricted males to reproduction with just one female due to alterations in female home-ranges (Emlen & Oring 1977; Whiteman & Côté 2004). Accordingly, previous studies have found correlations between foraging ecology, prey types, pairing behaviour and monogamous reproduction (e.g. Barlow 1987; Hourigan 1989).

Thus, assuming that pairing and monogamous reproduction have evolved for similar reasons in most reef fishes (except, for instance, burrowing gobies [f. Gobiidae]; e.g. Reavis & Barlow 1998; Pratchett et al. 2006), it appears reasonable to assume that there are parallels in the ecology of species that form pairs. Given that ecological traits are often manifested in morphological features (e.g. Motta 1988; Schmitz & Wainwright 2011b), one would predict that pairing reef fishes exhibit certain morphological features, shared between phylogenetically distinct species. Specifically, when considering previous findings relating ecological traits to monogamous reproduction in reef fishes, the question arises if species that occur in pairs display morphological adaptations that enable the foraging on small prey items.

Reef fishes that obtain their food by biting or scraping the reef substratum represent a promising group to explore this issue for several reasons. Firstly, a distinct set of lineages display this foraging strategy including the butterflyfishes (Chaetodontidae), angelfishes (Pomacanthidae), surgeonfishes (Acanthuridae), rabbitfishes (Siganidae), parrotfishes (Labridae, tribe Scarini), tetraodontiform fishes and several smaller lineages (e.g., Ephippidae, Kyphosidae) (Wainwright & Bellwood 2002; Konow et al. 2008), offering a diverse range of taxa. Secondly, their close association with the substratum and the associated benthic community has allowed these lineages to diversify in their cranial morphology and diet. This provides a broad spectrum of different morphologies (Konow et al. 2008; Goatley & Bellwood 2009). Finally, there is high variation in terms of the social associations formed by species within these lineages, making comparisons possible both within and between lineages.

Given that in the past, ecomorphological studies have contributed greatly to our understanding of reef fish ecology (Motta 1988; Wainwright 1991; Bellwood & Wainwright 2001; Ferry-Graham et al. 2001a; Fulton & Bellwood 2002; Collar et al. 2008; Konow et al. 2008), the goal of the present study was to compare the morphology of biting/scraping coral reef fish species in different social systems to identify possible ecomorphological patterns and determine if pair-forming species share any common morphological traits. Specifically, the aims were: 1) to examine the gross morphology of the head, snout, eyes and basic body shape of biting and scraping coral reef fishes to determine, if pair-forming, biting reef fishes share a similar morphospace and, if so, 2) to provide a hypothesis for the functional basis of such ecomorphological segregation.

3.2 Materials and methods

A total of 47 substratum biting or scraping species within the families Chaetodontidae, Pomacanthidae, Acanthuridae, Siganidae, Kyphosidae and scarine Labridae were examined. These groups of biting/scraping taxa were chosen as they are abundant on coral reefs and show a broadly similar foraging ecology, in that they feed by grasping or scraping items from the benthos (Konow et al. 2008).

3.2.1 Social systems

In order to compare the ecomorphology of species in different social systems, the most prevalent social system of each species was determined among 12 different sites on Lizard Island, Great Barrier Reef (GBR), Australia. At each site, the first encountered individual of each focal species was designated as being either solitary (no conspecifics within five metres of the focal individual), paired (two conspecifics in close proximity with coordinated movements and no antagonistic behaviour, no other conspecific individuals in close proximity), a trio (three conspecifics, coordinated movements, no antagonistic behaviour, no other conspecific individuals in close proximity), or in a school (more than three individuals in close proximity with coordinated movements). Each individual was classified on first observation, and then followed for 30 seconds after detection to ensure continuity of behaviour (all individuals retained the original designation). Furthermore, only one individual in each association was assessed, and only species with more than five observations were considered in the data analysis (mean of 58.6 ± 6.8 (SE) observations per species). A total of 2,753 focal observations were recorded from 47 species in the six families. Morphological measurements were then obtained for the observed species. The 47 species include the vast majority of biting and scraping teleosts found at Lizard Island.

3.2.2 Morphology

Morphological measurements were taken from published ‘Randall-style’ images of dead, pinned fishes (Woodland 1990; Froese and Pauly 2012). These have a standard presentation and permit accurate measurements of fishes in lateral presentation, with a mean of 2.1 images per species. All specimens were freshly caught and only mature individuals were considered. Five different morphological measurements were taken from each replicate: 1) the “snout angle” (S_A, **Figure 3.1**). After defining the midline (passing horizontally through the mid caudal peduncle), an eye-line was drawn perpendicular to the midline touching the front of the eye. A second line, perpendicular to the midline, was drawn half-way between the vertical eye-line and the anterior tip of the premaxilla. From this line, lines were drawn to the tip of the premaxilla from the point where the second line crossed the upper and lower margins of the snout. The angle formed by those two lines marks the snout angle; 2) the “head angle” (H_A, Fig. 1) is formed by the upper snout angle line and a line connecting the upper margin of the snout to the crossing of lines II and IV (parallel to midline touching the dorsal rim of the orbit) in front of the orbit; 3) body depth (B_D) is measured along a line, perpendicular to the midline, drawn from the first dorsal spine to the lower margin of the body; 4) eye diameter (E_D): Measured parallel to the midline, through the centre of the pupil and, 5) snout length (S_L) measured from a line drawn vertically through the centre of the eye and along a perpendicular, horizontal line to the tip of the premaxilla. All variables were expressed as residuals from measurements regressed against standard length (SL) of the respective measured specimens. A mean of each variable was calculated for each species. In addition, the maximum size of each species was obtained from the literature (Randall et al. 1997). Measurements were taken using vernier callipers and a protractor.

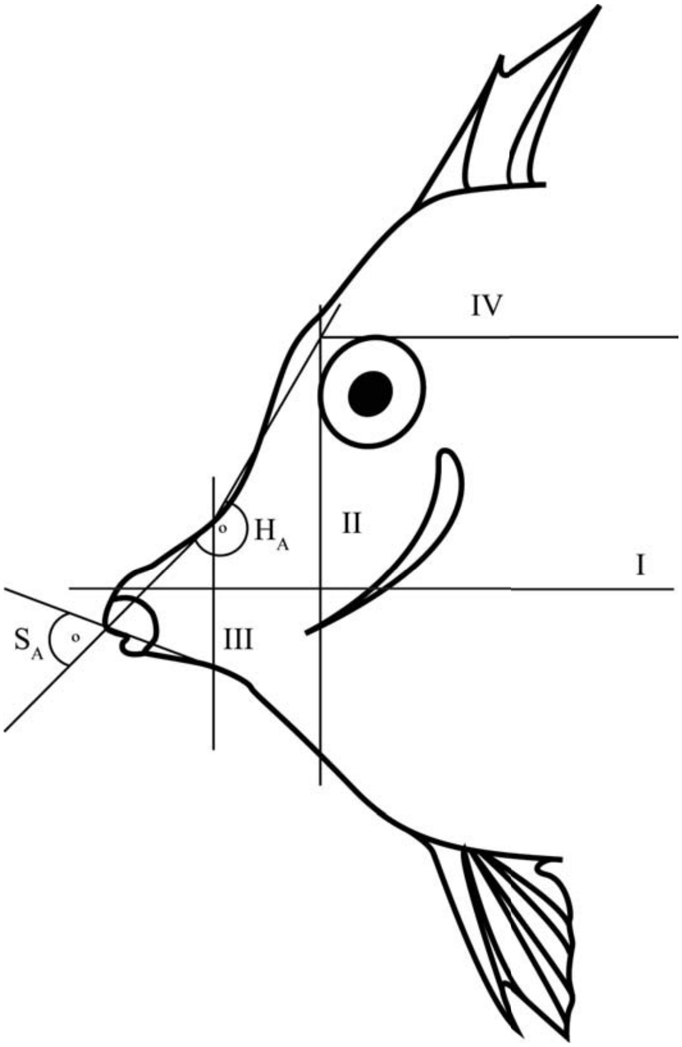

Figure 3.1: Morphological measurements of the head. From the midline (I), a perpendicular line (II) is drawn touching the anterior rim of the orbit. A second perpendicular line (III) is drawn half way between (II) and the anterior tip of the premaxilla. Where this line meets the upper and lower rim of the snout, lines are drawn to the tip of the premaxilla. The angle formed by these two lines defines the snout angle (SA). A third line is drawn parallel to the midline touching the dorsal margin of the orbit (IV). The head angle (HA) is the angle between the upper line of the snout angle and a line that connects the snout intercept with the crossing of lines (II) and (IV).

3.2.3 Statistical analysis

To explore morphological variation among species, a principal components analysis (PCA) was performed, using the mean of the residuals of each of the five morphological measurements for each species, and maximum size as variables. Species on either side (negative and positive) side of PC1 were compared with regards to the prevalence of solitary individuals, pairs, trios and schools using a non-parametric Mann-Whitney U test (to allow for unequal sample sizes). In order to test for the effect of size, each morphological variable was tested using analyses of covariance (ANCOVA) with standard length (SL) as continuous, pair-formation as categorical, and the respective morphological measurements as dependent variables. As the species used for this analysis represent non-independent samples due to their phylogenetic relationships, I used phylogenetic analysis to evaluate the consistency of patterns when accounting for phylogenetic relationships (Felsenstein 1985). This was only possible within families, as no published phylogeny exists for all of the species used in this study. For the Chaetodontidae and Siganidae, pruned phylogenies were obtained from Fessler and Westneat (2007) and Kuriiwa et al. (2007), respectively. These phylogenies contained all of the species examined in this study (except for *Chaetodon lunulatus*). No significant linear or non-linear trends were found in the data, leading to the assumption that all branch lengths were consistent with a Brownian motion model. To evaluate the relationship between morphology and pair-formation the scores on PC1 (as a representative summary of the morphological features) and the percentage of individuals in pairs were compared in linear regression analyses using the phylogenetically independent contrasts (PICs) for both variables (R Development Core Team 2012, packages '*ape*' and '*caper*'). Due to the lack of well resolved phylogenies that include the majority of species examined in this study, simple linear regression analyses were performed for the Acanthuridae and Labridae without accounting for phylogenetic biases. In the Chaetodontidae, *Chaetodon baronessa* was excluded from this analysis due to extensive collection by other researchers in the main observation sites immediately before the observation period. Thus, local populations of *C. baronessa* were not considered to be natural.

3.3 Results

The prevalence of pairing varied considerably within and between families: in the Siganidae (n = 731 observations), 53.1% of all individuals were observed in pairs, with the highest proportion in *Siganus vulpinus* (80.4%) and the lowest in *Siganus canaliculatus* (0%). This is followed by the Chaetodontidae (33.5%, n = 314), ranging from *Chaetodon lunulatus* with 61.2% of individuals in pairs to *Chaetodon plebeius* at 7.1%. The Pomacanthidae (n = 145) showed a comparable prevalence of pairing (30.6%), but with less variation; from the highest in *Centropyge vroliki* (35.7%) to lowest in *Pomacanthus sexstriatus* (25.8%). Within the Acanthuridae (n = 736), 13.6% of all fishes were encountered in pairs, with the highest prevalence in *Zebrasoma scopas* (43.3%) and the lowest proportions in *Acanthurus lineatus* and *Acanthurus blochii* (0%). In the Kyphosidae, only *Kyphosus vaigiensis* had sufficient observations (n = 26) and only 3.8% of these individuals were found in pairs. Similarly, only 3.5% of the scarine Labridae (n = 799) were found to be paired, with *Scarus rubroviolaceus* exhibiting the highest prevalence of pairing (13%), while *Scarus flavipectoralis, Scarus ghobban, Scarus globiceps* and *Scarus psittacus* were not observed to form pairs (0%).

3.3.1 Morphology

The PCA of the morphology of the 47 species showed a clear segregation of species along PC1, with the first axis explaining 40.8% of the variation (**Figure 3.2a,b**). Species with a high prevalence of pairing were located on the positive end of PC1. Except for the Labridae (exclusively negative), all families contained species that were located on both sides of

PC1.The second axis (PC2) explained 22.3% of the variation, with the Acanthuridae being exclusively on the negative side and the Pomacanthidae and Chaetodontidae on the positive side. All other families were scattered on both sides. Scores on PC1 were mostly driven by the eye diameter and the head angle (convexity or concavity of the forehead) and to a lesser extent by the snout angle, body depth, and maximum size. PC2 was predominantly driven by the snout length and to a lesser extent by maximum size (**Figure 3.2c**, **Table 3.1**). When comparing the prevalence of pairing on the negative (n=22 species) and positive (n=25) side of PC1, pair formation was significantly more prevalent in species on the positive (35.8 ± 4.7% (mean ± SE) of individuals in pairs) than on the negative (9.0 ± 3.2% (mean ± SE) of individuals in pairs) side (Mann-Whitney U test: $p < 0.001$). Schooling showed an inverse pattern (13.9 ± 4.7% (mean ± SE) individuals in schools on the positive side of PC1, 25.3 ± 4.8% (mean ± SE) on the negative side; Mann-Whitney U test: $p = 0.03$). Likewise, solitary individuals were significantly less prevalent on the positive side (47.4 ± 4.5% SE) than on the negative side (63.3 ± 4.3% SE) (Mann-Whitney U test: $p = 0.04$). The prevalence of trios was low on both sides of PC1 (2.9 ± 0.7% and 2.4 ± 1.3% SE, respectively; Mann-Whitney U test: $p > 0.05$).

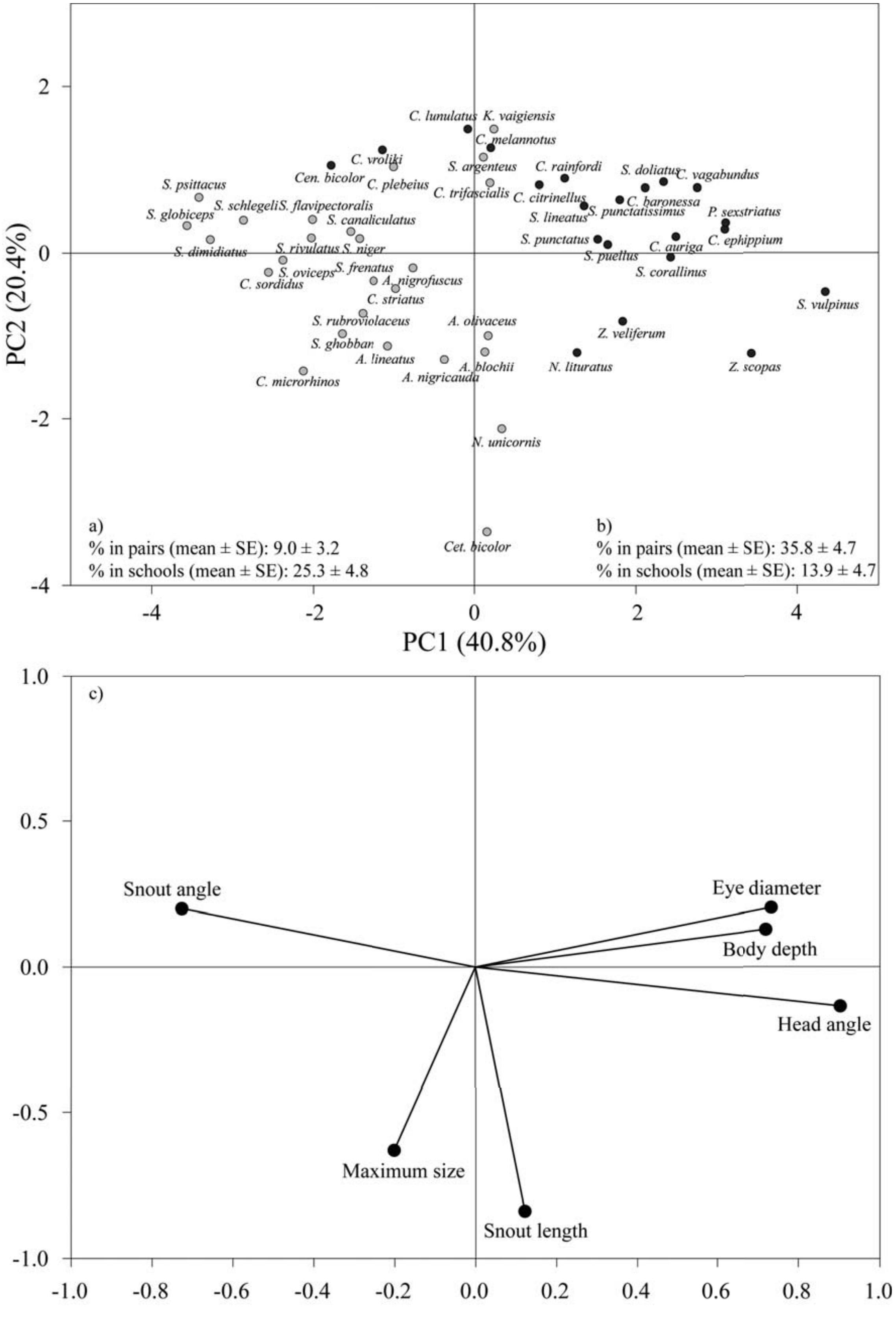
PC2 (20.4%)
PC1 (40.8%)
C. lunulatus
K. vaigiensis
C. melannotus
C. vroliki
Cen. bicolor
C. plebeius
S. argenteus
C. rainfordi
S. doliatus
C. vagabundus
S. psittacus
C. trifascialis
C. citrinellus
C. baronessa
S. schlegeli
S. flavipectoralis
S. globiceps
S. canaliculatus
S. lineatus
S. punctatissimus
P. sexstriatus
S. dimidiatus
S. rivulatus
S. niger
S. punctatus
S. puellus
C. auriga
C. ephippium
S. frenatus
S. oviceps
C. sordidus
A. nigrofuscus
S. corallinus
C. striatus
S. vulpinus
S. rubroviolaceus
A. olivaceus
Z. veliferum
S. ghobban
A. lineatus
A. blochii
N. lituratus
Z. scopas
C. microrhinos
A. nigricauda
N. unicornis
Cet. bicolor
a)
% in pairs (mean ± SE): 9.0 ± 3.2
% in schools (mean ± SE): 25.3 ± 4.8
b)
% in pairs (mean ± SE): 35.8 ± 4.7
% in schools (mean ± SE): 13.9 ± 4.7
2
0
-2
-4
-4
-2
0
2
4
c)
Snout angle
Eye diameter
Body depth
Head angle
Maximum size
Snout length
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0

Figure 3.2: Principal component analysis of morphological features and the distribution of species in morphospace. a) Species with low prevalence of pairing behaviour are located predominantly on the negative side of PC1 whereas b) species with high proportions of pairing are found on the positive side of PC1. Schooling proportions show an inverse pattern. Pairing species are represented by black dots, whereas non-pairing species are in black. c) shows the morphological attributes driving the pattern, with eye diameter, the head angle, snout angle and body depth being the main factors driving differentiation along PC1.

Table 3.1: Eigenvalues and factor loadings for the principal components analysis performed on residuals of morphological traits compared to standard length.

	Eigenvalue	% total variance	Cumul Eigenvalue	Cumul %
Factor 1	2.447455	40.79092	2.447455	40.7909
Factor 2	1.223603	20.39339	3.671059	61.1843
Factor 3	0.930829	15.51382	4.601888	76.6981
Factor 4	0.666249	11.10415	5.268137	87.8023
Factor 5	0.483022	8.05036	5.751158	95.8526
Factor 6	0.248842	4.14736	6.000000	100.0000

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6
$\mathbf{S_A}$	-0.728549	0.197066	0.035396	0.554128	-0.321502	0.136773
$\mathbf{H_A}$	0.900723	-0.137511	0.001422	-0.008800	-0.122124	0.393440
$\mathbf{B_D}$	0.717580	0.126305	-0.177412	0.567338	0.324868	-0.101190
$\mathbf{E_D}$	0.731271	0.202678	0.472616	0.033127	-0.389908	-0.218340
$\mathbf{S_L}$	0.119335	-0.841167	-0.431204	0.105151	-0.255069	-0.127060
$\mathbf{M_S}$	-0.203592	-0.633456	0.699140	0.158389	0.205222	0.035829

The ANCOVAs revealed that, size differences between species had no influence on the morphological segregation of pairing and non-pairing species. On average, pair-forming species had significantly larger eyes ($F_{1, 90} = 33.3$; $P < 0.001$), wider head angles (occasionally exceeding 180º, i.e. concave, $F_{1, 90} = 86.1$; $P < 0.001$), narrower snout angles (ANCOVA: $F_{1, 90} = 19.5$, $P < 0.001$), and deeper bodies ($F_{1, 90} = 25.4$; $P < 0.001$) than non-pairing species. Snout length did not vary significantly ($F_{1, 90} = 0.58$; $P = 0.448$). Only the head angle showed a weak negative relationship to standard length in pairing species (slope = -0.43, $r^2 = 0.18$), while no such relationship was found in non-pairing species (slope = 0.01, $r^2 < 0.01$). All other morphological features showed no significant size relationship.

The apparent relationship between morphology and pairing among all taxa is also evident when the species within families are tested in a phylogenetic analysis to account for non-independence of samples. For both, the Chaetodontidae and the Siganidae, linear regressions exploring the relationship between morphology and pair-formation showed a relationship when performed on the traits (Chaetodontidae: $r^2 = 0.59$, $P = 0.026$; Siganidae: $r^2 = 0.72$, $P = 0.004$; **Figure 3.3**). This was consistent when the regression was performed on phylogenetically independent contrasts of the traits (Chaetodontidae: $r^2 = 0.76$, $P = 0.014$; Siganidae: $r^2 = 0.49$, $P = 0.022$) (**Figure 3.4**). As the results of the uncorrected data were congruent with the results of the phylogenetically corrected data in two families, it is unlikely that phylogenetic effects are confounding the overall results. A significant relationship between morphological attributes and pair-formation was also found in the Acanthuridae ($r^2 = 0.82$, $p < 0.001$), while in the Labridae, where pair-formation is uncommon, no such relationship was found ($r^2 = 0.15$, $p = 0.166$). As *Chaetodon lunulatus* was a strong outlier showing high pairing prevalence and a comparably low score on PC1, and was not present in the phylogeny used for the phylogenetically independent contrasts, this species was excluded from the regression analysis ($r^2 = 0.20$; $P = 0.23$ including *C. lunulatus*).

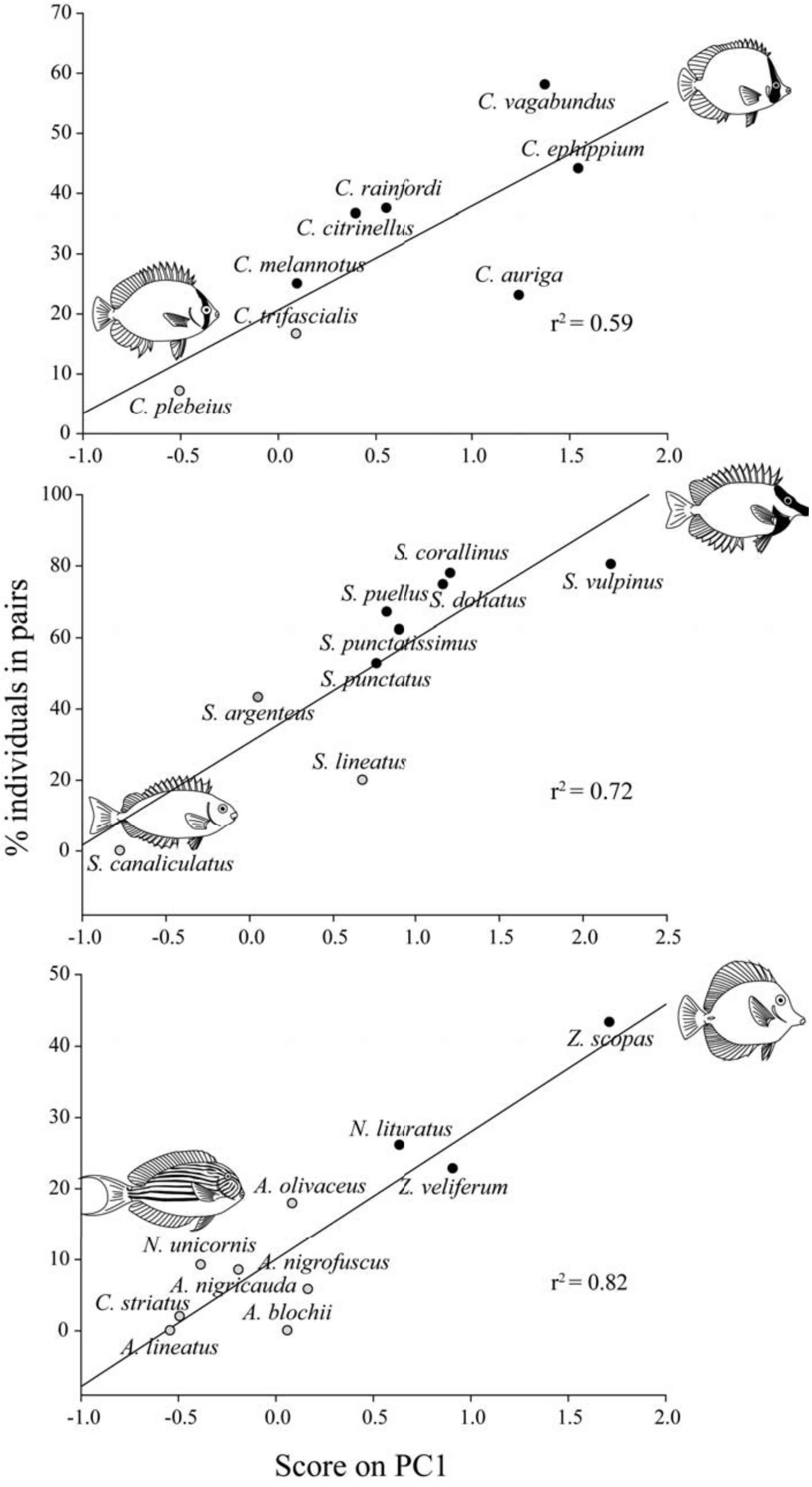
70
60
50
40
30
20
10
0
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
C. vagabundus
C. ephippium
C. rainfordi
C. citrinellus
C. melannotus
C. auriga
C. trifascialis
r² = 0.59
C. plebeius
100
80
60
40
20
0
S. corallinus
S. puellus
S. doliatus
S. vulpinus
S. punctatissimus
S. punctatus
S. argenteus
S. lineatus
r² = 0.72
S. canaliculatus
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
% individuals in pairs
50
40
30
20
10
0
Z. scopas
N. lituratus
Z. veliferum
A. olivaceus
N. unicornis
A. nigrofuscus
A. nigricauda
C. striatus
A. blochii
A. lineatus
r² = 0.82
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Score on PC1

Figure 3.3: The relationship between pair-formation and morphology (scores on PC1) in the Siganidae, Chaetodontidae and Acanthuridae. All families show a significant relationship between their overall morphology (score on PC1) and their tendency to form pairs (% individuals in pairs).

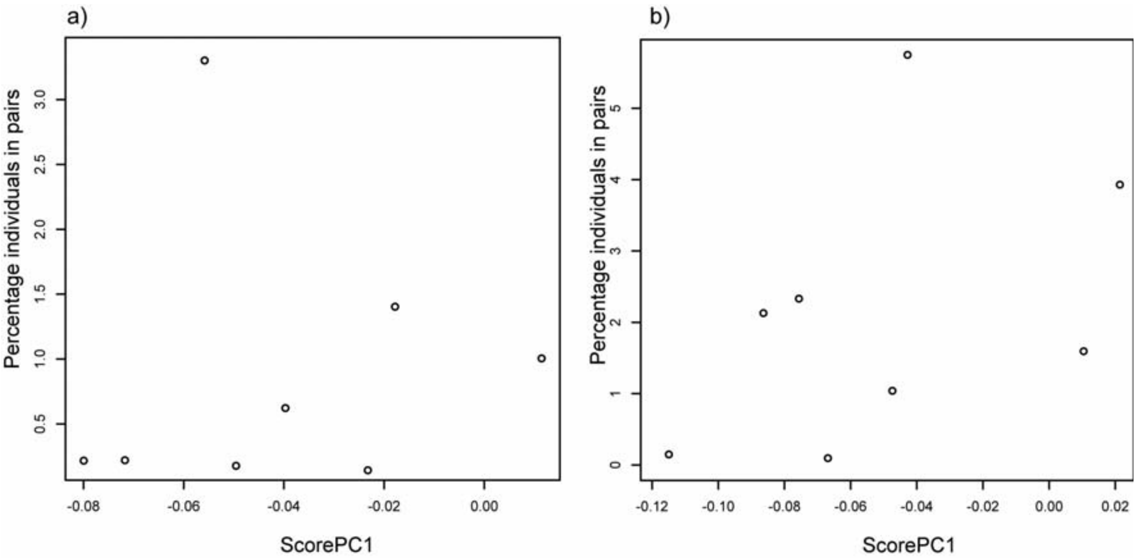

Figure 3.4: Plots of the linear regressions performed on phylogenetically independent contrasts of the score on PC1 and the prevalence of pairing for (a) the Chaetodontidae and (b) the Siganidae. Points represent respective nodes in the phylogeny.

3.4 Discussion

Among biting and scraping teleosts, the prevalence of pairing varied considerably. Pair-formation was most common in the Siganidae, followed by the Chaetodontidae, Pomacanthidae and Acanthuridae. It is negligible in the Kyphosidae and scarine Labridae. When mapped onto the morphological ordination, pair-forming taxa of all families occupied a similar morphospace, characterized by large eyes, an obtuse head angle (concave forehead), an acute snout angle (pointed snout), a deep body, and a relatively small maximum length. Interestingly, snout length was not correlated with pair-formation. A significant relationship between the species' position in morphospace and the proportion of individuals in pairs was also revealed within the Acanthuridae, Chaetodontidae and Siganidae. Phylogenetic relationships do not appear to be driving this pattern, as no phylogenetic effects were found in the Chaetodontidae and the Siganidae when examined using phylogenetically independent contrasts of the data. There was no relationship between pairing and morphology in the scarine Labridae.

The results raise two major questions: 1) what is the putative functional significance of the observed morphological features in pairing species and 2) how does this relate to the role of pair-formation in these species?

3.4.1 Functional significance of pair-forming morphology

The five morphological traits associated with pairs (large eyes, concave foreheads, pointed snouts, deep bodies, and small maximum sizes) are examined separately below. Larger eyes have been shown to improve the general visual capabilities of fishes, enhancing both acuity and sensitivity (Li et al. 1985; Fernald 1991; Miller et al. 1993; Schmitz & Wainwright 2011a). Thus, based on superficial morphology, and without considering physiological differences, pair-forming species appear to display relatively well-developed visual capacities. An enhanced visual performance is known to favour the detection and discrimination of small, delicate prey items (Wetterer 1989; Schmitz & Wainwright 2011a) especially in dim, weakly illuminated reef microhabitats like caves, crevices or sub-rubble systems (Marshall et al. 2003; Schmitz & Wainwright 2011b). Larger eyes would therefore allow for high foraging selectivity and may have important implications for the feeding behaviour, as prey detection is the first crucial step of a successful foray (Ferry-Graham et al. 2002b).

The concave forehead might also play a critical role in foraging. This relates to depth perception. Consumption of attached and motionless food sources requires considerable coordination, starting with targeting and approaching the prey at the right angle and distance (Rice & Westneat 2005). Depth perception is crucial at this stage for estimating distances and in the recognition of three-dimensional substratum structures. In fishes, depth perception is usually achieved with binocular visual fields, i.e. stereopsis (Wetterer 1989; Job & Bellwood 1996; but see Pettigrew et al. 2000). Stereopsis is established by an overlap of the monocular visual fields of each eye. The extent of this overlap, hence the binocular visual field, depends on the convergence distance from the centre of the eye to the convergence point (McComb & Kajiura 2008). Thus, shorter convergence distances yield larger overlapping areas, a broader binocular visual field, and ultimately, a larger visual field in which depth and three-dimensional structure can be recognized. This field is usually largest along the line of the visual axis (Tamura 1957). A concave forehead may substantially decrease the binocular convergence distance (**Figure 3.5**), thus yielding an improved depth perception as a function of a larger binocular field for these species, especially as the visual axis in substratum feeding species is expected to be anterio-ventral (Tamura 1957). While other factors, such as head width or lateral protrusion of the eyes, are likely to influence the convergence distance, it appears plausible that a concave, rather than a convex forehead, may decrease the convergence distance. Similarly, the alignment of the snout with the visual axis, in the binocular field, will be facilitated by a concave forehead and will help maintain accurate visual control of snout positioning during foraging (Martin & Katzir 1999; Guillemain et al. 2002). Thus, the concave forehead, as seen in pairing species, might enable improved visual perception of substratum topography and allow for precise close-range evaluation of the benthos in topographically complex microhabitats.

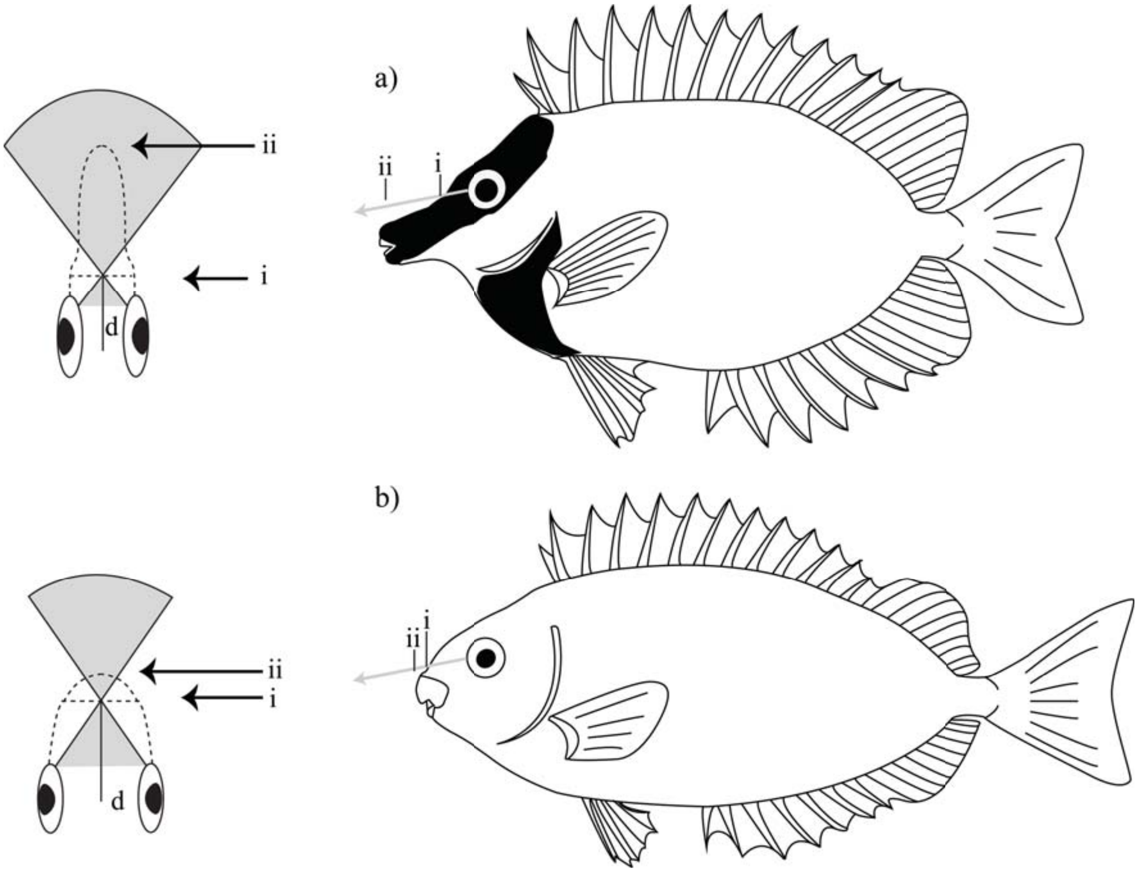

Figure 3.5: An estimate of possible differences in binocular visual fields of fishes with different morphologies. Pair-forming species' (example a, *Siganus vulpinus*) morphology may allow for a shorter convergence distance (d) and a convergence point closer to the eyes (i) despite maintaining an elongated snout (ii), located in the centre of a larger binocular field. Schooling species (example b, *Siganus canaliculatus*) lacking the morphological attributes of pairing species appear to show inverse patterns. Both fishes are drawn from photographs at the same scale. Distances and angles of the visual fields are estimates based on photographs, osteological and preserved material, without accounting for other factors that can influence the visual field such as lateral eye protrusion or aphakic apertures.

The pointed snout allows for delicate, dexterous movements and can function like a pair of forceps thus facilitating a selective foraging behaviour (Ferry-Graham et al. 2001b; 2008; Hernandez et al. 2009). Furthermore, this snout configuration grants access to small crevices and interstices, where concealed prey items, which cannot be exploited by other species, can be utilized. This is a well-known trait of some long-jawed butterflyfishes (Motta 1988; Ferry-Graham et al. 2001a, 2001b) and has recently been identified for pairing species within the Siganidae (Fox & Bellwood 2012). However, despite the pointed snout, some species would still be able to produce efficient gape expansion even while having their snout in interstices. Pair-forming Siganidae (*Siganus doliatus*) and Acanthuridae (*Zebrasoma veliferum*) both exhibit exceptional gape expansion due to intramandibular flexion (Konow et al. 2008), permitting them to achieve relatively large gapes even with a small mouth. High body depths might also contribute to this foraging pattern in enhancing manoeuvrability (Webb 1997; Gerstner 1999). Similarly, a smaller maximum size in pairing species would be beneficial in terms of accessing topographically complex habitats.

Overall, the large eyes, the concave forehead, pointed snout and general body proportions that unite pair forming fishes in a similar morphospace all appear to favour foraging on small, discrete and potentially concealed prey items. The prey can be detected and distinguished due to enhanced visual performance (large eyes), approached and targeted using improved depth perception due to the concave forehead, and ultimately reached and gathered utilizing a pointed snout.

This suite of morphological traits is found in all three families where pairing is common and shows a significant relationship to the prevalence of pairing in the examined species. In the Siganidae, *Siganus corallinus, Siganus puellus* and *Siganus vulpinus* exhibit all the mentioned morphological traits in a pronounced form, are strongly paired, and have recently been identified to forage selectively within small reef crevices and interstices (Fox &

Bellwood 2012). In contrast, siganid species lacking this morphology (*Siganus canaliculatus*, *Siganus argenteus* and *Siganus lineatus*) occur predominantly in groups and are reported to feed unselectively on a wide range of large, erect macroalgae or detrital matter (Woodland 1990; Paul et al. 1990; Fox & Bellwood 2008, 2011; Fox et al. 2009). In the Chaetodontidae, all examined species are known to feed on small, benthic prey items (Pratchett 2005). Generalists and micro-invertebrate feeders (e.g. *Chaetodon ephippium*, Pratchett 2005) appear to be more frequently paired and possess a more pronounced morphology. Accordingly, the extreme long-snouted genera *Forcipiger* and *Chelmon* are usually found in pairs (Allen et al. 1998; Ferry-Graham et al. 2001a, 2001b) and are reported to exploit reef crevices and interstices (Motta 1988). There are no dietary differences between the remaining species, despite marked variation in their pairing prevalence. This suggests that there may be other factors in the foraging ecology of the Chaetodontidae (such as the choice of feeding microhabitats), underpinning the differences in pairing prevalence. *Chaetodon lunulatus* was excluded from my analyses as it was the only strong outlier. Belonging to the crown-subgenus *Corallochaetodon*, this species has a different morphology, dentition patterns and greatly exceeds other *Chaetodon* species in intramandibular flexion (Motta 1988, 1989; Konow et al. 2008), suggesting different bite kinematics and a different foraging strategy. Finally, in the Acanthuridae, species in the genus *Zebrasoma* are most frequently paired and possess the most modified morphological attributes. Correspondingly, these species are reported to differ from other acanthurids in their foraging ecology in exploiting a wide range of microhabitats (Robertson et al. 1979; Robertson & Gaines 1986; Montgomery et al. 1989; Fouda & El-Sayed 1994). In contrast, most members of the genus *Acanthurus* rarely form pairs and appear to have a morphology unsuitable for selectively foraging on small, benthic prey items. Matching this, most members of the genus *Acanthurus* are described as relatively unselective grazers of the open EAM (epilithic algal matrix) (Russ 1984; Fox & Bellwood

2012). Likewise, parrotfishes are known to relatively unselectively scrape algae, detritus and associated matter off planar EAM-covered substrata (Bellwood & Choat 1990; Bonaldo & Bellwood 2011; Fox & Bellwood 2012), suggesting that their foraging strategy does not entail the need for pairing. There was no significant relationship between morphological features and pair-formation in parrotfishes.

These results are highly consistent with one of the prevailing hypothesis for the evolution of monogamy in reef fishes, based on the restricted ability of males to guard more than one female, as a function of altered home-ranges which are shaped by foraging on small, widely dispersed, high quality food items (Emlen & Oring 1977). Thus, given that this way of foraging appears to be a consistent feature of the majority of pair-forming species examined in this study, it appears likely that the species that form pairs may also do so for reproductive reasons and that they mate monogamously. This is supported by observations on, for instance, *Zebrasoma scopas*, *Zebrasoma veliferum* and *Chaetodon lunulatus*, which are reported to reproduce in pairs and are probably monogamous (Robertson 1983; Yabuta 1997; Whiteman & Côté 2004). However, for other species, including all species within the Siganidae and the butterflyfish *Chaetodon ephippium*, there is no record of pair spawning. Conversely, the latter species and the rabbitfish *Siganus punctatus*, both strongly pairing and with the associated morphological features, are reported to spawn in aggregations (Johannes 1981; Yabuta 2007), offering little potential for monogamous reproduction (Emlen & Oring 1977). While the lack of data makes it difficult to assess the importance of monogamous reproduction as a driving force behind pairing, it does appear to be a significant factor in some species. Overall, my observations support the suggestion that pairing arose as a response to foraging on small, high quality, but dispersed, food items, which may also be associated with, or gave rise to, monogamous reproduction.

3.4.2 An ecological role for pair-formation?

In species that forage on small, inaccessible prey items, vulnerability to predation may be a crucial factor. Vulnerability to predation appears to be significantly decreased when feeding in groups (Ryer & Olla 1998; Overholtzer & Motta 2000; White & Warner 2007a; DeMartini et al. 2011). In contrast, vulnerability increases with handling-time of prey (Popp 1988), restricted visual fields (Guillemain et al. 2002), and an increased body angle during foraging (Krause & Godin 1996). A foraging strategy targeting small, concealed, benthic prey appears to be particularly dangerous by virtue of time- and attention-consuming dexterous movements and restricted visual fields when in close proximity to the substratum. Thus, although deep bodies, as exhibited by pairing species, may decrease vulnerability while foraging (e.g., Persson et al. 1996), feeding on small and concealed prey is likely to increase the overall vulnerability of the fish to predation (cf. Krause & Godin 1996; Ferry-Graham et al. 2001b, 2008; Rice & Westneat 2005). Given high selectivity for small prey items coupled with inaccessible, structurally complex microhabitats and a patchy distribution of prey, large group sizes may not be compatible with efficient feeding because of decreasing feeding efficiency (White & Warner 2007b). Accordingly, schooling is largely absent in species occupying the ‘pairing’ morphospace (highest prevalence of schooling in *Naso lituratus*, 13%) and is significantly more common among species with ‘non-pairing’ morphological traits (25.3% ± 4.8% (mean ± SE) of individuals in schools).

Associating with only one individual would result in increased vigilance (vs. solitary feeding) while limiting reductions in feeding efficiency and prey accessibility (vs. schooling) (Ryer & Olla 1998; White & Warner 2007b). In theory, in pairs, one fish can function as an observer while the other fish forages. Performed in an alternating pattern, this benefits both pair members (Wickler 1985). While previous studies have not found a significant increase in feeding rate of paired vs. solitary individuals (Bonaldo et al. 2005; Gregson et al. 2008), it is possible that feeding on small, concealed prey is only performed effectively when fishes are arranged in a pair, whilst solitary individuals display a more conservative foraging strategy. Hence, species, which are morphologically equipped to forage in this way, might execute this feeding mode only when they are able to rely on the safety provided by a partner.

Overall, the pattern of pairing species occupying a similar ecological morphospace appears to be consistent both among and within families. Using only superficial morphological traits, it appears that species with higher pairing proportions occupy a similar morphospace characterized by large eyes, concave foreheads, pointed snouts, deep bodies, and small maximum sizes. This relationship held for the Acanthuridae, Chaetodontidae, Pomacanthidae and Siganidae, whereas the scarine Labridae and Kyphosidae show no such pattern. This appears to be the first study to reveal a distinct ecomorphospace for pairing reef fish species. It is hypothesized that the morphological attributes allow for selective foraging on small, delicate prey items on micro-topographically complex substrata including reef caves, crevices and interstices. Given this, it is likely that pairing arose for ecological reasons and subsequently gave rise to shared reproductive traits, with several species exhibiting a monogamous mating system. The presence of pairs in species with apparently non-monogamous reproductive strategies suggests that there may be additional factors underpinning the formation and maintenance of pairs. While at this stage, I am unable to resolve the evolutionary history of foraging ecology, pair-formation and monogamy, there does appear to be a strong link between morphology, sociality and ecology in biting coral reef fishes that warrants further investigation.

Chapter 4: Coordinated vigilance provides evidence for direct reciprocity in coral reef fishes

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4.1 Introduction

Cooperation is widespread among animals (Dugatkin 1997), and it is now widely accepted that cooperation is also present among unrelated individuals (Trivers 1971; Mesterton-Gibbons & Dugatkin 1992; Dugatkin & Mesterton-Gibbons 1996; Nowak 2006). In this context, reciprocity or 'reciprocal altruism', which involves a costly action beneficial for another individual, based on an expected future payoff through reciprocation, has garnered particular interest (Trivers 1971; Axelrod & Hamilton 1981; Schino & Aureli 2010). This interest has arisen from the notion that cooperative individuals should be prone to exploitation by their respective partners if the latter defects after having received help (Ghoul et al. 2014), therefore leading to fitness declines in cooperating individuals. However, it has been suggested that reciprocity can be evolutionarily stable, even if modelled under an iterated prisoner's dilemma (IPD), in which both players employ a strategy called 'tit-for-tat' (Axelrod & Hamilton 1981; Nowak & Sigmund 1992). The IPD and several other game-theoretical models have subsequently provided frameworks for the evaluation of reciprocity in animals and throughout the last few decades, the presence of reciprocity has been suggested in fishes (Zöttl et al. 2013; Taborsky 1984; Fischer 1988; Milinski et al. 1990; Milinski 1987), birds (Godard 1993; Krama et al. 2012; Krams et al. 2008), and mammals (Carter & Wilkinson 2013; Wilkinson 1984; Rutte & Taborsky 2008; Cheney et al. 2010; Hauser et al. 2003).

However, almost all reported occurrences of direct reciprocity in animals have now been challenged (Clutton-Brock 2009), as many aspects of reciprocity are thought to require a suite of complex cognitive abilities. This includes the recognition of individual partners, the capacity to recall their previous actions, or the ability to make intentional investments under the expectation that it will entail a future reward (Stevens & Hauser 2004; Pfeiffer et al. 2005). For this reason, it has been questioned whether direct reciprocity exists in animals which are assumed to lack complex social and cognitive skills (Clutton-Brock 2009; Clements & Stephens 1995; Milinski & Wedekind 1998; Russell & Wright 2009; Connor 2010; Melis & Semmann 2010), and most evidence of direct reciprocity to date is confined to a few cases in birds and mammals (Carter & Wilkinson 2013; Rutte & Taborsky 2008; Hauser et al. 2003; Taborsky 2013). Yet, in response to these criticisms, it has also been posited that most of the cognitively demanding actions of reciprocity stem predominantly from the theoretical framework in which reciprocity is investigated (Schino & Aureli 2010; Taborsky 2013; Raihani & Bshary 2011; Brosnan et al. 2010). Specifically, many aspects of game-theoretical models such as tit-for-tat in the IPD have been questioned over the last two decades (Connor 1995; Noë 2006). Most recently, the discrete time structure of the IPD and other models, as well as their incapacity to allow for the exchange of information among partners during cooperative interactions, have been identified as a major weakness of these models (Sirot 2012; van Doorn et al. 2014). These weaknesses undermine our capacity to adequately judge whether or not reciprocity is present (Carter 2014), particularly given the often emphasized need for continuous information exchange among cooperating partners in a natural setting (Boesch & Boesch 1989; Milinski et al. 1990; Krams et al. 2008).

Teleost fishes have contributed substantially to the debate about cooperation and reciprocity in animals, and a variety of systems have been discussed in the context of the reciprocal exchange of commodities. This includes 1) egg-trading in hermaphroditic hamlets

(f. Serranidae), which describes the exchange of costly eggs for fertilization by the partner (Fischer 1984, 1988), 2) helping behaviour in cooperatively breeding cichlids (f. Cichlidae), which involves the trading of resource access against the provision of brood care and territorial defence (helpers ‘pay-to-stay’; Bergmüller & Taborsky 2005; Bergmüller et al. 2005), 3) interspecific cleaning behaviour by pairs of cleaner wrasses (f. Labridae), which involves the removal of parasites from client fishes (Trivers 1971; Bshary & Grutter 2006; Bshary & Schäffer 2002), and 4) predator inspection in sticklebacks (f. Gasterosteidae) and other small fishes (Dugatkin 1997; Dugatkin & Alfieri 1991), which involves a pair of fishes approaching a predator in order to assess the threat arising from its presence, for which the presence of a partner provides a safer situation than if the fish were to approach the predator alone (Milinski et al. 1990; Dugatkin & Alfieri 1991). While most of these systems were initially identified as cases of reciprocity, subsequent assessments and syntheses have argued that they are based on pseudo-reciprocity and by-product mutualism rather than direct reciprocity (Clutton-Brock 2009; Connor 1992, 1996, 2010; Stephens et al. 1997), invoking the limited potential of teleost fishes to cope with the cognitive and social demands of reciprocity. However, there is now substantial evidence for many complex social processes in fishes (Bshary et al. 2002, 2014; Brown 2015; Brown et al. 2011; Ward et al. 2008, 2011), including image scoring (Bshary & Grutter 2006), punishment (Bshary & Grutter 2005), pre-emptive appeasement (Bergmüller & Taborsky 2005; Bergmüller et al. 2005), or partner preference (Croft et al. 2006). Thus, teleost fishes appear to provide a promising group for the investigation of reciprocity (Taborsky 2013; Bshary et al. 2002).

Rabbitfishes (f. Siganidae) are an Indo-Pacific family of teleost fishes, which includes 28 species and is separated in two major groups (Woodland 1990). The first group consists of predominantly schooling species, which are drab-coloured and commonly associated with mangrove and estuarine habitats, while the second group consists of species which occur mostly in stable pairs, are brightly coloured, and are commonly associated with coral reefs (Brandl & Bellwood 2013a,b). In the latter group, the presence of same-sex pairs has spurred research exploring the potential ecological role of pairing behaviour in this family, and it has been proposed that their foraging habits, which entail the penetration of cracks and crevices in the reef matrix, may necessitate the presence of a vigilant partner (Brandl & Bellwood 2014a,b). Consequently, it has recently been suggested (based on photographic evidence) that pair members may cooperate in order to achieve high levels of vigilance during foraging (Fox & Donelson 2014). However, the potential presence of cooperation among pair members in rabbitfishes has not been evaluated quantitatively and individual costs and benefits are unknown, undermining our ability to judge whether vigilance behaviour in pairing rabbitfishes may be based on reciprocity.

The goal of the present study, therefore, was to quantify the major aspects of pairing behaviour in rabbitfishes, and to assess whether the behaviour exhibited by rabbitfish pairs may satisfy the basic requirements of reciprocal cooperation, such as reciprocal alternation between feeding bouts and a costly investment by one individual that directly benefits the partner.

4.2 Materials & Methods

4.2.1 Data collection

All fieldwork was conducted on coral reefs around Lizard Island, a granitic mid-shelf island in the northern Great Barrier Reef, Australia (14°40′08″S 145°27′34″E). Four different species of pairing rabbitfishes were considered (*Siganus corallinus, S. doliatus, S. puellus,* and *S. vulpinus*), as they represented the most abundant pairing species in the study area (Big Vicki’s Reef). The four examined species differ in their dietary preferences, with *S. corallinus* and *S. doliatus* feeding predominantly on red corticated and red filamentous algae, while *S. puellus* feeds mainly on sponges, and *S. vulpinus* predominantly on cyanobacteria (Hoey et al. 2013). However, all species are similar in their foraging behaviours, as all four species have been reported to exploit cryptic reef micro-habitats such as cracks and crevices in the substratum (Brandl & Bellwood 2014a). In addition, all four species are strongly pair-forming, with approximately 80% of all adult individuals occurring in pairs in *S. corallinus*, *S. doliatus*, and *S. vulpinus*, and approximately 70% in *S.* puellus (Brandl & Bellwood 2013a).

Haphazardly encountered pairs of the four species were followed while SCUBA diving and video footage of their behaviour was collected for a period of 12 minutes for each pair (using Sony DCR-SR300E camcorders). Care was taken to sample different sites on the reef in order to avoid re-sampling of the same pairs. For each pair, the size was estimated, and video recording commenced one minute after the fish were observed to feed, in order to prevent behavioural biases due to the presence of the observer (foraging was interpreted as a sign that fish had acclimatized to the observer). Observers aimed to keep a constant distance from the recorded fish; video sequences in which the distance to the fish resulted in unreliable examination of fish behaviour or obvious behavioural responses to the observer were discarded from the analyses. Videos were collected during three different times of day (0600 to 1000h; 1000 to 1400h; 1400 to 1800h) and subsequently analysed in 5-second intercepts. Specifically, videos were paused every five seconds to determine the current behaviour of the partners as a point measure. For every 5-second point intercept at which both members of the pair were visible in the video, the angles of both individuals (θA and θB) relative to a vertical line perpendicular to the substratum were measured using a protractor that was superimposed on the computer screen (**Figure 4.1**). Angles were assessed quantitatively to describe a conspicuous behaviour, henceforth termed ‘vigilance position’, in which one individual was found hovering high above the substratum with its head oriented upwards (**Figure 4.1c**). In addition, the fish's height above the substratum (cm), the distance between pair members (cm), the complexity of the surrounding microhabitat (1 = lowest complexity to 5 = highest complexity, Wilson et al. 2007), and the behaviour of individuals (swimming, foraging, hovering, or displaying) were recorded. These parameters were recorded because of their potential influence on the behaviour exhibited by the partners (for instance, higher complexity of the surrounding environment may reduce the threat arising from predation through the provision of shelter (Beukers & Jones 1998). Swimming was defined as active, directional movements, while foraging was defined as at least one of the two individuals engaged in active feeding (i.e. biting from the substratum). Hovering entailed both individuals being stationary and motionless (similar to the vigilance position), and displaying was noted when individuals engaged in displays towards other pairs of the same species. The incidence of fin-flicks (rapid flashing of dorsal, pelvic, or anal fin spines) was also noted, along with specific information on the identity of the fin-flicking fish and the subsequent behaviours of both individuals. This was recorded based on evidence from other families of fishes, that suggests that fin-flicks serve as a communicative signal (Murphy & Pitcher 1987; Brown et al. 1999; Tricas et al. 2006; Parmentier et al. 2011), and the potential importance of communication in reciprocal cooperation (Sirot 2012; van Doorn et al. 2014). All occurrences of presumed flight behaviour (i.e. an individual rapidly abandoning its position followed by extensive swimming behaviour) were likewise recorded, specifying which individual initiated the behaviour, whether the fish's visual fields were obstructed or not, and if the partner followed the flight. I observed 15 pairs each for three species (*S. corallinus*, *S. doliatus*, *S. vulpinus*), and 14 pairs for *S. puellus*, resulting in a grand total of 59 pairs, all of which were filmed for a period of 12 minutes. As only data points were included in which both pair members were in the video frame, and not visibly disturbed by the observer, the average number of non-independent data points (5-second intercepts) extracted per pair was 83.8 (± 5.1 SE) for *S. corallinus*, 71.7 (± 8.1 SE) for *S. doliatus*, 53.4 (± 5.9 SE) for *S. puellus*, and 71.0 (± 7.2 SE) for *S. vulpinus*.

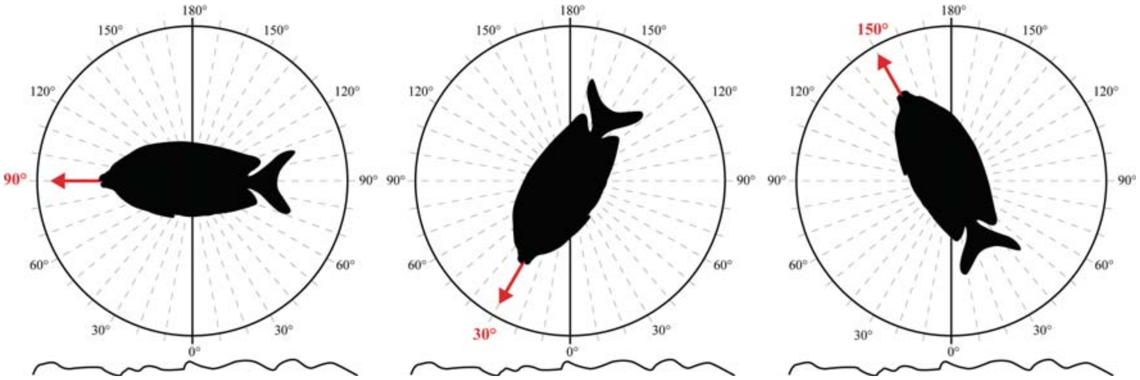

Figure 4.1: Schematic description of the assessment of angles exhibited by rabbitfishes. Angles were assessed based on a vertical line perpendicular to the substratum using a protractor superimposed on the screen. 90° denotes a horizontal position parallel to the substratum (a), while 30° mark a head-down position (b), and 150° mark a head-up position (c). The head-up position (ranging from ~90° to 180°) was identified as a vigilance position.

To determine whether pair members sequentially alternated their roles between feeding bouts, I also counted the occurrence of alternating (A to B, B to A) and repeated (A to A, B to B) foraging bouts, with the latter also including instances where both pair members were feeding simultaneously (AB to A, AB to B, A to AB, B to AB, AB to AB). One foraging bout was defined as active foraging behaviour by either or both of the pair members (A, B, or AB) at a given 5-second intercept until it was interrupted by a different behaviour (or a change of the identity of the forager) at the next 5-second intercept. The next feeding bout commenced at the next 5-second intercept at which one of the individuals (or both) engaged in foraging behaviour. If the individual feeding during the previous bout was feeding again, repeated foraging behaviour was recorded. If the individual not engaged in foraging at the last 5-second intercept engaged in foraging, alternated foraging was recorded. Data were collected for all pairs in all species (n = 59).

In addition to the videos of pairing fish, 24 videos of solitary individuals in all four species (average of 6.0 ± 0.44 SE individuals per species; *S. corallinus: n* = 8; *S. doliatus: n* = 3; *S. puellus*: *n* = 7; *S. vulpinus: n* = 6; average observation period of 459.8 ± 41.6 SE seconds per individual) were collected and analysed to quantify the length of vigilance bouts, the number of bites per foray (foray defined as a continuous sequence of bites from the substratum), and the maximum substratum penetration depth during forays. Vigilance bouts refer to the duration (in s) over which a fish was observed in the assumed vigilance posture (a stationary ‘head-up’ position in the water column, exhibiting an angle > 90°), without interruption by feeding or active swimming. The number of bites per foray was quantified as the number of consecutive bites taken by a fish without engaging in other behaviour such as vigilance (defined above). The penetration depth was estimated as the extent (in cm) to which a foraging fish penetrated into cracks in the substratum (Brandl & Bellwood 2014a). The same protocol was performed with 32 randomly selected videos of pairs (eight per species), where one haphazardly selected individual of the pair was selected for the duration of the video.

4.2.2 Statistical procedures

I used linear and additive mixed effects models to separately analyse the angles of pair members during swimming and foraging (which, when combined, accounted for 92.8% of the behaviours displayed) for each species. I tested whether the angle of one individual in a pair (*θA*) was independent from predictor variables, including environmental factors (time of day, microhabitat complexity), or variables associated with the partner (the angle of the partner [*θB*], its height above the substratum, and the distance between pair members). For all analyses, pair ID was included as a random factor to account for non-independence of points taken from the same pair. For the data gathered during foraging activity, residual plots indicated non-linearity for *θA* as a dependent variable in all species. Thus, data were analysed using generalized additive mixed effects models (GAMMs) with a Gaussian error distribution and a cubic regression spline smoother, calculated by automatic cross-validation, for *θB* and *heightB* during foraging (hastie & Tibshirani 1990). Due to temporal non-independence of behaviours (i.e. an individual might be more likely to assume an angle close to the angle from the previous data point), a temporal autocorrelation function was also added (Zuur et al. 2009). The analysis was repeated for *θB* as the dependent variable for all species. Variables included in the final model were selected using likelihood ratio tests, and model fits were assessed using residual plots. Angles during swimming were analysed in the same fashion but using generalized linear mixed effects models (GLMMs) with pair ID included as a random factor and incorporating a temporal autocorrelation coefficient. This was performed in order to demonstrate that the observed behavioural patterns during foraging are not simply a random behaviour, which is also present during other aspects of the fishes’ daily activity.

To test whether pair members alternated their roles more often than they performed the same role consecutively over the 12-minute observation period, occurrences of sequential changes in the identity of the foraging individual (either alternating or repeated foraging) were analysed. All transitions to or from bouts where both individuals were feeding simultaneously were assigned to be repeated in order to yield conservative estimates. The occurrence of alternating or repeated foraging bouts was analysed using four species-wise zero-inflated GLMMs with a negative binomial error distribution, using counts of alternated and repeated foraging events within pairs as dependent variables and pair ID as a random factor to account for the non-independence of data collected from the same pair. For all GLMMs, model fits were assessed using residual plots, all of which were satisfactory. For each pair, I also calculated the deviation from a balanced (0.5) proportion of 5-second intercept points at which individual A or B were foraging, and tested the overall distribution of feeding by pair members in each species against a balanced distribution using Pearson’s Chi-squared tests. The relative occurrence of fin-flicks during different behaviours (standardized as the number of fin-flicks per 5-second intercept during which a given behaviour was displayed) was analysed using a frequency test (Pearson’s Chi-squared test).

To examine potential behavioural differences between solitary and paired fish, solitary and paired individuals were compared for each species, separately, using GLMMs with the respective individual fitted as a random factor to account for non-independence of repeated measures for each fish. All data were modelled using a negative binomial error distribution as non-normality and overdispersion were detected during the modelling process. I tested the effects of the social status (solitary or paired) on the time spent in the vigilance posture (seconds), the number of consecutive bites per foray (bite counts), and the maximum extent to which individuals penetrated the substratum during foraging (cm). The value 1 was subtracted from the count dataset in order to prevent inaccurate estimates due to zerotruncation (i.e. as at least one bite was necessary to constitute a foray, there were no zeros in the count dataset, possibly resulting in inappropriate model estimates in a Poisson or negative binomial model; Zuur et al. 2009). For the time spent in vigilance posture, seconds were transformed to centiseconds to yield integer values. When the anterior structures of individuals were concealed due to penetration of the substratum, bites per foray were determined by the occurrence of caudal and pectoral fin-movements, which precede food acquisition in rabbitfishes (Pink & Fulton 2014). All analyses were performed using the software R and the packages *mgcv*, *nlme*, and *glmmADMB*.

4.3 Results

In all four rabbitfish species, when foraging, one pair member commonly assumed a stationary, upright position in the water column above the substratum (entailing an angle of 90° or larger), while the partner was feeding. The feeding individual often penetrated deep into cracks and crevices in the substratum with substantial obstructions to its visual field (**Figure 4.2**). Possible flight responses (entailing rapid abandonment of vigilance position or foraging activity) were almost exclusively initiated by the individual positioned head-up in the water column (95.1% of instances), which always had an unobstructed field view of the surrounding environment. In contrast, at the onset of flights, the forager's eyes were often not visible (15.7%), but it followed the fleeing individual in 94.1% of cases, suggesting that individuals in the water column were more vigilant than the forager and that information was rapidly communicated to the foraging fish. It is possible that some of the presumed flight responses were not due to the threat imposed by potential predators but rather in order to engage in territorial defence or simply to move on to another foraging location. However, the high density of predatory fish in the study area (and the presence of the observer as a potential threat) suggest that at least a proportion of the observed responses were associated with predator-oriented vigilance.

Figure 4.2: Foraging and vigilance postures in four species of pairing rabbitfishes. The foraging individual (in the head-down position) feeds in cracks and crevices in the substratum, while the vigilant individual is positioned in the water column with its head up. Note the obstructions to the visual field of the forager, suggesting high vulnerability to predation and the unobstructed field of perception of the vigilant fish. (a) *Siganus corallinus*, (b) *S. vulpinus*, (c) *S. doliatus*, (d) *S. puellus*.

Pair members strictly coordinated their vigilance efforts, which is reflected by the angles assumed during foraging (**Figure 4.3**). A low angle (= head down, foraging) in individual A (θ_A) was complemented by a large angle (= head up, vigilant) in individual B (θ_B) and *vice versa* in all four species. The GAMMs confirmed that pair members' angles were non-independent and arranged in a contrasting manner (GAMM_{AB}: *S. corallinus*: *edf* = 5.781; $F = 11.23$; $P < 0.0001$; *S. doliatus*: *edf* = 3.512; $F = 11.94$; $P < 0.0001$; *S. puellus*: *edf* = 3.802; $F = 5.105$; $P = 0.0009$; *S. vulpinus*: *edf* = 5.116; $F = 4.438$; $P = 0.0005$), suggesting that individuals take turns in being vigilant. The height of individual B likewise showed a significant inverse relationship with θ_A (GAMM_{AB}: *S. corallinus*: *edf* = 3.865; $F = 13.96$; $P < 0.0001$; *S. doliatus*: *edf* = 3.716; $F = 10.39$; $P < 0.0001$; *S. puellus*: *edf* = 2.576; $F = 2.576$; $P < 0.0001$; *S. vulpinus*: *edf* = 3.668; $F = 20.057$; $P < 0.0001$), suggesting that an unobstructed field of perception (i.e. a large angle and a position high above the substratum) in one fish represents the best predictor for foraging (i.e. a low angle) in the partner (*S. corallinus*: *adj.* $R^2 = 0.428$; *S. doliatus* = *adj.* $R^2 = 0.433$; *S. puellus* = *adj.* $R^2 = 0.570$; *S. vulpinus* = *adj.* $R^2 = 0.397$). Except for *S. corallinus*, in which the time of day exhibited a small effect on the angle of individual A ($P = 0.004$; *adj.* $R^2 = 0.443$), the angle and height of the partner were the only variables retained, as likelihood ratio tests indicated that the inclusion of other variables did not significantly improve the model fit. The analyses yielded similar results when repeated using θ_A and height_{A} as predictors for θ_B (GAMM_{BA}: *S. corallinus*: *adj.* $R^2 =$ 0.413; *S. doliatus* = *adj.* $R^2 = 0.462$; *S. puellus* = *adj.* $R^2 = 0.529$; *S. vulpinus* = *adj.* $R^2 =$ 0.327). In contrast to the angles during foraging, the angles of pair members while swimming showed a clear positive, linear relationship (GLMM_{AB}: *S. corallinus*: $\beta = 0.718$; $t = 22.56$; $P < 0.0001$; *S. doliatus*: $\beta = 0.761$; $t = 28.87$; $P < 0.0001$; *S. puellus*: $\beta = 0.644$; $t = 18.01$; $P < 0.0001$; *S. vulpinus*: $\beta = 0.673$; $t = 23.22$; $P < 0.0001$), indicating that individual angles are non-independent and linearly synchronized during movement, with no other variables eliciting a significant effect in any of the four species (**Figure 4.4**). Thus, pairs of rabbitfishes travelled together synchronously, but performed contrasting, complementary roles during foraging, which were strongly coordinated with minimal overlap in vigilance behaviour.

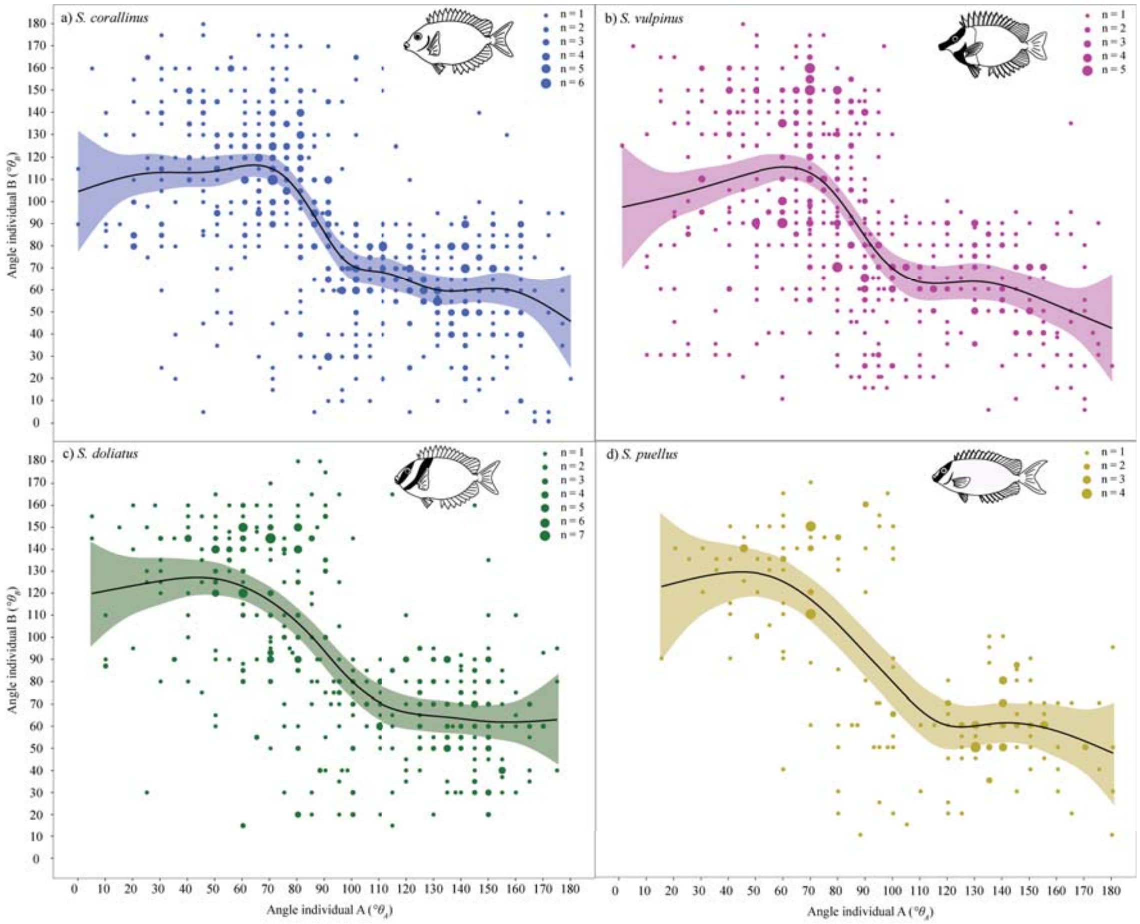

Figure 4.3: Graphical representation of coordination between foraging and vigilance in four species of rabbitfish pairs. Axes mark the angles of individuals in pairs (θA, θB), while each point represents the angle assumed at a given 5-second point intercept with the size varying according to the number of overlying points. The four predicted smoothed lines mark the predicted fits from generalized additive mixed effects models (GAMMs) and their upper and lower 95% confidence interval. In all species, data are predominantly spread between the upper left and lower right quartile of the plot. The smoothing function, fit by automatic cross-validation, suggests that individuals assume contrasting angles (<90° and >90°); however, the extent of the angle is negligible once a certain threshold is reached (~120° and 60°,

respectively). The observed pattern was consistent among species. a) *S. corallinus* (*n* = 15), b) *S. vulpinus* (*n* = 15), c) *S. doliatus* (*n* = 15), d) *S. puellus* (*n* = 14). *n* = number of independent pairs represented in the plot.

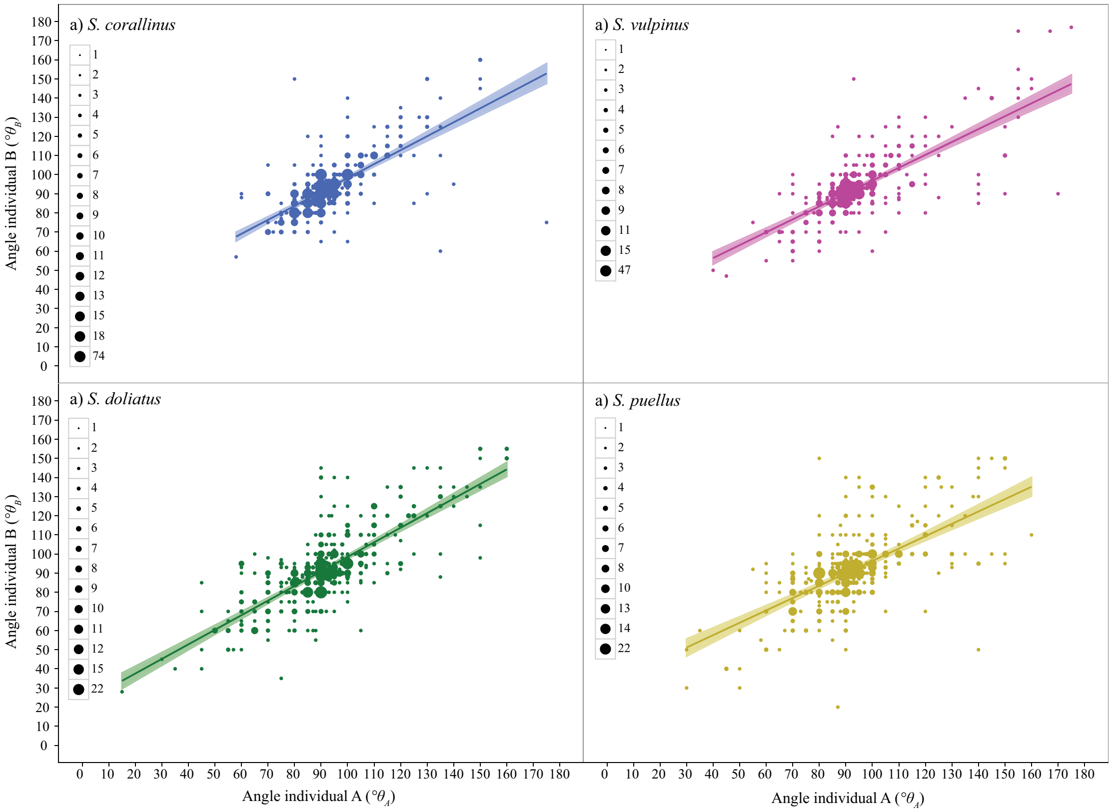

Figure 4.4: Angles exhibited by pair members during swimming behaviour. In all four species, angles are synchronized linearly, with the angle of individual B being the best linear predictor of the angle of individual A. The size of dots marks the number of overlying data points. Data represent repeated observations on 15 independent pairs in a) *S. corallinus*, b) *S. vulpinus*, c) *S. doliatus* and 14 independent pairs in d) *S. puellus*. Trendlines represent the predicted fit (± 95% confidence intervals) from GLMMs performed for each species separately.

Across all pairing rabbitfish species examined, a vigilant individual (i.e., a stationary individual not engaged in foraging activity and exhibiting an angle >90°) was present during 82.6% of foraging activity (i.e. when at least one individual was feeding). When feeding, pair members alternated their roles significantly more often than they continued in the same role (**Figure 4.5**a), with a higher proportion of alternated foraging bouts compared to repeated foraging bouts in all species (**Figure 4.5b**; parameter estimates for repeated counts compared to alternated counts: *S. corallinus*: $\beta = -1.538$; $z = -12.6$; $P < 0.0001$; *S. doliatus*: $\beta = -0.826$; $z = -5.61$; $P < 0.0001$; *S. puellus*: $\beta = -1.858$; $z = -7.99$; $P < 0.0001$; *S. vulpinus*: $\beta = -1.094$; $z = -7.70$; $P < 0.0001$). The average deviation from a balanced proportion of feeding events per individual (0.5) was relatively small across pairs in all species (0.14), and within species, the distribution of feeding events was not statistically different from an expected balanced distribution (Pearson's Chi-squared test; *S. corallinus*: $\chi^2 = 2.419$, $df = 1$, $P = 0.120$; *S. doliatus*: $\chi^2 = 2.294$, $df = 1$, $P = 0.130$; *S. puellus*: $\chi^2 = 2.630$, $df = 1$, $P = 0.105$; *S. vulpinus*: $\chi^2 = 3.480$, $df = 1$, $P = 0.062$), although these estimates have to be interpreted with care due to the relatively small sample size.

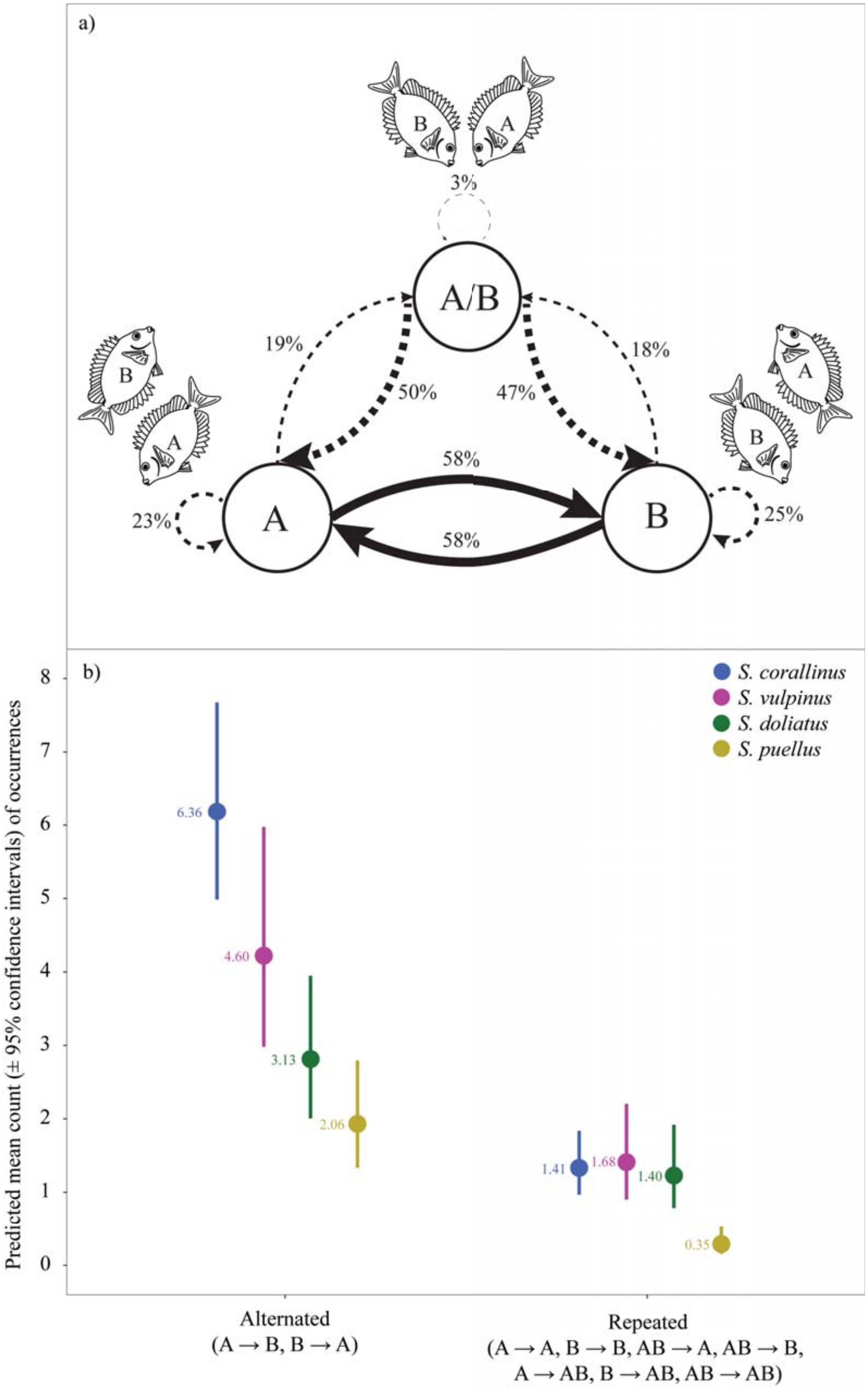
a)
B
A
3%
A/B
19%
18%
50%
47%
B
A
A
B
58%
23%
A
B
25%
58%
b)
S. corallinus
S. vulpinus
S. doliatus
S. puellus
Predicted mean count (± 95% confidence intervals) of occurrences
8
7
6
5
4
3
2
1
0
6.36
4.60
3.13
2.06
1.41
1.68
1.40
0.35
Alternated
(A → B, B → A)
Repeated
(A → A, B → B, AB → A, AB → B,
A → AB, B → AB, AB → AB)

Figure 4.5: Patterns of alternated or repeated foraging bouts in pair members. a) Schematic figure showing the percentage of different pathways pooled for all pairs in all species (n = 59). In cases where only one of the pair members is foraging (A or B), a subsequent foraging bout by the partner (B or A) is most common (58% and 58% of all sequential foraging bouts; solid arrows). In contrast, repeated foraging bouts were significantly less common (23% and 25%, respectively; dashed arrows) and so were changes to foraging bouts performed simultaneously by both individuals (19% and 18%, dashed lines). Foraging bouts performed by both pair members simultaneously were almost always succeeded by foraging bouts performed by a singular fish (50%A and 47%B). b) The occurrence of alternated or repeated foraging bouts by pair members in all four species. Circles represent average values for a 12-minute period, predicted from zero-inflated generalized linear mixed effects models (GLMMs) with lines marking the upper and lower 95% confidence intervals. While the average number of both alternating and repeated foraging bouts varied among species as a function of the overall foraging activity, alternated foraging bouts (i.e. individuals taking turns) were significantly more common than repeated foraging bouts in all species (see text for statistical results). Observed values are provided to indicate model fits. Blue = *S. corallinus* (*n* = 15), magenta = *S. vulpinus* (*n* = 15), green = *S. doliatus* (*n* = 15), gold = *S. puellus* (*n* = 14). *n* = number of independent pairs represented in the plot.

The behaviour of solitary and paired rabbitfish individuals differed in all species (**Figure 4.6**). Compared to solitary rabbitfishes, paired rabbitfishes exhibited significantly longer vigilance bouts except in *S. doliatus*, in which estimates followed the same trend but fell outside the α-level of 0.05 (parameter estimates for solitary individuals compared to paired individuals: *S. corallinus*: $\beta = -0.733$; $z = --4.12$; $P < 0.0001$; *S. doliatus*: $\beta = -0.621$; $z = -1.64$; $P = 0.09$; *S. puellus*: $\beta = -0.934$; $z = -6.37$; $P < 0.0001$; *S. vulpinus*: $\beta = -0.695$; $z = -7.34$; $P < 0.0001$). In all species, paired individuals took significantly more bites per foray (parameter estimates for solitary individuals compared to paired individuals: *S. corallinus*: $\beta = -0.360$; $z = -2.48$; $P = 0.013$; *S. doliatus*: $\beta = -0.792$; $z = -2.29$; $P = 0.022$; *S. puellus*: $\beta = -0.935$; $z = -7.14$; $P < 0.0001$; *S. vulpinus*: $\beta = -0.461$; $z = -1.96$; $P = 0.05$). In *S. corallinus* and *S. doliatus*, paired individuals penetrated deeper into the substratum than solitary individuals and while the same trend was visible in *S. puellus* and *S. vulpinus*, estimates in the latter two species were not statistically significant (parameter estimates for solitary individuals compared to paired individuals: *S. corallinus*: $\beta = -0.578$; $z = -3.99$; $P < 0.0001$; *S. doliatus*: $\beta = -1.665$; $z = -2.58$; $P = 0.0099$; *S. puellus*: $\beta = -0.323$; $z = -1.75$; $P = 0.08$; *S. vulpinus*: $\beta = -0.308$; $z = -1.73$; $P = 0.084$). Overall, differences between solitary and paired individuals were highly consistent among species. All species showed the same trends, varying only slightly in extent. The lack of significance in some variables may have arisen from small sample sizes in solitary individuals, which were both rare and exceptionally easily disturbed.

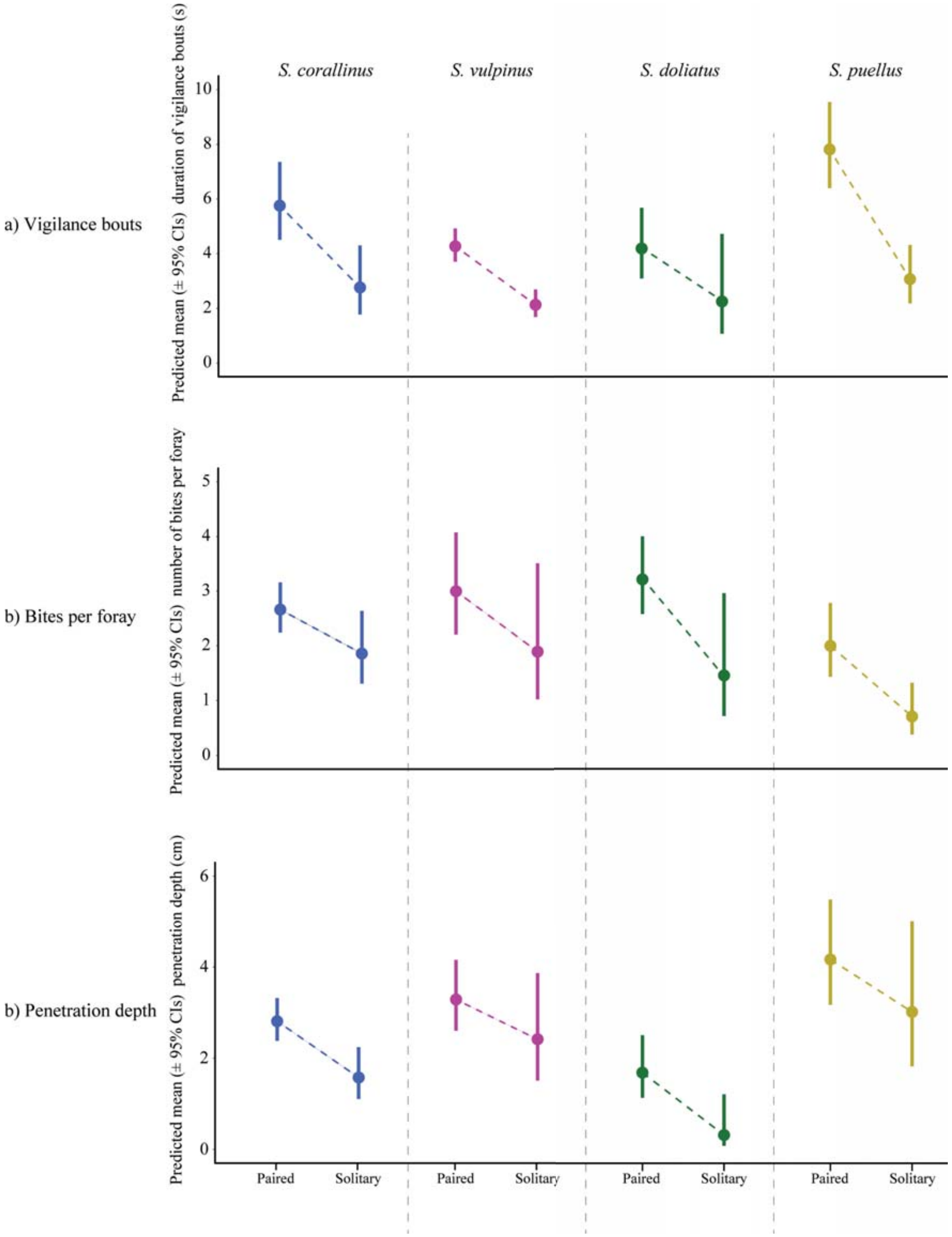

Figure 4.6: Behavioural differences between paired and solitary individuals in all four species. a) Average predicted duration of vigilance bouts (± 95% confidence

intervals) in paired and solitary individuals. b) Average predicted number of bites per foray (± 95% confidence intervals). c) Average predicted maximum penetration into cracks and crevices in the reef substratum during forays (± 95% confidence intervals). All values were obtained from GLMMs performed separately on all four species. Blue = *S. corallinus* (pair *n* = 8; solitary *n* = 8), magenta = *S. vulpinus* (pair *n* = 8; solitary *n* = 6), green = *S. doliatus* (pair *n* = 8; solitary *n* = 3), gold = *S. puellus* (pair *n* = 8; solitary *n* = 7). *n* = number of independent individuals on which observations were performed.

The relative frequency of fin-flicking differed significantly among behaviours (Pearson’s Chi-squared test: $\chi^2 = 231.250$, $df = 3$, $P < 0.001$), occurring significantly more often during foraging activity (i.e. when at least one of the fishes was engaged in foraging) and while displaying to other pairs (aggressive interaction) and hovering, while significantly less fin-flicks were performed during swimming. When one fish was in the vigilance position, while its partner was foraging, almost all observed fin-flicks were produced by the vigilant fish (92.4% of recorded fin-flicks during foraging activity) and subsequent actions (abandonment of current positions, switching positions, chasing) were taken by individuals on average 2.3 ± 0.2 seconds after the fin-flicking, suggesting that feeding individuals may respond to fin-flicks by the vigilant fish. This is further supported by the observation that 61.8% of all observed flight responses were preceded by fin-flicks.

4.4 Discussion

In this study, I provide field-based observational evidence for a coordinated, cooperative vigilance system in four species of pairing rabbitfishes. Specifically, I demonstrate that during foraging, pair members strongly coordinate their positions: while one individual forages with its head down, its partner assumes an elevated, upright position in the water column, allowing for an unobstructed visual field to scan the surrounding environment. Paired fishes alternate frequently between foraging and the vigilance position. Compared to solitary individuals, individuals in pairs exhibit longer vigilance bouts than their solitary counterparts, but appear to benefit from the presence of the partner by exhibiting more consecutive bites per foray and deeper penetration into crevices in the substratum.

The posture assumed by one of the rabbitfishes while its partner is foraging closely matches reports in birds and mammals, where vigilant individuals are commonly identified by raised heads and/or elevated positions (Radford et al. 2009; McGowan & Woolfenden

1989; Favreau et al. 2010; Pays et al. 2009), a behaviour that has only recently been reported for teleost fishes (Fox & Donelson 2014). For rabbitfishes, the upright position is likely to favour vigilance as it potentially enables a greater ability to detect predators (and possibly also competitors) compared to foraging fishes, probably due to a less obstructed visual field (Fernández-Juricic et al. 2004; Arenz & Leger 1997). The assumed angle may allow an unobstructed field of view while remaining close to the reef and the partner. While I am unable to demonstrate that the upright position serves primarily for the detection of predators, my observations and previous evidence suggest that scanning the surroundings for competitors, potential new partners, or food are of limited importance when compared to predator detection. While rabbitfishes do occasionally engage in aggressive behaviour with other pairs, these interactions are infrequent (<1% of the total behaviours observed in this study) and home-ranges of pairs are non-exclusive (Brandl & Bellwood 2013b), suggesting that scanning the surroundings for competitors may only play a minor role. In addition, pair bonds between rabbitfishes are relatively stable (Brandl & Bellwood 2013a,b), questioning the need to continuously look out for a new partner. Finally, the foraging strategy of rabbitfishes along with their dietary preferences for small and cryptic algae, sponges and cyanobacteria (Brandl & Bellwood 2014a; Hoey et al. 2013), which require careful and close examination of concealed micro-habitats, make it unlikely that an elevated position will be beneficial for the detection of food. However, as I am unable to quantify the relative contributions of these various roles, I use the term ‘vigilance’ in its widest sense as being aware of the surrounding environment.

Whenever the pair was observed to rapidly abandon its positions (i.e. engaged in rapid directional swimming behaviour), the vigilant individual had an unobstructed view of the surrounding environment, while the visual field of the forager was often blocked by the reef substratum. Upon the vigilant individual abandoning its position (which was far more frequent than the forager abandoning its position first), the forager consistently trailed the vigilant individual, suggesting that foraging individuals reliably (94.1% of all cases) respond to actions or potential warning cues generated by the vigilant individual. While peripheral vision and social monitoring by the forager may facilitate the reaction to the vigilant partner's behaviour (Fernández-Juricic et al. 2005), the frequent occurrence of fin-flicks prior to abandoning the vigilance position may indicate intentional communication (Hollén et al. 2008; Wickler 1985; Manser 1999). Although the significance of fin-flicks has not yet been investigated in rabbitfishes, fin-flicks are known to generate an acoustic signal in another family of reef fishes in which pairing is prevalent (f. Chaetodontidae; Tricas et al. 2006; Parmentier et al. 2011) and fin-flicks have been described as an important warning signal in other fish species (Brown et al. 1999; Murphy & Pitcher 1987). Thus, although the role of fin-flicking remains to be determined in rabbitfishes, it seems likely that fin-flicks serve as a communication signal and that the forager is able to perceive these signals despite visual restrictions. My findings that the vast majority of fin-flicks in rabbitfishes occurred in situations in which communication is beneficial (i.e. when one fish was foraging while the partner was vigilant or while displaying to other pairs) support a role of fin-flicks in in the maintenance of coordination between the forager and the vigilant fish.

Interestingly, the described scenario, in which foraging severely compromises vigilance while information is readily available from a vigilant conspecific, precisely matches the conditions under which coordinated vigilance should be favoured (Sirot 2012; Fernández-Juricic et al. 2004). This is strongly supported by the angles rabbitfishes assume during foraging episodes where one fish's angle and height above the substratum are the best predictors for complementary behaviour in the partner (**Figure 4.3**). Clearly, pairs of rabbitfishes coordinate their positions during foraging and possibly do so through communication via fin-flicks.

Given this, the question then arises whether the coordinated behaviour in rabbitfish pairs represents a cooperative system based on by-product mutualism/pseudo-reciprocity (Connor 1995, 2010), or if rabbitfishes may satisfy the requirements of direct reciprocity. Several recent papers have emphasized the lack of evidence supporting the fundamental characteristics of direct reciprocity in animals (Clutton-Brock 2009; Connor 2010; Melis & Semmann 2010). These include: i) continuous cooperation between the same individuals, ii) behavioural adaptations to assist the partner, iii) adjustment of assistance provided according to received assistance, iv) cooperation not restricted to kin or potential mates, v) assistance entailing momentary net fitness costs to the assisting individual, and vi) cooperative behaviour being found in wild populations (after Clutton-Brock 2009).

For rabbitfishes, there is evidence supporting all of these requirements. (i) As rabbitfish pairs are stable and remain together for extended periods of time (Woodland 1990; Brandl & Bellwood 2013b), cooperation is likely to occur continuously between the same individuals. (ii) My results show that individuals prolong the length of vigilance bouts in the presence of a partner. This may represent a behavioural adaptation to assist the partner, as paired fishes exhibited an increased number of bites per foray (*S. doliatus*, *S. puellus*, *S. corallinus*) or deeper substratum penetration (*S. corallinus*, *S. doliatus*), therefore increasing the likelihood of a higher overall food intake (as reported for pied babblers *Turdoides bicolor*; Hollén et al. 2008). (iii) Pair members frequently alternate between foraging and vigilance and the ratio between assistance provided and assistance received appears to be well balanced. While feeding was unevenly distributed in a few of the observed pairs, this may be a consequence of the length of observations, and a more balanced distributions may be observed if fish were monitored over an entire day. (iv) The observation that feeding within pairs is not generally skewed toward one individual suggests that cooperation is not solely based on male mate-guarding (as found in sleepy lizards, *Tiliqua rugosa*; Bull &

Pamula 1998), and the common occurrence of same-sex pairs in rabbitfishes (Brandl & Bellwood 2013b) suggests that cooperation is not limited to reproductive pairs (Annett et al. 1999). Due to the reproductive strategies of reef fishes and their pelagic larval stage, cooperation limited to kin is also highly unlikely.

(v) Fitness costs may include predation risk and lost foraging opportunities during vigilance behaviour but such costs are inherently difficult to quantify (Carter 2014; Bednekoff 1997). As in other animals where mutual vigilance has been described as a potential cooperative system (Radford et al. 2009; Hollén et al. 2008; Wright et al. 2001; Ridley et al. 2013), the vigilant individual in rabbitfish pairs is positioned above the underlying substratum with its head elevated, making vigilance beneficial for the overall awareness of the surroundings and therefore potentially self-serving rather than costly (provided predators selectively target foraging individuals). However, given the nutritive constraints of marine herbivory (or spongivory), which necessitate constant and intensive grazing, prolonged vigilance bouts are probably nutritionally costly rather than self-serving (Choat & Clements 1998). This is further supported by the low levels of simultaneous vigilance (both pair members hovering motionless above the substratum, 6.6% of behaviours across all pairs), which would indicate competition for vigilance in a scenario where predators preferentially target foragers (Sirot 2012; Bednekoff 1997; Sirot et al. 2009; Clutton-Brock et al. 1999). Thus, while gaps in foraging activity associated with prolonged vigilance are likely to represent a significant cost, the deeper penetrations into crevices, as well as the higher number of bites per foray appear to be an intuitive reward for the partner. The lack of a clear difference between solitary and paired individuals in *S. puellus* and *S. vulpinus* in terms of penetration depth may point towards differences in the dietary preferences of these two species or their morphological adaptations. While *S. corallinus* and *S. doliatus* feed predominantly on filamentous and corticated red algae, food that is readily used by other herbivorous fish species (Hoey et al. 2013; Choat et al. 2002), only a few reef fishes feed on cyanobacteria, which are the main food source for *S. vulpinus*. Thus, the latter might be more readily available in more accessible microhabitats. In addition, *S. vulpinus* exhibits the morphological characteristics most suited for the exploitation of crevices among the four investigated species, suggesting that even solitary individuals might be able to penetrate into the substratum with no substantial obstructions to the visual field (Brandl & Bellwood 2013a). *S. puellus*, in turn, exhibits the most fusiform morphology among the examined species (Brandl & Bellwood 2013a), suggesting that quick escape from predators might play a bigger role in this species, possibly permitting solitary individuals to penetrate into the substratum despite the lack of a vigilant partner. However, given the relatively small sample size, the lack of significance in these comparisons should be interpreted with caution. These minor differences notwithstanding, there appear to be clear costs (vigilance bouts) and benefits (foraging efficiency) associated with cooperative vigilance in all four rabbitfish species examined. Finally, vi) all observations were conducted on the reef, indicating that the described vigilance system occurs in wild populations. Thus, the coordination of foraging and vigilance in rabbitfish pairs appears to satisfy all the basic requirements for reciprocal cooperation.

While I cannot hope to fully resolve the question of reciprocity with observational evidence alone, my findings are consistent with direct reciprocity. Thus, my study corroborates the tenor of several recent studies, which posit that reciprocity may be a lot more common under natural settings than when forced into the stringent rules of game-theoretical models (Taborsky 2013; Raihani & Bshary 2011; Brosnan et al. 2010; Carter 2014; van Doorn 2014). Indeed, my results help us to understand why we may find reciprocity in animals, which lack the presumed cognitive requirements for reciprocity (Clutton-Brock 2009). First, cooperative interactions among rabbitfishes are restricted to just one partner at a time. This alleviates frequently-cited cognitive issues arising from recognizing a range of individuals and remembering their previous actions in a large group of animals (Milinski et al. 1990; Stevens & Hauser 2004; Milinski & Wedekind 1998) in order to repay for the behaviour of a previous partner, as has been posited for predator inspection and egg-trading in fishes (Clutton-Brock 2009; Connor 1992, 1996). Second, continuous foraging activity, immediate alternation, and the similar and simultaneous needs (food and safety) for both pair members in rabbitfishes prevent long time-lags between rounds in an IPD, as often found in, for instance, primates (Brosnan et al. 2010; De Waal & Brosnan 2006). This again relaxes the need for complex cognitive abilities, such as memory, to underpin reciprocal cooperation (Rutte & Taborsky 2008). Third, rabbitfishes cooperate continuously with the same partner over an extended period of time. There is now considerable evidence that such interdependence between social partners can foster high levels of cooperation in an IPD, as individuals do not systematically surrender to the short-term temptation of cheating on the partner (Roberts 2005; St-Pierre er al. 2009), therefore making tit-for-tat (or, more specifically ‘generous tit-for-tat’) a strategy with high levels of cooperation. Finally, my study provides preliminary evidence for the continuous exchange of social information between partners by means of fin-flicks and suggests that individuals quickly react to the behaviour displayed by the partner, as indicated by high levels of coordination (Sirot 2012). Such elimination of discrete rounds in the IPD and the continuous exchange of information have been proposed as a major factor in favouring cooperation (either by coaction or reciprocity), as it lowers the cost for cooperating individuals (van Doorn et al. 2014). Given the low levels of simultaneous vigilance observed in the present study, reciprocity appears more likely to operate in rabbitfishes than coaction, which would incline individuals to simply copy the partner’s behaviour (van Doorn et al. 2014).

In summary, my study identifies pairing rabbitfishes as an intriguing group of animals in the context of reciprocity, cooperation, and cognition. Although limited to observational data, I provide strong evidence for a clear coordination of foraging and vigilance behaviour in pairs and demonstrate that pair members frequently alternate their foraging. I further show that rabbitfish pairs have the potential to satisfy all the basic requirements of reciprocity and discuss a range of conditions, which may favour reciprocal exchange in animals. My evidence suggests that the complex cognitive and social skills, frequently assumed to be necessary for the evolution of direct reciprocity in animals, may be advantageous but, as in fishes, may not be essential.

Chapter 5: Individual-based analyses reveal limited functional overlap in a coral reef fish community.

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5.1 Introduction

All over the world, ecosystems are changing. Human domination is altering both the biotic diversity and habitat structure of ecosystems, leading to fundamental changes in ecosystem processes (Chapin et al. 1997; Hooper et al. 2005). This can ultimately result in the loss of goods or services provided by an ecosystem (Vitousek et al. 1997). Biodiversity in all its facets (e.g. taxonomic diversity, phylogenetic diversity and functional diversity) is accepted as a key factor for the persistence of ecosystems (Duffy et al. 2003; Hooper et al. 2005; Gamfeldt et al. 2008). Functional diversity, in particular, has been the focus of many recent studies evaluating stability or changes in ecosystem processes (Petchey & Gaston 2006; Mouillot et al. 2012). In this context, the functional role of a species is frequently treated as an equivalent to its ecological niche (Halpern & Floeter 2008; Mouillot et al. 2011).

The ecological niche of a species is commonly described as the volume occupied in a multidimensional hyperspace, symbolizing the ecosystem (Hutchinson 1957; Whittaker et al. 1973; Devictor et al. 2010). If this volume is based on a species’ impact on the ecosystem, the niche is usually described as a species’ *functional niche* (Hutchinson 1957; Rosenfeld 2002). Beyond this, the classification of a species’ niche can be extended to its fundamental or realized niche. The *fundamental niche* refers to the potential volume along all axes that a species could theoretically occupy, if species-specific, intrinsic characteristics, such as morphological or physiological attributes, were the only determinants. In contrast, the *realized niche* is the volume a species actually occupies when constrained by biotic and abiotic factors (Hutchinson 1957; Whittaker et al. 1973; Devictor et al. 2010). Most studies that seek to evaluate species' ecosystem roles use a functional-diversity framework with multiple phenotypic traits from which a classification of the respective species niches are derived (Petchey & Gaston 2006; Villéger et al. 2008; Villéger et al. 2011), thus measuring species' fundamental niches (Hutchinson 1957; McGill et al. 2006; Wright et al. 2006). Realized niches, however, can only be assessed using data on the species *in situ*, where restricting abiotic or biotic agents are operating. Unfortunately, there is a notable lack of empirical studies that incorporate field observations to determine the realized functional niche of species across communities, particularly in high diversity marine ecosystems (Hooper et al. 2005).

Among marine systems, coral reefs harbour exceptional diversity but are also subject to intense human pressure (Vitousek et al. 1997; Hooper et al. 2005). Despite providing vital goods and services to millions of people, human impacts are progressively altering the biodiversity, structure and processes on coral reefs (Hughes et al. 2003). One critical functional process on coral reefs that is under threat is the removal of algae by herbivorous fishes (Bellwood et al. 2004; Nyström 2006). Herbivorous species are traditionally classified into distinct functional groups according to their taxonomic affiliation (e.g. families Acanthuridae, Labridae, Siganidae), dietary preferences (e.g. macroalgae, turf algae, detritus) or their way of acquiring food (e.g. scraper, excavator, grazer) (Nyström 2006; Green & Bellwood 2009; Cheal et al. 2012). Using these classifications, many studies have investigated links between herbivorous species assemblages and the health or resilience of coral reefs (Burkepile & Hay 2008; Green & Bellwood 2009; Cheal et al. 2010). However, these classification schemes are inherently problematic.

While facilitating a broad overview of the functional composition of a community, functional-group approaches have several shortcomings leading to a significant loss of information. Many studies measure only the fundamental niche and, to date, most studies only consider *which species* feeds on *what* and *how* they do it (Nyström 2006; Johansson et al. 2013), while other components such as *where* species feed are rarely accounted for (but see Fox & Bellwood 2013). Furthermore, existing classification schemes are often equivocal and consensus about functional group membership has yet to be achieved (Green & Bellwood 2009; Cheal et al. 2012). Most importantly, arranging species in a broad classification scheme discounts variability among individuals, a widely neglected but potentially important component of biodiversity that can contain valuable information on species' functional niches (Messier et al. 2010; Violle et al. 2012).

To address some of these issues, I compare the realized functional niches of herbivorous coral reef fishes, with regards to fine-scale spatial characteristics of their functional impact (i.e. *where* the fish feed). I present a novel way of assessing the realized functional niche of species that uses behavioural data, and takes individual variation into consideration, to examine patterns of redundancy and complementarity in functionally important species. Based on field data on the feeding behaviour of 21 herbivorous coral reef fish species, I use a recently developed multidimensional framework (Villéger et al.; Villéger et al. 2011; Mouillot et al. 2012) to provide estimates of the functional impact of each species (the volume occupied in functional niche hyperspace) and the functional overlap between species (the volume shared between species in this hyperspace). I offer this method as an alternative way of assessing the functional niche of species that allows for a more nuanced assessment of the functional role of species beyond traditional functional-group frameworks. Specifically, the objectives of my study were to: 1) develop a multidimensional framework to examine functional niche overlap between species using a high-diversity herbivorous reef fish community as a model, 2) compare the results of my analyses to traditional classification schemes to assess the sensitivity and applicability of the analyses, 3) provide a novel, continuous rather than categorical representation of the functional niches of herbivorous reef fishes based on their microhabitat utilization patterns and 4) evaluate the ecological implications of these findings.

5.2 Materials and methods

5.2.1 Data collection

The study was conducted during April and May 2012 on Lizard Island (14°40′08″S 145°27′34″E), a granitic mid-shelf island in the northern Great Barrier Reef (GBR). Lizard Island has a rich herbivorous fish fauna, encompassing the vast majority of herbivorous fishes found on the GBR (Cheal et al. 2012). Behavioural observations were made on the crest and upper slope (1-8 m) of two fringing reefs on the sheltered side of the island, in Mermaid Cove and off Turtle Beach (**Figure 5.1**).

Figure 5.1: Lizard Island and the two sample sites, Mermaid Cove and Turtle Beach. Sites are located on the sheltered side of the island.

Observations were carried out on adult individuals of 21 species from three families (Acanthuridae, Labridae, Siganidae). The 21 species represent the majority of roving herbivores present on these reefs. No other roving herbivorous species were sufficiently abundant on the sampled reefs to be included in the analyses. A haphazardly selected individual was followed until it took a bite from the reef. I then recorded the surface type (open horizontal [A], open vertical [B], underside [C], concealed vertical [D] or concealed horizontal [E]) and the substratum type (branching coral, encrusting coral, massive coral, dead coral skeleton, macro-algae, coral rubble, soft coral, sand, sponge, turf covered reef matrix or other substratum types such as giant clams). Surfaces were considered A or B if they were exposed, planar microhabitats, C was on the underside of overhanging surfaces, while surfaces D and E were recorded if herbivores fed in concavities that required the penetration into holes between 1 and 30 cm across in the substratum. These latter microhabitats ranged from small holes, crevices or fissures in the reef matrix to the microhabitat between the branches of branching, corymbose corals. A further criterion for surfaces D and E was that the concavity depth had to equal or exceed its smallest width. I also recorded the extent of penetration into the substratum exhibited by individuals, distinguishing between feeding in concavities with its snout (from the premaxilla tip to the anterior rim of orbit) or with its body (from anterior rim of orbit to the caudal fin margin) (Fox & Bellwood 2013). Vernier callipers were used to measure the penetration depth. To minimize the likelihood of recording the same individual within a 24 h period, reefs were sampled on alternating days and different sampling areas of the reef were used throughout the day. Observations were discarded if fish exhibited a detectable response to the observer. To ensure consistent recordings, all data were collected by two observers throughout the study. Overall, a total of 1,734 observations were recorded (with a mean of 82.5 observations per species) (**Table 5.1**).

Table 5.1: Microhabitat utilization patterns of herbivorous reef fishes. FG = Traditional functional group affiliation; GD = grazer/detritivore; AB = algal browser.

Family	Species	FG	Surface					Substrate						Penetration			
			A	B	C	D	E	DC	MA	SD	RB	TR	$\Sigma_{(Others)}$	P_{B} %	$P_{B x}$ (mm)	P_{S} %	$P_{S x}$ (mm)
Acanthuridae	***A. nigricauda***	GD	89	6.5	0	3.8	0.8	1.2	0	47.3	12	38.5	1	0	0	0	0
	A. nigrofuscus	AB	69.6	18.3	0	4	8.1	19.5	2.5	0	17.3	59	1.7	0	0	17.5	18.6
	A. olivaceous	GD	85.1	14	0	0	0.9	0	0	21.1	10.7	68.2	0	0	0	0	0
	***C. striatus***	GD	66.3	32.3	0	1.3	0	12.6	3.4	4.8	5.5	73.6	0	0	0	0	0
	N. unicornis	AB	45	41.7	0	1.7	11.7	11.7	0	0	17.2	71.1	0	0	0	7.5	23.3
	Z. scopas	AB	26.1	23.5	0.6	24.4	25.4	21.5	0	0	0.4	77	1.1	1	40	37.1	17.8
	Z. veliferum	AB	34.9	30.6	2.3	20	12.2	14.7	0	0	8.4	75.5	1.4	0	0	29.2	14.4
Labridae	***C. microrhinos***	EX	64	36	0	0	0	14	0	0	3.7	82.4	0	0	0	0	0
	C. sordidus	EX	72.6	18.7	2.3	5.6	0.8	34.1	0	0	11.2	52.2	2.5	1.2	300	2.4	25
	S. dimidiatus	SC	74.9	20.7	0	0	4.4	19.6	0	0	9.9	70.5	0	1.8	100	1.8	30
	S. frenatus	SC	59.3	37	0	1.6	2	17.5	0	0	6.9	75.6	0	0	0	3.1	20
	***S. niger***	SC	52.4	32.9	5.7	6	3.1	25.1	0	0	6	65	4	2.4	85	3.7	16.7
	S. oviceps	SC	65.3	32.7	0	0	2	29.3	0	0	2	65.3	3.4	0	0	1.5	30
	S. rivulatus	SC	69.2	25.4	0	3.5	2	7.5	0.8	2.1	5.4	84.2	0	0	0	2.6	35
	S. schlegeli	SC	67.7	25.1	0.9	3.7	2.5	3.8	1.1	15.8	10.4	68.5	0.5	1.7	60	3.4	25
Siganidae	***S. argenteus***	AB	63.6	22	0	3	11.4	7.5	20.8	1.2	21.4	49.1	0	0	0	15.5	16.7
	S. corallinus	AB	7.9	8.7	2.2	30.7	50.5	46.6	1.5	0	22.2	28	1.8	11.3	106.4	70.7	24.9
	S. doliatus	AB	25.2	16.2	1.3	29.2	28.1	31.1	4.2	1.1	14	48.9	0.7	8.3	160.7	45.3	20.5
	***S. puellus***	AB	24.5	22.8	5	31	16.6	14.6	8.5	4.4	11.5	52.4	8.5	23.5	130.4	29.6	23.4
	S. punctatus	AB	27.9	20.8	1.5	25.3	24.5	33.5	7.1	0.9	11.7	43.1	3.7	9.2	70	33.7	19.4
	S. vulpinus	AB	13.2	6	2	21.2	57.6	67.4	0	0	13.2	15.4	3.9	5.3	87.1	74	31.1

5.2.2 Individual-based analyses of species' realized functional niches

To assess the realized functional niche of species, a multidimensional functional niche space can be created using the behavioural observations made on individuals. In this study, I used the number of bites taken by an individual during a feeding foray, the surface position, substratum type and the extent of body- or snout-penetration. As behavioural observations often include data of different types (such as categorical and numeric data), I used Gower's metric (Gower 1966) to calculate a distance matrix that serves as the basis for an ordination. Based on a Gower's distance matrix, a principal co-ordinate analysis (PCoA) can be performed using appropriate corrections for negative eigenvalues (Legendre & Legendre 1998). PCoA is a useful way of representing patterns from pairwise distance measures and is designed to function with multiple distance metrics. The values yielded by the PCoA serve as synthetic trait values (i.e. new trait values based on the relative importance of behavioural traits in the initial dataset). These new synthetic trait values are then used to establish the distribution of individuals in multidimensional space (Laliberté & Legendre 2010), thus creating a synthetic functional niche hyperspace (i.e. a multidimensional space that encompasses all possible trait combinations), from which individual coordinates can be extracted.

Based on these individual coordinates, a species' functional niche volume can be calculated that encompasses all individuals of a species within a given ecosystem (Cornwell et al. 2006; Villéger et al. 2011). The niche volume (a convex hull volume) is delimited by the individuals with the most extreme positions in multidimensional space (called vertices). In practice, this means that species with large niche volumes have vertices that are widely dispersed in multidimensional space, suggesting that individuals in this species exhibit a high degree of variation in their realized functional niche. In contrast, the niche volume is small when individuals of the species deliver only a restricted range of functions. In my study, this would equate to the use of a limited range of microhabitats.

The overlap among species' functional niche volumes can also be calculated. To describe distances between species in assemblages, the term "functional dissimilarity" has been proposed (Villéger et al. 2011). For coral reef fishes, recent studies stress the concept of complementary functions for herbivorous fishes (Burkepile & Hay 2008, 2011; Rasher et al. 2013). I therefore use the term functional complementarity as a measure of the overlap between species' volumes in functional niche space. Functional complementarity is the inverse of functional redundancy (species with high overlap have high redundancy but low complementarity and *vice versa*) and can be expressed as the percentage of overlap between the niche volumes of two species. This is calculated as the ratio between the volume of the overlap (intersection) and the overall volume of the respective niches. Thus, if individuals in two species implement the same functions, the volume shared by those two species would be expected to be large (> 50% overlap). This can be considered functional redundancy. In contrast, little or no overlap between species provides a measure of complementarity (< 50% overlap).

In addition, the effect of niche volume on the overlap of species should be considered. Specifically, a small niche volume can only have limited overlap with another volume. Thus, it is desirable to know whether little overlap between two species is the result of two large volumes overlapping only marginally (species A and B) or a consequence of a small volume (species C) being entirely or partially nested within a larger volume (species D). In both cases, the volume of overlap is small, yet the ecological consequences are fundamentally different. In the first case, individuals of the two species perform highly dissimilar functions and only few individuals are located in the same area of multidimensional space. In contrast, in the second case, most individuals of species C are located within the volume occupied by species D but perform only a small fraction of the functions executed by individuals of species D, which, in turn, performs all functions administered by species C. This distinction has originally been proposed for decomposing β-diversity, where the respective contributions of either scenario have been termed “turnover” (the scenario of species A and B) and the “nestedness” (C and D) components (Baselga 2010, 2012; Villéger et al. 2013). Using the distribution of individuals in functional niche space and the resulting niche volumes, the contribution of the turnover and nestedness components to the functional niche overlap between species can be calculated (Villéger et al. 2013).

5.2.3 Realized functional niches and complementarity in herbivorous coral reef fishes

Using Gower’s distance metric and a PCoA, I calculated the realized functional niche volumes of 21 herbivorous reef fish species based on their microhabitat utilization patterns during foraging. To account for different sample sizes, subsamples of 30 individuals were used to calculate functional impacts using 999 randomized permutations within each species. The niche volume of each species was then standardized against the total volume of niche space occupied by all species. While this provides insights into the functional impact of a species, it is also desirable to know whether or not the volume of a species is significantly lower than expected based on the total niche space volume. To test this, I used randomized permutation testing (Manly 1997), running 999 randomized iterations where 30 individuals were chosen from the whole community regardless their taxonomic identity (to represent hypothetical species). The volumes occupied by individuals of the focal species were then compared to the distribution of the hypothetical species volumes, to determine if the volumes of observed species differ significantly from hypothetical species (based on a random draw from individual values across the entire community).

I also calculated the overlap between species' niche volumes. As the overlap is highly dependent on the extent of niche volumes, values were standardized against the total volume occupied by the two species (Villéger et al. 2011). These values were then compared to values yielded by 999 randomized iterations to evaluate if the calculated overlap differs significantly from a null expected value based on random volumes in total niche space. To construct a null-model, two sets of 30 individuals (hypothetical species), drawn randomly from the total pool, were used to create an overlap between two niche volumes (i.e. overlap between two hypothetical species, again standardized against the total volume of the two hypothetical species volumes). To avoid bias toward increased overlap between the two hypothetical species, the permutations were coded to automatically exclude individuals that have been assigned to one of the two hypothetical species.

Using pairwise overlaps of the 21 focal species, a non-metric multidimensional scaling (nMDS) analysis and Ward's hierarchical clustering analysis were performed to visualize the obtained pairwise distance matrix. Finally, I calculated the contribution of the turnover and nestedness component to the overlap between species following the equations given by Baselga (2012) and Villéger et al. (2013) to account for the different sizes of niche volumes among species.

All analyses were carried out on four dimensions of the functional niche hyperspace as a result of a trade-off between computation time and the percentage of variation within the original dataset expressed on these four dimensions (69.8% explained by four dimensions). Statistical computations were performed using the packages *ape*, *cluster*, *geometry*, *rcdd* and *vegan* as well as the functions *CHVintersect* and *betapart* (Villéger et al. 2011, 2013; Baselga 2012) in the software R (R Development Core Team 2012), using the HPC unit at James Cook University, Townsville, Australia.

5.3 Results

5.3.1 Realized functional niche volumes

The functional niche volumes of the 21 species varied markedly. Volumes varied from just 0.8% of the total niche space in the excavating parrotfish *Chlorurus microrhinos* to 58.8% in the rabbitfish *Siganus punctatus* (**Figure 5.2**). The functional volume of *Chlorurus microrhinos* was thus only 1.4% of the volume occupied by *Siganus punctatus*. Aside from *S. punctatus*, nine other species had niche volumes that were not found to be significantly different from expected volumes (i.e. compared to hypothetical species based on a random draw; randomized permutation testing: $P > 0.05$). These species included all rabbitfishes (*Siganus*) and surgeonfishes in the genera *Zebrasoma* and *Naso,* as well as *Acanthurus nigrofuscus*. The functional niche volumes of all other species were significantly lower than expected under the null model. This was highly significant ($P < 0.001$) in the grazing, detritivorous surgeonfishes in the genus *Acanthurus* and in *Ctenochaetus striatus*, as well as the parrotfishes *Chlorurus microrhinos* and *Scarus oviceps*. Moderate significance levels ($P = 0.01 – 0.001$) were found for all scraping parrotfishes (*Scarus*, **Figure 5.2**).

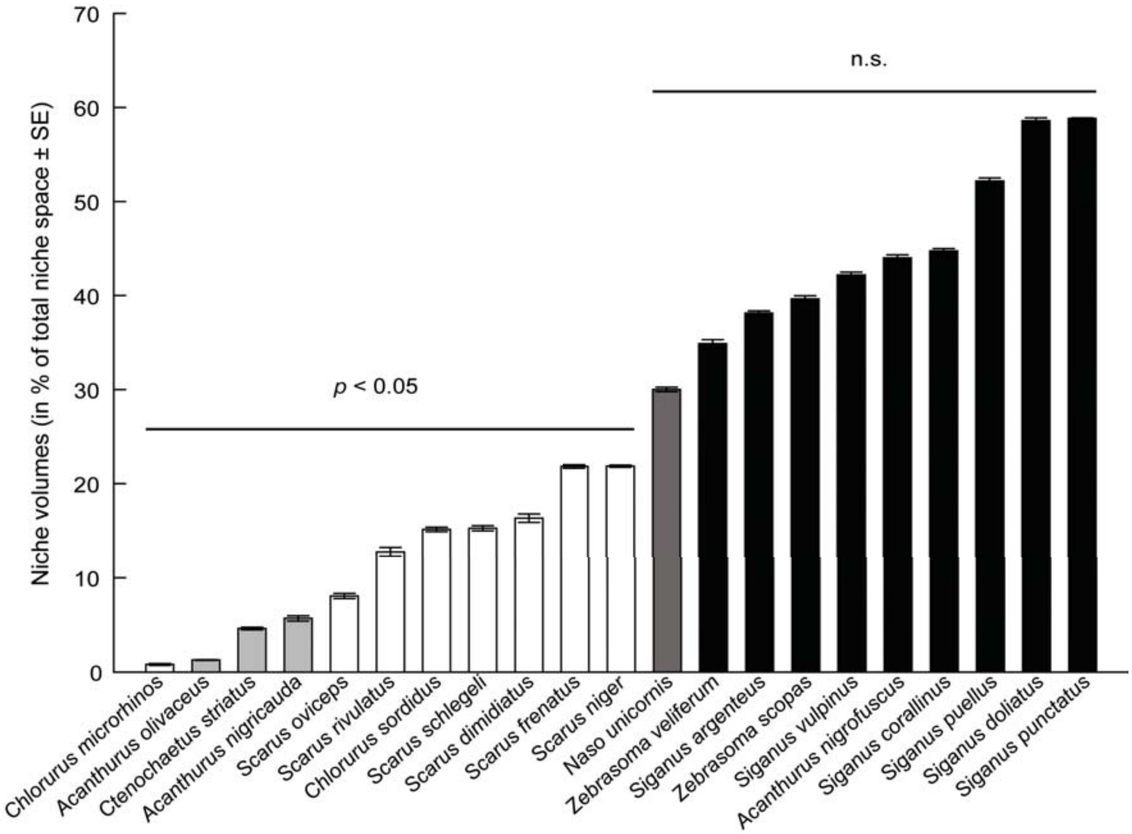

Figure 5.2: The relative volumes of herbivorous fishes in functional niche space based on feeding microhabitat preferences. Bars mark the percentage of niche space occupied relative to the total niche space available. Niche volumes with $p < 0.05$ are significantly lower than expected, based on hypothetical volumes (drawn randomly from the total niche space; n = 999). Black bars = croppers; dark grey = browsers; light grey = detritus feeders; white = scrapers/excavators.

5.3.2 Functional redundancy vs. complementarity

Based on the occupied niche volumes of species, the overlap between all species pairs was calculated, supplying a measure of pairwise, functional complementarity (i.e. a pairwise, functional dissimilarity matrix; Table **5.2, 5.3**). There was extensive complementarity among herbivorous fish species. The mean overlap of functional niche volumes among species was just 15.2% ± 0.1 SE, and the highest overlap between two species amounted to only 42.6% between the rabbitfishes *Siganus doliatus* and *Siganus punctatus*. Based on my 50% cut-off, no species pair displayed redundancy in microhabitat utilization.

Table 5.2: Percentages of non-overlapping volumes between species of herbivorous species resulting in a pairwise dissimilarity matrix. Note that values indicating zero would have to be interpreted with caution as zero overlap on a single dimension may mask existing ecologically important overlap on other dimensions.

	Agri	*Agro*	*Aoli*	*Cstr*	*Scor*	*Sdol*	*Stus*	*Sdim*	*Sriv*	*Ssch*	*Snig*	*Sovi*	*Sfre*	*Zsco*	*Zvel*	*Svul*	*Spue*	*Sarg*	*Nuni*	*Cmic*	*Csor*
Agri																					
Agro	0.917																				
Aoli	0.825	0.977																			
Cstr	0.897	0.908	0.941																		
Scor	0.995	0.677	1.000	0.970																	
Sdol	0.932	0.677	0.995	0.978	0.622																
Stus	0.981	0.625	0.996	0.945	0.682	0.574															
Sdim	0.884	0.874	0.988	0.731	0.964	0.931	0.861														
Sriv	0.866	0.841	0.985	0.872	0.953	0.902	0.848	0.766													
Ssch	0.845	0.811	0.966	0.867	0.911	0.833	0.913	0.826	0.861												
Snig	0.947	0.815	0.992	0.856	0.859	0.836	0.741	0.833	0.877	0.805											
Sovi	0.968	0.888	0.974	0.839	0.941	0.918	0.950	0.905	0.921	0.854	0.925										
Sfre	0.850	0.740	0.996	0.909	0.896	0.756	0.733	0.816	0.751	0.699	0.754	0.884									
Zsco	0.970	0.698	0.995	0.945	0.741	0.701	0.676	0.897	0.916	0.880	0.833	0.955	0.746								
Zvel	0.958	0.672	0.989	0.981	0.810	0.706	0.614	0.815	0.890	0.755	0.744	0.893	0.707	0.639							
Svul	0.957	0.804	0.999	0.987	0.671	0.635	0.678	0.891	0.903	0.846	0.935	0.980	0.834	0.780	0.751						
Spue	0.978	0.653	0.996	0.967	0.633	0.642	0.580	0.831	0.859	0.852	0.798	0.864	0.753	0.667	0.638	0.691					
Sarg	0.957	0.657	0.985	0.953	0.747	0.740	0.617	0.748	0.868	0.841	0.789	0.905	0.737	0.751	0.710	0.655	0.664				
Nuni	0.943	0.686	0.991	0.981	0.706	0.700	0.683	0.846	0.919	0.842	0.842	0.847	0.735	0.719	0.710	0.699	0.776	0.672			
Cmic	0.965	0.987	0.998	0.933	0.998	0.988	0.991	0.937	0.962	0.962	0.970	0.932	0.964	0.995	0.985	0.995	0.992	0.984	0.981		
Csor	0.948	0.827	0.996	0.867	0.930	0.849	0.901	0.787	0.793	0.793	0.744	0.904	0.783	0.802	0.843	0.780	0.927	0.858	0.853	0.946	

Table 5.3: Associated *P*-values obtained under the null model (n = 999). *P*-values > 0.95 indicate significantly less overlap than expected given the sample size and the total niche volume.

	Agri	*Agro*	*Aoli*	*Cstr*	*Scor*	*Sdol*	*Stus*	*Sdim*	*Sriv*	*Ssch*	*Snig*	*Sovi*	*Sfre*	*Zsco*	*Zvel*	*Svul*	*Spue*	*Sarg*	*Nuni*	*Cmic*	*Csor*
Agri																					
Agro	0.997																				
Aoli	0.989	0.999																			
Cstr	0.997	0.999	0.999																		
Scor	0.999	0.689	0.999	0.999																	
Sdol	0.999	0.781	0.999	0.999	0.359																
Stus	0.999	0.415	0.999	0.999	0.766	0.128															
Sdim	0.997	0.989	0.999	0.822	0.999	0.999	0.995														
Sriv	0.975	0.993	0.999	0.985	0.999	0.998	0.998	0.946													
Ssch	0.990	0.953	0.999	0.980	0.997	0.985	0.995	0.989	0.983												
Snig	0.999	0.979	0.999	0.982	0.995	0.975	0.935	0.965	0.970	0.979											
Sovi	0.999	0.996	0.999	0.989	0.999	0.999	0.997	0.973	0.997	0.995	0.996										
Sfre	0.989	0.924	0.999	0.997	0.996	0.970	0.925	0.992	0.926	0.736	0.971	0.996									
Zsco	0.999	0.822	0.999	0.998	0.864	0.778	0.724	0.993	0.994	0.991	0.982	0.998	0.915								
Zvel	0.999	0.731	0.999	0.999	0.944	0.829	0.356	0.987	0.995	0.881	0.953	0.995	0.898	0.514							
Svul	0.999	0.927	0.999	0.999	0.740	0.471	0.671	0.998	0.997	0.995	0.995	0.999	0.996	0.944	0.936						
Spue	0.999	0.636	0.999	0.999	0.495	0.566	0.170	0.997	0.996	0.994	0.983	0.994	0.935	0.710	0.515	0.823					
Sarg	0.999	0.644	0.999	0.999	0.925	0.917	0.351	0.839	0.994	0.990	0.978	0.991	0.962	0.889	0.870	0.612	0.648				
Nuni	0.999	0.812	0.999	0.999	0.818	0.736	0.756	0.988	0.991	0.991	0.987	0.984	0.898	0.887	0.911	0.786	0.818	0.604			
Cmic	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.998	0.999	0.999	0.999	0.999	0.999	0.999	0.999		
Csor	0.999	0.978	0.999	0.989	0.999	0.951	0.987	0.982	0.968	0.984	0.933	0.998	0.974	0.976	0.984	0.937	0.990	0.991	0.993	0.998	

An ordination based on non-metric multidimensional scaling of the dissimilarity matrix revealed two distinct groups (**Figure 5.3**), characterized by differences in the extent of their functional niche volumes and functional complementarity. The groupings were consistent with the hierarchical clustering analysis (**Figure 5.4**) and reflect the differences in the functional impact among species with a major division between species with limited overlap (mean overlap: 11.5% ± 1.1 SE) and small volumes (detritus feeders, scrapers and excavators) and species with higher overlap (31.5% ± 0.8 SE) and large volumes (croppers and browsers).

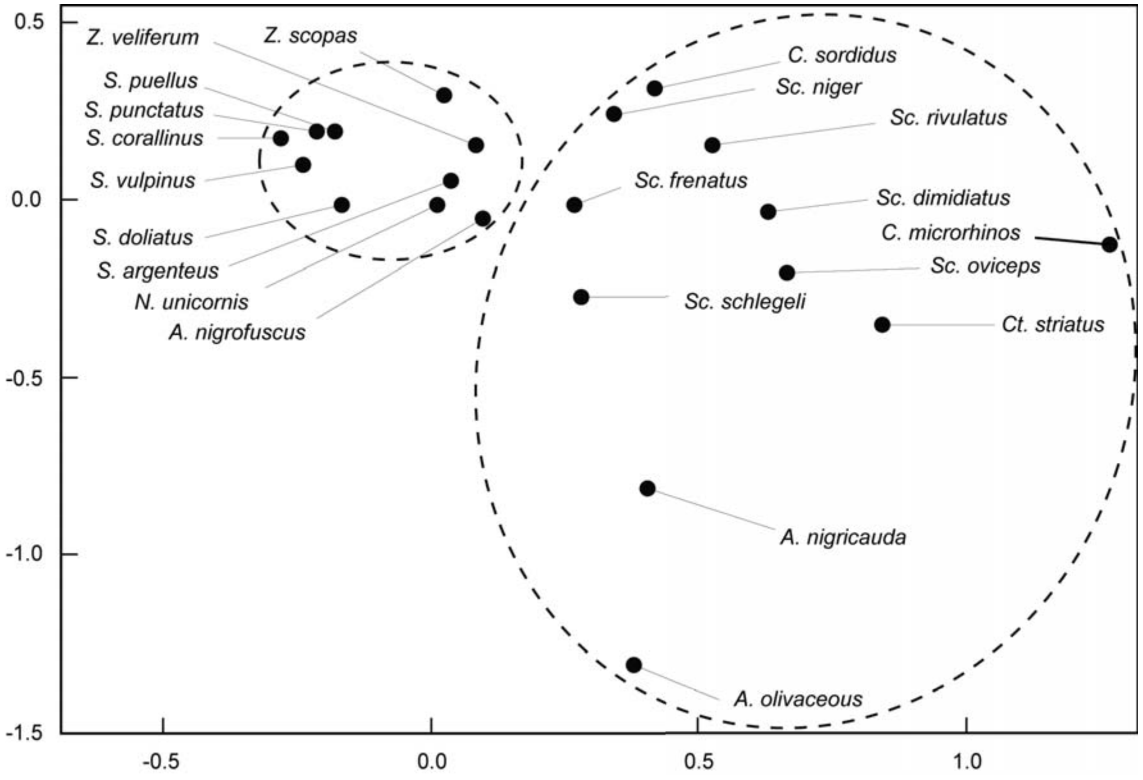

Figure 5.3: Functional distances between herbivorous reef fish species. The ordination plot represents the results from a non-metric multidimensional scaling analyses, performed on the pairwise dissimilarity matrix yielded by the analysis of overlap between niche volumes. Groupings are based on Ward's hierarchical clustering and indicate the functional overlap/distance between herbivore species, showing two distinct groups that differ markedly in their functional impact. The larger group on the right includes species with small niche volumes with minimal overlap, the smaller group on the left is characterized by species with large niche volumes and more overlap.

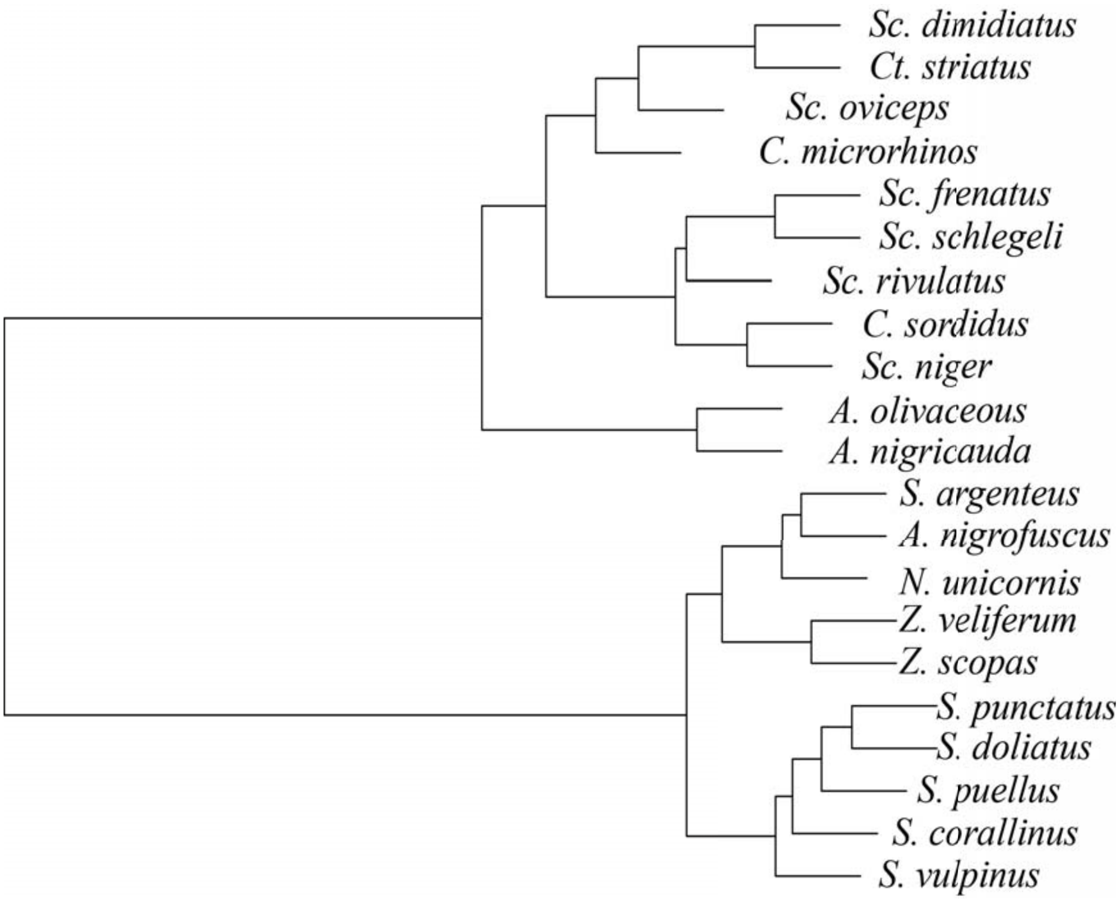

Figure 5.4: Ward's hierarchical clustering analysis, revealing a split into two distinct groups of herbivorous reef fishes based on their preferred feeding microhabitats.

These patterns are best exemplified by focusing on three species: the surgeonfish *Acanthurus nigricauda*, the parrotfish *Scarus schlegeli* and the rabbitfish *Siganus doliatus* and their utilization of different surface types (A, B, C, D and/or E) during foraging. These species show marked differences in their functional niche volumes (*Acanthurus nigricauda*, 4.6% ± 0.1 SE; *Scarus schlegeli*, 15.1% ± 0.2 SE; *Siganus doliatus*, 58.6% ± 0.3 SE; values as percentages of the total niche space occupied). The volume occupied by *Acanthurus nigricauda* amounts to only 7.9% of the space occupied by *Siganus doliatus.* As one would expect, these species also show varying degrees of functional complementarity (**Figure 5.5**). *Acanthurus nigricauda* and *Scarus schlegeli*, both characterized by small niche volumes and united in the same group, overlap by 15.5% of their (combined) functional volumes. In contrast, *Acanthurus nigricauda* and *Siganus doliatus* only show an overlap of 6.8%. These differences strongly reflect the foraging patterns of the respective species (**Figure 5.6**). When considering targeted reef surfaces, for example, individuals of *Acanthurus nigricauda* almost exclusively target horizontal, open surfaces [A] (88.9% ± 0.8 SE of all bites) and do not feed on any other surfaces to a significant extent. Individuals of *Scarus schlegeli* show slightly more variation by also feeding on vertical, open surfaces [B] (25.1% ± 1.3 SE) while still targeting predominantly horizontal, open surfaces (67.7% ± 1.4 SE). In contrast, individuals of *Siganus doliatus* exhibit the broadest niche on this axis by feeding on almost all available surfaces on the reef (except undersides [C]) (**Table 5.1**). This segregation is reinforced by differences in the targeted substratum types and the extent of substratum penetration. Both *A. nigricauda* and *S. schlegeli* forage predominantly on the reef matrix or sandy substrata while *S. doliatus* utilizes a wide range of substrata and frequently penetrates the substratum when feeding.

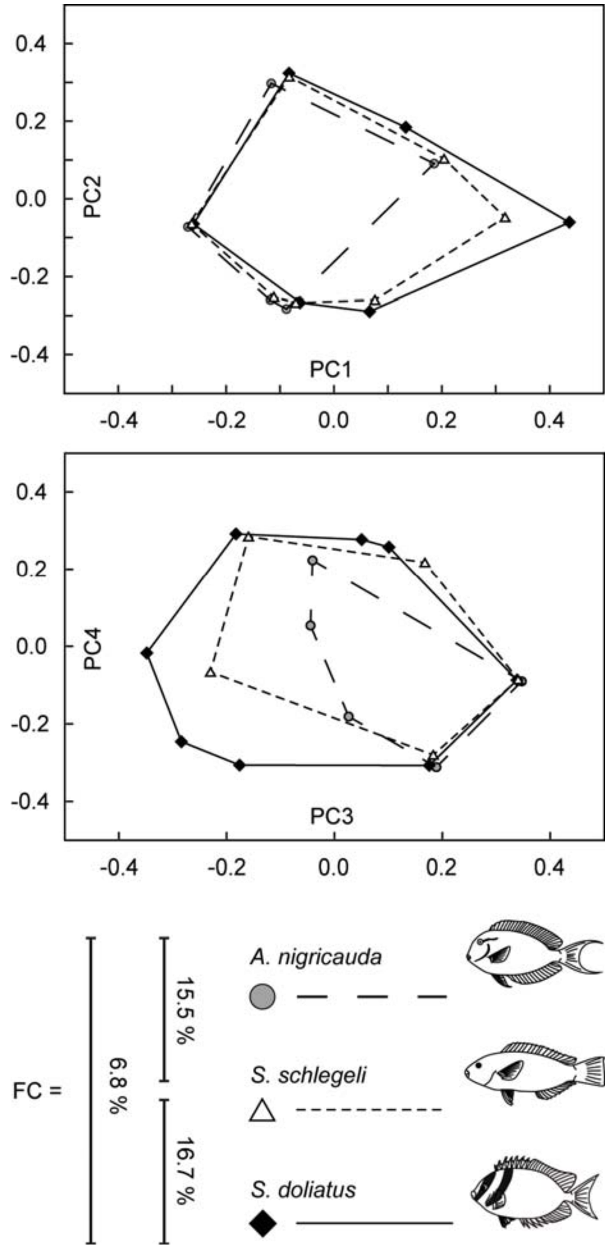

Figure 5.5: Multidimensional niche volumes of *Acanthurus nigricauda*, *Scarus schlegeli*, and *Siganus doliatus* calculated over four axes. Symbols mark the most extreme individuals (vertices) from which niche volumes (convex hull volumes) are calculated. Note the changes in niche volumes when considering more than two axes. Functional complementarity (FC) between species is expressed in % overlap between niche volumes of the respective species.

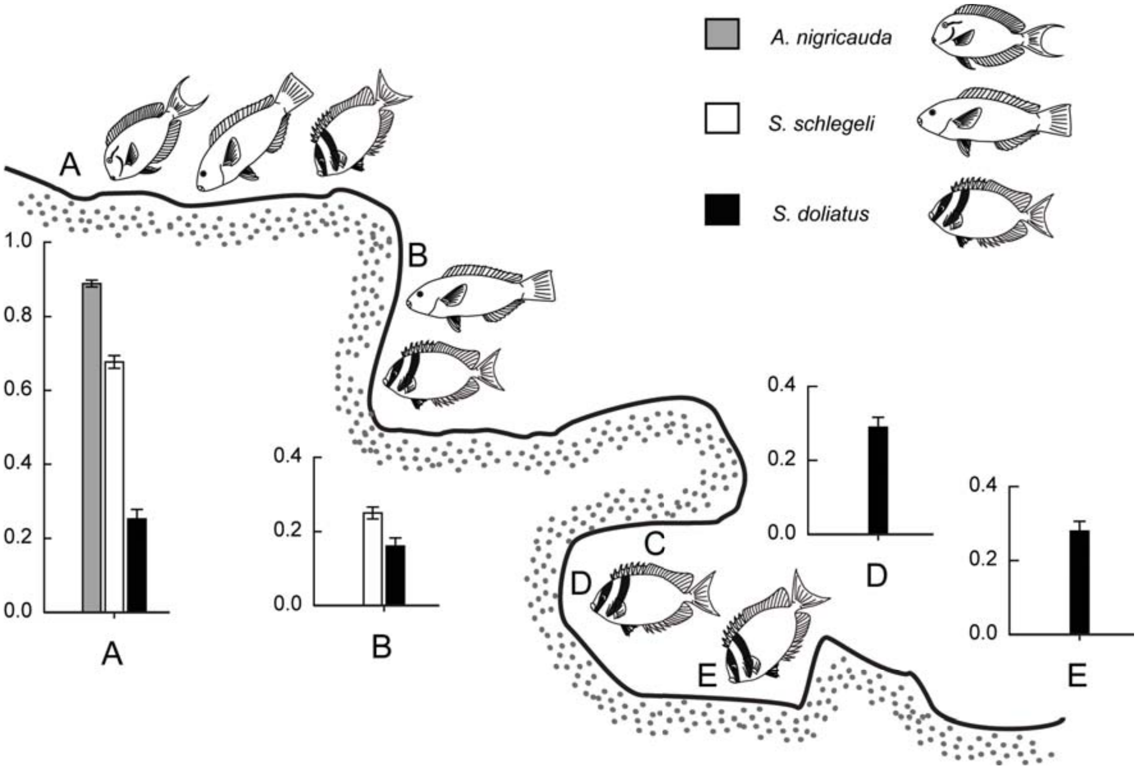

Figure 5.6: Microhabitat utilization patterns in three species exemplified by surface type use of *A. nigricauda, S. schlegeli* and *S. doliatus*. Barplots indicate proportions of bites taken from different surfaces (only surfaces with > 0.15 of the total bites illustrated). Observed patterns show low variation in the choice of feeding microhabitats in *A. nigricauda* and slightly more variation in *S. schlegeli*, while *S. doliatus* targets almost all surfaces to a roughly equal extent. Surfaces are coded according to the main text (A = open, horizontal; B = open, vertical; C = underside; D = concealed, vertical; E = concealed, horizontal).

Decomposing the dissimilarity into its turnover and nestedness components further reveals the nature of the niche partitioning among the three species. The overlap between *A. nigricauda* and *S. schlegeli* is predominantly due to the nestedness of the small niche volume of *A. nigricauda* within the volume of *S. schlegeli* (72.3% overlap due to nestedness; **Figure 5.7**) and both species' niches are nested within the large volume of *S. doliatus* (52.5% and 73.7% nestedness, respectively).

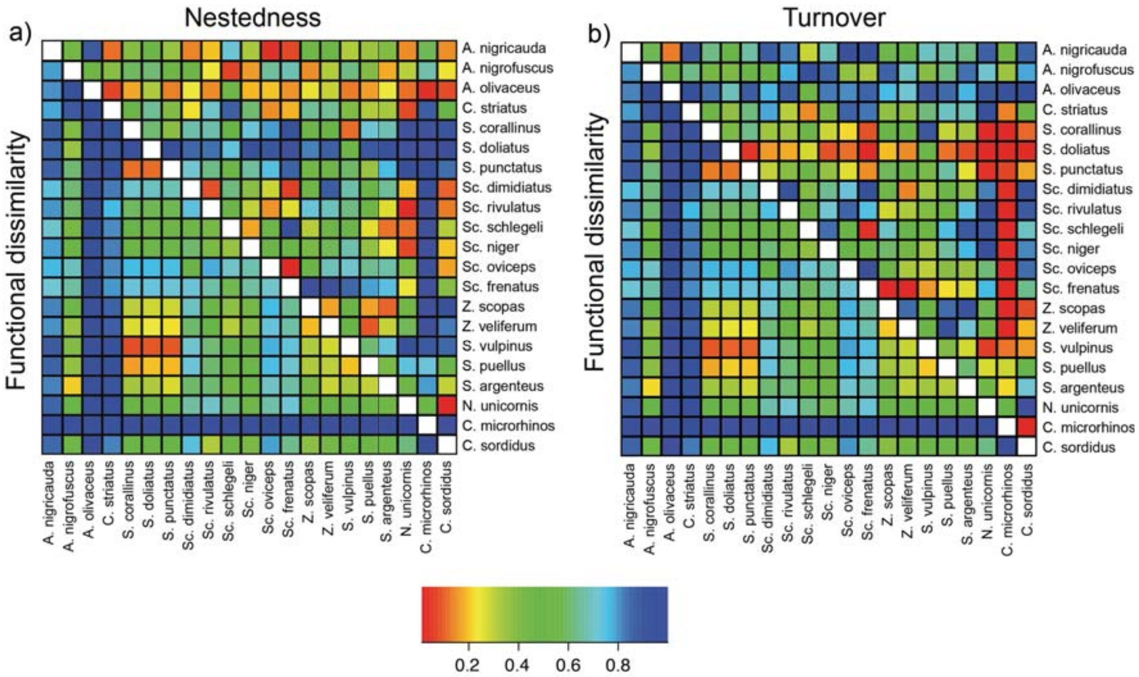

Figure 5.7: Contribution of turnover and nestedness components to functional overlap among herbivorous fishes. In both heatmaps, the lower left matrix marks the functional dissimilarity, while the upper right triangular matrix denotes the contribution of, a) the nestedness component and b) the turnover component of the overlap.

5.4 Discussion

Using a new multidimensional analysis of species' functional niches based on individual observations, I provide evidence for extensive complementarity among herbivorous reef fishes when considering their choice of feeding microhabitats. Some species deliver their function over a wide range of microhabitats while other species appear to be restricted in their microhabitat utilization patterns, occupying less than 5% of the largest niche volume. In calculating the functional complementarity (i.e. the overlap between niche volumes of species), I show that herbivorous species can be broadly divided into two distinct groups, which are not revealed in traditional functional classifications. These groups, characterized by the choice of feeding microhabitats, show striking differences. One group exhibits little individual variation, leading to small functional niches and extensive complementarity, while species in the other group show high variance among individuals, large functional niche volumes and, as a result, less complementarity. These results may have important implications for our understanding of herbivorous processes on coral reefs and highlight the benefits of the new approach in complementing and extending traditional functional groupings.

5.4.1 Individual-based analyses vs. traditional groupings

The assessment of the foraging ecology of herbivorous reef fishes using individual-based analyses provides a finely-graded perspective of functional niche occupation and the extent of overlap among species within a herbivore community. Traditional classification schemes provide a broad, categorical framework. In contrast, my analysis presents a largely concordant but finer-scaled picture that places all species and individuals within a continuous range of functional niches, thus permitting a deeper understanding of functional variation within and among herbivorous species and within traditional functional groups. As a consequence, we can quantitatively explore the extent of functional redundancy or complementarity within functional groups of herbivorous reef fishes.

The differences between traditional groupings and the results yielded by my analyses are apparent when comparing, for example, the functional role of rabbitfishes (f. Siganidae). All 28 members of this family are united in one genus, *Siganus*, and are considered to exhibit limited variation in their taxonomy and general morphology (Borsa et al. 2007). As a result, their functional niche is assumed to be relatively uniform (Green & Bellwood 2009; Cheal et al. 2012). While this view is partially supported when examining the foraging microhabitats of rabbitfishes (all species are in the same cluster), the results of my analyses suggest that there are marked differences between species, as the maximum functional overlap between the two most similar species (*S. doliatus* and *S. punctatus*) was only 42.6%. The extent of separation is even more apparent when examining the functional overlap between *S. corallinus* and *S. argenteus*, which only have an overlap of 25.3%. Such functional differences have been suggested based on morphological traits (Brandl & Bellwood 2013a) and dietary analyses (Hoey et al. 2013). However, it is only by using *in situ* observations that we are able to reveal the extent of segregation in the functional niches of rabbitfishes.

Another advantage of the new analyses compared to traditional groupings is the species-specific assessment based on individuals. This can be illustrated using the rabbitfish *S. doliatus*. Occupying more than half of the available functional niche space with regards to feeding microhabitat selection, *S. doliatus* appears to exhibit remarkable flexibility and the ability to exploit virtually all available locations. Although some studies suggest an exceptional functional role for *S. doliatus* on coral reefs (Fox & Bellwood 2007; Cheal et al. 2010; Brandl & Bellwood 2013b), the capabilities of *S. doliatus* to utilize a range of different microhabitats and, consequentially, its large functional niche volume have not been considered in traditional groupings. The large occupied niche volume in *S. doliatus* can be attributed to a high degree of individual variation within this species. Despite the fact that previous individual-based observations have shown that coral reef fishes display high flexibility in their foraging behaviour (Dill 1983; Biro et al. 2010; Fox & Bellwood 2011), traditional groupings often neglect this aspect. My results emphasize the potential importance of assessing variance among individuals within a species when determining its functional niche (Messier et al. 2010; Violle *et al.* 2012).

An additional benefit of the analyses is the potential to incorporate multiple axes (Rosenfeld 2002). Traditional groupings or assessments of niche overlap are commonly based on a single factor, e.g. diet or feeding mode (Nyström 2006; Green & Bellwood 2009; Cheal et al. 2012; Fox & Bellwood 2013). However, redundancy is likely to decrease with the incorporation of multiple axes, which can reveal important information when assessing the functional structure of a species assemblage (Rosenfeld 2002). Again, rabbitfishes provide a good example. The only previous study on the feeding microhabitats of rabbitfishes (Fox & Bellwood 2013) reported *S. corallinus*, *S. puellus* and *S. vulpinus* to overlap almost entirely in their occupied niche (calculated solely by the extent to which fishes penetrated the substratum). I find that while there is significant overlap between these three species, the consideration of surface type, substratum type and penetration depth reveals a marked reduction in their functional overlap (e.g. 30.9 % between *S. puellus* and *S. vulpinus*, with a turnover component of 38.8%). In addition, factors such as dietary specialization (Hoey et al. 2013) are likely to further differentiate functional niches, underlining the importance of multiple axes in disentangling functional niches within a species community.

Our approach also permits comparisons between traditional functional groups. For instance, the surgeonfish *A. nigricauda* and the rabbitfish *S. doliatus* have previously been classified in either the same (‘grazers/detritivores’; Green & Bellwood 2009) or different functional groups (‘grazers/detritivores’ and ‘browsers’; Cheal et al. 2012). My analysis identified their functional niche volumes to be markedly different (4.6 ± 0.1 % SE and 58.6 ± 0.3 % SE of the total niche space, respectively with just 6.8 % of overlap in volumes). Thus, irrespective of their functional group membership, these species differ in their microhabitat utilization and my analyses allow for a quantitative estimate of the disparity between species.

Even more detail can be revealed when considering the components contributing to the overlap between species. For example, *Z. scopas* and *S. argenteus*, both classified as browsers (Cheal et al. 2012), exhibit a 24.9% overlap in their niche volumes and are grouped in the same cluster. My analyses reveal that 89.7% of the dissimilarity between these two species is due to high turnover, i.e. functionally dissimilar individuals (**Figure 5.7**). Thus, even if both are browsers, both species comprise of individuals that feed in microhabitats not utilized by the other species. A similar picture emerges within parrotfishes, which have been assumed to exhibit relatively similar functional niches (Bellwood & Choat 1990; Cardoso et al. 2006; Green & Bellwood 2009; Price et al. 2010; Cheal et al. 2012). However, when examining the two scraping parrotfishes *Scarus frenatus* and *S. oviceps*, these species appear to differ considerably in their functional niches (11.2 % of overlap), with *S. frenatus* targeting more coral rubble and concealed surfaces than *S. oviceps*. This is again predominantly due to high turnover. In marked contrast, while the two excavating parrotfishes *Chlorurus microrhinos* and *C. sordidus* also only overlap in 5.4% of their niche volumes, 97.2% of this dissimilarity is due to nestedness, with the relatively small niche volume of *C. microrhinos* almost entirely nested within the volume of *C. sordidus*. This suggests that, based on microhabitat utilization patterns, *C. sordidus* may be able to compensate for the loss of *C. microrhinos* but not *vice-versa*. Although parrotfishes are clustered in the same broad group, the detail my analyses can provide emphasizes the variation within the cluster (Fig. S2) and provides an indication of the extent and nature of functional complementarity.

The differences within all three families highlight the broad pattern seen in microhabitat use. While siganids are generally croppers and parrotfishes generally scrapers, the former exhibit broad microhabitat utilization whereas the latter only use a limited range of microhabitats. Thus, parrotfishes may not show the extent of redundancy one may assume. In all these cases, the quantitative estimates yielded by individual-based analyses of functional niche overlap show that traditional groupings offer only a first step in disentangling the complex functional structure of high diversity assemblages. My approach may be of benefit to ecologists in other fields who seek to resolve functional niche partitioning in highly diverse species communities. Thus, it may be useful to tease apart the functional niches of, for instance, birds (e.g. Şekercioğlu 2006), insects (Andersen 1997), or across various groups of animals with similar ecosystem functions, such as pollinators (Clark et al. 2001).

In summary, my approach offers a high-resolution quantitative method to explore functional niche occupation and the extent and nature of functional overlap among species. Several recent studies have emphasized that there are areas of potential weaknesses that can arise from assuming redundancy in key functional groups (Petchey et al. 2007; Cheal et al. 2013; Johansson et al. 2013). My analyses provide means to go beyond functional interpretations based on the abundance of species in an ecosystem to quantitatively evaluate species’ actions and activities.

5.4.2 Ecological implications

From an ecological perspective, the results of the present study point to two distinct herbivore groups with extensive niche partitioning within both these and traditional functional groups. This calls for caution when assessing reef resilience based on broad functional groupings. Several species, mostly surgeon- and parrotfishes, appear to graze heavily on open, exposed reef surfaces and sandy substrata. There are, however, subtle differences in the foraging behaviour of these species. This is particularly evident within scraping parrotfishes, which appear to partition the available, exposed substratum very finely by having relatively distinct foraging behaviour characterized by little intraspecific variation and high functional turnover, leading to extensive complementarity. This is consistent with observations on parrotfish foraging behaviour in the Caribbean (Cardoso et al. 2006). In the parrotfishes, explaining the coexistence of so many morphologically and trophically similar species in a single ecosystem has been a challenge (Choat & Bellwood 1990; Streelman et al. 2002; Price et al. 2010; Choat et al. 2012). My analyses suggest that fine-scale niche partitioning of feeding microhabitats may be an important factor in explaining these patterns. This implies that scraping parrotfishes, which are generally assumed to have very similar functional niches (thus showing high functional redundancy), may provide yet another example of limited functional redundancy in herbivorous reef fishes (Bellwood et al. 2003; Hoey & Bellwood 2009), as their ability to remove algae appears to depend strongly on species-specific microhabitat utilization patterns.

In contrast to the first group (small niches, predominantly parrotfishes), only a limited suite of species (mostly rabbitfishes and several surgeofishes) graze on concealed reef microhabitats. However, individuals in these species are highly flexible in their microhabitat utilization patterns; all feed on a wide range of different microhabitats, including those targeted by species with limited niche volumes. Flexibility in the use of different microhabitats has been suggested previously for some rabbitfishes and surgeonfishes (Robertson et al. 1979; Robertson & Gaines 1986; Fox & Bellwood 2013) and may suggest that either, a) concealed microhabitats do not provide enough resources to maintain these species if they feed solely in concealed areas, or b) that species feeding on open microhabitats competitively exclude the more flexible species from feeding on easily accessible surfaces (Robertson et al. 1979; Robertson & Gaines 1986; Alwany et al. 2005). The latter scenario may be particularly important for reef management as species with high flexibility in their foraging microhabitat selection may be critical for the resilience of reef ecosystems because of their ability to remove algae from inaccessible microhabitats (Brandl & Bellwood 2013a; Fox & Bellwood 2013).

Overall, using a new multidimensional framework to analyse feeding microhabitat utilization among herbivorous reef fishes, my study demonstrates the sensitivity of individual-based *in situ* behavioural observations when evaluating a species' realized functional niche, especially in high diversity ecosystems. I find that herbivorous species vary greatly in their functional impact with regards to their microhabitat utilization patterns. Indeed, I found no functional redundancy (based on a 50% cut-off) among herbivorous fish species in their microhabitat use. Herbivores broadly divide into species that feed predominantly on open surfaces and species that also exploit concealed microhabitats. Species within the first group appear to partition their feeding microhabitats very finely, resulting in small functional niche volumes with high complementarity. In contrast, individuals of species feeding on concealed microhabitats show high variation in their foraging behaviour, leading to higher overlap of niche volumes (mostly due to a strong turnover component, thus maintaining functional complementary rather than redundancy). These results underscore the potential sensitivity of the analyses and their ability to reveal details of species' functional niches and their role in ecosystem processes.

Applied to coral reef fish communities, my results emphasize the need for caution when assessing reef resilience based solely on assessments of biodiversity and broad functional groups and stress the importance of complementarity among herbivorous reef fish species. Studies using traditional functional groups may find high redundancy; however, this can arise as a result of either true overlap in functions or excessively broad functional categories. My results suggest that the latter may be more common than previously thought. Given the global threat of changing environmental conditions and the progressive loss of biodiversity, the key question now is: to what extent can a species' functional niche shift in response to changing environments or changing patterns of biodiversity?

Chapter 6: Exploring the nature of ecological specialization in a coral reef fish community: morphology, diet, and foraging microhabitat use

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6.1 Introduction

The fundamental characteristics of species' niches shape ecological communities across the globe. Within communities, species differ not only in their positions in niche space, but also in the respective sizes of the volumes they occupy (Whittaker et al. 1973). Specialist species, often considered as taxa that occupy the smallest niche volumes, have evoked particular interest in a wide range of fields (Futuyma & Moreno 1988). Ecological specialization is accepted as a key factor for countless facets of organismal biology, affecting speciation (Schluter 2000), species distribution patterns (Emery et al. 2012), and ecosystem functioning and stability (Clavel et al. 2010). Yet, as ecological specialization can occur on various levels (e.g. fundamental vs. realized or individuals vs. populations; Bolnick et al. 2003; Poisot et al. 2011; Ferry-Graham et al. 2002a), many aspects of its ecosystem impacts remain unresolved.

Two of the most commonly studied features of ecological specialization are morphological/physiological attributes and behavioral traits relating to foraging (Futuyma & Moreno 1988), and their respective relationships. By identifying morphological traits that directly relate to prey capture or procurement capacities, numerous studies have established strong correlations between morphological and dietary specialization in birds (Grant & Grant 1996), reptiles (Henderson et al. 2013), fishes (Huckins 1997), and mammals (Aguirre et al. 2002), suggesting a tight link between fundamental and realized niches and permitting the inference of simple directional evolutionary pathways. Consequently, relating morphological features to dietary preferences has become one of the most widespread techniques used to extrapolate ecological function (Wainwright & Reilly 1994). Ichthyologists, in particular, have made extensive use of ecomorphological techniques to interpret the ecology of fishes, especially when sustained observational studies are unfeasible (Wainwright 1988, 1996; Douglas & Matthews 1992; Wainwright & Bellwood 2002; Pouilly et al. 2003; Snorrason et al. 1994; Sturmbauer et al. 1992; Hulsey & García de León 2005).

However, in the last two decades, there have been a number of intriguing studies that have revealed high behavioral plasticity in morphologically specialized fish species (Liem 1980; Motta et al. 1995; Barnett et al. 2006; Bellwood et al. 2006; Sanderson 1990). It appears that morphological specialization in teleost fishes does not always entail dietary specialization and that, in many cases, a species' realized (dietary) niche is largely unrelated to its morphology (Alfaro et al. 2005; Wainwright et al. 2005). One of the most striking examples of this scenario was described in African cichlids, where the apparent mismatch between morphological features and dietary niches in ecologically specialized species has been termed "Liem's Paradox" (i.e. why are morphological specialists often dietary generalists; Liem 1980; Robinson & Wilson 1998). The most common explanation for the paradox is that specialized morphological traits enable exploitation of "fallback foods" when preferred resources are low. It is posited that this has arisen as a result of competition-driven morphological specialization during low-resource situations, while retaining the capacity to exploit a range of preferred resources under more typical circumstances (Robinson & Wilson 1998). This hypothesis has been supported by both empirical and theoretical work on a wide range of taxa (Fontaine et al. 2008; Ungar e al. 2008), and appears to be the most prevalent explanation in teleost fishes (Bouton et al. 1998; Janovetz 2005).

As the marine analogues to cichlids in African Rift Lakes, coral reef fishes with their extreme diversity offer an outstanding opportunity to investigate ecological specialization (Wainwright & Bellwood 2002). Despite extreme morphological specialization in numerous reef fishes lineages (Ferry-Graham et al. 2002a), attempts to relate these features to dietary niche partitioning have had mixed success (Bellwood et al. 2006; Price et al. 2010). Herbivorous reef fishes *sensu lato* (Clements et al. 2009) provide an excellent group for exploring patterns of ecological specialization. Herbivore communities are of critical importance for the benthic structure of shallow reef environments and have been the subject of intensive research with regards to their diet (Choat et al. 2002; Hoey et al. 2013), foraging behavior (Rasher et al. 2013), and evolutionary history (Choat et al. 2012). However, patterns of ecological specialization in herbivore families have rarely been examined. This is particularly interesting given the variation in morphological diversification among and within herbivorous families (Choat et al. 2012; Brandl & Bellwood 2013a), and the presence of dietary niche partitioning across distinct phylogenetic lineages (Choat et al. 2002; Robertson & Gaines 1986; Robertson et al. 1979). Furthermore, there is evidence for subtle partitioning of feeding microhabitats in many families (Robertson & Gaines 1986; Brandl & Bellwood 2014a), which has been linked to morphological traits (Brandl & Bellwood 2013a; Fox & Bellwood 2013) but has not been considered with regards to ecological specialization, despite its potential importance in aquatic ecosystems (Holbrook & Schmitt 1992). There is, therefore, strong indication of the potential for ecological specialization in herbivorous reef fishes along three distinct but interrelated niche axes: morphology, diet, and foraging microhabitat utilization. In addition, in light of the functional importance of herbivores in shaping benthic dynamics, and the tendency of ecological specialists to be among the first species to succumb to human-induced disturbances (Clavel et al. 2010), detecting ecological specialists among herbivorous fish species may be important for coral reef management, particularly given current anthropogenic pressures (Bellwood et al. 2012; Edwards et al. 2014).

To assess the relationship between fundamental (morphological) and realized (behavioural) specialization on coral reefs, I examined an assemblage of ten species of surgeonfishes (f. Acanthuridae). I first identified morphological specialization among species using external features, and then considered two distinct behavioural niche axes, diet and foraging microhabitat utilization. For each behavioural axis, I examined behavioral specialization using an individual-based multidimensional framework Brandl & Bellwood 2014a), which allows for a representation of all species along a quantitative generalist-specialist continuum. I examined the relationship between morphological specialization and the two behavioural niche axes based on three underlying hypotheses: 1) no relationship (as a null-hypothesis), 2) a positive relationship following the ‘traditional’ ecomorphological paradigm where morphological specialists are behavioral specialists, and 3) an inverse relationship (potentially consistent with Liem’s Paradox) (**Figure 6.1**).

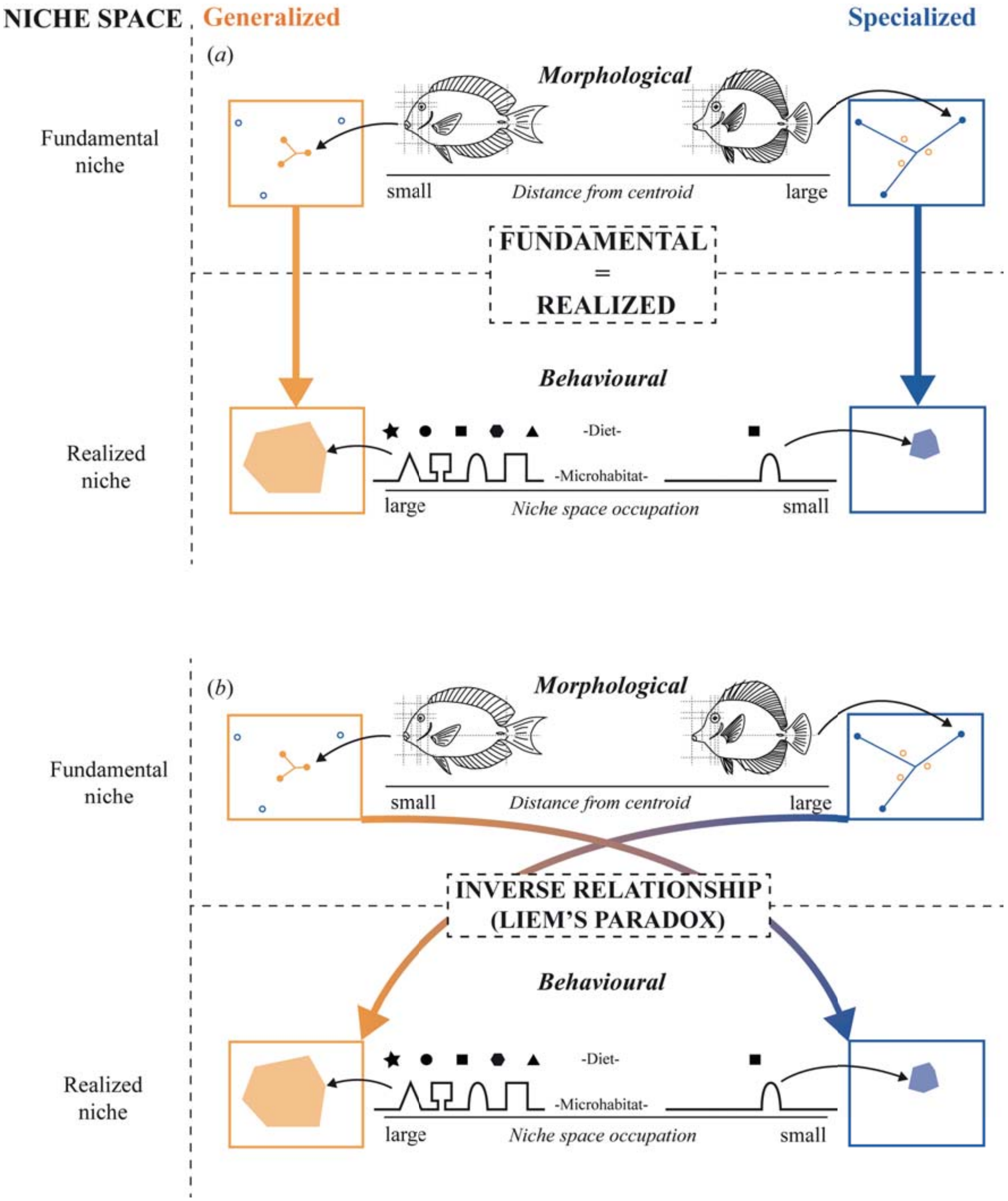


Figure 6.1: A conceptual synthesis of the potential relationships between fundamental (morphological) and realized (behavioural, i.e. diet [filled symbols] or foraging microhabitat utilisation [open symbols]) specialization in surgeonfishes. The three hypotheses were, i) no relationship between morphological and behavioural

specialization (not figured), ii) morphological specialists are behavioural specialists (*a*), or iii) morphological specialists are behavioural generalists and *vice versa*, potentially consistent with a phenomenon termed Liem's paradox (*b*).

6.2 Materials and methods

All fieldwork and sampling was conducted on reefs around Lizard Island, a mid-shelf island in the northern Great Barrier Reef (GBR), Australia (14°40′08″S 145°27′34″E). Data were collected from adult individuals of ten surgeonfish species in four genera, *Acanthurus blochii*, *A. lineatus*, *A. nigricauda*, *A. nigrofuscus*, *A. olivaceus*, *Ctenochaetus striatus*, *Naso lituratus*, *N. unicornis*, *Zebrasoma scopas*, and *Z. velifer*. These species represent 40% of the surgeonfish species recorded from the GBR and encompass all numerically abundant species at the study site (Cheal et al. 2012).

6.2.1 Morphological characterization

Species were characterized using a set of morphological traits consisting of 19 distance-based measurements and three angle measurements. All morphological measurements were selected based on previous linkages between the morphology and functional aspects of the species' foraging ecology, such as feeding, locomotion, or sensory abilities (Douglas & Matthews 1992; Bellwood et al. 2014). All values were transformed to ratios by standardizing them against head or standard length, as required (e.g., snout length ÷ head length). As none of the ratios showed a significant relationship with standard length, analyses were performed using the standardized values rather than residuals. The average number of individuals measured for each species was 3.8 ± 0.3 (SE). Details are provided in Bellwood et al. (2014). A list of morphological features measured and their ecological significance is provided in **Table 6.1**.

Table 6.1: List of morphological traits measured and their ecological significance. All measurements are explained in greater detail in Bellwood et al. 2014 and references therein.

Morphological trait	Measured as	Affects
Body depth	Body depth/standard length	Predator avoidance, maneuvreability
Head length	Head length/standard length	Sensory and trophic capabilities
Narrowest point on caudal peduncle	Width caudal peduncle/body depth	Swimming speed
Body aspect ratio	Body depth^2/body area	Predator avoidance, maneuvreability
Medial caudal fin ray length	Medial fin ray/longest fin ray	Swimming ability and speed
Snout length	Snout length/head length	Precision in prey acquisition
Eye diameter	Eye diameter/head length	Visual acuity
Head depth	Head depth/body depth	Hydrodynamics, maneuvrability
Lower jaw length	Lower jaw length/head length	Range of prey items ingested
Anterior of orbit to forehead	Anterior of orbit/head length	Binocular vision
Hoirzontal eye position	Distance posterior the orbit/ head length	Field of perception
Vertical eye position	Distance ventral of orbit/head depth	Field of perception
Mouth-eye distance	Orbit centroid to premaxilla/head length	Eye-snout coordination
Mouth position	Ventral of snout/head depth	Prey acquisition
Longest dorsal spine	Longest dorsal spine/body depth	Predator avoidance, maneuvreability
Snout angle	Angle charactizing tip of snout	Prey acquisition
Head angle	Angle characterizing anterior cranial region	Prey acquisition
Snout-eye angle	Angle between snout and eye	Eye-snout coordination

6.2.2 Diet

Specimens were collected from the reef using spearguns and barrier nets. Specimens were kept on ice and the whole alimentary tract was removed and preserved in 10% buffered formalin within 1h of capture. Contents were identified using microscopic analysis (4x10 magnification) along transects of a 100×100mm grid on a Perspex plate. For detrital feeders with considerable amounts of fine organic matter in alimentary tracts, examination was performed using 10x40 magnification to allow for the identification of microalgae and other microscopic dietary items. An average of 6.6 ± 0.3 (SE) specimens per species were analyzed. The methods are described in detail in (Choat et al. 2002). A list of dietary categories is provided in **Table 6.2**.

Table 6.2: List of categories of dietary items found in alimentary tracts of the examined species.

Categories of dietary items
Arthropoda
Brown filamentous algae
Brown foliose algae
Brown thallous algae
Calcareous sediment
Chitinous matter
Chitons
Crustacea
Echinoids
Eggs
Fish scales
Foraminifera
Gastropoda
Gelatinous zooplankton
Green filamentous algae
Green foliose algae
Green thallous algae
Heteropod mollusca
Hydroids
Organic matter
Red filamentous algae
Red foliose algae
Red thallous algae
Silaceous material
Spicule
Sponge spicule
Stomatopoda
Sponges
Gelatinous matter

6.2.3 Foraging microhabitat preferences

Observations on foraging microhabitat selection were carried out on SCUBA or while snorkeling (during April/May 2013). Haphazardly chosen individuals were followed until the first foray. Then, the surface orientation and accessibility [open horizontal (A), open vertical (B), underside (C), concealed vertical (D) or concealed horizontal (E)], the substratum type (live coral [LC], dead coral skeleton [DC], macro-algae [MA], coral rubble [RB], sand [SD], turf covered reef matrix [TR]) and the number of bites taken from the respective microhabitat were recorded. In addition, the extent to which an individual penetrated the substratum was measured using vernier calipers. The average number of observations per species was 49.8 ± 1.3 (SE) (details in Brandl & Bellwood 2014b).

6.2.4 Microhabitat availability

The abundance of different microhabitats was also estimated during April/May 2013, using 20 ten-meter chain intercept transects laid parallel to the reef crest (following Goatley & Bellwood 2011). A transect tape was laid conforming to the reef benthos to include concealed microhabitats. The underlying microhabitat was recorded every 20cm, using vernier calipers to measure the depth of crevices and depressions. Measurements were taken perpendicular to the substratum. To match the foraging microhabitat observations, microhabitat characteristics included the surface orientation and exposure (A, B, C, D, E), substratum type (live coral, dead coral, rubble etc.), and depth of interstices and crevices.

6.2.5 Statistical procedures

In terms of morphological specialization, analyses were performed at the species level. Morphological data (traits averaged for each species) were analyzed using a principal co-ordinate analysis (PCoA) based on Gower’s dissimilarity matrix. Distances were calculated among species based on the average trait measurements for each species. Using the coordinates for each species in the first two dimensions, I calculated the distance from the centroid of the ordination for each species as a proxy for morphological specialization (following Bellwood et al. 2006). While this quantification is dependent on the relative proportions of species morphotypes used, the species were selected to broadly reflect the relative proportions of surgeonfish types in GBR assemblages.

I used an individual-based multidimensional framework for the calculation of behavioural niche spaces yielding quantitative, continuous estimates of niche space occupation for both dietary and microhabitat selection data based on inter-individual variation for each species. First, I calculated the pairwise distances between all individuals of all species using Gower's distance metric. Following this, a PCoA was performed using Cailliez' correction for negative eigenvalues (Laliberté & Legendre 2010), yielding a distribution of all individuals in a synthetic dietary/microhabitat niche space. Subsequently, I computed species niche space occupation for diet and microhabitat utilization in the same fashion, based on individuals with the most extreme coordinates using convex hulls (Ackerly & Cornwell 2007; Cornwell et al. 2006). To account for unequal sample sizes in both datasets (i.e. different numbers of observations among species, which may lead to biased estimates of niche volumes as a matter of chance) and to decrease the effect of few extreme individuals on the overall volume for each species, I performed randomized permutations (*n* = 999) with a constant subsample of individuals for each species and calculated the mean niche space occupation for each species for further analyses (i.e. for each species, 999 volumes were calculated from subsamples of individuals). Thus, my measure of species' degree of specialization was a function of inter-individual variability within populations, a common metric of species' ecological niches (Whittaker et al. 1973; Colwell & Futuyma 1971). Due to restrictions in the dimensionality of the data and because I did not directly compare dietary and microhabitat specialization, dietary niche space occupation was computed on two dimensions, whereas microhabitat niche space occupation was conducted on both two- and three-dimensional space to maximize extraction of information.

For foraging microhabitat specialization, I also computed Manly's χ^2 log-likelihood statistic ($\chi_{L2}{}^2$) (Manly et al. 2002), which quantifies a population's selectivity for a given resource based on availability within the ecosystem. I used model design I with sampling protocol A (Manly et al. 2002), which measures resource selection on the population level, to calculate selection ratios for each species (used/available). High ratio values indicate high levels of specialization, while low ratio values suggest a generalist strategy.

I investigated the relationships between morphological specialization (as measured by the distance from the centroid in morphospace), dietary specialization, microhabitat specialization (both of the latter quantified as the dietary/microhabitat niche space occupied by individuals within a species, i.e. inter-individual variability across time and space), and microhabitat selectivity (Manly's χ^2 log-likelihood statistic ($\chi_{L2}{}^2$)) using Bayesian linear models with morphology as a fixed effect and the respective behavioural variable as response. Uninformative default priors were used on the fixed effect estimates (0 on intercept and regression coefficient, variance of 100,000,000 for both parameters; Hadfield 2010). For the residual variance, I specified uninformative inverse Wishart priors with V = 1 and nu = 0.002. Models were run for 2,000,000 iterations with a burnin of 50,000 and a thinning interval of 1,000. Chain convergence was validated using trace chain plots.

6.2.6 Phylogenetic correction and evaluation of assumed relationships

To account for biases due to shared ancestry, I used a phylogenetically corrected principal component analysis (PCA) on the morphological data using phylogenetic distances from a pruned tree (**Figure 6.2**) based on Sorensen et al. (2013) (Martin & Wainwright 2011; Revell

2012). In this ordination, evolutionary independence is achieved by incorporating estimated ancestral states for each character into the analysis, therefore reducing phylogenetic correlation among scores on each axis to zero. Subsequently, I examined the relationship between morphological and dietary/microhabitat specialization using phylogenetic Bayesian Mixed Models (BMMs). Again, phylogenetic relatedness was determined from a pruned tree (Sorensen et al. 2013) and fitted as a random factor under a Brownian motion model of evolution in the BMM (Hadfield 2010). In order to evaluate whether phylogenetic correction altered the results from my previous models, and due to the small sample size of only ten species in three distinct phylogenetic groups, I specified informative priors using the parameter estimates obtained from the previous uncorrected models for each relationship. This was done as my prior belief in the respective relationships was based on the uncorrected model estimates. For both random and residual variance, I again specified uninformative inverse Wishart priors and the number of iterations was specified as above. In addition, I performed a sensitivity analysis in order to assess the effect of the specified priors on the posterior estimates. Specifically, I specified three informative, but arbitrary, priors for each relationship, suggesting the relationship between morphology and the three behavioural variables to be either positive (mu = 1, V = 0.2), non-existent (mu = 0, V = 0.2), or negative (mu = -1, V = 0.2). All analyses conducted in this paper were performed in the software *R* (R Core Team 2014) using the packages *ape* (Paradis et al. 2004), *MCMCglmm* (Hadfield 2010), *phytools* (Revell 2012), *geometry* (Habel et al. 2014), *rcdd* (Geyer & Meeden 2014), *cluster* Maechler et al. 2015), *adehabitat* Calenge 2006), and *geiger* (Harmon et al. 2008).

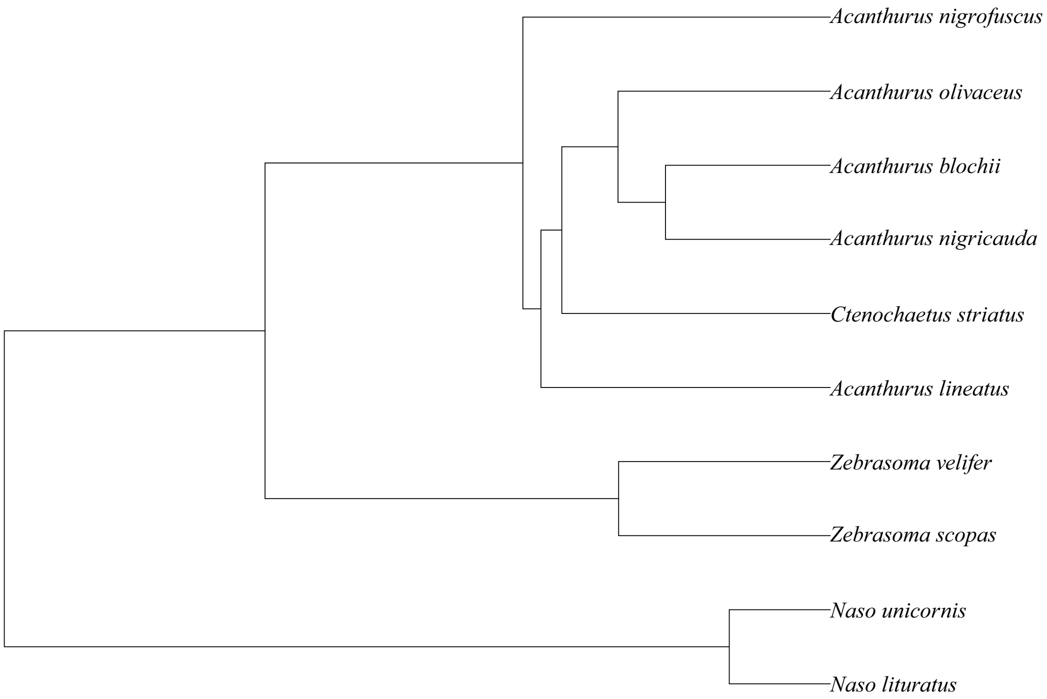


Figure 6.2: Pruned phylogenetic tree after Sorensen et al. 2013, which was used for all phylogenetic corrections.

6.3 Results

I found marked differences in morphological and behavioral specialization patterns among surgeonfish species. Morphologically, *Z. velifer*, *N. unicornis*, and *Z. scopas* were most specialized, exhibiting the greatest distance from the centroid of the biplot (**Figure 6.3**). The least specialized morphologies were found for *C. striatus, A. nigricauda*, *A. olivaceus*, and *A. blochii.* In the dietary niche space, *A. blochii* occupied the greatest area, followed by *N. unicornis*. The smallest areas were occupied by *A. olivaceus* and *Z. scopas* (**Figure 6.4a**). In terms of microhabitat utilization (in three dimensions), *Z. scopas* exhibited the largest niche volume, followed by *A. nigrofuscus* and *Z. velifer.* The other members of the genus *Acanthurus* occupied the smaller niche volumes (**Figure 6.4b**). Patterns were similar when using only two dimensions. When accounting for the availability of different microhabitats by using Manly's χ^2 log-likelihood ratio, *Z. velifer* and *A. nigrofuscus* had the lowest specialization scores, while *A. blochii* and *A. nigricauda* had the highest scores, therefore suggesting the latter species to be most specialized (**Figure 6.5**). The most abundant microhabitat in terms of benthic cover was open horizontal rock substratum (29.2%), followed by live coral (16.5%). The most common concealed microhabitat were crevices in horizontal rocky substrata (7.1%). Overall, concealed microhabitats accounted for 24.6% of available foraging microhabitats, while open microhabitats accounted for 75.4%.

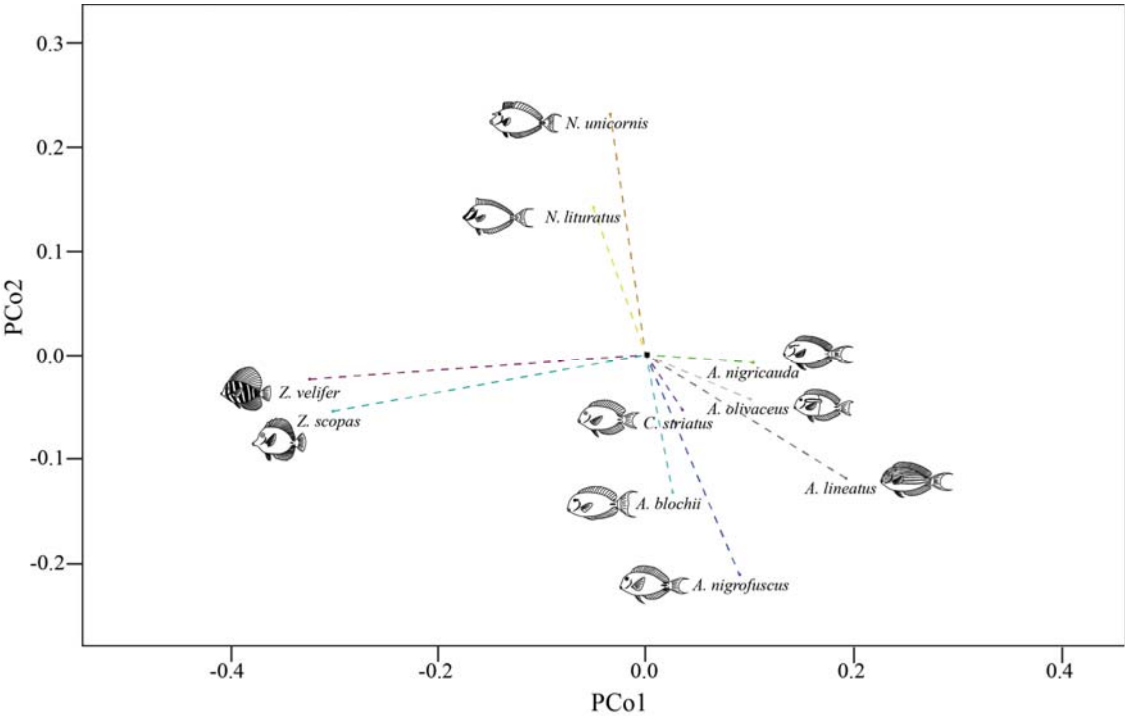
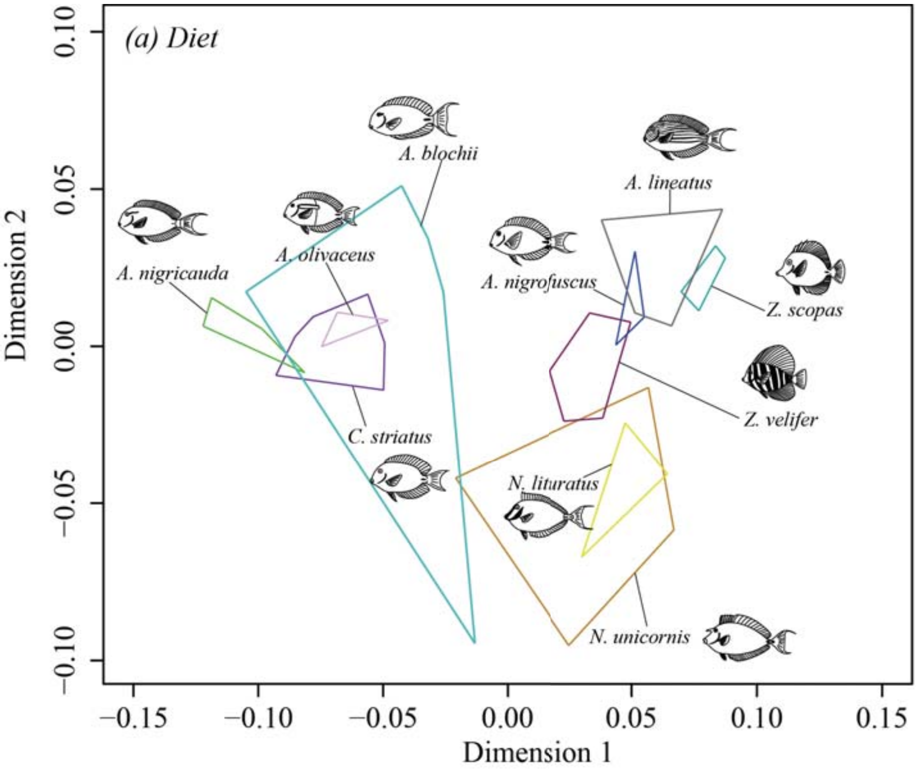


Figure 6.3: Morphological ordination from which species-level morphological specialization was inferred by calculating the distance from the centroid of the ordination.


(a) Diet
A. blochii
A. lineatus
A. olivaceus
A. nigricauda
A. nigrofuscus
Z. scopas
Z. velifer
C. striatus
N. lituratus
N. unicornis
Dimension 2
0.10
0.05
0.00
−0.05
−0.10
−0.15
−0.10
−0.05
0.00
0.05
0.10
0.15
Dimension 1

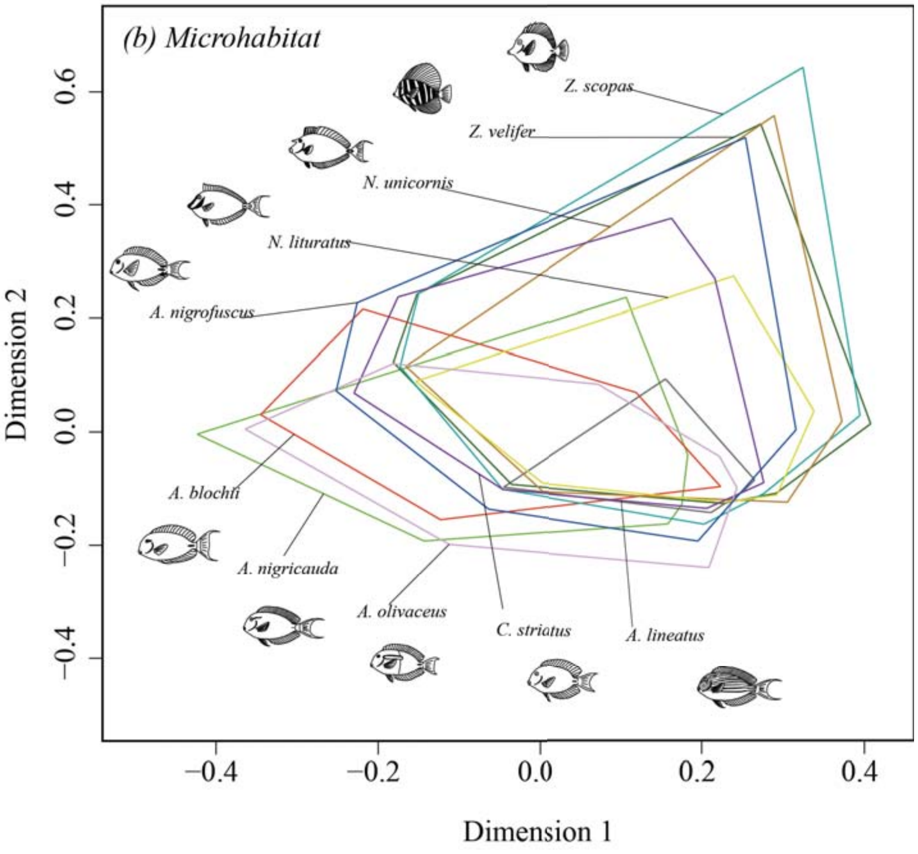

(b) Microhabitat
Z. scopas
Z. velifer
N. unicornis
N. lituratus
A. nigrofuscus
A. blochii
A. nigricauda
A. olivaceus
C. striatus
A. lineatus
Dimension 2
0.6
0.4
0.2
0.0
−0.2
−0.4
−0.4
−0.2
0.0
0.2
0.4
Dimension 1

Figure 6.4: Niche volumes for ten species of surgeonfishes in two-dimensional niche space for (b) diet and (c) foraging microhabitat utilization.

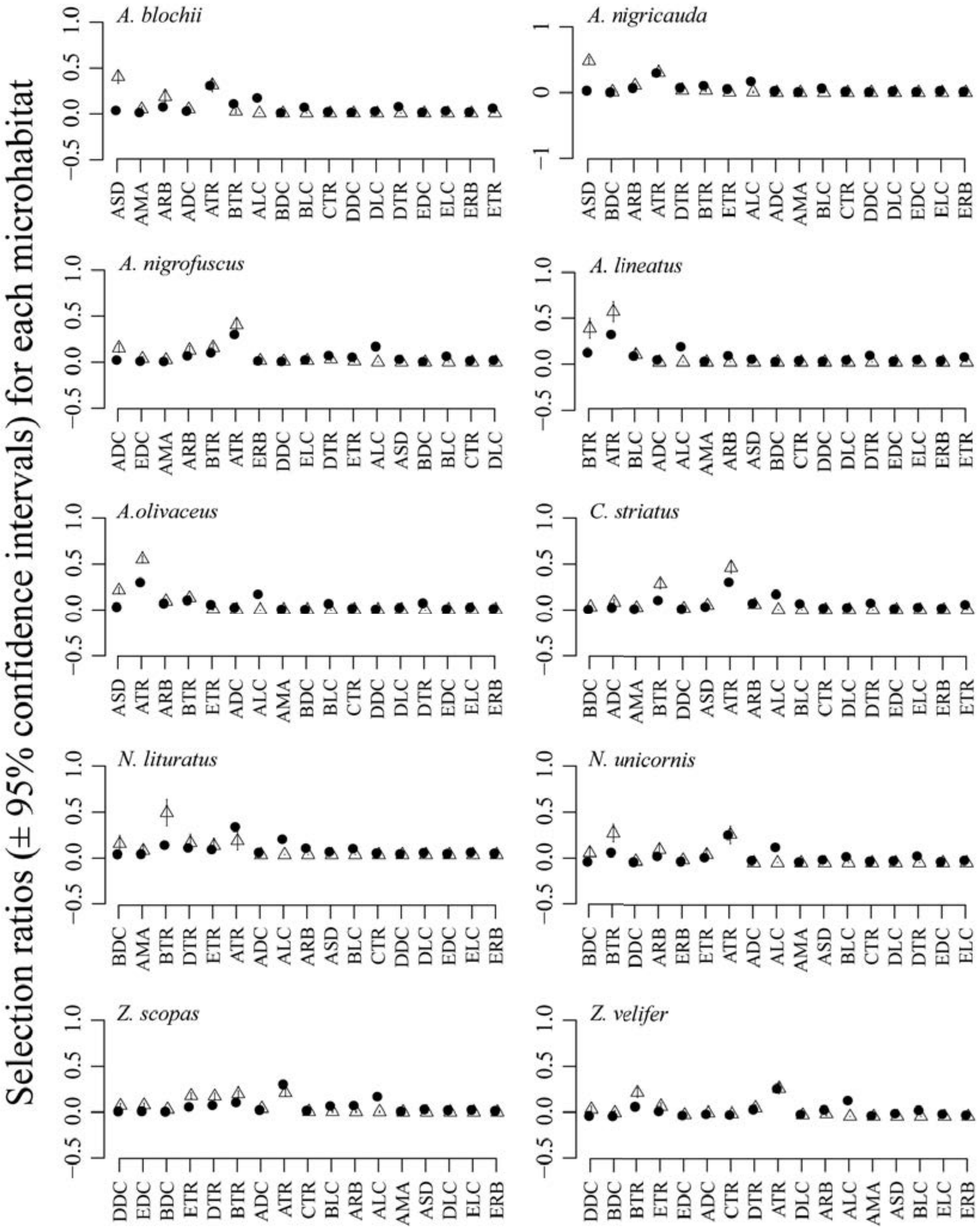


Figure 6.5: Resource selection ratios for respective microhabitats in ten species of surgeonfishes. Open triangles are the usage, while filled circles mark the availability of the respective microhabitat. Acronyms consist of the surface orientation (A,B,C,D,E) and the given substratum type (DC, TR, RB, LC, MA, SD).

Morphological specialization had a markedly different relationship with dietary and microhabitat specialization (**Figure 6.6**), respectively. There was virtually no relationship between morphological and dietary specialization (Bayesian linear model: posterior mean density estimate β = -0.025, 95% credible interval (*CI*) = -0.096 to 0.043). In contrast, morphological specialization showed a negative relationship with foraging microhabitat utilization specialization (β = -0.392, *CI* = -0.679 to -0.106), with morphologically specialized species exhibiting the largest niche volumes, i.e. being the most behaviorally generalized species. There was a similar trend in the relationship between morphology and microhabitat selectivity (Manly's χ^2 log-likelihood statistic), although 95% CIs of the mean posterior estimate also extended beyond zero (β = -1.020, *CI* = -2.876 to 1.172).

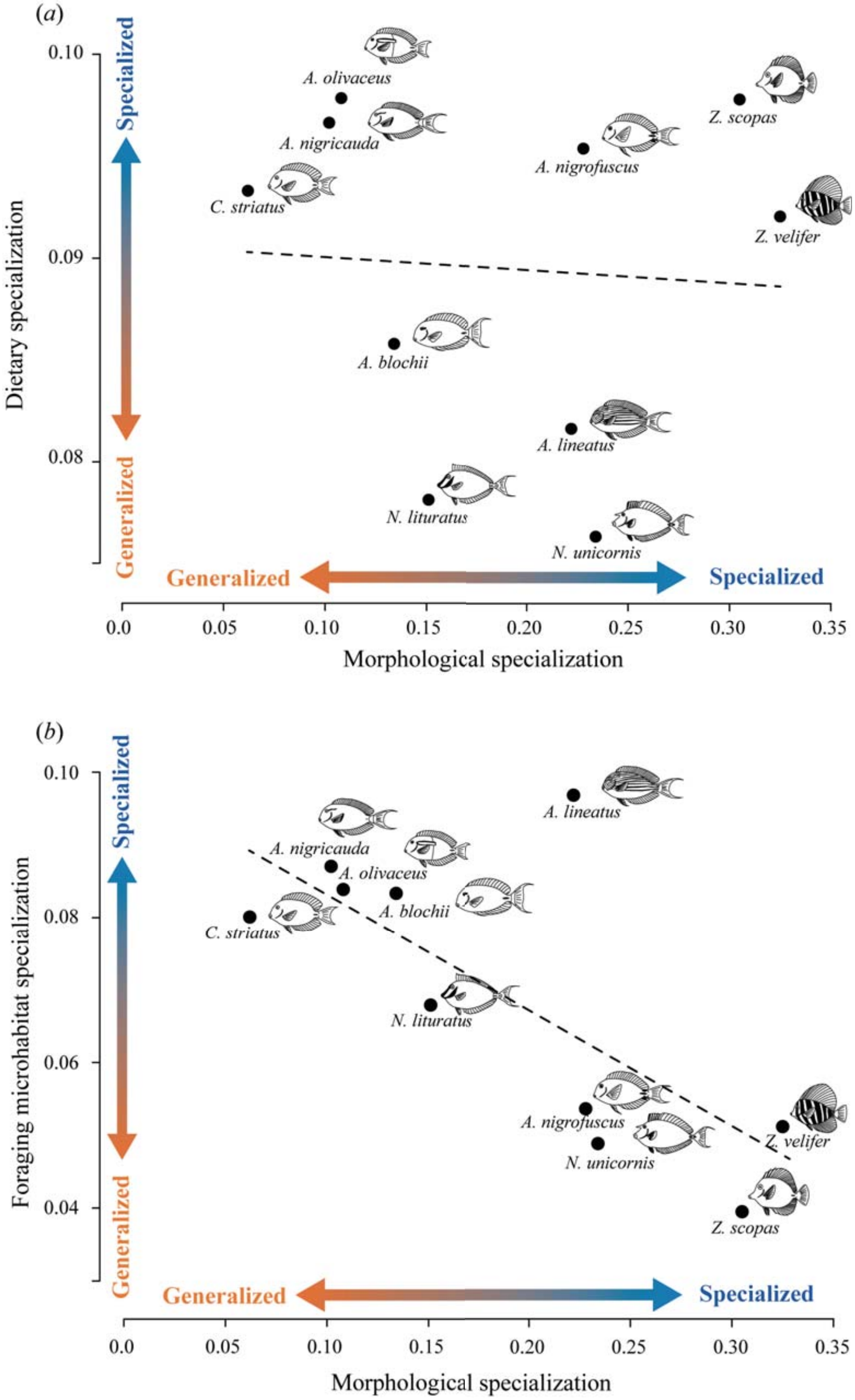

(a)
Dietary specialization
0.10
0.09
0.08
Specialized
Generalized
A. olivaceus
A. nigricauda
C. striatus
A. nigrofuscus
Z. scopas
Z. velifer
A. blochii
A. lineatus
N. lituratus
N. unicornis
Generalized
Specialized
0.0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Morphological specialization
(b)
Foraging microhabitat specialization
0.10
0.08
0.06
0.04
Specialized
Generalized
A. lineatus
A. nigricauda
A. olivaceus
A. blochii
C. striatus
N. lituratus
A. nigrofuscus
N. unicornis
Z. velifer
Z. scopas
Generalized
Specialized
0.0
0.05
0.10
0.15
0.20
0.25
0.30
0.35
Morphological specialization

Figure 6.6: Relationships between morphological and behavioural specialization for (*a*) diet and (*b*) foraging microhabitat utilization. Morphological specialization and dietary niche space occupation showed no relationship, while there was a strong relationship between morphological specialization and microhabitat niche space occupation. For graphical purposes, behavioural specialization on the Y-axis was inverted by subtracting the occupied niche space value from 0.1.

Accounting for shared ancestry in a morphological PCA and in the phylogenetic BMMs did not change the overall result, although it slightly altered the effect sizes and CIs (**Figure 6.7**). For the relationship between morphological and dietary specialization, the mean posterior estimate for the fixed effect was centered around zero (**Figure 6.7a**) (phylogenetic BMM: β = -0.020, *CI* = -0.081 to 0.039), with both the 95% and 50% CIs intersecting zero. The relationship between morphological specialization and microhabitat specialization (based on species' niche volumes) was less diffuse (**Figure 6.7b**) with consistently negative estimates for the mean (β = -0.294, *CI* = -0.527 to -0.084) despite a slight shift towards zero compared to the uncorrected model. When regressing morphological specialization against Manly's χ^2 log-likelihood statistic of resource specialization (figure 3c), the relationship also showed a negative trend but 95% CIs did intersect zero (β = -0.929, *CI* = -2.117 to 0.326).

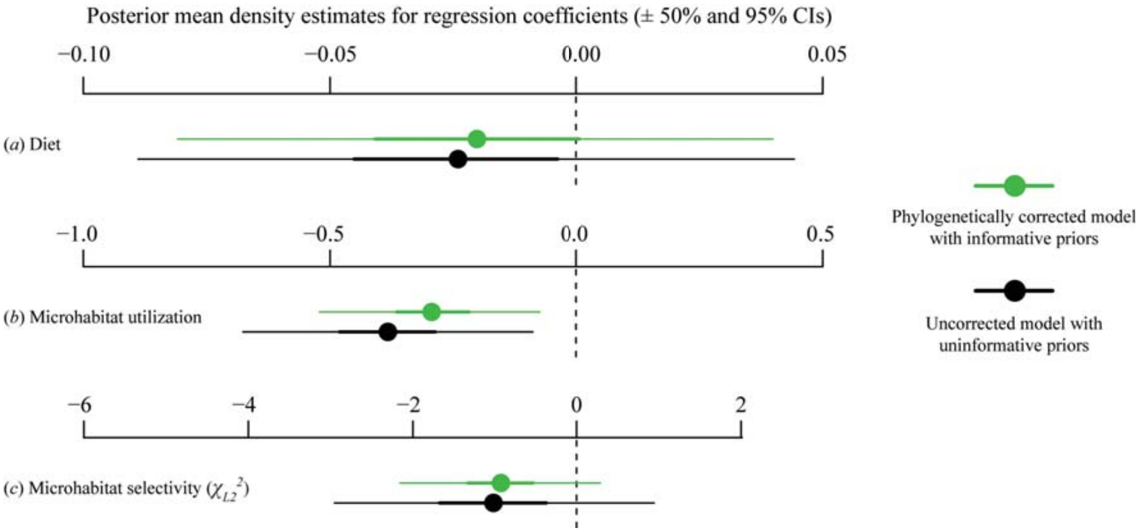


Figure 6.7: Comparisons of models estimating the relationship between morphological specialization and (a) dietary specialization, (b) foraging microhabitat specialization, and (c) microhabitat selectivity. Plots show the mean posterior density estimates of regression coefficients and their 50% and 95% CIs in phylogenetically corrected (green) and uncorrected models (black). Relationships between morphological and behavioural specialization were consistent after phylogenetic corrections, with no relationship between morphological and dietary specialization (*a*). In contrast, a clear negative relationship is seen between morphological and microhabitat utilization specialization regardless of phyloegentic correction (*b*). A possible negative relationship is seen between morphological specialization and microhabitat selectivity; however, 95% CIs extend beyond zero (*c*).

While the results from the phylogenetically corrected BMMs indicate that substantial information for the posterior estimates came from the specified priors, the decrease of the CIs surrounding the posterior estimates in the phylogenetic BMMs suggests that the data did support the initial findings (**Figure 6.7**). This is further supported by the results of the sensitivity analysis (**Figure 6.8, Table 6.3**). For the relationship between morphological and dietary specialization, none of the models yielded a clear trend, regardless of the specified priors. In contrast, an unambiguous negative relationship between morphological specialization and microhabitat specialization was present in the models featuring the negative priors, while there was no clear relationship when neutral or positive priors were specified. The same pattern was present for the relationship between morphological specialization and Manly's χ^2 log-likelihood statistic of resource specialization, with a clear relationship only found when a negative prior was used. Thus, although the data did not override the neutral/positive priors, for both aspects of microhabitat specialization, the models with the negative priors resulted in a clear negative relationship in the posterior, suggesting that the data supported such negative relationship. Therefore, although small sample sizes may limit the strength of the support, the main suggestion of my analyses is that morphological specialization is negatively related to microhabitat utilization specialization, while dietary specialization shows no relationship with morphology.

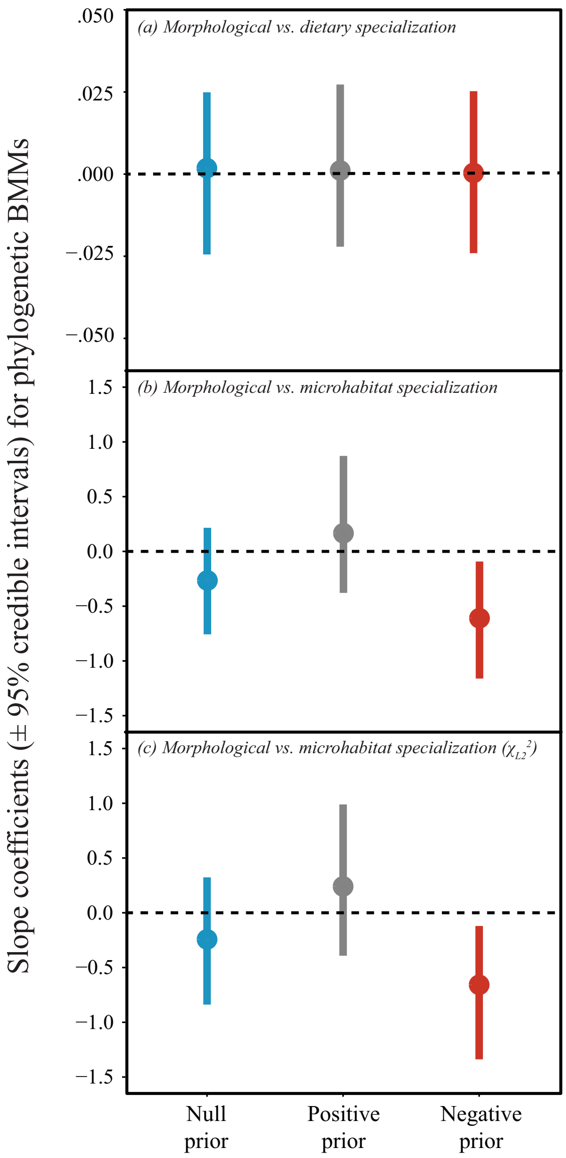


Figure 6.8: Results of the sensitivity analysis. The plot shows the mean posterior estimates of phylogenetic Bayesian Mixed Models (BMMs) testing the effect of morphological specialization on dietary and foraging microhabitat specialization (niche volumes and Manly's χ^2 log-likelihood statistic). The y-axis denotes the mean posterior estimate for the slope parameter. Three different priors were used to simulate prior beliefs about the relationship between morphological and behavioural specialization, specifically a) no relationship ("null prior"), b) a positive relationship

(i.e. morphological specialists are behavioural specialists, “positive prior”), and c) a negative relationship (i.e. morphological specialists are behavioural generalists, “negative prior”). For both metrics of foraging microhabitat specialization, only the negative prior yielded an unambiguous negative relationship. No effect was found for dietary specialization regardless of the used prior.

Table 6.3: Prior specifications and posterior parameter estimates for sensitivity analysis. Symbol indicates the nature of the prior (no relationship, positive, negative).

Relationship modeled	Direction	Fixed effects prior: intercept (α)	Fixed effects prior: slope (β)	Mean posterior slope estimate	Lower/upper 95% CIs
Morphology vs. dietary niche volume	(0)	Pr(μ) ~ N(0, 0.2)	Pr(μ) ~ N(0, 0.2)	0.002	-0.03 / 0.03
	(+)	Pr(μ) ~ N(0, 0.2)	Pr(μ) ~ N(1, 0.2)	0.001	-0.02 / 0.03
	(−)	Pr(μ) ~ N(1, 0.2)	Pr(μ) ~ N(-1, 0.2)	0.0004	-0.02 / 0.03
Morphology vs. microhabitat niche volume	(0)	Pr(μ) ~ N(0, 0.2)	Pr(μ) ~ N(0, 0.2)	-0.265	-0.76 / 0.22
	(+)	Pr(μ) ~ N(0, 0.2)	Pr(μ) ~ N(1, 0.2)	0.166	-0.38 / 0.87
	(−)	Pr(μ) ~ N(1, 0.2)	Pr(μ) ~ N(-1, 0.2)	-0.610	-1.16 / -0.09
Morphology vs. microhabitat selectivity (χ_{L2}^2)	(0)	Pr(μ) ~ N(0, 0.2)	Pr(μ) ~ N(0, 0.2)	-0.243	-0.84 / 0.32
	(+)	Pr(μ) ~ N(0, 0.2)	Pr(μ) ~ N(1, 0.2)	0.241	-0.39 / 0.99
	(−)	Pr(μ) ~ N(1, 0.2)	Pr(μ) ~ N(-1, 0.2)	-0.658	-1.34 / 0.12

6.4 Discussion

6.4.1 Ecological specialization in surgeonfishes

Links between morphological specialization and dietary strategies are widespread, supporting the paradigm that specialized morphological features are related to dietary specialization (Forister et al. 2012; Ferry-Graham et al. 2002a; Douglas & Matthews 1992). However, I found no such relationship in coral reef surgeonfishes, supporting a small number of similar studies in teleost fishes (Liem, 1980; Motta et al. 1995; Barnett et al. 2006; Bellwood et al. 2006; Wainwright et al. 2005). Basically, morphologically similar surgeonfish species showed marked differences in the range of food items ingested (e.g. *A. blochii* vs. *A. nigricauda*), while morphologically disparate species shared a quantitatively similar dietary range (*A. olivaceus* vs. *Z. scopas*). These results call for caution when identifying functional groups based solely on morphological similarity or phylogenetic relatedness: realized niches need to be examined carefully if we are to understand and monitor ecosystem functioning of coral reefs (Bellwood et al. 2004).

In contrast, I found an interesting, negative relationship between morphological specialization and foraging microhabitat preferences in surgeonfishes. While foraging microhabitat utilization has been identified as an important axis of niche partitioning in fishes (Brandl & Bellwood 2014a), few ecomorphological studies have considered the relationship between microhabitat specialization and morphological specialization in a broad quantitative framework (but see Snorrason et al. 1994). For surgeonfishes, it has been proposed that certain morphological characteristics such as a small and deep body, large eyes, a truncate caudal fin, or a concave forehead are linked to the exploitation of concealed resources and that these features enable species to utilize a broad range of resources (Brandl & Bellwood 2013a; Robertson & Gaines 1986). This was supported by my results: morphologically specialized species are microhabitat generalists, while morphological generalists are foraging microhabitat specialists. Two extreme examples are *Z. scopas* and *A. nigricauda*. While *Z. scopas* exhibits a highly specialized morphology, distinguishing it from most other surgeonfish species, this species foraged over the widest range of microhabitats. In contrast, despite exhibiting the generalized *Acanthurus* morphology, *A. nigricauda* almost exclusively targeted flat and exposed rocky substrata.

Furthermore, these patterns are possibly consistent, when the availability of microhabitats is accounted for. For example, the three closely related species *A. blochii*, *A. nigricauda,* and *A. olivaceus* forage almost exclusively on flat horizontal surfaces and although these surfaces are readily available, their disproportional use of open sand, rubble, and rock microhabitats results in a high level of selectivity. In contrast, species such as *Z. velifer* and *A. nigrofuscus* appear to distribute their foraging efforts relatively evenly across available microhabitats, resulting in low selectivity scores for these species. Such patterns of specific habitat or microhabitat use by specialized species has been reported previously in parrotfishes (Bellwood & Choat 1990), but not to the extent seen in surgeonfishes.

The links between morphological and behavioural specialization in surgeonfishes are, in part, driven by phylogenetic relatedness. For example, the two species of *Zebrasoma* are closely related to each other, but phylogenetically distinct from most species within the *Acanthurus* clade (Sorenson et al. 2013). It is therefore not surprising that the two *Zebrasoma* species exhibit a similar morphology and foraging strategies but differ markedly from most of the *Acanthurus* species. Despite this clear influence of shared ancestry, the phylogenetically corrected BMMs suggest that the observed relationships are robust and still supported when phylogeny is accounted for. Thus, there appears to be no relationship between morphological and dietary specialization, while the negative relationship between morphological and microhabitat specialization is consistent for the overall niche volume measures and, to a lesser extent, possibly for microhabitats selectivity (Manly's χ^2 log-likelihood ratio). However, given the small sample size of the phylogenetically corrected dataset and the influence of the used priors on the posterior estimates (revealed in the sensitivity analysis), the broader validity of these findings will have to be confirmed using a more extensive sampling protocol, ideally across a broader phylogenetic sample.

Interestingly, the described relationship between morphological and foraging microhabitat specialization is strikingly similar to patterns found in terrestrial plant-pollinator networks. In both arthropod and avian pollinator communities, species with “specialized” morphologies such as long probosces or bills have been identified as generalists, feeding on a wide range of flower types, while species with shorter mouthparts are restricted to flowers with shallow tubes (Borrell 2005; Temeles et al. 2009). These ecological parallels may not be coincidental. Algal and detrital resources on coral reefs and nectar in plant-pollinator communities are both replenished at high rates (Thomson et al. 1989; Bonaldo & Bellwood 2011) and form a highly diverse network of resources with varying accessibility (Jordano et al. 2003). Furthermore, similar to flowers with long tubes, which provide high rewards in terms of available nectar (Gómez et al. 2008), inaccessible microhabitats appear to harbor richer algal resources (Brandl et al. 2014), potentially offering higher rewards than flat microhabitats. Thus, although the two systems exhibit different consumer-producer relationships (mutualism vs. prey-predator relationships; Johnson & Steiner 2000), the ecological processes shaping both plant-pollinator and herbivore-benthos dynamics may be more similar than previously thought. This further suggests that the relationship between morphological and foraging microhabitat specialization present in both systems may be more broadly applicable.

6.4.2 The role of microhabitat specialization for the evolution of coral reefs

The observed pattern in surgeonfishes is superficially consistent with a phenomenon termed Liem's paradox. While the idea of Liem's paradox operating on coral reefs seems appealing in light of the extraordinary diversity present in reef fishes, there are theoretical inconsistencies in the context of my findings. The most popular evolutionary framework for Liem's paradox posits that the basic strategy for every species is to forage on an easily exploitable resource, which is subsequently followed by 'secondary' specialization on less abundant or accessible resources (Snorrason et al. 1994). In the Acanthuridae, however, specialized morphotypes similar to *Zebrasoma* or *Naso* are recorded from coral reefs in the Eocene 60 Ma (Bellwood et al. 2014), suggesting that microhabitat generalists have been present on reefs throughout most of their evolutionary history. Furthermore, although generalized morphs were also present in the Eocene (Sorenson et al. 2013), the expansion of morphological generalists specialized on flat microhabitats appears to have been a later trend (rapidly increasing species richness and relative abundance in the Miocene ca. 25 Ma), questioning the applicability of Liem's paradox in this case. Interestingly, reef parrotfishes which predominantly target open microhabitats (Price et al. 2010; Brandl & Bellwood 2014a), also appeared on scleractinian-dominated reefs around the same time as surgeonfishes of the genus *Acanthurus* (Choat et al. 2012), supporting the hypothesis that increased exploitation of open microhabitats occurred predominantly in the Miocene. It appears probable that morphological specialists added the exploitation of open microhabitats to their initial feeding repertoire and that the subsequent major radiations in surgeonfish lineages specialized on flat open microhabitats may be due to the increased availability of these foraging surfaces.

There are three non-exclusive hypotheses that may explain this trend: first, mirroring recent trends towards the loss of topographical complexity on coral reefs (Alvarez-Filip et al. 2009), coral reefs may have undergone a transition from complex, micro-topographically intricate systems to flatter, less complex systems over the last fifty million years through increasing rates of external bioerosion (Bonaldo et al. 2014), resulting in an increase in the proportion of planar surfaces with easily accessible resources for herbivorous/detritivorous fishes. Second, biotic or abiotic processes such as sea level fluctuations or increasing calcification and accretion may have increased the extent of reef flats, a habitat that frequently supports the largest area of hard, open surfaces on modern coral reefs (Bellwood & Wainwright 2002) in the most productive zone of primary production (Steneck 1988). Finally, reef flats may have been available throughout the last 60 Ma, but the establishment of a nutritionally attractive epilithic algal matrix and its associated detrital resources may have only arisen once coral reef fishes increased grazing intensities throughout their radiation in the Miocene (Bellwood et al. 2014; Steneck 1983; Cowman & Bellwood 2013), leading to the evolution of specialized herbivores foraging exclusively on flat open surfaces. In all three cases, the expansion of specialized open-microhabitat foraging species appears to have been an essential step in the establishment of modern herbivorous coral reef fish assemblages.

6.4.3 Significance, limitations, and future perspectives

Ecomorphological assessments attempting to relate morphological specialization to dietary specialization have been invaluable for our understanding of the ecology and evolution in animals. However, there is increasing evidence that the relationship between morphological specialization and dietary preferences is multifaceted and often less clear and linear than expected. I do not suggest that the link between morphological specialization and diet in reef fishes (or, more specifically, surgeonfishes) is absent; such a conclusion would be unwarranted given the potential for more detailed assessments of this relationship (such as a higher resolution classification of morphology or dietary items or the mapping of the latter onto different microhabitats). However, my study serves as a cautionary note, suggesting that there is a potential for more than one ecologically significant axis that one may find reflected in a species' morphology.

Our findings present an intriguing case for the exploration of foraging microhabitats as a potentially important niche axis in benthic feeding reef fishes. Although limited by the relatively small sample size of ten species with shared ancestries within a large lineage, the results suggest that the identified pattern may persist if the assessment is expanded. Furthermore, the list of factors that may influence the foraging behavior and microhabitat selection of reef fishes is long: exploring the range of dietary items present in various microhabitats and their rate of replenishment, a finer classification of dietary items, or nutritional analyses of resources in different microhabitats and their post-ingestive utilization by both specialists and generalists would offer interesting avenues for future research and may help uncover more detail about the dynamics between benthic organisms and mobile consumer communities on coral reefs. Here, I am only scraping the surface of a largely untouched ecological niche axis. Nevertheless, my findings, particularly regarding the similarities between plant-pollinator communities and coral reef herbivores and the superficial parallels to Liem's paradox, are encouraging for future investigations of foraging microhabitat utilization on coral reefs.

6.4.4 Conclusion

Our study shows that morphological specialization and its behavioural correlates are not as easily inferred as frequently assumed. I demonstrate that there is no evidence for a correlation between morphological specialization and dietary specialization, but reveal a potential link between morphological specialization and foraging microhabitat specialization. However, this relationship is inverted: species with specialized morphologies are foraging microhabitat generalists while generalized morphotypes are behaviorally specialized on exposed microhabitats. These results suggest that we may need to look beyond the most commonly investigated links between species’ morphological and behavioural niches and that on coral reefs, morphological specialization may be tightly intertwined with foraging microhabitat utilization. Consequently, the use of different microhabitats may be an important ecological axis to understand the past, present, and future of coral reefs.

Chapter 7: Micro-topography mediates interactions between corals, algae, and herbivorous reef fishes on a mid-shelf reef

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7.1 Introduction

The last two to three decades have seen the degradation of many coral reef systems around the world. Although subject to various stressors, degraded reef systems are commonly characterized by marked changes to the benthic community composition (Bellwood et al. 2004; Norström et al. 2009). One of the most prominent is a shift from scleractinian corals to macroalgae as the dominant benthic component (Hughes 1994; Cheal et al. 2010; Rasher et al. 2013). If we are to understand the basis of such transitions, it is essential to understand the population dynamics of both corals and macroalgae, and the factors that shape their interactions (McCook et al. 2001; Vermeij et al. 2009; Sotka & Hay 2009; Diaz-Pulido et al. 2010).

The life history and population dynamics of scleractinian corals have attracted much attention. Due to their planktonic larval stage, coral populations are largely shaped by the addition of new individuals from the pelagic environment (i.e., settlement) and early post-settlement mortality (Baird & Hughes 1997; Hughes et al. 1999; Mundy & Babcock 2000; Ritson-Williams et al. 2010). The settlement of corals has been studied in both the field and laboratory using experimental settlement surfaces (e.g., terracotta tiles), which are readily colonized by coral planulae (e.g., Harriott & Fisk 1987; Mundy 2000; Penin et al. 2010). These studies suggest that coral planulae actively choose microhabitats based on environmental factors, including exposure (Maida et al. 1994), depth (Baird et al. 2003) or the presence and type of crustose coralline algae (CCA) (Raimondi and Morse 2000;

Harrington et al. 2004). Similarly, by settling recruits on experimental tiles and transplanting the tiles onto the reef, many studies have investigated spatial variation in post-settlement survival of coral spat (e.g., Babcock & Mundy 1996; Ritson-Williams et al. 2010; Penin et al. 2011). The most frequently identified environmental factors influencing the post-settlement survival of juvenile or newly settled corals include sedimentation, grazing pressure by herbivorous fishes or invertebrates, and competition with other benthic organisms, particularly algae (Sammarco 1980; Hodgson 1990; Birrell et al. 2008).

Several studies have emphasized the importance of algal competition and herbivorous grazing in shaping post-settlement mortality in corals (Mundy and Babcock 2000; Arnold et al. 2010; Penin et al. 2010; Trapon et al. 2013a,b), identifying three main types of interaction. Firstly, macroalgae can be detrimental for the settlement and survival of coral recruits as they compete for space (e.g., Box & Mumby 2007). Although the mechanisms of algal interference with coral juveniles are not well resolved (Vermeij et al. 2009), and may depend on algal and coral identity (Birrell et al. 2008), mechanical and chemical/allelopathic defenses of macroalgae do appear to play an important role (Rasher et al. 2011). Secondly, coral reef herbivores control algal growth and can facilitate coral survival and replenishment by removing algal competitors and opening space for settlement (Hughes et al. 2007; Arnold et al. 2010; Rasher & Hay 2010; Rasher et al. 2012, 2013). Finally, herbivores may also increase mortality of small or recently settled corals via incidental grazing. This has been reported for both echinoid grazers (e.g., Sammarco 1980) and scraping parrotfishes (e.g., Brock 1979; Day 1983; Penin et al. 2010, 2011). Given the influence of algae and herbivores on the post-settlement survival of juvenile corals, it may be postulated that algal competitors and grazing fishes would play a key role in shaping abundance patterns of juvenile corals. However, their relative importance in shaping patterns of settlement and post-settlement mortality remains to be determined, especially for corals on natural reef substrata.

It is often assumed that many corals settle in cryptic habitats to avoid mortality due to incidental grazing, despite intense competition for space in these concealed microhabitats (Day 1983; Carlon 2001; Edmunds et al. 2004). In most experimental frameworks, coral planulae settle preferentially to cryptic habitats (i.e., the undersurfaces of tiles) as opposed to open, exposed surfaces (Maida et al. 1994; Babcock & Mundy 1996; Vermeij 2005; Arnold et al. 2010). Further, the availability of micro-crevices on settlement tiles has been shown to significantly increase the survival of corals in the first year post-settlement (Nozawa 2008). However, in the few observational field studies that have reported microhabitat associations on natural reef surfaces, juvenile corals have been found to be most abundant on open surfaces (Florida Keys: Edmunds et al. 2004; Palmyra Atoll: Roth & Knowlton 2009; Great Barrier Reef: Trapon et al. 2013a). This apparent disparity between coral settlement preferences on artificial substrata and observations of micro-habitat associations on natural reef substrata may be related to the relative size of the crevices, differential settlement preferences and/or juvenile survival patterns, or be an artefact of the experimental set-ups. For example, coral larvae may settle into micro-crevices and then outgrow the micro-crevice to become associated with more open substrata as a juvenile. Alternatively, the common use of artificial surfaces in experimental studies and the exclusion of extrinsic factors such as competition or predators under experimental conditions may have contributed to differences between experimental and observational studies. There is a clear need to understand the role of these extrinsic factors in shaping juvenile coral assemblages.

Of the observational studies assessing the microhabitat associations of juvenile coral none included distributions of potential competitors, and only one study (Trapon et al. 2013a) evaluated the intensity of herbivorous grazing on juvenile coral survival. Grazing pressure on juvenile corals is believed to be an important source of mortality and is commonly associated with echinoids and / or scraping and excavating parrotfishes (f. Labridae). The vast majority of studies assessing the effect of herbivores on juvenile corals do not distinguish the relative impact of the various herbivorous groups (Brock 1979; Penin et al. 2010, 2011; but see Sammarco 1980; Trapon et al. 2013a). Yet herbivorous fishes differ markedly in their diet and feeding mode and can have highly dissimilar impacts on the reef substratum and its benthic community (Bellwood & Choat 1990; Burkepile & Hay 2008, 2011; Green and Bellwood 2009; Rasher et al. 2013; Hoey et al. 2013), including corals (Bonaldo and Bellwood 2011). As such, parrotfishes are more likely to cause incidental damage through non-selective scraping of the reef substratum, while the more selective removal of algal filaments by cropping and browsing species is less likely to affect coral juveniles (Trapon et al. 2013b). It thus appears necessary to evaluate the functional relationship between corals, algae and individual taxa of herbivores, rather than examining the distribution of herbivorous fishes *per se*, in order to explore their possible impact on benthic organisms (Baria et al. 2010).

The aims of the present study, therefore, were to 1) quantify the distribution patterns of juvenile corals and early life-stages of a potential macroalgal competitor, *Turbinaria ornata* (Gleason 1996; Shearer et al. 2012) with regards to microhabitats and reef zones, and 2) to examine their distribution in relation to abundance patterns of large grazing herbivorous fishes.

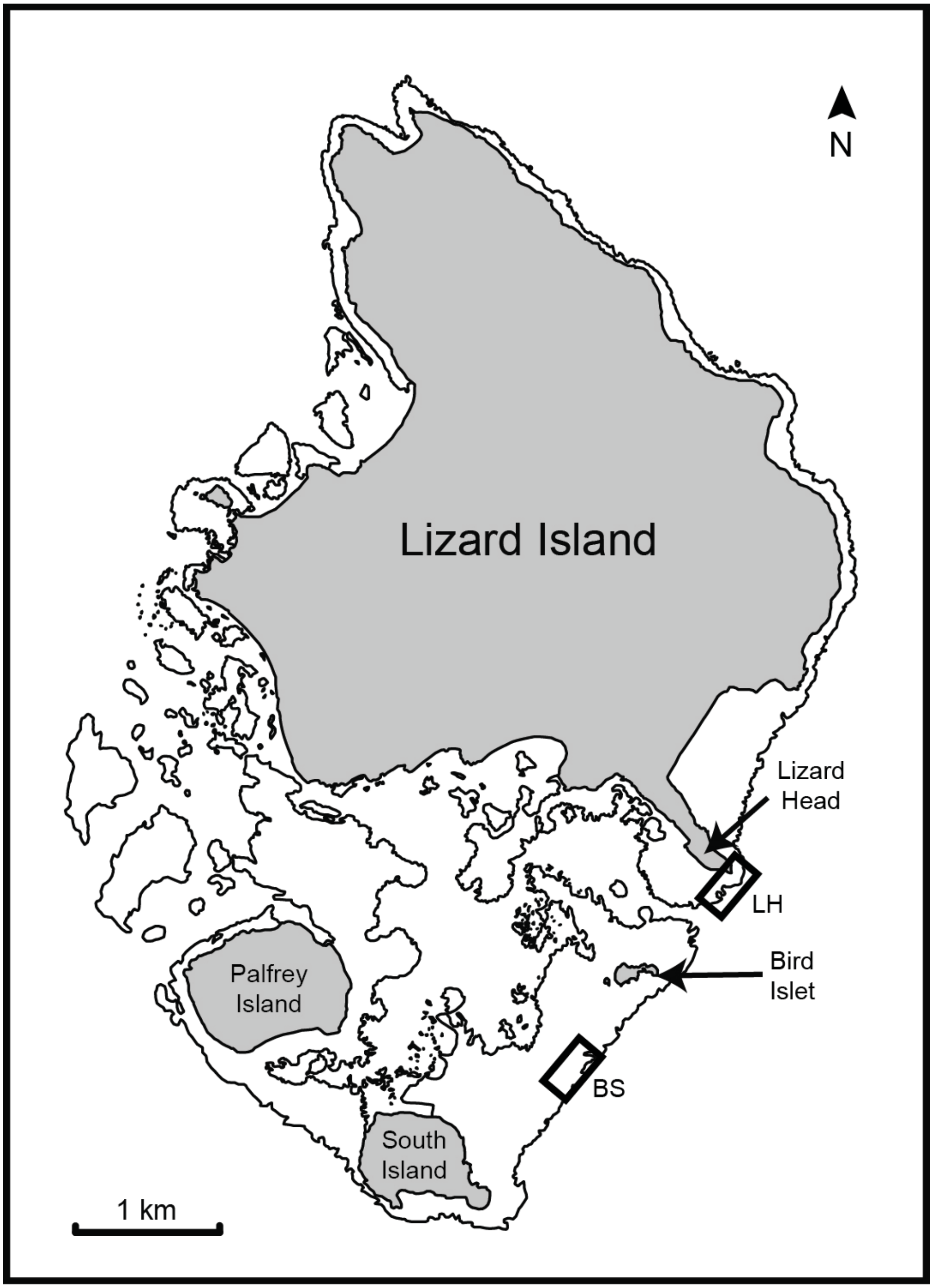


Figure 7.1: Map of Lizard Island. The two sites (BS = Bird – South; LH = Lizard Head) are marked by rectangles.

7.2 Materials and methods

The study was conducted on reefs around Lizard Island, a mid-shelf island in the Northern Great Barrier Reef, Australia (14°40’08”S 145°27’34”E). Two reef sites were examined, between Bird Islet and South Island (BS) and Lizard Head (LH) (**Figure 7.1**). Both sites are typical exposed reef systems and display distinct topographic zonation patterns. This includes a reef base, a distinct reef crest and a low complexity reef flat. The reef crest at both sites was marked by high adult coral cover and low macroalgal abundance, while the reef flat in both areas was characterized by low adult coral cover and the presence of large, erect macroalgae, particularly the fleshy brown alga *T. ornata* (Fucales, Phaeophyceae). Juvenile corals and algal thalli were quantified in two zones, the reef crest and the outer reef-flat (approximately 10 – 15 m behind the crest). These zones were chosen because they offer the highest potential for interactions between juvenile corals and macroalgae, as both adult coral colonies and macroalgal thalli were present in the immediate vicinity.

7.2.1 Benthic transects

To quantify the distribution of juvenile corals and macroalgae, five quadrats (1m^2) were placed haphazardly along a 50 m belt transect, laid parallel to the reef crest. Five transects were laid in each reef zone (crest, outer flat), at each site (BS, LH) resulting in a total of 20 transects and 100 quadrats. In each quadrat, juvenile corals (< 50mm diameter; following Rylaarsdam 1983) and early life-stage macroalgal thalli (< 50mm high) were counted using SCUBA. Due to low abundances and difficulties in reliably distinguishing between juveniles and partial mortality remnants in massive corals, the juvenile coral assessment was restricted to the families Acroporidae and Pocilloporidae. For the investigation of macroalgal distribution patterns, *T. ornata* was chosen, as it was by far the most abundant macroalgal species in the area (> 95% of all fleshy macroalgae observed) and allowed for reliable identification of early life-stages based on the height of the thalli. The microhabitat of every sampled juvenile coral colony or macroalgal thallus was characterized as concealed, semi-concealed or open. Microhabitats were considered concealed if the colony / thallus was found within a feature that was only accessible from one direction (i.e., holes or crevices). Semi-concealed habitats had access from two different directions (i.e., grooves or ledges), while in open microhabitats, the colony / thallus was fully exposed and accessible from every lateral direction within 20 cm of the colony / thallus. Grooves are defined as long concavities accessible from the top and two sides while ledges are defined as steps in the substratum with the organism growing in the angle. Concealed and semi-concealed microhabitats represented less than 10% of the total available area within all quadrats examined. All sampled colonies or thalli were measured using vernier calipers (corals: length, width and height with the 50mm cutoff based on mean colony diameter; algae: height) and photographed. Each quadrat was searched systematically for a minimum of 15 minutes and from four different angles to ensure standardized, comprehensive sampling of juvenile coral colonies and *T. ornata* thalli. Each *T. ornata* thallus recorded was examined for any evidence of feeding by macro-herbivores. Feeding events were readily identified by hemispherical bite marks and clearly severed blades.

7.2.2 Fish transects

The herbivorous fish community was assessed using underwater visual censuses along haphazardly laid 50 x 5 m belt transects in the same reef zones and sites as above (5 transects per zone at each site). All large mobile, herbivorous fishes (families Acanthuridae, Labridae, Siganidae) were counted while deploying the transect tape, to minimize disturbance (Dickens et al. 2011). Smaller, sedentary herbivores such as territorial pomacentrids were not included as they were extremely uncommon at the examined sites (cf. Ceccarelli et al. 2005; Hoey &

Bellwood 2010a). Fishes were identified to species and placed in six 5 cm size classes (10 – 15cm etc. to 35cm and > 35cm) based on visual assessments. Above 35 cm total length, a size estimate was recorded to allow for a more accurate assessment of fish biomass. All observations were performed by the same trained observer (SJB) between 1000 and 1600 hrs.

7.2.3 Statistical analysis

The distribution patterns of juvenile corals and macroalgae were analyzed using a generalized linear mixed effects model (GLMM) with a Poisson error distribution and log-link function. GLMMs were chosen as the data violated parametric assumptions even after transformation. Site, zone and microhabitat were treated as fixed effects, while transects were treated as a random factor. Deviance statistics were generated for different models and Chi-squared tests were implemented on the deviance statistics to compare the significance of explanatory variables in the models. GLMMs were applied to coral and macroalgae counts separately. Models were selected using the Akaike information criterion (AIC). In addition, the occurrence of bite marks on macroalgal thalli was compared between the crest and the outer flat using Pearson’s Chi-squared test. To visualize results and obtain a distance matrix for the BEST ENV-BIO routine (see below), a non-metric multidimensional scaling analysis was performed using Euclidean distances of juvenile corals and early life-stage macroalgae in different microhabitats, grouped by transects.

Fish abundance data were converted to biomass 250 m^{-2} (using published length-weight relationships; following Hoey & Bellwood 2009), and then differences between sites and zones were analyzed using a two-way analysis of variance (ANOVA). Assumptions of the ANOVA were tested using a Shapiro-Wilk test for normality of residuals and Bartlett’s test for homogeneity of variances. The species community composition within transects was analyzed using non-metric multidimensional scaling of a Bray-Curtis distance matrix of the abundance data.

Subsequently, a BEST ENV-BIO routine was performed using the two distance matrices for coral juveniles / macroalgae and fish abundance (following Clarke and Ainsworth 1993; Clarke & Warwick 2001). This procedure allows for the exploration of relationships between two distance matrices, one of which being patterns observed in selected biota (i.e., coral and algal distribution patterns) while the other distance matrix is based on extrinsic or environmental factors (in this case abundance of herbivorous fish species). To this end, a Spearman's rank correlation coefficient (ρ) between the two matrices is calculated for every combination of variables, extrapolating the combination of extrinsic factors (i.e. a suite of herbivorous fish species) that best predicts the observed distribution patterns. The significance of explanatory variables was assessed using 999 randomized permutations under the null hypothesis that there is no correlation of variables between distance matrices (Clarke et al. 2008). The BEST ENV-BIO routine was performed using the software PRIMER. All other statistical analyses were performed using the software R and the packages *lme4* and *MuMIn* (R Development Core Team 2012).

7.3 Results

Overall, 424 juvenile coral colonies and 122 juvenile macroalgae thalli were recorded across the study area. The mean number of juvenile corals per quadrat was 4.2 ± 0.3 colonies m^{-2} (SE) and early life-stage *T. ornata* thalli was 1.2 ± 0.2 thalli m^{-2} (SE).

7.3.1 Distribution patterns of juvenile coral colonies

The majority of juvenile corals were found in concealed microhabitats and were most abundant on the reef crest (**Figures 7.2, 7.3**). Concealed microhabitats supported more than three times more colonies (2.9 ± 0.2 colonies m^{-2} SE) than semi-concealed (0.8 ± 0.1 m^{-2} SE) or open (0.5 ± 0.1 m^{-2} SE) microhabitats. Coral juveniles were almost twice as abundant on the reef crest (5.5 ± 0.4 colonies m^{-2} SE) than on the outer flat (3.0 ± 0.3 colonies m^{-2} SE). This was reflected in the GLMM, where the outer flat ($P < 0.001$) and semi-concealed and open microhabitats ($P < 0.001$) showed a significant negative association with the abundance of juvenile corals. The model including only reef zone and microhabitat performed better than a GLMM including site as a fixed factor ($\chi^2 = 0.8$, $P = 0.4$) and/or a site × zone interaction term ($\chi^2 = 2.5$, $P = 0.3$, **Table 7.1**), suggesting that sites had no significant effect on the observed distribution patterns. In only 1.6% of all records (6 occasions) were juvenile corals and early life-stage *T. ornata* found in the same hole or crevice (**Figure 7.3**).

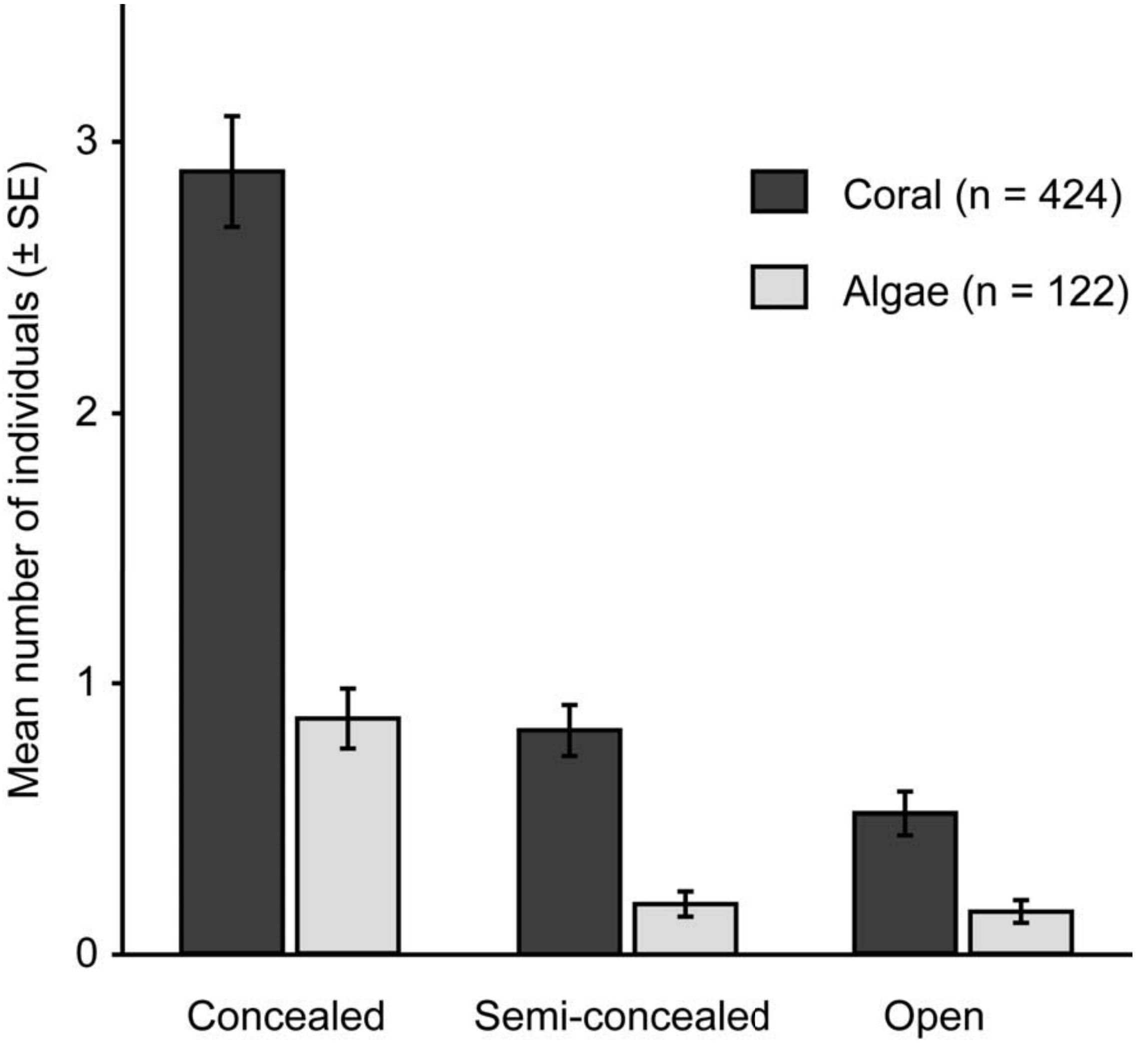


Figure 7.2: Distribution patterns of juvenile corals and early life-stage *Turbinaria ornata* thalli among microhabitats. The average number of individuals per quadrat is significantly higher in concealed microhabitats for both organisms with more than four times more individuals present in concealed microhabitats than in semi-concealed or exposed habitats.

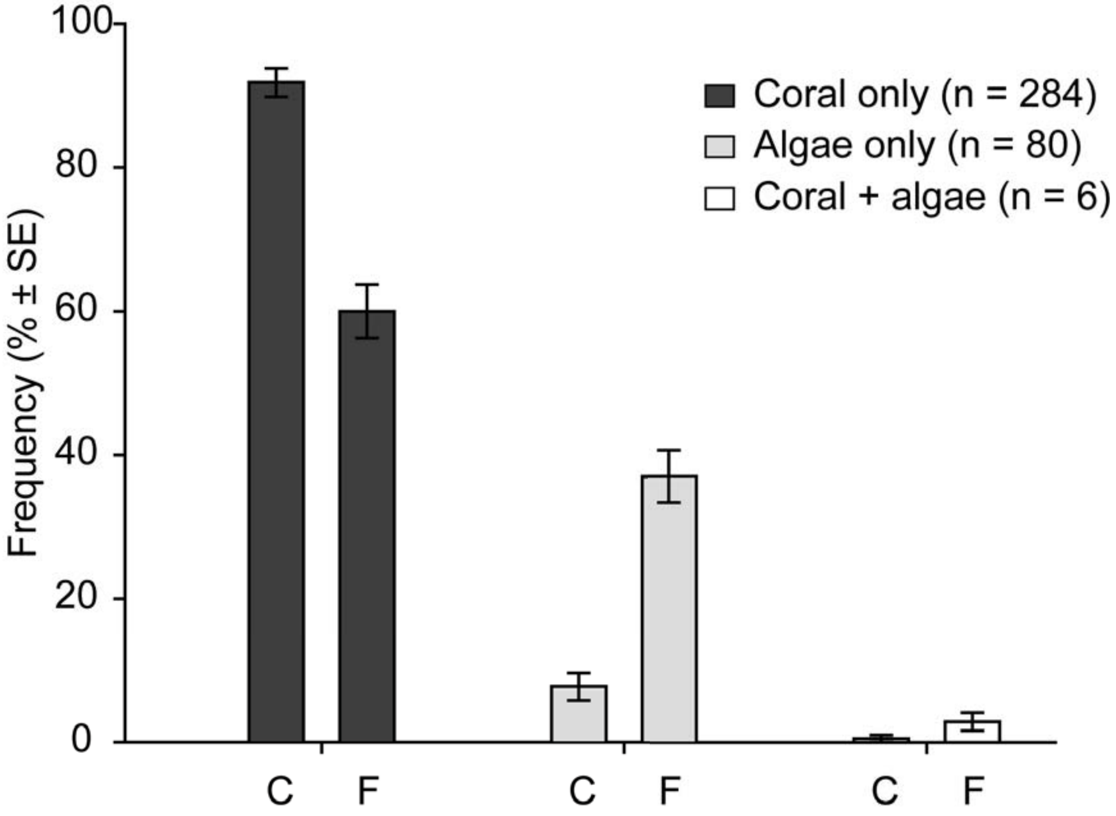


Figure 7.3: Proportion of juvenile corals, algae and both organisms in crevices in different reef zones. On the crest, 92% of records were corals only, while only 60% of records on the flat were corals only. Records of both organisms within the same crevice are rare in both reef zones (n = 6), amounting to only 1.6% of all records. C = Crest, F = Flat.

Table 7.1: Summary of generalized linear mixed model (GLMM) using a Poisson error distribution. Models are compared using the Akaike information criterion (AICc). Only models that perform better than the null model and the null model itself are considered. Shown are degrees of freedom (df), model maximum log-likelihood (logLik), Akaike's information criterion (AICc), changes in the AIC (Δ) and AIC weight (wAIC).

Coral models	df	logLik	AICc	Δ	wAIC
Exposure + Zone	4	-177.73	363.6	0.00	0.507
Exposure + Site + Zone	5	-177.33	364.9	1.27	0.269
Exposure + Site + Zone + Site×Zone	6	-176.48	365.2	1.65	0.223
Exposure	3	-185.36	376.8	13.21	0.001
Exposure + Site	4	-185.15	378.4	14.84	0.000
Zone	3	-283.85	573.8	210.18	0.000
Site + Zone	4	-283.44	575.0	211.43	0.000
Site + Zone + Site×Zone	5	-282.59	575.4	211.80	0.000
Null	2	-291.48	587.0	223.4	0.000

Algae models	df	logLik	AICc	Δ	wAIC
Exposure + Zone	4	-108.76	225.7	0.00	0.480
Exposure + Site + Zone	5	-108.06	226.3	0.68	0.341
Exposure + Site + Zone + Site×Zone	6	-107.67	227.6	1.97	0.179
Exposure	3	-120.98	248.0	22.40	0.000
Exposure + Site	4	-120.90	249.9	24.29	0.000
Zone	3	-142.07	290.2	64.56	0.000
Site + Zone	4	-141.37	290.0	65.23	0.000
Site + Zone + Site×Zone	5	-140.98	292.2	66.51	0.000
Null	2	-154.21	314.5	88.85	0.000

7.3.2 Distribution patterns of juvenile algal thalli

As in corals, early life-stage *T. ornata* were more abundant in concealed microhabitats (0.9 ± 0.1 thalli m^{-2} SE) than in semi-concealed (0.2 ± 0.1 m^{-2} SE) or open (0.1 ± 0.0 m^{-2} SE) microhabitats (**Figures 7.2**). However, in contrast to coral juveniles, early life-stage *T. ornata* were more abundant on the outer flat (2.1 ± 0.2 thalli m^{-2} SE) than on the crest (0.4 ± 0.1 m^{-2} SE) (**Figure 7.3**). This was reflected in the GLMM, which identified a significant negative association of *T. ornata* thalli abundance with the reef crest ($P < 0.001$) and semi-concealed and open microhabitats ($P < 0.001$). As in the model describing the distribution of juvenile coral colonies, this model was preferred over models including site as a fixed factor ($\chi^2 = 1.4$, $P = 0.2$) and/or an interaction term between site and zone ($\chi^2 = 2.2$, $P = 0.3$, **Table 7.1**), indicating that site had again no significant effect on the observed distribution patterns. The distribution of bite marks on early life-stage *T. ornata* varied significantly between reef zones, with a higher proportion of bite marks present on thalli from the reef crest (42.1% with bite marks) than on the outer flat (21.2% with bite marks) ($\chi^2 = 4.5$, $P < 0.05$).

7.3.3 Distribution patterns of herbivorous reef fishes

A total of 1,234 herbivorous fishes, in 30 species within three families (Acanthuridae, Labridae, Siganidae) were recorded. The average biomass of herbivorous fishes displayed no consistent relationships between habitats or sites (Site × Zone: $F_{1,20} = 9.2$, $P = 0.008$). On the reef crest the average biomass of herbivorous fish was lower at BS than LH (13.9 ± 1.9 and 21.8 ± 3.8 kg.250m^{-2} SE, respectively), while on the outer reef flat herbivorous fish biomass was lower at LH than BS (10.5 ± 3.0 and 18.8 ± 1.3 kg.250m^{-2} SE, respectively). Sites and reef zones alone had no significant effect on fish biomass (Site: $F_{1,20} = 0.003$, $P = 0.957$; Zone: $F_{1,20} = 1.4$, $P = 0.249$).

Non-metric multidimensional scaling of the distance matrices computed for coral juveniles / early life-stage *T. ornata* and fish data both yielded a clear separation of the reef crest from the outer flat (**Figure 7.4**). Corals, in all three microhabitats, characterized the reef crest, while the outer flat was distinguished by *T. ornata*. Among herbivorous fish species, the reef crest was characterized by the surgeonfishes *Zebrasoma scopas* and *Ctenochaetus striatus*, pairing rabbitfishes (including *Siganus doliatus, S. vulpinus, S. corallinus, S. punctatus*) and some scraping parrotfishes (*Scarus niger*, *S. dimidiatus, S. oviceps*). The outer reef flat was characterized by schooling rabbitfishes (*Siganus argenteus* and *S. canaliculatus*), several scraping parrotfishes (*Scarus psittacus, S. rivulatus* and *S. schlegeli*) and surgeonfishes (*Acanthurus nigrofuscus*, *A. lineatus*, *A. olivaceous*). The BEST ENV-BIO routine identified pairing rabbitfishes (*Siganus puellus*, *S. punctatus*) and the surgeonfish *Zebrasoma scopas* to be the species that best predicted the observed patterns in the abundance of coral juveniles and early life-stage *T. ornata* (Spearman rank correlation obtained under 999 permutations: $r_s = 0.72$, $P < 0.001$). All three species were completely absent from reef flat habitats and, although not numerically abundant (mean 2.0 ± 0.5 individuals $250m^{-2}$), were consistently present on the reef crest, suggesting a positive relationship between the abundance of the three species and the observed distribution of corals and a negative relationship with the distribution of *T. ornata* when considering the resultant MDS plots (**Figure 7.5**).

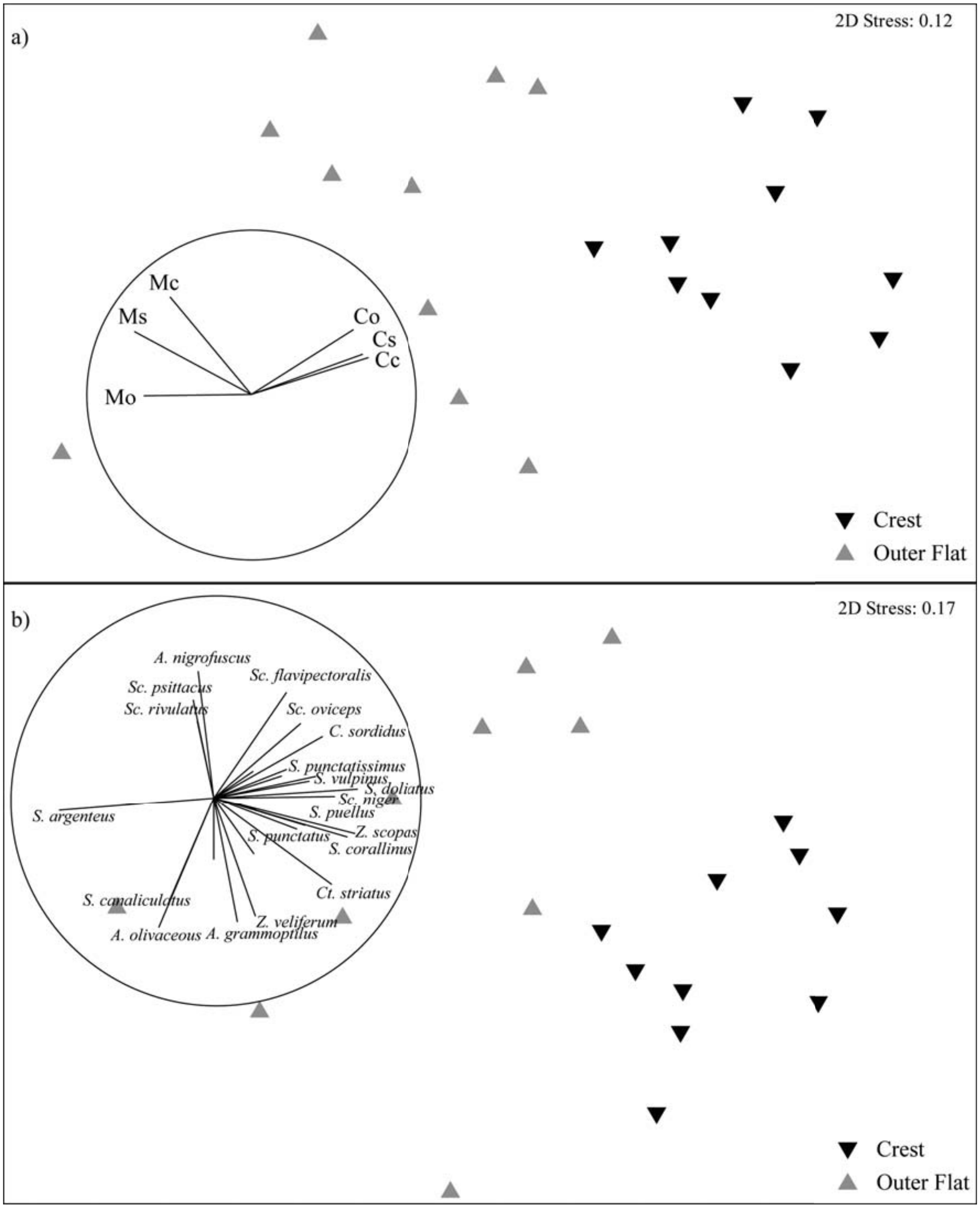


Figure 7.4: Non-metric multidimensional scaling analyses performed on distance matrices for (a) benthic patterns and (b) the distribution of herbivorous fishes. Both ordination plots show a clear segregation in transects on the crest and outer flat. (a)

The crest is characterized by corals in all microhabitats (Cc = coral concealed, Cs = coral semi-concealed, Co = coral open) while the outer flat supports macroalgal thalli in all microhabitats (Mc = macroalgae concealed, Ms = macroalgae semi-concealed, Mo = macroalgae open). (b) Fish species characteristic for the different reef zones. The reef crest is characterized predominantly by pairing rabbitfishes, *Zebrasoma spp.* and several scraping parrotfishes while the outer flat is dominated by schooling rabbitfishes, detritivorous surgeonfishes and scraping parrotfishes.

7.4 Discussion

Cryptic microhabitats, such as holes and crevices, are often assumed to be important habitats for early life stages of benthic coral reef organisms, primarily as a spatial refuge from predation (Penin et al. 2011; Trapon et al. 2013a, b). There are, however, surprisingly few studies examining the role of these concealed microhabitats for corals and macroalgae, especially on natural reef substrata. My study provides evidence that highlights the potential importance of concealed microhabitats to juvenile corals and macroalgae on the exposed reef crest and outer reef flat zones. Despite juvenile corals and early life-stage *T. ornata* displaying different among-habitat distributions, both were 4-5 times more abundant within concealed microhabitats (i.e., holes and crevices) than in semi-concealed (i.e., cracks and ledges) or open microhabitats. This association with concealed microhabitats is even more striking given that these habitats account for less than 10 % of the available area at the study sites. Furthermore, the observed distribution patterns of juvenile corals and algae were best explained by three fish species, the rabbitfishes *S. puellus* and *S. punctatus*, and the surgeonfish *Z. scopas*. Interestingly, these three species have recently been reported to feed extensively in holes and crevices (Fox & Bellwood 2013), the microhabitat where most juvenile corals and algae were found. This provides correlative evidence, suggesting that microhabitat characteristics may play an important role in the early benthic life-stages of corals and macroalgae, which may add another facet to the complex dynamics between corals, algae and grazing fishes on coral reefs.

7.4.1 Distribution patterns of juvenile corals and macroalgal thalli

The distribution patterns observed in the present study suggest that juvenile corals survive predominantly in concealed microhabitats. This is consistent with previous experimental studies that have found a strong preference for coral planulae to settle in narrow cracks and crevices (Harriott & Fisk 1987; Babcock & Mundy 1996; Raimondi & Morse 2000; Vermeij 2006). However, the results of the present study are in marked contrast to previous field observations (Edmunds et al. 2004; Roth & Knowlton 2009; Trapon et al. 2013a), in which the majority of coral juveniles were found in open, exposed microhabitats. The reasons for these differences are not readily apparent but may be related to variation in the reef zone examined, scale and definition of open vs. concealed microhabitats, availability and size of microhabitats, or a range of biotic (e.g., grazing rates, benthic assemblages) and abiotic (e.g., sedimentation, wave action) factors. Of these, the size of the available crevices may have a large bearing on the microhabitat associations of juvenile corals. Corals may preferentially settle to micro-crevices (<10mm; Nozawa 2008), and then outgrow the microhabitat to appear as a juvenile colony on open, or exposed, substratum. Furthermore, two of these studies were located in biogeographically distinct locations with relatively low-diversity coral communities (Palmyra Atoll: Roth & Knowlton 2009; Florida Keys: Edmunds et al. 2004) and may not be directly comparable to the present study. The third study, however, was conducted on exposed reef crests of nine reefs on the GBR, including those around Lizard Island (Trapon et al. 2013a). Trapon et al. (2013a) reported that relatively few juvenile corals (10-50mm diameter) were found within crevices, but there was significant variation among coral genera and latitudes (i.e. between the southern, central, and northern GBR). The microhabitat associations of juvenile corals may thus depend strongly on local abiotic and biotic factors.

A common explanation for the preference for cryptic habitats by coral planulae is that these habitats reduce post-settlement mortality through incidental grazing by reef herbivores, especially scraping and excavating parrotfishes (Brock 1979; Sammarco 1980; Penin et al. 2011; Evans et al. 2013). Indeed, a recent study at one of the sites used in the present study (BS) demonstrated that the exclusion of herbivorous fishes increased early post-settlement survival of coral recruits on settlement tiles (Trapon et al. 2013b). Furthermore, the survivorship of coral recruits on tiles exposed to herbivores was negatively correlated with the density of parrotfish feeding scars on tiles.

Although there was no relationship between the distributions of juvenile corals or macroalgae and scraping and excavating parrotfishes in the present study, these fishes were present at both sites and in both reef zones, suggesting that grazing pressure on open surfaces (cf. Fox & Bellwood 2013) was high. Grazing-induced mortality as a result of feeding by parrotfishes may have contributed to the abundance of juvenile corals and algae in concealed microhabitats. However, there are many other factors that may contribute to these patterns, including increased survival of juveniles due to reduced abrasion (Hunte & Wittenberg 1992) or decreased potential of dislodgement (Madin & Connolly 2006). Alternatively, crevices may present preferred settlement locations due to, for instance, favourable light regimes (Maida et al. 1994; Babcock & Mundy 1996; Mundy & Babcock 1998; Baird et al. 2003) or the presence of specific coralline algae (Harrington et al. 2004). Given the number of processes that influence settlement choice and post-settlement survival of corals, the grazing pressure administered by herbivorous fishes is likely to be only one of many factors influencing microhabitat distribution patterns of juvenile corals.

Juvenile *T. ornata* were also most abundant in concealed microhabitats, emphasizing the possible importance of concealed microhabitats for the ecology of macroalgae (Diaz-Pulido & McCook 2004). Spatial refuges are assumed to be a beneficial factor for the settlement and survival of macroalgae (Fletcher & Callow 1992) but the effect of crevices on mortality of early life-stage macroalgae have rarely been assessed in the field (but see Diaz-Pulido & McCook 2004). As for corals, multiple factors (e.g., larval supply, water motion, sedimentation) are likely to influence the settlement preferences (Fletcher and Callow 1992), and post-settlement growth and survival (e.g., nutrients, herbivory) of algae. Among these, herbivorous grazing is known to have a major influence on the survival and distribution of algae on coral reefs (e.g., Wright & Steinberg 2001; Hughes et al. 2007; Cheal et al. 2010).

Our two study habitats, the reef crest and outer reef flat, are commonly identified as areas of high herbivore activity (Hay 1981; Fox & Bellwood 2007). Given the detrimental effects of grazing on early life-stages of macroalgae, including *T. ornata* (Vadas et al. 1992; Lotze et al. 2001; Diaz-Pulido & McCook 2003; Stiger & Payri 2005), the high rates of herbivory within these habitats are likely to have reduced the survivorship of any *T. ornata* propagules that settled on exposed microhabitats. Moreover, variation in the consumption of adult or large fleshy fucalean macroalgae (*Sargassum swartzii* and *S. cristafolium*) among seven habitats around Lizard Island, revealed that herbivory was greatest on the exposed reef crest and outer flat, including one of the sites in the present study (Hoey & Bellwood 2009, 2010b). Such high rates of grazing and browsing lends support to the hypothesis that herbivory may be contributing to the observed association of *T. ornata* with concealed microhabitats. However, the differential distribution of adult algae among zones suggests that other factors, such as wave action, sedimentation or larval supply, are also influencing reef-scale distribution patterns of *T. ornata*.

7.4.2 Coral-algae interactions

Although corals and algae are most abundant in concealed microhabitats, they rarely occupied the same hole or crevice. The majority of crevices contained either juvenile corals only, or small *T. ornata* only. In the few cases (n = 6), where a juvenile coral and a small *T. ornata* were found in the same crevice, the corals showed signs of bleaching and/or tissue loss that may reflect the outcomes of competitive interactions (tissue loss, bleaching; **Figure 7.5**). Mechanisms and consequences of algae-coral interactions are still not well resolved, especially between juvenile corals and early life-stage macroalgae (McCook et al. 2001;

Vermeij et al. 2009). However, it is commonly assumed that erect macroalgae can have detrimental effects on corals, especially during their early life stages (Sammarco 1980; Birrell et al. 2008; Diaz-Pulido et al. 2010). *T. ornata* has been suggested to have negative impacts on coral health, growth and recruitment, most likely through mechanical effects such as shading and abrasion (Gleason 1996; Rasher et al. 2012; Shearer et al. 2012). It is possible, therefore, that early life-stages of *T. ornata* may compete with juvenile corals for space within crevices. However, the factors influencing the potential competition between these organisms as well as the results of their competitive interactions are unclear. Thus, future experimental studies are needed to assess if juvenile corals interact with early life-stage macroalgae such as *T. ornata* and, if so, whether concealed microhabitats are a significant venue for these interactions.

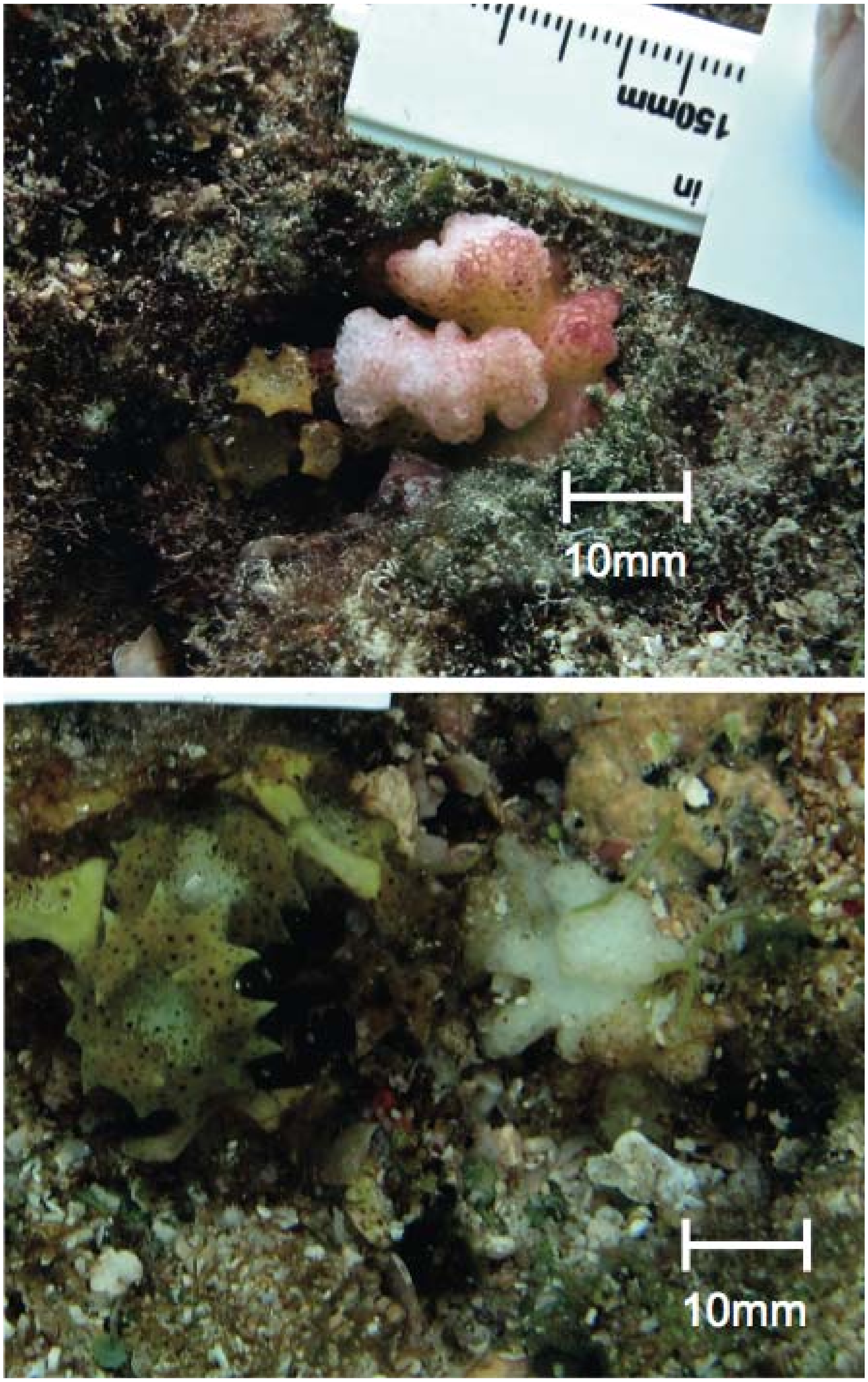


Figure 7.5: Juvenile corals and early life-stage *T. ornata* thalli in the same crevice. a) The *T. ornata* appears to be in direct contact with the juvenile pocilloporid coral, which shows signs of tissue loss and abrasion. b) With *T. ornata* in close proximity,

the juvenile coral is fully bleached. In both cases, the coral exhibits clear signs of competitive interactions with the algae. Signs of bleaching were observed in 66.7% of cases, where corals and algae were found in the same crevice (n = 6), whereas only 6.7% of all other colonies (n = 418) showed signs of bleaching. Photographs are taken at similar magnifications (scale = 10mm).

7.4.3 The distribution of herbivorous reef fishes

Reef crests have been repeatedly reported to support higher species richness and biomass of herbivorous fishes than adjacent reef zones (e.g., Russ 1984; Fox & Bellwood 2007; Hoey & Bellwood 2008). In the present study total herbivore biomass did not differ consistently between the two reef zones, but there was marked variation in the composition of herbivorous fish assemblages between the two zones. Grazing parrotfishes and surgeonfishes were common throughout the study areas, and are known to feed heavily the epilithic algal matrix on exposed surfaces (Bellwood 1995; Fox & Bellwood 2013). Grazing by parrotfishes and surgeonfishes may therefore have contributed to the low abundances of juvenile corals and *T. ornata* on exposed surfaces, however, these fish groups avoid concave surfaces and crevices when feeding (Bellwood and Choat 1990; Bellwood 1995; Fox & Bellwood 2013), which suggests that their influence on the benthos within concealed microhabitats will be limited.

In contrast to the widespread parrotfishes, pairing rabbitfishes and surgeonfishes in the genus *Zebrasoma* were largely restricted to the reef crest in the present study. Interestingly, these species are among a limited suite of nominally herbivorous fishes that have the capacity to exploit a wide range of microhabitats, including holes and crevices, when feeding (Robertson & Gaines 1986; Brandl & Bellwood 2013a,b; Fox & Bellwood 2013). It thus appears that the reef crest harbours a significantly larger biomass of herbivorous species with the capacity to feed on organisms within coral reef crevices, and that the distribution of these species was related to the distribution of juvenile corals (positively) and early life-stage *T. ornata* (negatively) across the study sites. Although only correlative, these relationships point to a potential link between these crevice-feeding fishes and the benthic community within crevices. However, further experimental studies are required to explore the role of fishes in the dynamics of benthic organisms in concealed microhabitats.

The results of the present study provide a useful insight into the interactions between juvenile corals, macroalgae, and grazing herbivores. My data suggests that concealed microhabitats, such as holes and crevices, may play an important role in the early life-stages of corals and algae. Although only providing a preliminary snapshot, my study highlights the potential importance of micro-topography in the dynamics of reef systems, and will hopefully stimulate further research on the role of concealed microhabitats in structuring reef assemblages.

Chapter 8: Micro-topographic refuges drive consumer-producer dynamics by mediating consumer functional diversity

Currently in review as: Micro-topographic refuges drive consumer-producer dynamics by mediating consumer functional diversity (in review).

8.1 Introduction

Herbivory is universally accepted as a critical ecosystem process in vegetated environments (Gruner et al. 2008). Through the disturbance induced by feeding, herbivorous organisms affect producer communities in terms of their biomass, diversity, and productivity (Olff and Ritchie 1998; Worm and Duffy 2003). However, herbivory is multifaceted, and numerous different aspects can influence the dynamics between consumer and producer communities. One crucial factor relates to the functional identity of herbivores. In almost every ecosystem, herbivore communities comprise multiple species that vary in their functional niches, which modulates their effects on producer communities (Sommer 1999). Similarly, producer avoidance of, or tolerance to, herbivory affects dynamics between consumer and producer communities (Duffy and Hay 1990; Rasher et al. 2013). While intrinsic mechanisms to avoid being grazed, such as morphological or chemical defense mechanisms, have received considerable attention (Berenbaum 1995), extrinsic factors that permit producers to escape herbivore pressure are less well understood (Milchunas and Noy-Meir 2002).

Extrinsic factors underlying grazer-avoidance include both biological and physical protection from grazing, i.e. refuges (Duffy and Hay 1990). Biological refuges comprise positive interactions among plant-species, in which species susceptible to grazing gain associational refuge by growing close to an unpalatable or non-preferred species (Pfister and Hay 1988; Stachowicz 2001). Physical refuges usually relate to physical or geological features, which reduce the accessibility of producers to herbivorous grazers (Milchunas and

Noy-Meir 2002). Compared to biological refuges, such physical refuges have received relatively little consideration, despite their demonstrated importance in both terrestrial (Shitzer et al. 2008) and aquatic (Hay 1981; Bergey 2005) environments. Importantly, physical refuges can vary dramatically in scale, ranging from entire islands (Milchunas and Noy-Meir 2002) to micro-topographic structures on the scale of a few millimetres (Menge and Lubchenco 1981; Dudley and D'Antonio 1991; Bergey 2005). Although often inconspicuous, the latter can significantly influence consumer-producer dynamics, especially when grazing pressure is intense (Menge and Lubchenco 1981; Milchunas and Noy-Meir 2002; Bergey 2005).

Many primary producers in marine environments are subject to particularly rigorous consumer control (Gruner et al. 2008; Bennett et al. 2015) and among marine habitats, benthic communities experience the strongest level of herbivore control (Poore et al. 2012). On tropical coral-dominated reefs, grazing pressure is particularly strong and reductions of grazing pressure often lead to the rapid establishment of fleshy macroalgae (Burkepile and Hay 2008; Cheal et al. 2010; Rasher et al. 2013). As a consequence, tight links between strong consumer control by herbivorous fishes and the resilience of coral reefs have been established (Nyström et al. 2008; Graham et al. 2015).

This emphasizes the potential importance of grazing refuges in these ecosystems (Littler et al. 1986). Several cases of biological refuges, in which readily consumed algae associate with species unpalatable to most herbivores, have been reported from coral reefs (Littler et al. 1986; Pfister and Hay 1988). Likewise, physical refuges exist at several different scales, ranging from regional refuges (inner shelf vs. outer shelf on the Great Barrier Reef (GBR) (Wismer et al. 2009), to reef zones (inner flat or sandy plains vs. crest, (Hay 1981; Fox and Bellwood 2007). However, micro-topographic refuges from grazing pressure (i.e. the three-dimensional structure of the reef on the scale of a few centimetres) also represent a widespread type of physical refuge within coral reef systems, occupying up to 25% of the available microhabitats on coral reefs (Brandl et al. 2015). While crevices appear to be critical for the recruitment and survival of scleractinian corals (Brock 1979; Nozawa 2008; Arnold et al. 2010; Brandl et al. 2014; Edmunds et al. 2014), and represent an important ecological axis for niche partitioning in herbivorous fishes (Robertson and Gaines 1986; Fox and Bellwood 2013; Brandl and Bellwood 2014; Brandl et al. 2015), no examination of the overarching effect of micro-topographic refuges on consumer-producer dynamics exists to date.

The purpose of the present study, therefore, was to provide an experimental evaluation of the effects of micro-topographic refuges on grazing dynamics on coral reefs. In quantifying grazing pressure, average turf lengths, the functional identity of grazer communities, and the community composition of the benthos in different microhabitats, we sought to provide answers to the following questions: i) Do micro-topographic refuges reduce the grazing pressure exerted by herbivorous fishes on the benthic community? ii) Is this exclusion evenly spread among fish species and functional groups? and iii) How do changes in grazing pressure and grazer identity affect the benthic community?

By answering these questions, we demonstrate that micro-topographic complexity leads to two distinct grazing regimes on coral reefs, which coexist at the scale of a few centimetres and may represent a key feature of consumer-producer dynamics in reef ecosystems.

8.2 Materials and methods

8.2.1 Data collection

To assess the effects of micro-topographic refuges on fish grazing patterns and the benthic community, I constructed two distinct grazing surfaces. The first, flat surface, consisted of a flat rectangle (length = 115mm, width = 65mm, height = 15mm). The second, complex surface, featured the same dimensions but included six evenly spaced vertical cylinders (radius = 10mm, h = 35mm; spaces between cylinders = 25mm) in two rows of three, to simulate micro-topographic refuges as found on coral reefs (specifically related to dead coral skeletons). On these surfaces, three distinct microhabitats were identified (**Figure 8.1**): flat and exposed (flat tiles without cylinders, henceforth ‘flat’), complex and exposed (the outside and top of cylinders, henceforth ‘exposed’), and complex and concealed (the inside of cylinders and the flat area between, henceforth ‘concealed’). To ensure uniformity among surfaces, I used standardized moulds made from neutral cure sealant, dry cornstarch, and mineral spirits (2:2:1 by volume). Flat surfaces had only the recess (10mm) for the flat rectangular base. For complex surface moulds, holes (depth = 35mm, radius = 10mm) were cut out of the mould using a drill press with a hole-saw fitting. To cast surfaces, a mixture of powdered coral rubble (dried for 72 hours, and pulverized using a sledge hammer), river sand, and cement (1:1:1) was mixed with water and poured into the moulds. This mixture was selected following a pilot study that revealed no differences in the benthic community between natural tiles of dead coral and the rubble-cement mixture (cf. Hixon & Brostoff 1985). After setting the concrete mixture for 48 hours, surfaces were extracted from the moulds and each surface was set centrally in a 750ml disposable plastic container filled with a standard concrete mixture. After setting for 48 hours, the containers were tied together for stability, producing grazing arrays of 20 surfaces (10 of each type). Six arrays were created yielding a total of 120 surfaces with 180 grazing microhabitats (flat *n* = 60, exposed *n* = 60, concealed *n* = 60). Arrays were deployed in groups of three at two different sites along the reef crest between Bird Islets and South Island (near Lizard Island, northern GBR) in the beginning of June 2013.

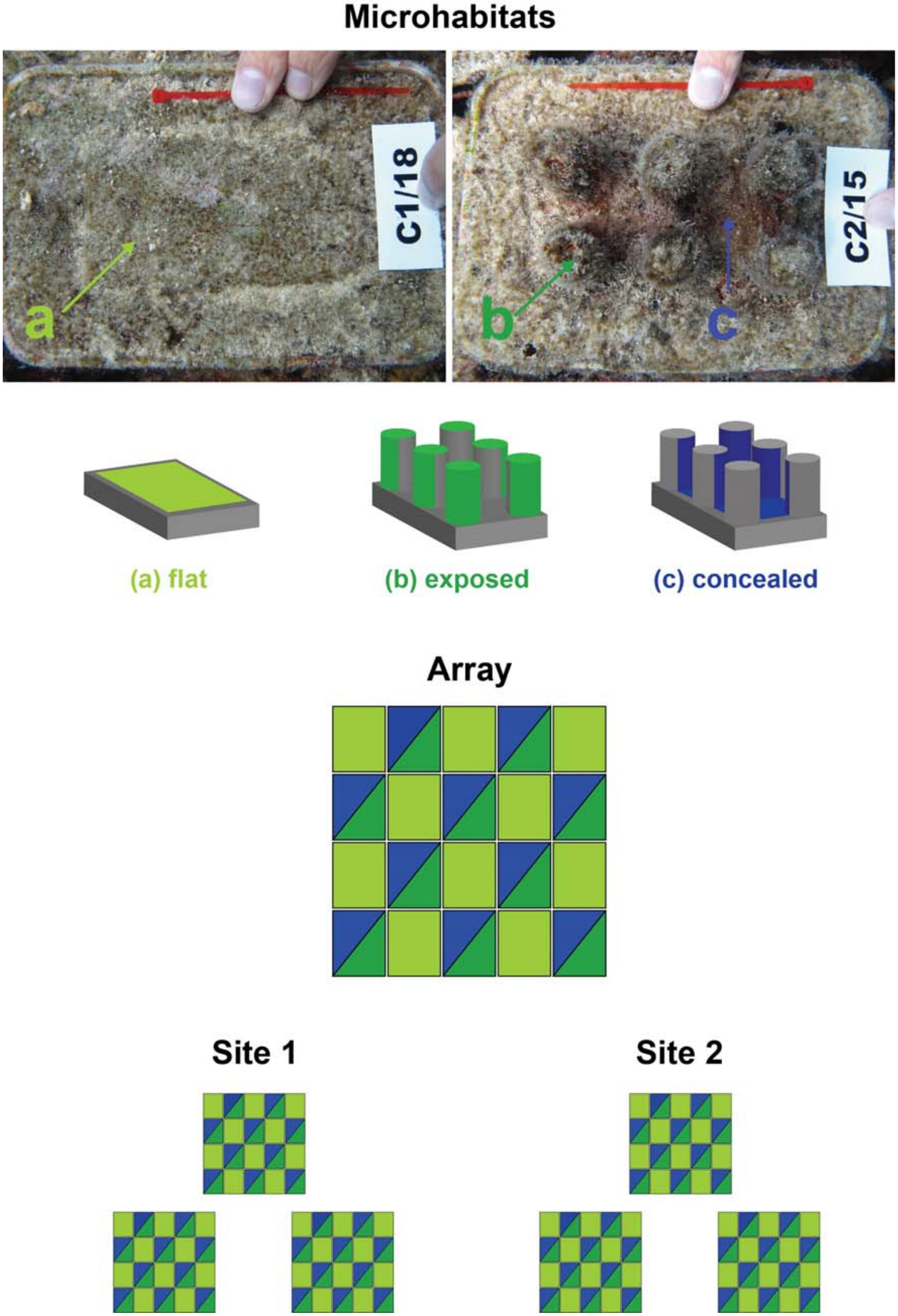

Microhabitats
C1/18
a
C2/15
b
c
(a) flat
(b) exposed
(c) concealed
Array
Site 1
Site 2

Figure 8.1: Description of the three focal microhabitats and deployment of the expierment. Flat microhabitats (a) are flat and exposed, exposed microhabitats (b) are complex and exposed on the outside or top of cylinders, and concealed microhabitats (c) are on the inside of cylinders and in the flat area between cylinders. Arrays consist of ten flat surfaces and 10 surfaces with cylinders, creating 30 non-independent microhabitats per array. Three arrays were deployed at each site.

The arrays were left on the reef for 35 weeks to establish natural benthic communities. Subsequently, the lengths of epilithic turf filaments from each microhabitat were measured using vernier callipers. To do so, the turf filament closest to a haphazardly chosen point was straightened and its vertical extension measured to the nearest millimetre. Ten measurements were taken from each microhabitat. No measurements were taken within 5mm of the edge of the rectangular base to avoid edge effects. Photographs were taken of each microhabitat from a fixed distance of approximately 10 cm to quantify the benthic community composition. Finally, the foraging activity of fish assemblages grazing on the microhabitats was monitored using remote underwater videos (GoPro Hero III) in January/February 2014. Each array was filmed for three to four hours on at least five non-consecutive days, resulting in a total observation period of 111 hours and an average of 18.52 ± 0.07 hours per microhabitat. Subsequently, both benthic photographs and grazing videos were analysed in the lab. On each photograph, I quantified the proportional cover of different benthic organisms from a planar view of the respective microhabitats (all of the flat microhabitat, upward facing circular surfaces for exposed microhabitats, horizontal surface between bases of cylinders for concealed microhabitats). Benthic organisms were assigned to a functional category (Steneck & Dethier 1994), and their proportional cover estimated using the software ImageJ. Videos were analysed by counting the number of bites taken on each microhabitat by all large (>10 cm) mobile herbivorous fish species (*sensu* Choat et al. 2002), since identification of smaller fishes was impossible in the videos.

Published data were used to characterize fish species in terms of their morphology, diet, and gut short-chain fatty acid (SCFA) profile (**Table 8.1**). For the morphology, five traits previously linked to foraging microhabitat utilization (body depth, eye diameter, snout length, snout angle, and head angle), were considered (Brandl & Bellwood 2013a). Trait measurements were regressed against standard length in a dataset comprising 260 individuals in 99 species and residual values were averaged for each species. For the dietary data, due to differences among sources in the functional categorizations of dietary items, a broad classification scheme was created to ensure congruent dietary classifications across taxa. Categories included sediment, organic material, filamentous algae, fleshy/thallous algae, and other items such as benthic invertebrates or foraminifera. For the SCFA profiles, the overall amount of dominant SCFAs (Acetate, Butyrate, Isovalerate, and Proprionate) present in the gut segment with the highest SCFA concentrations was used, as well as the proportional composition of SCFAs.

Table 8.1: Published functional traits describing the morphology, diet, and gut SCFA profiles of the herbivorous fish species present in the study. Morphological trait values are averaged individual residuals extracted from a linear model regressing the respective trait against the measured individuals' standard length (Brandl & Bellwood 2013). Diet values are averaged proportional values of each group of items in the examined individuals' guts (Choat 1969; Choat et al. 2002; Hoey et al. 2013). SCFA values represent the averaged total SCFA concentration in the guts of examined individuals and its proportional composition (Clements & Choat 1995).

Morphology					
Species	**M1**	**M2**	**M3**	**M4**	**M5**
Acanthurus nigricauda	0.018	0.568	0.031	0.021	-0.064
Acanthurus nigrofuscus	0.008	0.397	0.019	0.020	-0.005
Chlorurus spilurus	-0.069	0.379	-0.061	0.011	-0.070
Ctenochaetus striatus	0.043	0.555	-0.025	-0.002	0.014
Scarus frenatus	-0.057	0.339	-0.056	-0.001	-0.040
Scarus globiceps	-0.048	0.339	-0.060	0.008	-0.078
Scarus niger	-0.011	0.338	-0.040	0.006	-0.049
Scarus psittacus	-0.026	0.349	-0.065	0.002	-0.040
Scarus schlegeli	-0.038	0.317	-0.060	-0.013	-0.035
Siganus corallinus	0.009	0.414	0.008	-0.045	0.066
Siganus punctatissimus	0.035	0.315	0.117	0.027	0.084
Siganus punctatus	0.010	0.381	0.040	0.015	0.022
Zebrasoma scopas	0.142	0.600	-0.013	-0.088	0.080
Zebrasoma velifer	0.089	0.625	0.072	-0.055	0.085

Diet					
Species	**D1**	**D2**	**D3**	**D4**	**D5**
Acanthurus nigricauda	37.310	56.197	5.240	0.310	0.943
Acanthurus nigrofuscus	0.829	0.501	0.167	36.652	61.048
Chlorurus spilurus	25.000	16.400	0.000	58.600	0.200
Ctenochaetus striatus	72.581	18.455	1.964	2.957	3.278
Scarus frenatus	10.800	26.700	1.500	55.000	1.600
Scarus globiceps	8.200	27.200	2.300	60.600	1.700
Scarus niger	6.800	27.400	0.400	63.000	2.400
Scarus psittacus	9.700	43.700	1.800	37.700	4.100
Scarus schlegeli	9.700	43.700	1.800	37.700	4.100
Siganus corallinus	7.600	1.000	1.100	28.700	59.750

Siganus punctatissimus	20.500	17.500	21.350	12.200	28.250
Siganus punctatus	11.700	8.000	38.600	6.250	36.100
Zebrasoma scopas	0.000	0.045	2.365	31.368	59.065
Zebrasoma velifer	0.763	0.683	0.297	4.844	92.562

Gut SCFAs **Species**	**S1**	**S2**	**S3**	**S4**	**S5**
Acanthurus nigricauda	9.660	63.730	2.500	2.340	30.820
Acanthurus nigrofuscus	18.180	86.590	4.310	6.190	2.490
Chlorurus spilurus	11.480	87.000	3.070	1.230	8.020
Ctenochaetus striatus	9.070	63.710	3.880	7.030	25.070
Scarus frenatus	9.800	85.260	1.310	1.830	11.290
Scarus globiceps	12.070	75.430	4.340	2.640	17.610
Scarus niger	9.800	85.260	1.310	1.830	11.290
Scarus psittacus	6.170	70.830	1.860	0.910	23.900
Scarus schlegeli	6.170	70.830	1.860	0.910	23.900
Siganus corallinus	10.790	85.390	10.180	1.760	1.640
Siganus punctatissimus	21.860	82.510	10.600	2.240	2.770
Siganus punctatus	14.290	80.990	11.820	2.500	3.000
Zebrasoma scopas	31.940	68.100	25.080	5.240	0.780
Zebrasoma velifer	36.970	72.420	17.150	8.540	1.050

M1:	Body depth	**D1:**	Organic particulates	**S1:**	Total gut SCFAs
M2:	Snout length	**D2:**	Calcareous sediment	**S2:**	Acetate
M3:	Eye diameter	**D3:**	Others	**S3:**	Propionate
M4:	Snout angle	**D4:**	Filamentous algae	**S4:**	Butyrate
M5:	Head angle	**D5:**	Fleshy algae	**S5:**	Isovalerate

8.2.2 Statistical analysis

To assess differences in the overall grazing pressure (number of bites.day^{-1}.cm^{-2}) and the length of turf algal filaments (mm) on the three microhabitat types, Bayesian Mixed Models (BMMs) were performed specifying the microhabitat type (flat, exposed, concealed) as a fixed effect. To account for the spatial non-independence of microhabitats within an array, array was specified to have a random effect. In addition, site was included as a fixed effect as the estimation of random variance can be unreliable if only two levels are available. For the comparison of grazing pressure among microhabitat types (overall grazing pressure model), a Poisson error distribution with a log-link function was specified. Furthermore, bite counts for each microhabitat were modelled against an offset specifying the overall observation period (time in d) and the area available for grazing (area in cm^2). To do so, the log of time and area were included as fixed effects, and informative priors were formulated for the regression coefficients of both factors, specifying a β-parameter of 1 with a variance of 0.000001. Uninformative priors were used on the other fixed effect parameters (mu = 0, V = 100,000,000), and informative priors (V = 0.000001, nu = 100) were used for the residual variance due to over-dispersion in the response variable. The model was run for 10,000,000 iterations, while all other models (throughout the study) were run for 3,000,000 iterations. Chain convergence was validated using trace chain plots. For the comparison of algal filament length (turf length model), a Gaussian error distribution with a link function was used, as data were approximately normally distributed. Uninformative priors were used on the fixed effects and inverse Wishart priors on the random and residual variance (V = 1, nu = 0.002).

To investigate the consumer community feeding on different microhabitat types, as well as their benthic communities, two non-metric multidimensional scaling ordinations were performed on Manhattan distance matrices. Subsequently, permutational multivariate analyses of variance (PERMANOVA) with 999 permutations were performed to investigate compositional differences among microhabitat types, again fitting array as a random effect. I also calculated patterns of consumer species richness interacting with the benthic community, and functional group richness for and benthic communities, respectively, and compared these patterns among microhabitat types using BMMs with a Poisson error distribution and uninformative priors.

Furthermore, I evaluated the functional composition of consumers feeding on the different microhabitat types. I combined the three trait datasets (morphology, diet, and SCFAs) and normalized data to a mean of zero and a standard deviation of 1. I then calculated pairwise distances among species using Gower's distance metric and divided the community into functional groups using a hierarchical clustering analysis with Ward's method. This resulted in two broad functional groups. I then extracted the number of bites taken on each microhabitat by the two functional groups and computed the bite-weighted trait means for the grazer community feeding on each microhabitat.

In order to compare the grazing pressure exerted on the different microhabitat types by each of the two functional groups, I used two zero-inflated Poisson BMMs (one for each group). I modelled the number of bites against two offset variables specifying the observation period and grazing area (as for the overall grazing pressure model above). Microhabitat type was formulated as a fixed effect and specified to interact with both the Poisson part of the response (counts of fish bites) and the binomial part denoting the probability of an observation being zero. Due to the presence of near complete separation in the data, I used weakly informative Cauchy distributed priors on the fixed effects (Hadfield 2010). Remaining priors were specified as in previous models, although the random (array) and residual variance were fixed to 1 in the binomial part of the model. Finally, to examine the average traits of fishes feeding on the three microhabitat types in terms of their morphology, diet, and SCFA profiles, I compared the functional trait means for the consumer community of each microhabitat type using three multi-response BMMs to account for the non-independence of the five trait variables in each broader category. To provide comparable estimates, all response variables were normalized to a mean of zero and a standard deviation of 1. Again, the microhabitat type was specified as a fixed effect while array was specified to have a random effect. A Gaussian error distribution was specified for all response variables. Uninformative priors were specified for the fixed effects. Parameter expanded priors were used on the random variance (Hadfield 2010). Residual variance-covariance matrices were assessed to extrapolate the covariance of the five trait variables in each model.

More detail on model specifications is provided in the appendix. All analyses were performed in the software R, using the packages *vegan* (Oksanen et al. 2013), *FD* (Laliberté & Legendre 2010), and *MCMCglmm* (Hadfield 2010).

8.3 Results

8.3.1 Overall grazing pressure and turf filament length

I found marked differences in grazing pressure among the three investigated microhabitat types. The overall grazing pressure was strongest on flat microhabitats (2.86 ± 0.15 [mean ± SE] bites.day^{-1}.cm^{-2}), followed by exposed microhabitats (0.81 ± 0.05 bites.day^{-1}.cm^{-2}), while the lowest grazing pressure occurred on concealed microhabitats (0.17 ± 0.02 bites.day^{-1}.cm^{-2}). Concealed microhabitats had an order of magnitude fewer bites compared to flat microhabitats (**Figure 8.2a**). There was no difference among sites, and random variance was small (**Table 8.2**).

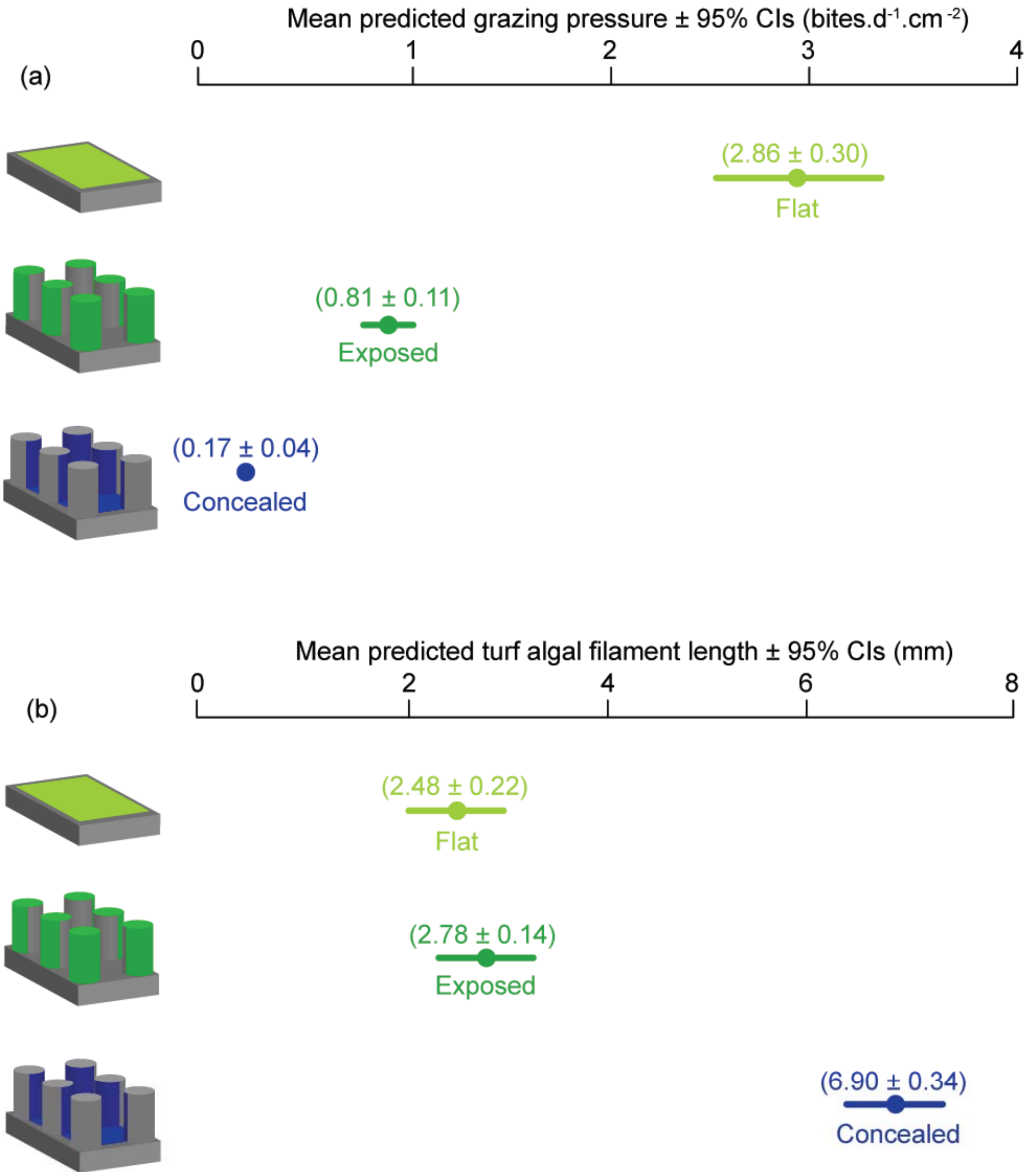


Figure 8.2: Predicted mean values from the grazing pressure model (a) and the turf length model (b), with observed means in parentheses. Flat microhabitats are subject to the highest grazing pressure, while concealed microhabitats experience the lowest grazing pressure. In contrast, turfs are longest in concealed microhabitats, while exposed and flat microhabitats both have shorter turfs. Plots show the

predicted mean ± 95% credible intervals (CIs). Statistical significance can be assumed where CIs do not overlap with the mean of another treatment.

Table 8.2: Model output from the Poisson Bayesian Mixed Model comparing grazing pressure among microhabitat types and sites. Microhabitat type and site were specified as fixed effects with uninformative priors (mu = 0, V = 100,000,000), while the two offset parameters, time and area, were fixed effects with informative priors (mu = 1, V = 0.000001). Due to overdispersion, priors on the residual variance were specified as V = 0.000001 and nu = 100, while uninformative priors were used for the random variance (V = 1, nu = 0.002). To achieve well-mixed chains, the model was run for 10,000,000 iterations. Estimates for effect levels are based on a global intercept containing estimates for microhabitat type “flat” and site 1. Where 95% CIs do not intersect 0, statistically significant differences can be inferred.

Grazing pressure model

Iterations:	100001:9990001
Thinning interval:	10000
Sample size:	990

G-structure (random variance):	~array			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
array	0.3384	0.02386	0.9559	990

R-structure (residual variance):	~units			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
units	0.1517	0.119	0.1834	865

Fixed effects:	Number of bites ~ microhabitat type + site + log(time.d) + log(cm.sq)			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
type(flat)	0.91894	0.36830	1.59062	990
type(exposed)	-1.20772	-1.35678	-1.06948	990
type(concealed)	-2.91238	-3.05042	-2.73961	990
site1	0.91894	0.36830	1.59062	990
site2	0.08132	-0.83559	0.93921	990
log(time.d)	1.00006	0.99819	1.00226	1324.1
log(cm.sq)	1.00004	0.99801	1.00196	1119.5

In contrast to grazing pressure, there were strong, but opposite, differences in the average turf filament length among the three microhabitat types. Flat microhabitats had the shortest turf filaments (2.48 ± 0.11 mm), closely followed by exposed microhabitats (2.78 ± 0.07 mm), while concealed microhabitats had by far the longest turf filaments (6.90 ± 0.17 mm) (**Figure 8.2b)**. As for grazing pressure, site had no effect and random variance from the different arrays was small (**Table 8.3**).

Table 8.3: Model output from the Gaussian Bayesian Mixed Model comparing turf filament length among microhabitat types and sites. Microhabitat type and site were specified as fixed effects with uninformative priors (mu = 0, V = 100,000,000). Uninformative priors were used for the residual and random variance parameters (V = 1, nu = 0.002). Estimates for effect levels are based on a global intercept containing estimates for microhabitat type “flat” and site 1. Where 95% CIs do not intersect 0, statistically significant differences can be inferred.

Turf length model

Iterations:	10001:299001
Thinning interval:	1000
Sample size:	2990

G-structure (random variance):	~array			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
array	0.1208	0.0002547	0.4463	2990

R-structure (residual variance):	~units			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
units	0.9308	0.7487	1.141	2990

Fixed effects:	Turf filament length ~ microhabitat type + site - 1			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
type(flat)	2.46588	1.98738	2.92477	2990
type(exposed)	0.29921	-0.06599	0.63978	2849
type(concealed)	4.41391	4.05343	4.75424	3169
site1	2.46588	1.98738	2.92477	2990
site2	0.03930	-0.62722	0.60480	2808

There was also a distinct difference in the mean number of species feeding on the three microhabitat types (species richness). While flat and exposed microhabitats were statistically indistinguishable (flat: 3.85 ± 0.16 [mean ± SE] number of species feeding on a given microhabitat over the entire observation period; exposed: 3.18 ± 0.17 species), concealed microhabitats had substantially less grazer species richness (1.93 ± 0.14 species). Interestingly, patterns of mean functional group richness of the benthic communities showed the opposite trend, with flat microhabitats supporting a markedly lower number of functional groups (3.15 ± 0.15 [mean ± SE] number of groups per microhabitat), compared to both exposed and concealed microhabitats (exposed: 4.333 ± 0.14 functional groups; concealed: 4.75 ± 0.15 functional groups). Again, site had no effect on the observed patterns and random variance was small (**Tables 8.4, 8.5**). Therefore, site data were pooled for subsequent analyses.

Table 8.4: Model output from the Poisson Bayesian Mixed Model comparing the number of grazer species observed to feed on a given microhabitat among microhabitat types and sites. Microhabitat type and site were specified as fixed effects with uninformative priors (mu = 0, V = 100,000,000). Uninformative priors were used for the residual and random variance parameters (V = 1, nu = 0.002). Estimates for effect levels are based on a global intercept containing estimates for microhabitat type “flat” and site 1. Where 95% CIs do not intersect 0, statistically significant differences can be inferred.

Grazer species richness model

Iterations:	10001:299001
Thinning interval:	1000
Sample size:	2990

G-structure (random variance):	~array			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
array	0.04014	0.0002354	0.1269	2990

R-structure (residual variance):	~units			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
units	0.003819	0.0001635	0.01174	2990

Fixed effects:	Number of grazer species ~ microhabitat type + site			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
type(flat)	1.169238	0.909828	1.434785	2990
type(exposed)	-0.193356	-0.377083	0.006359	2637
type(concealed)	-0.692251	-0.925175	-0.474703	2311
site1	1.169238	0.909828	1.434785	2990
site2	0.311634	-0.022325	0.668442	3262

Table 8.5: Model output from the Poisson Bayesian Mixed Model comparing the number of benthic functional groups present on each microhabitat among microhabitat types and sites. Microhabitat type and site were specified as fixed effects with uninformative priors (mu = 0, V = 100,000,000). Uninformative priors were used for the residual and random variance parameters (V = 1, nu = 0.002). Estimates for effect levels are based on a global intercept containing estimates for microhabitat type "flat" and site 1. Where 95% CIs do not intersect 0, statistically significant differences can be inferred.

Benthic functional group richness model

Iterations:	10001:299001
Thinning interval:	1000
Sample size:	2990

G-structure (random variance):	~array			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
array	0.02866	0.0001762	0.08015	2990

R-structure (residual variance):	~units			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
units	0.002871	0.0001734	0.008534	2990

Fixed effects:	Number of functional groups ~ microhabitat type + site			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
type(flat)	1.17987	0.95788	1.38807	2990
type(exposed)	0.31975	0.14029	0.50751	2065
type(concealed)	0.41193	0.23086	0.60103	2589
Site1	1.17987	0.95788	1.38807	2990
Site2	-0.07846	-0.21591	0.06792	2990

8.3.2 Community compositions

The three microhabitat types showed distinct differences in the grazer and benthic communities (**Figure 8.3**). The nMDS ordination for the grazer communities showed a clear separation between concealed microhabitats and the two other microhabitat types, but not between flat and exposed microhabitats (**Figure 8.3a**). The separation was driven largely by rabbitfishes (*Siganus corallinus, S. punctatus, S. punctatissimus*), and the two surgeonfish species *Zebrasoma scopas* and *Acanthurus nigrofuscus*, fishes that characteristically grazed in concealed microhabitats. In contrast, flat and exposed microhabitats were characterized by parrotfishes (*Scarus frenatus*, *S. globiceps*, *S. niger*, *S. psittacus*, *S. schlegeli*, *Chlorurus spilurus*) and the surgeonfish species *A. nigricauda* and *Ctenochaetus striatus*. This separation of microhabitat types was statistically significant in the PERMANOVA (pseudo $F_{2,174} = 37.12$, $P < 0.001$), explaining approximately one third of the variation ($R^2 = 0.30$).

Benthic communities likewise varied markedly, with the nMDS ordination again showing a clear distinction between concealed microhabitats and the two remaining microhabitats, which showed extensive overlap (**Figure 8.3b**). While concealed microhabitats were composed of a wide array of benthic organisms, including scleractinian corals and various stands of filamentous, fleshy, and foliose algae, as well as fish faeces, both flat and exposed microhabitats showed a more uniform community composition, comprising a polycultural turf algal mat, occasionally with exposed crustose coralline algae (CCA), cyanobacterial mats, and a few non-coralline sessile invertebrates (on exposed microhabitats). Again, these differences distinctly characterized the respective microhabitat types in the PERMANOVA (pseudo $F_{2,180} = 128.16$, $P < 0.001$), explaining more than half of the variance ($R^2 = 0.59$).

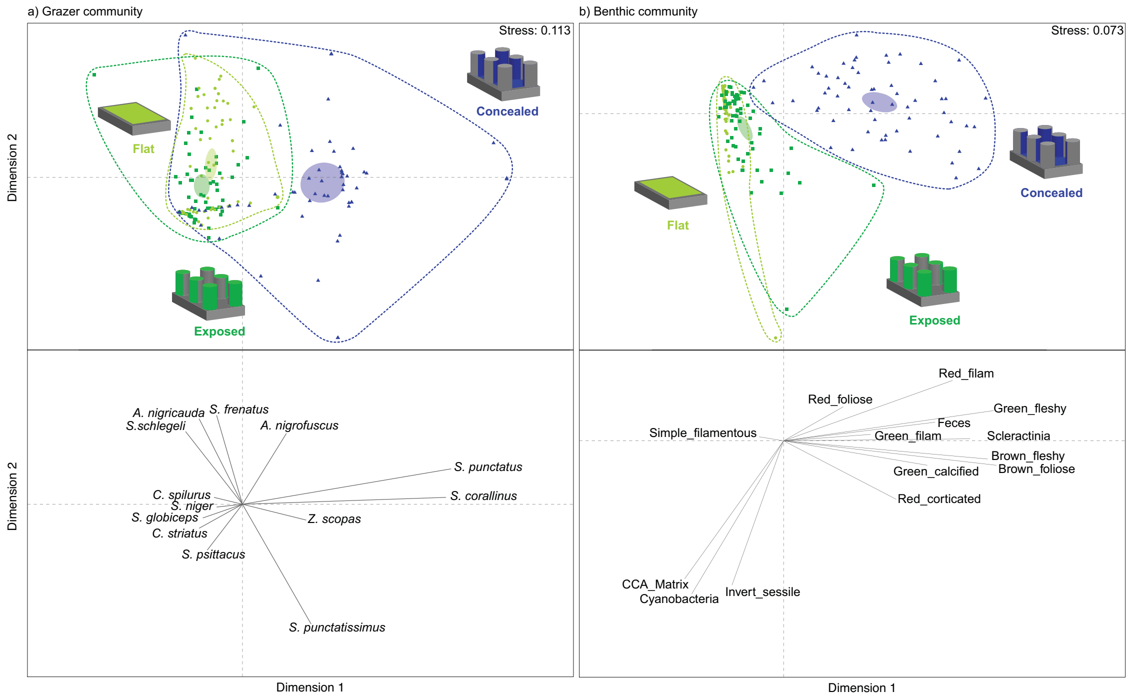
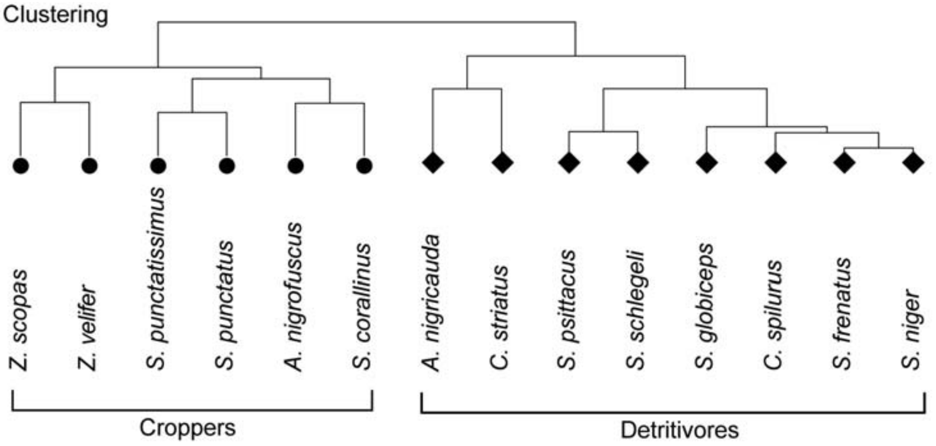


Figure 8.3: The grazer communities and benthic communities of the three microhabitat types. Ordinations represent nMDS ordinations with each symbol representing a microhabitat type. Shaded ellipses represent the 95% confidence intervals of the centroids, while coloured dashed lines comprise all samples within a given microhabitat. Bottom panels represent vectors. Concealed microhabitats are markedly different from flat and exposed habitats with regards to both their grazer communities (a), and benthic community composition (b). For the grazer community, six concealed microhabitats were omitted due to no grazing.

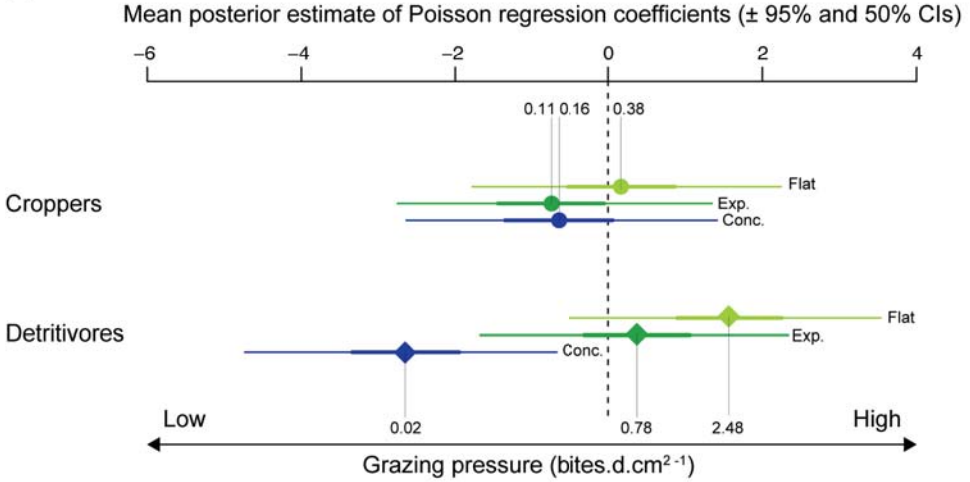
8.3.3 Functional profiles of grazer communities

When dividing grazer communities into functional groups based on their morphology, gut contents, and SCFA profiles, I found further, and consistent, differences in the grazing pressure exerted on the three microhabitat types. The first group encompassed the fish community typically feeding on concealed microhabitats (see nMDS above) and consisted of all observed rabbitfishes (*S. corallinus, S. punctatissimus, S. punctatus*), both surgeonfishes in the genus *Zebrasoma* (*Z. scopas, Z. velifer*), and *Acanthurus nigrofuscus*. Collectively, these species are 'croppers', feeding largely on the apical portions of algae. The second group encompassed the fish community typically feeding on flat and exposed microhabitats (see nMDS above), and comprised all observed parrotfishes (*C. spilurus*, *S. frenatus*, *S. globiceps*, *S. niger, S. psittacus*, *S. schlegeli*), and the two surgeonfish species *C. striatus* and *A. nigricauda*. Collectively, these species are 'detritivores', which remove both filamentous algae and particulate matter, or just the particulate portion of the epilithic algal matrix, when feeding. There were no differences in the grazing pressure exerted on the respective microhabitat types by croppers, as both bite counts and the probability of zero counts were similar among microhabitats. In strong contrast, grazing pressure by detritivores differed extensively, with concealed microhabitats being substantially less heavily-grazed and having a much higher probability of zero counts than flat or exposed microhabitats, for which zero-counts were absent (**Figure 8.4, Table 8.6**).

(a) Clustering



(b) Bite counts



(c) Zero-inflation

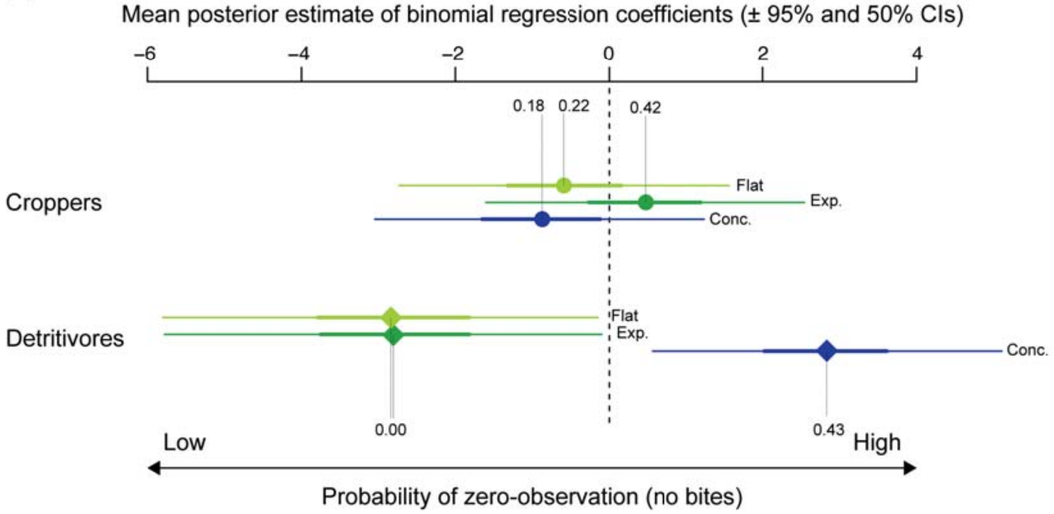


Figure 8.4: The grazing pressure of the two functional groups on the respective microhabitats. Ward’s clustering analysis of the trait dataset (a) divided herbivores into two functional groups, croppers and detritivores. The model coefficients from a zero-inflated Poisson BMM indicate that there are no differences in the grazing pressure exerted on different microhabitats by croppers, with regards to both the bite rate (b) and the likelihood of no bites at all (c). In stark contrast, concealed microhabitats are significantly less grazed on by detritivores, as indicated by both the bite counts and zero-probability.

Table 8.6: Model output from the zero-inflated Poisson Bayesian Mixed Model comparing the grazing pressure of croppers and detritivores, respectively, among the three microhabitat types. Due to complete separation in the data, weakly informative priors were used on the fixed effect microhabitat type (mu = 0, V = 1+ $\pi^{2/3}$), while highly informative priors were specified for the two offset parameters controlling for time and area (mu = 1, V = 0.0000001). For the Poisson component of the model, uninformative priors were used on the residual and random variance (V = 1, nu = 0.002), while residual and random variance were fixed at 1 and 0.000001, respectively, for the binomial zero-inflation component of the model. Microhabitat type was specified to interact with both the Poisson and the binomial part of the model to obtain estimates of the effects of microhabitat type on the grazing rates and the likelihood of complete avoidance (zero counts). To facilitate interpretation, the global intercept was suppressed.

Functional group grazing pressure model: (a) Croppers

Iterations:	10001:299001
Thinning interval:	1000
Sample size:	2990

G-structure (random variance):	~array			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
array	0.055537	0.0002152	0.195891	2990
ZI-array	0.000001	0.000001	0.000001	0

R-structure (residual variance):	~units			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
units	0.6144	0.4393	0.8112	2990
ZI-units	1.0000	1.0000	1.0000	0

Fixed effects:	Number of bites ~ trait – 1 + trait(Poisson)*microhabitat type + trait(ZI)*microhabitat type + trait(Poisson)*log(time.d) + trait(Poisson)*log(cm.sq)			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size

P(bite)	-1.2636	-3.2340	0.8421	2800
ZI(bite)	-0.9651	-2.9121	1.1923	2990
P(bite)*type(flat)	0.1786	-1.8414	2.2165	2780
P(bite)*type(exp)	-0.7377	-2.9541	1.1963	2788
P(bite)*type(con)	-0.6485	-2.6633	1.3711	2781
ZI(bite)*type(flat)	-0.5873	-2.6187	1.5552	2990
ZI(bite)*type(exp)	0.4780	-1.5740	2.6354	2990
ZI(bite)*type(con)	-0.8578	-2.9655	1.3290	3351
P(bite)*log(time)	1.0000	0.9982	1.0019	2990
P(bite)*log(area)	1.0000	0.9981	1.0020	2990

Functional group grazing pressure model: (b) Detritivores

Iterations: 10001:299001
Thinning interval: 1000
Sample size: 2990

G-structure (random variance):	~array			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
array	0.144413	0.012310	0.410385	2990
ZI-array	0.000001	0.000001	0.000001	0

R-structure (residual variance):	~units			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
units	0.2097	0.154	0.2717	2983
ZI-units	1.0000	1.0000	1.0000	0

Fixed effects:	Number of bites ~ trait + trait(Poisson)*microhabitat type + trait(ZI)*microhabitat type + trait(Poisson)*log(time.d) + trait(Poisson)*log(cm.sq)			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. sample size
Poisson	-0.7581	-2.8416	1.2167	2990
ZI	-2.7932	-5.1436	-0.6116	1366.8
Poisson*type(flat)	1.5777	-0.3790	3.6576	2990
Poisson*type(exp)	0.3793	-1.5568	2.4992	2990
Poisson*type(con)	-2.6341	-4.5617	-0.4463	2990
ZI*type(flat)	-2.8630	-5.7930	-0.1750	744.2
ZI*type(exp)	-2.8041	-5.8088	-0.2844	745.4
ZI*type(con)	2.8661	0.5453	5.0674	1343.2
Poisson*log(time)	1.0000	0.9982	1.0019	2990
Poisson*log(area)	1.0000	0.9981	1.0020	2990

The fundamental differences in the feeding pressure exerted on the three microhabitat types by croppers and detritivores is closely reflected in the bite-weighted average functional profiles of fishes feeding on the respective microhabitats. Compared to fishes grazing on flat and exposed microhabitats, fishes feeding on concealed microhabitats exhibit larger head angles (i.e. a concave head), smaller snout angles (i.e. pointed snouts), larger eyes, and deeper bodies. Furthermore, fishes grazing on concealed microhabitats exhibit higher proportions of fleshy algae, filamentous algae, and other benthic material in their guts, and substantially lower amounts of calcareous sediments and organic particulates. These dietary differences are also apparent in the SCFA profiles, with fishes feeding on concealed microhabitats exhibiting high levels of SCFAs, containing high levels of acetate and propionate but low levels of isovalerate (**Figure 8.5, Table 8.7**).

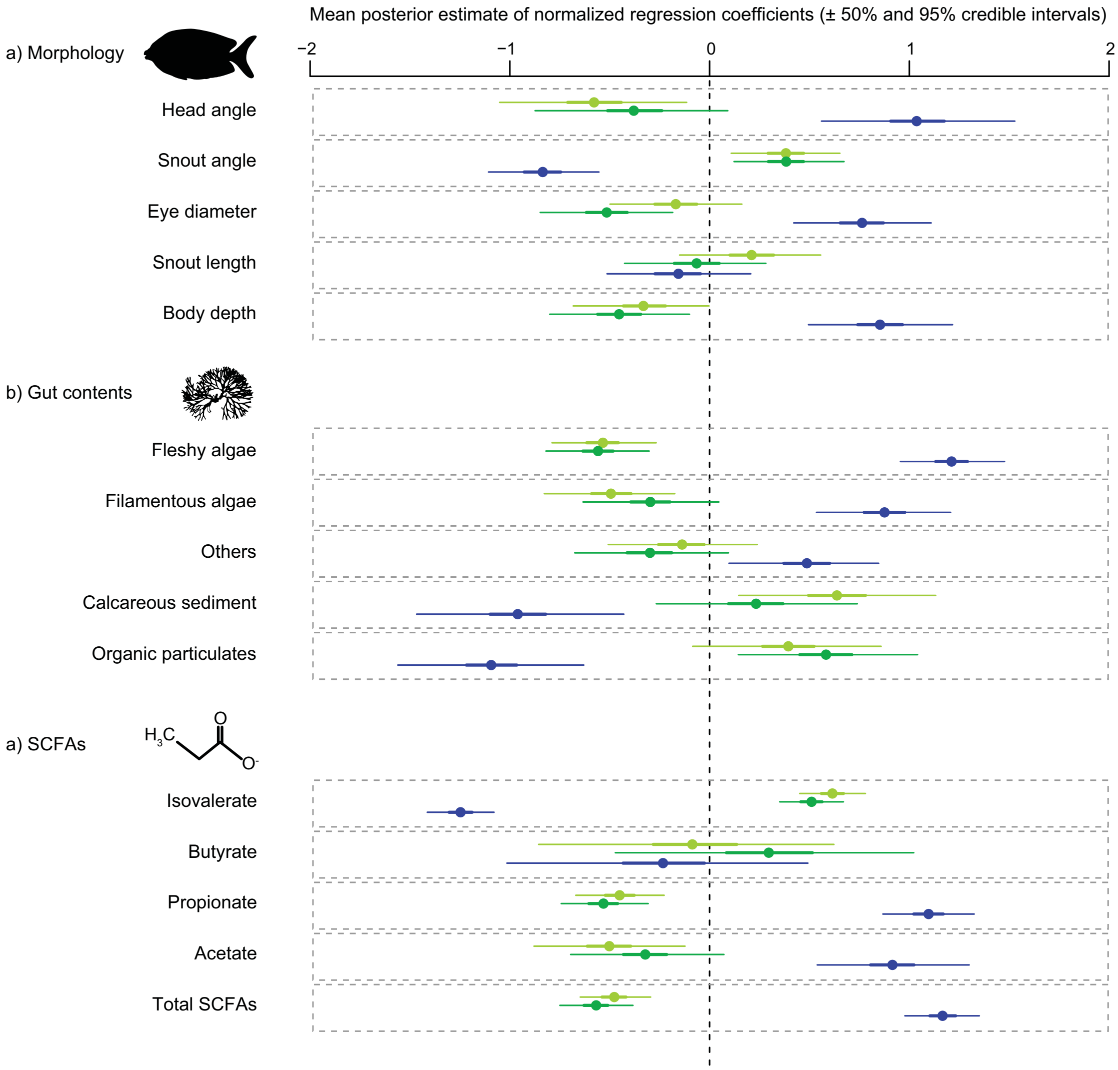


Figure 8.5: The average trait values of consumer communities feeding on the three microhabitat types. There were strong differences between concealed and exposed microhabitats in terms of morphology (a), gut contents (b), and SCFA profiles (c). Consumer communities feeding on concealed microhabitats were characterized by concave foreheads, pointed snouts, large eyes, and deep bodies. They predominantly consume fleshy and filamentous algae, while taking only little calcareous sediment and organic particulates. This is supported by the SCFA profiles, which show low levels of isovalerate, but high levels of propionate, acetate,

and total SCFA concentrations. Light green = flat microhabitats, dark green = exposed microhabitats, blue = concealed microhabitats.

Table 8.7: Model output from the three multi-response models comparing the bite-weighted average trait means of consumers in terms of morphology, diet, and SCFAs among the three microhabitat types. For all three model, uninformative priors were specified on the fixed effect (microhabitat type). For the random variance, parameter expanded priors (V = 1, nu = 5.02, alpha.mu = 0, alpha.V = 1000) were specified on an idh-structure, while residual variance was specified to co-vary among the different response variables under an us-structure (priors: V = 1, nu = 5.02). To facilitate interpretation, the global intercept was suppressed.

(a) Morphology

Iterations:	10001:2999001
Thinning interval:	1000
Sample size:	2990

G-structure (random variance):	~idh(trait):array			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. Sample size
Body depth.array	0.132	0.000	0.419	2990
Snout length.array	0.121	0.000	0.332	2592
Eye diameter.array	0.103	0.000	0.348	2990
Snout angle.array	0.042	0.000	0.145	2990
Head angle.array	0.328	0.021	0.946	2990

R-structure (residual variance-co-variance)	~us(trait):array					
		Body d	Snout l	Eye d	Snouta	Head a
Body depth	Post. Mean	0.631				
	lower 95% CI	0.498				
	upper 95% CI	0.767				
Snout length	Post. Mean	0.587	0.977			
	lower 95% CI	0.446	0.771			
	upper 95% CI	0.747	1.195			
Eye diameter	Post. Mean	-0.160	-0.312	0.719		
	lower 95% CI	-0.262	-0.458	0.550		
	upper 95% CI	-0.052	-0.180	0.866		
Snout angle	Post. Mean	-0.553	-0.506	0.367	0.714	
	lower 95% CI	-0.677	-0.656	0.243	0.564	
	upper 95% CI	-0.416	-0.356	0.491	0.868	
Head angle	Post. mean	0.329	0.154	0.026	-0.336	0.411

	lower 95% CI	0.244	0.061	-0.057	-0.428	0.329
	upper 95% CI	0.426	0.256	0.110	-0.242	0.501

Fixed effects:	(body d, snout l, eye d, snout a, head a) ~ (trait:microhabitat type - 1)			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. Sample size
Body d*type(flat)	-0.331	-0.677	-0.002	2990
Snout l*type(flat)	0.210	-0.142	0.559	2781
Eye d*type(flat)	-0.169	-0.508	0.151	3225
Snout a*type(flat)	0.382	0.099	0.638	3263
Head a*type(flat)	-0.578	-1.008	-0.083	2990
Body d*type(exp)	-0.453	-0.797	-0.098	2488
Snout l*type(exp)	-0.065	-0.434	0.268	2990
Eye d*type(exp)	-0.515	-0.835	-0.179	2990
Snout a*type(exp)	0.384	0.125	0.674	2830
Head a*type(exp)	-0.380	-0.876	0.086	2990
Body d*type(con)	0.853	0.482	1.202	2428
Snout l*type(con)	-0.156	-0.498	0.215	2990
Eye d*type(con)	0.763	0.431	1.114	2990
Snout a*type(con)	-0.835	-1.107	-0.554	2740
Head a*type(con)	1.037	0.532	1.491	2990

(b) Diet

Iterations:	10001:2999001
Thinning interval:	1000
Sample size:	2990

G-structure (random variance):	~idh(trait):array			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. Sample size
Organic_matter.array	0.341	0.017	0.880	1612
Calc_sediment.array	0.324	0.019	0.955	2718
Others.array	0.133	0.000	0.410	3172
Filamentous.array	0.097	0.000	0.318	2990
Fleshy.array	0.074	0.000	0.220	2832

R-structure (residual variance-co-variance)	~us(trait):array					
		Organics	Sediment	Others	Filaments	Fleshy
Organic matter	Post. Mean	0.353				
	lower 95% CI	0.279				
	upper 95% CI	0.431				
Calcareous sediment	Post. Mean	0.097	0.509			
	lower 95% CI	0.031	0.412			
	upper 95% CI	0.166	0.628			

Others	Post. Mean	0.016	0.225	0.893		
	lower 95% CI	-0.078	0.117	0.702		
	upper 95% CI	0.094	0.335	1.075		
Filamentous algae	Post. Mean	-0.360	-0.237	-0.247	0.640	
	lower 95% CI	-0.454	-0.331	-0.369	0.508	
	upper 95% CI	-0.272	-0.145	-0.130	0.787	
Fleshy algae	Post. mean	-0.221	-0.304	-0.152	0.258	0.338
	lower 95% CI	-0.287	-0.388	-0.247	0.179	0.268
	upper 95% CI	-0.159	-0.231	-0.072	0.342	0.414

Fixed effects:	(organics, sediment, others, filamentous, fleshy) ~ (trait:microhabitat type -1)			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. Sample size
Organics*type(flat)	0.394	-0.041	0.879	2990
Sediment*type(flat)	0.638	0.141	1.122	2990
Others*type(flat)	-0.138	-0.523	0.214	2990
Filamentous*type(flat)	-0.494	-0.843	-0.197	2990
Fleshy*type(flat)	-0.534	-0.775	-0.258	2990
Organics*type(exp)	0.583	0.126	1.014	2990
Sediment*type(exp)	0.233	-0.284	0.707	3411
Others*type(exp)	-0.298	-0.693	0.072	3107
Filamentous*type(exp)	-0.297	-0.650	0.019	3562
Fleshy*type(exp)	-0.558	-0.838	-0.322	2828
Organics*type(con)	-1.093	-1.546	-0.621	2990
Sediment*type(con)	-0.961	-1.521	-0.491	3486
Others*type(con)	0.487	0.110	0.856	2990
Filamentous*type(con)	0.876	0.527	1.190	2990
Fleshy*type(con)	1.212	0.953	1.471	4019

(c) SCFAs

Iterations:	10001:2999001
Thinning interval:	1000
Sample size:	2990

G-structure (random variance):	~idh(trait):array			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. Sample size
totalscfa.array	0.009	0.000	0.034	2990
acetate.array	0.163	0.003	0.516	2990
proprionate.array	0.027	0.000	0.092	2710
butyrate.array	0.896	0.045	2.273	2990
isovalerate.array	0.010	0.000	0.044	2822

R-structure (residual variance-co-variance)	~us(trait):array

		Total	Acetate	Prop	But	Iso
Total SCFA	Post. Mean	0.419				
	lower 95% CI	0.328				
	upper 95% CI	0.508				
Acetate	Post. Mean	-0.037	0.572			
	lower 95% CI	-0.110	0.455			
	upper 95% CI	0.039	0.702			
Propionate	Post. Mean	0.379	-0.128	0.485		
	lower 95% CI	0.294	-0.212	0.385		
	upper 95% CI	0.473	-0.050	0.592		
Butyrate	Post. Mean	0.074	-0.116	0.021	0.717	
	lower 95% CI	-0.007	-0.212	-0.069	0.565	
	upper 95% CI	0.163	-0.050	0.114	0.880	
Isovalerate	Post. mean	-0.247	-0.216	-0.237	-0.025	0.322
	lower 95% CI	-0.312	-0.290	-0.305	-0.098	0.254
	upper 95% CI	-0.178	-0.143	-0.166	0.049	0.389

Fixed effects:	(total scfa, acetate, propionate, butyrate, isovalerate) ~ (trait:microhabitat type - 1)			
	Post. mean parameter est.	lower 95% CI	upper 95% CI	Eff. Sample size
TotalSCFA*type(flat)	-0.478	-0.648	-0.296	2990
Acetate*type(flat)	-0.503	-0.855	-0.107	2990
Propionate*type(flat)	-0.451	-0.657	-0.216	2990
Butyrate*type(flat)	-0.087	-0.856	0.625	2990
Isovalerate*type(flat)	0.614	0.456	0.783	3085
TotalSCFA*type(exp)	-0.569	-0.746	-0.383	2990
Acetate*type(exp)	-0.323	-0.728	0.036	3890
Propionate*type(exp)	-0.532	-0.741	-0.306	2990
Butyrate*type(exp)	0.295	-0.522	0.966	2990
Isovalerate*type(exp)	0.510	0.358	0.676	2990
TotalSCFA*type(con)	1.165	0.978	1.351	2990
Acetate*type(con)	0.914	0.543	1.299	2990
Propionate*type(con)	1.096	0.877	1.332	3742
Butyrate*type(con)	-0.234	-0.984	0.501	2990
Isovalerate*type(con)	-1.248	-1.410	-1.078	2810

8.4 Discussion

My results reveal that micro-topographic refuges profoundly affect the dynamics between grazing herbivorous fishes and benthic organisms on coral reefs. Specifically, increased complexity at the scale of a few centimetres alters the grazing rates of consumer communities comparable to variation previously reported on coral reefs at local, regional, and global scales. Furthermore, micro-topographic refuges fundamentally change the functional identity of the consumer communities, essentially restricting the spectrum of herbivorous fishes that can feed on concealed microhabitats to few algae-cropping species. In contrast, detritivorous species, which incorporate large proportions of organic particulates and calcareous sediments into their diet, appear to be excluded from concealed microhabitats, although they exert intense grazing pressure on flat and exposed microhabitats. Thus, micro-topographic refuges appear to eliminate an entire ecosystem process, the removal of particulates. As a consequence, the benthic communities vary drastically between concealed and flat or exposed microhabitats. While algal turfs dominate both communities, turf filaments are markedly longer in concealed microhabitats and incorporate a wide range of algal forms and other benthic components, including juvenile scleractinian corals. I suggest that the refuge from grazing provided by micro-topographic complexity creates an environment that fosters benthic diversity through intermediate grazing pressure by a few selected cropping species.

8.4.1. Effects of micro-topographic refuges on grazing

Micro-topographic refuges clearly reduce the grazing pressure exerted by herbivorous fishes, resulting in a more than tenfold decrease in the number of bites per day per cm^2 within refuges. This corroborates the results of previous studies in both aquatic and terrestrial environments (Menge and Lubchenco 1981; Dudley and D'Antonio 1991; Bergey 2005; Shitzer *et al.* 2008). In the context of coral reefs, the effect of micro-topographic complexity on grazing rates rivals well-documented differences at larger scales. The approximately tenfold differences observed between flat and concealed microhabitats resemble the variation in grazing pressure outside and inside of damselfish territories (Hixon and Brostoff 1996), and are comparable with the variation along some major reef habitats. Specifically, Hay (1981) demonstrated a tenfold difference in the consumption of *Thalassia* blades between seaward sides of outer fore-reefs (9.0% consumed) and rubble areas of back reefs (92.8% consumed). Furthermore, if grazing pressure scales approximately linearly with herbivorous reef fish biomass, then the difference between open and concealed microhabitats exceeds both regional (0.8 to 7.2kg.100m^{-2} on the inner shelf of the GBR, compared to 5.0 to 31.7kg.100m^{-2} on the outer shelf, Wismer *et al.* 2009) and global disparities in grazing pressure on coral reefs (mean of 20.9g.m^{-2} in Brazil compared to 83.7g.m^{-2} in New Caledonia; supplementray material in Edwards *et al.* 2014). The gradient reported herein is also greater than the gradient in herbivorous fish biomass induced by fishing pressure globally (20.5g.m^{-2} in fished areas compared to 56.4g.m^{-2}, Edwards *et al.* 2014) and exceeds herbivore biomass reductions achieved through the employment of herbivore exclusion cages (Hughes *et al.* 2007). Thus, the presence of micro-topographic complexity on the scale of a few centimetres appears to profoundly affect consumer pressure, equivalent to some of the largest gradients in grazing rates reported for coral reef ecosystems.

Besides overall grazing pressure, however, micro-topographic refuges profoundly affect the functional diversity of consumer species capable of interacting with the benthos. Concealed microhabitats are only grazed by a subset of fish species, resulting in marked reductions of consumer taxonomic and functional diversity. Microhabitat utilization has been recognized as a strong axis of niche partitioning in herbivorous fishes (Brandl and Bellwood 2014; Adam et al. 2015), but the effects of this environmental filter on functional processes performed by herbivorous fishes are largely unknown. Our results show that there is a clear morphological segregation, as feeding in concealed microhabitats appears to be restricted to ‘cropping’ species, with relatively large eyes, deep bodies, concave foreheads, and pointed snouts, all of which favour the exploitation of small prey items in complex environments (Brandl and Bellwood 2013). Furthermore, micro-topographic complexity almost completely eliminates feeding by ‘detritivorous’ fishes that remove organic and inorganic particulate material. Previously reported dietary information (Choat et al. 2002) and evidence of digestive use of ingested material (SCFA profiles; Clements and Choat 1995), suggest that there is very little extraction of either the entire epilithic algal matrix (including particulates; Wilson et al. 2003), or the particulate component alone, in concealed microhabitats. Instead, grazing pressure exerted on concealed microhabitats is almost exclusively restricted to the selective cropping of the apical portions of both filamentous and foliose/fleshy algae, leaving the base layers of the turf community largely intact (Hixon and Brostoff 1996). Thus, the identity of consumer communities and the ecosystem processes they deliver differ vastly among microhabitats. This segregation may explain previously reported effects of herbivore identity and species richness on benthic community composition and succession on coral reefs (Burkepile and Hay 2008, 2010; Cheal *et al.* 2010).

Despite these striking functional differences between grazer species, many of the species observed in the present study have been consistently placed in the same functional group (grazers/detritivores) in order to assess their status or ecosystem function (e.g. Green and Bellwood 2009; Cheal et al. 2010; Doropoulos et al. 2013; Edwards et al. 2014). For example, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* have been considered to be functionally equivalent in several instances (Green and Bellwood 2009; Marshell and Mumby 2011); yet, my results demonstrate that they vary drastically in their use of microhabitats and resources therein. This is likewise applicable to *Acanthurus nigrofuscus* and the rabbitfishes observed in this study (Green and Bellwood 2009). Hence, the results of the present study emphasize the need for caution when assigning species to functional groups and assuming within-group functional equivalence. Clearly, differences in the utilization of foraging microhabitats need to be considered when characterizing species with regards to their functional impact (Adams et al. 2015) and indeed, it would not be surprising if even finer partitioning of foraging microhabitats, dietary items, or digestive use of resources would create a unique functional role for most herbivorous fish species on coral reefs.

8.4.2. Effects of micro-topographic refuges on benthic communities

As expected, given the differences in both grazing pressure and the functional identity of grazers, the benthic communities varied strongly among microhabitat types. In close agreement with the reduced grazing pressure, we found an almost three-fold increase in the length of turf algal filaments in concealed microhabitats. This closely matches situations in which herbivory is naturally or experimentally suppressed (Arnold et al. 2010; Bonaldo and Bellwood 2011; Rasher et al. 2012). The lack of a difference between turf filaments growing on flat and exposed microhabitats suggests that there is a grazing threshold above which short turf filaments are maintained. Specifically, lower grazing pressure on exposed microhabitats (0.81 ± 0.05 bites.day^{-1}.cm^{-2}) appears to be sufficient to maintain a closely cropped turf community, while the even lower grazing pressure on concealed microhabitats (0.17 ± 0.02 bites.day^{-1}.cm^{-2}) clearly allows for longer turf filaments, suggesting a threshold between 0.17 and 0.81 bites.day^{-1}.cm^{-2} (**Figure 8.2**).

While algal turfs dominated all microhabitats, we found a marked difference between the benthic communities of open and concealed microhabitats. This highlights a fundamental problem when describing benthic communities on coral reefs merely as algal turfs (or the epilithic algal matrix), as these communities are far from uniform (Connell et al. 2014; Harris et al. 2015). The benthic community on flat and exposed microhabitats appears to closely resemble a state of ‘successional deflection’ (*sensu* Hixon and Brostoff 1996), where extreme and destructive grazing by a wide range of fish species only permits the existence of short, low-complexity algal filaments, CCA, and cyanobacterial mats (Hixon and Brostoff 1996; Wismer et al. 2009). In contrast, the benthic community in concealed microhabitats was far more diverse, including a wide array of algal growth forms as well as juvenile scleractinian corals. This not only corroborates previous findings, which suggest that micro-topographic complexity can be beneficial to benthic organisms by providing a refuge from grazing pressure (Brandl et al. 2014; Edmunds et al. 2014; Franco et al. 2015), but it also supports the role of micro-topographic complexity, or any refuge from intense grazing, in fostering benthic diversity across ecosystems (Menge and Lubchenco 1981; Hixon and Brostoff 1985, 1996; Casey et al. 2014). Indeed, the communities present in concealed microhabitats appear analogous to a successional state of peak diversity (*sensu* Hixon and Brostoff 1996), which is commonly maintained by intermediate levels of consumer-mediated disturbance (Worm et al. 2002). This may apply herein, as detritivorous parrotfish species that scrape the entire turf community off the substratum, therefore representing a severe disturbance, are excluded from concealed microhabitats. In contrast, the selective cropping of algae by fishes feeding in concealed microhabitats may represent a partial and therefore intermediate level of disturbance.

Thus, micro-topographic refuges on coral reefs create two distinct regimes, which are maintained by two separate groups of grazers: detritivorous fishes, which feed on the entire epilithic algal matrix (EAM) or its particulate component, maintain a short, intensively grazed, low-diversity epilithic turf community, while cropping herbivores sustain a longer turf community with diverse algal growth forms and juvenile corals.

8.4.3. Effects of micro-topographic refuges on coral reef ecosystems

Our results suggest that the relationship between grazing herbivorous fishes and benthic communities is overwhelmingly influenced by micro-topographic refuges, and as such, far more complex than previously assumed. Since the identification of herbivory as a critical process for coral reef ecosystems, many studies have identified the direct positive effect of grazing herbivores on reef resilience (reviewed by Bellwood et al. 2004; Nyström et al. 2008; Roff and Mumby 2012; Graham et al. 2015). While there is clear evidence that it is the failure of coral recruitment, which causes the large-scale and long-term decline of coral-dominated reefs (Hughes and Tanner 2000; Hughes et al. 2007), our results suggest that micro-topographic refuges may play a critical role in the dynamics between herbivorous grazing and coral replenishment (**Figure 8.6**). Coral replenishment is tightly linked to the survival of juvenile corals, which depends on the avoidance of mortality induced by both intense grazing pressure and the smothering by algal turfs (Arnold *et al.* 2010; Steneck *et al.* 2014). My results suggest that by creating an interface between open and concealed microhabitats, micro-topographic refuges represent an environment that permits corals to avoid both threats, provided that the herbivore community comprises fishes capable of cropping algae within refuges, and detritivorous fishes that maintain a shortly grazed EAM outside refuges. In essence, by selectively trimming algae within refuges, cropping grazers prevent the smothering of coral recruits from within refuges. Simultaneously, detritivorous grazers maintain a short EAM outside refuges, enabling corals to access light whilst being sheltered from grazing damage within refuges. Thus, although easily overlooked in a world of global syntheses, micro-topographic complexity on the scale of a few centimetres, and the functional roles of herbivorous fishes grazing within and outside of micro-topographic refuges, may be a critical aspect of the dynamics between herbivorous fishes and the benthic community in coral reef ecosystems.

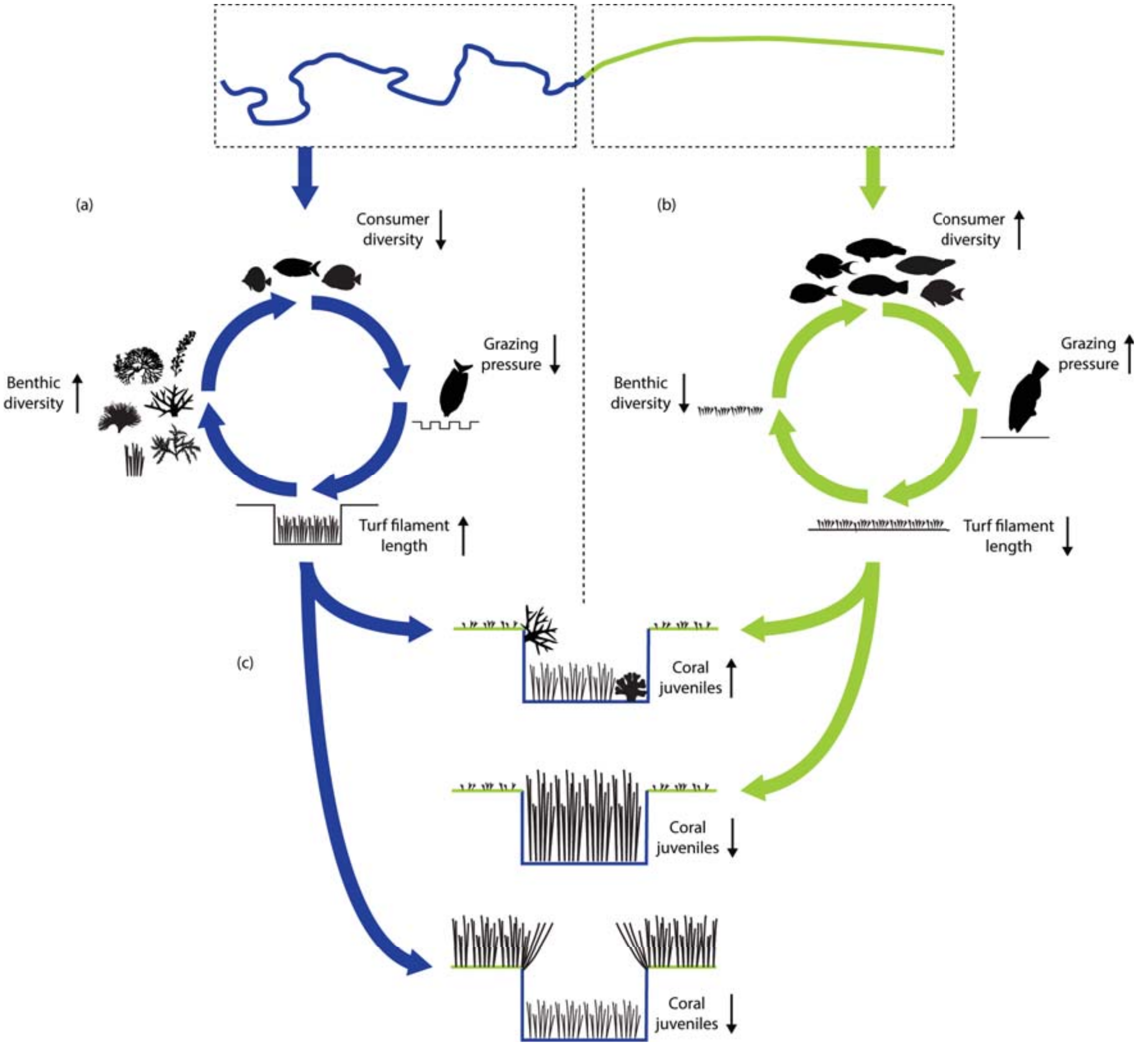


Figure 8.6: Conceptual synthesis of the effects of refuges. Refuges restrict the grazer community to a few cropping species, which exert moderate grazing pressure. Consequently, turf algal filaments grow longer and a diverse benthic community can establish (a). In contrast, a diverse assemblage (incl. croppers and detritivores), grazes on flat microhabitats, leading to intense overall grazing pressure. Algal filaments are tightly grazed and a low-diversity epilithic algal matrix is established (b). Thus, three possible scenarios emerge (c): if both regimes coexist, corals can settle in refuges to avoid grazing pressure, and can outgrow these microhabitats, as turfs are controlled within and outside refuges. If no croppers are

present, corals become smothered by algal turfs in refuges. If detritivores are absent, grazing pressure is reduced, but corals are smothered by algae expanding from flat microhabitats.

In summary, I demonstrate that micro-topographic complexity can act as an environmental refuge for benthic organisms by means of excluding a suite of high-intensity grazers, while permitting the grazing activity of low-intensity grazers that crop algal filaments. As a consequence, two fundamentally different benthic regimes can coexist at the scale of a few centimetres. I suggest that a balance between these two regimes underpins processes relating to coral replenishment on coral reefs and propose that the role of micro-topographic complexity and functional differences among herbivorous fishes be considered in future assessments of grazing dynamics on coral reefs.

Chapter 9: General Discussion

Although the interest in species diversity *per se* continues (Mora et al. 2011; Fisher et al. 2015), the question of what species are doing within a given ecosystem has established itself as one of the most urgent issues in ecology (Diaz & Cabido 2001; Cardinale et al. 2002; Naeem et al. 2012; Cardinale et al. 2012). Yet, as more and more information is compiled into global databases of species' functional traits (Kattge et al. 2011), the call for the consideration of realized niches, which include individual variability in environments governed by countless, and often unquantified, biotic and abiotic interactions, is intensifying (Schleuter et al. 2010; Violle et al. 2012; Albert et al. 2012; Brandl & Bellwood 2014a).

The importance of this approach is demonstrated in this thesis. In Chapter 2 and 3, I extracted social and morphological traits that can serve as predictors for species' fundamental niches, suggesting that pairing species with large eyes, concave foreheads, pointed snouts, and deep bodies may be able to feed in more topographically complex microhabitats. While Chapter 4 presented evidence for one of the mechanisms driving this relationship, it also shows that intraspecific plasticity in the social system can have significant implications for a species' realized functional niche. Chapter 5 then demonstrated, how species that have been consistently placed in the same functional group by previous work (Green et al. 2009; Cheal et al. 2012; Doropoulos et al. 2013), thus implying that their impact on reefs is equivalent, can vary dramatically in their functional role when realized niches are considered. This realization was facilitated by the introduction of a new framework for the community-wide analysis of realized niche overlap. Chapter 6 further supported the necessity of considering realized niches: while it is intuitive to infer that morphologically specialized species will have specialized realized niches, the opposite can be the case, as found in coral reef surgeonfishes. Finally, Chapter 7 and 8 provided observational and experimental evidence for how small variation in the realized niches of species can markedly modify their functional role within ecosystems and how, in the case of herbivorous fishes, this may lead to significant changes in benthic communities. In disentangling the relationship between pair-formation, herbivorous fishes, micro-topographic complexity, and the benthic community on coral reefs, this thesis contributes to our knowledge of the effects of *realized* functional diversity for coral reef ecosystems. The information provided in this thesis, therefore, may be considered in future assessments of functional diversity on coral reefs, in order to improve the accuracy with which we can predict the contribution of biodiversity to ecosystem functioning in one of the world's most diverse ecosystems.

Consumer control of primary producers is extraordinarily strong on coral reefs and many studies have emphasized the importance of herbivorous fishes in preventing the proliferation of macroalgae (e.g. Hughes 1994; Bellwood et al. 2004; Hughes et al. 2007; Burkepile & Hay 2006; Graham et al. 2015). The investigation of herbivorous fishes and their functional roles on coral reefs has flourished throughout the last two decades of the 20th century (e.g. Robertson et al. 1979; Robertson & Gaines 1986; Choat & Bellwood 1985; Hay 1991; Hay & Fenical 1988; Choat & Clements 1993; Bellwood & Choat 1990; Bellwood 1995; Clements & Choat 1995), laying the foundation for subsequent functional classifications. Since then, many researchers have engaged in studies that monitor herbivore abundances (Floeter et al. 2005; Wismer et al. 2009; Cheal et al. 2012), assess herbivore biomass and diversity on large spatial scales (Edwards et al. 2014), investigate the effects of herbivore extraction (McClanahan et al. 2001; Bellwood et al. 2012), or examine the socio-ecological factors that can lead to over-exploitation of herbivorous fishes (Cinner et al. 2009; Cinner et al. 2012). While the advances made in these fields are arguably indispensible for our overarching goal to manage and conserve coral reefs, the vast majority of studies incorporating herbivore functional diversity into their framework use classification schemes that are, at best, coarse representations of species' fundamental niches, suggesting extensive functional overlap between species within groups.

This contrasts strongly with the burgeoning evidence of differences in the realized niches of herbivorous fishes. Over the last five years, research has revealed marked differences among herbivorous fish species commonly considered to be functionally equal. These differences relate to their diet (Fox et al. 2009; Mantyka & Bellwood 2007a,b; Hoey & Bellwood 2011; Hoey et al. 2013; Rasher et al. 2013), spatial ecology (Marshell et al. 2011; Claisse et al. 2011; Fox & Bellwood 2011; Welsh & Bellwood 2012; Brandl & Bellwood 2013b), foraging microhabitat utilization (Cardoso et al. 2006; Fox & Bellwood 2013; Brandl & Bellwood 2014a [Chapter 5]), or their overall impact on the benthic community (Burkepile & Hay 2008; 2010; 2011; [Chapter 8]). Yet, unfortunately, little of the information provided by these studies has since been incorporated into studies attempting to extrapolate the functional structure of herbivore communities and the effects of human-mediated pressure on ecosystem function. This is concerning as it suggests that many studies underestimate the functional diversity of herbivorous fishes, and thus overestimate the extent of functional redundancy (Bellwood et al. 2003; Johannsson et al. 2013; Micheli et al. 2013). Thus, I posit that more dedicated efforts need to be made to incorporate current findings with regards to functional differences among herbivorous reef fishes, as provided in this thesis, into evaluations of herbivore diversity and ecosystem functioning. At present, the continued use of functional classification schemes that have been shown to be of limited resolution impedes our attempts to fully understand herbivory as an ecosystem process and the effect of current environmental changes on herbivorous grazing on coral reefs.

Several of the results presented in this thesis may provide an impetus for future research. Notably, the results of Chapters 2, 3, and 4 present pair-formation in fishes in a new light. While fishes are often assumed to associate predominantly for the purpose of reproduction (Pratchett et al. 2006), I demonstrate that direct ecological benefits of associating with a partner may override potential reproductive advantages. Given the frequency of pair-formation in reef fishes (Brandl & Bellwood 2014b [Chapter 2]), the potential for case studies examining pairing behaviour from an ecological perspective is vast, and likely to yield other cases in which both reproductive and direct ecological benefits underpin pairing behaviour in fishes. Chapter 4 builds on the social-ecological aspect of pair-formation in fishes and, as such, presents rabbitfishes as a model organism for the study of the cognitive and social capacities that allow fishes to engage in cooperative relationships. While the last decade has seen the establishment of fishes as a group of organisms that can cope with the complex cognitive and social demands of cooperative interactions (Bshary et al. 2002; Bshary & Grutter 2006; Brown 2015), the cooperative vigilance system observed in rabbitfishes opens several avenues for research that could be considered. First, genetic parentage analyses would provide a useful tool in order to examine whether kinship may play a role in the maintenance of cooperation among pair members. Kinship has long been argued to be a crucial factor for the evolution of cooperation in animals (Axelrod & Hamilton 1981; Dugatkin 1997; Clutton-Brock et al. 2001; Clutton-Brock 2009), but its effect on cooperation between rabbitfishes has yet to be determined. While the pelagic larval phase of rabbitfishes (Thresher 1984) makes close kinship between pair members rather unlikely, it appears possible that kin selection plays a factor in maintaining high levels of cooperation. Second, further exploration of the factors that stabilize cooperation in pairs of coral reef rabbitfishes could be performed, such as experimental manipulations of the partner’s cooperativeness or the ambient predation pressure. In addition, the potential role of fin-flicking behaviour as a communicative signal could be examined using experimental setups. Third, the cognitive demands of cooperation between rabbitfishes could be assessed by confronting rabbitfsihes with challenges such as individual recognition or memorization of individual’s previous actions. Along with these assessments, a closer examination of life-history parameters in rabbitfish pairs would be helpful to determine the fishes' sex, age, and respective body condition. Finally, the reproductive strategies of rabbitfishes are still largely unexplored. Aside from anecdotal information, which suggests that pairing rabbitfishes spawn in large aggregations (Johannes 1981), no spawning observations have been made to date.

The results from the remaining chapters suggest that a closer examination of the interactions between micro-topograhic complexity and the foraging behaviour of fishes may provide interesting information on consumer-producer dynamics on coral reefs. First, a detailed account of the benthic communities within crevices *in situ* could be performed, including assessments of particulate components. The dynamics of sediment and organic particulates, in particular, may provide interesting insights. In addition, a species-level assessment of the benthic communities in different types of concealed microhabitats (e.g. scaling in size) along with high-resolution examinations of the dietary preferences of herbivorous fishes, potentially making use of stable isotope analyses, may reveal interesting aspects of grazing dynamics on coral reefs and enable us to further unravel niche overlap among herbivorous fishes and its effect on the benthic community. Finally, a replication of the experiment presented in Chapter 8 in different locations would be desirable. It is striking that none of the genera identified to feed in concealed environments on the Great Barrier Reef are present in the Caribbean. If herbivory in concealed environments represent a critical ecosystem process on Indo-Pacific coral reefs, the question arises whether this process is equally important in the Caribbean, and if so, which species are responsible for performing the functional role. Given the comparably low diversity of Caribbean coral reefs, such approach would yield interesting details and may reveal one pathway that has led to the large-scale degradation of Caribbean coral reefs.

Finally, I suggest that the findings of this thesis be incorporated into larger-scale assessments of the functional diversity of herbivorous fishes. This could make use of either the morphological information provided in Brandl & Bellwood (2013a [Chapter 3]), or classify species based on their realized microhabitat realization in order to extract their contribution to overall ecosystem functioning. In this context, the assembly of a catalogue of morphological and categorical ecological traits for coral reef organisms may prove to be a valuable endeavour. In such a catalogue, current information about the fundamental and realized niches of coral reef organisms, such as fishes, could be regularly updated and made accessible to researchers, while encouraging authors to provide information about the functional niches of coral reef organisms in a standardized format. For instance, a similar framework to the one suggested in Brandl & Bellwood (2014a [Chapter 5]) may be applied in order to examine functional niche partitioning in consumer assemblages and standardized estimates of niche overlap could be entered in the database. If used continuously in various locations around the world, larger-scale evaluations of functional diversity and ecosystem processes will enable researchers to consider information on the realized niche of fishes, rather than their potential function within the ecosystem. Given the downward trajectory of coral reefs and the worldwide losses of diversity (Knowlton 2009), such approaches will become more and more critical in order to predict the response of reef systems to anthropogenic disturbances or the implementation of conservation measures to counteract these disturbances.

In summary, this thesis presents evidence for fine-scale functional niche partitioning among herbivorous coral reef fishes. Herbivorous fish species differ markedly in their use of different benthic foraging microhabitats, and ecological segregation that is facilitated by the differences in morphological features, social preferences, and environmental variation among microhabitats. While this thesis is restricted to coral reef environments, processes similar to the ones described herein may also be operating in other ecosystems.

References

Able, K.W., Grimes, C.B., Cooper, R.A. & Uzmann, J.R. 1982. Burrow construction and behavior of tilefish, *Lopholatilus chamaeleonticeps*, in Hudson Submarine Canyon. *Environmental Biology of Fishes* **7**, 199–205.

Ackerly, D.D., Cornwell, W. 2007. A trait-based approach to community assembly: partitioning of species trait values into within-and among-community components. *Ecology Letters* **10**, 135-145.

Adkins-Regan, E. 2002. Development of sexual partner preference in the zebra finch: a socially monogamous, pair-bonding animal. *Archives of Sexual Behavior* **31**, 27–33.

Adrian, O., Kaiser, S., Sachser, N., Jandewerth, P., Löttker, P., Epplen, J.T. & Hennessy, M.B. 2008. Female influences on pair-formation, reproduction and male stress responses in a monogamous cavy (*Galea monasteriensis*). *Hormones and Behavior* **53**, 403–412.

Aguirre, L.F., Herrel, A., Van Damme, R., Matthysen, E. 2002. Ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community. *Proceedings of the Royal Society London B* **269**, 1271-1278.

Ahlgren, J., Åbjörnsson, K. & Brönmark, C. 2011. The influence of predator regime on the behaviour and mortality of a freshwater amphipod, *Gammarus pulex*. *Hydrobiologia* **671**, 39–49.

Albert, C.H., de Bello, F., Boulangeat, I., Pellet, G., Lavorel, S., & Thuiller, W. 2012. On the importance of intraspecific variability for the quantification of functional diversity. *Oikos* **121**, 116-126.

Alfaro, M.E., Bolnick, D.I., Wainwright, P.C. 2005. Evolutionary consequences of many-to-one mapping of jaw morphology to mechanics in labrid fishes. *American Naturalist* **165**, 140-154.

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

Allen, G.R., Steene, R., Allen, M. 1998. *A guide to angelfishes and butterflyfishes*. Odyssey Publishing, Perth

Allen, G.R. & Munday, P.L. 1995. Description of four new gobies (Gobiidae) from the western Pacific Ocean. *Revue française d'aquariologie* **22**, 99–104.

Allen, G.R. & Rajasuriya, A. 1995. *Chrysiptera kuiteri*, a new species of damselfish (Pomacentridae) from Indonesia and Sri Lanka. *Records of the Western Australian Museum* **17**, 283–286.

Allen, G.R. 1987. Descriptions of three new pseudochromid fishes of the genus *Pseudoplesiops* from Australia and surrounding regions. *Records of the Western Australian Museum* **13**, 249–261.

Allen, G.R. 1991. *Damselfishes of the world*. Melle, Germany: Mergus Publishers.

Allen, G.R., Steene, R.C., Humann, P. & DeLoach, N. 2003. *Reef fish identification: Tropical Pacific*. Jacksonville, FL: New World Publications.

Almany, G.R. & Webster, M.S. 2006. The predation gauntlet: early post-settlement mortality in reef fishes. *Coral Reefs* **25**, 19–22.

Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., Watkinson, A.R. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society London B*, rspb20090339.

Alwany, M., Thaler, E. & Stachowitsch, M. 2005. Territorial behaviour of *Acanthurus sohal* and *Plectroglyphidodon leucozona* on the fringing Egyptian Red Sea reefs. *Environmental Biology of Fishes*, **72**, 321-334.

Andersen, A.N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. *Journal of Biogeography*, **24**, 433–460.

Ang, T.Z. & Manica, A. 2010. Benefits and costs of dominance in the angelfish *Centropyge bicolor*. *Ethology* **116**, 855–865.

Annett, C.A., Pierotti, R. & Baylis, J.R. 1999. Male and female parental roles in the monogamous cichlid, *Tilapia mariae*, introduced in Florida. *Environmental Biology of Fishes* **54**, 283-293.

Araujo, M.B., & Guisan, A. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* **33**, 1677-1688.

Arenz, C.L. & Leger, D.W. 1997. The antipredator vigilance of adult and juvenile thirteen-lined ground squirrels (Sciuridae: *Spermophilus tridecemlineatus*): visual obstruction and simulated hawk attacks. *Ethology* **103**, 945-953.

Arnold, S.N., Steneck, R. & Mumby, P.J. 2010. Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series* **414**, 91-105.

Atema, J., Jacobson, S., Karnofsky, E., Oleszko-Szuts, S. & Stein, L. 1979. Pair-formation in the lobster *Homarus americanus*: behavioural development, pheromones and mating. *Marine and Freshwater Behaviour and Physiology* **6**, 277–296.

Axelrod, R. & Hamilton, W. D. The evolution of cooperation. *Science* **211**, 1390-1396.

Aydin, M. 2011. Growth, reproduction and diet of pufferfish (*Lagocephalus sceleratus*, Gmelin, 1789) from Turkey's Mediterranean Sea coast. *Turkish Journal of Fisheries and Aquatic Sciences* **11**, 589–596.

Babcock, R.C., Mundy, C.N. 1996. Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. *Journal of Experimental Marine Biology and Ecology* **206**, 179–201.

Baird, A.H., Babcock, R.C. & Mundy, C.P. 2003. Habitat selection by larvae influences the depth distribution of six common coral species. *Marine Ecology Progress Series* **252**, 289–293.

Baird, A.H. & Hughes, T.P. 1997. Spatial variation in coral recruitment around Lizard Island, Australia. *Proceedings of the 8th International Coral Reef Symposium* **2**, 1207–1210

Baird, A.H., Guest, J.R. & Willis, B.L. 2009. Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics* **40**, 551–571.

Baird, T.A. & Baird, T.D. 1992. Colony formation and some possible benefits and costs of gregarious living in the territorial sand tilefish, *Malacanthus plumieri*. *Bulletin of Marine Science* **50**, 56–65.

Baria, M.V.B., Guest, J.R., Edwards, A.J., Alino, P.M., Heyward, A.J. & Gomez ED 2010. Caging enhances post-settlement survival of juveniles of the scleractinian coral *Acropora tenuis*. *Journal of Experimental Marine Biology and Ecology* **394**, 149–153

Barlow, G.W. 1987. Spawning, eggs and larvae of the longnose filefish *Oxymonacanthus longirostris*, a monogamous coralivore. *Environmental Biology of Fishes* **20**, 183–194.

Barlow, G.W. 1974. Extraspecific imposition of social grouping among surgeonfishes (Acanthuridae, Pisces). *Journal of Zoology* **174**, 333–340.

Barlow, G.W. 1981. Patterns of parental investment, dispersal and size among coral-reef fishes. *Environmental Biology of Fishes* **6**, 65–85.

Barlow, G.W. 1984. Patterns of monogamy among teleost fishes. *Archiv für Fischereiwissenschaft* **35**, 75–123.

Barnett, A., Bellwood, D.R. & Hoey, A.S. 2006. Trophic ecomorphology of cardinalfish. *Marine Ecology Progress Series* **322**, 249–257.

Barreiros, J.P., Morato, T., Santos, R.S., & Borba, A.E. 2003. Interannual changes in the diet of the almaco jack *Seriola rivoliana* (Perciformes: Carangidae) from the Azores. *Cybium* **27**, 37–40.

Barros, B., Sakai, Y., Hashimoto, H. & Gushima, K. 2008. Feeding behavior of leaf-like juveniles of the round batfish *Platax orbicularis* (Ephippidae) on reefs of Kuchierabu-jima Island, southern Japan. *Journal of Ethology* **26**, 287–293.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* **19**, 134–143.

Baselga, A. 2012. The relationship between species replacement and dissimilarity derived from turnover and nestedness. *Global Ecology and Biogeography* **9**, 134–143.

Bednekoff, P. A. 1991. Mutualism among safe, selfish sentinels: a dynamic game. *American Naturalist* **150**, 373-392.

Bellwood, D.R. 1995. Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef, Australia. *Marine Biology* **121**, 419–429

Bellwood, D.R., Goatley, C.H.R., Brandl, S.J. & Bellwood, O. 2014. Fifty million years of herbivory on coral reefs: fossils, fish and functional innovations. *Proceedings of the Royal Society London B* ***281*** (doi:10.1098/rspb.2013.3046).

Bellwood, D.R., Hoey, A.S. & Hughes, T.P. 2012. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society London B* **279**, 1621—1629.

Bellwood, D.R., Hughes, T.P. & Hoey AS 2006. Sleeping functional group drives coral-reef recovery. *Current Biology* **16**, 2434–2439.

Bellwood, D.R. & Wainwright, P.C. 2001. Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* **20**, 139–150.

Bellwood, D.R., Wainwright, P.C., Fulton, C.L. & Hoey, A.S. 2006. Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society London B* **273**, 101-107.

Bellwood, D.R. & Wainwright, P.C. 2002. *The history and biogeography of fishes on coral reefs*. Coral reef fishes: dynamics and diversity in a complex ecosystem, (ed. PE Sale), pp. 5-32. San Diego, CA: Academic Press.

Bellwood, D.R. & Choat, J.H. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* **28**, 189–214.

Bellwood, D.R., Hoey, A.S & Choat, J.H. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem functionon coral reefs. *Ecology Letters* **6**, 281–285.

Bellwood, D.R., Hoey, A.S., Ackerman, J.L. & Depczynski, M. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology* **12**, 1587–1594.

Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. 2004. Confronting the coral reef crisis. *Nature* **429**, 827-833.

Bellwood, D.R., Klanten, S., Cowman, P.F., Pratchett, M.S., Konow, N. & Van Herwerden, L. 2010. Evolutionary history of the butterflyfishes (f: Chaetodontidae) and the rise of coral feeding fishes. *Journal of Evolutionary Biology* **23**, 335–349.

Bellwood, D.R., Renema, W. & Rosen, B.R. 2012. *Biodiversity hotspots, evolution and coral reef biogeography: a review.* In Biotic evolution and environmental change in Southeast Asia, D.J. Gower, K.G. Johnson, J.E. Richardson, B.R. Rosen, L. Rüber, & S.T. Williams (eds.). Cambridge, UK: Cambridge University Press, 216–245.

Beltran, S., & Boissier, J. 2008. Schistosome monogamy: who, how, and why? *Trends in Parasitology* **24**, 386–391.

Bennett, S., & Bellwood, D.R. 2011. Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Marine Ecology Progress Series* **426**, 241-252.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J. & Saunders, B.J. 2015. Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters* (in press) DOI: 10.1111/ele.12450.

Berenbaum, M.R. (1995). The chemistry of defense: theory and practice. *Proceedings of the National Academy of Sciences USA* **92**, 2-8.

Bergey, E.A. 2005. How protective are refuges? Quantifying algal protection in rock crevices. *Freshwater Biology* **50**, 1163-1177.

Bergmüller, R. & Taborsky, M. 2005. Experimental manipulation of helping in a cooperative breeder: helpers ‘pay to stay’ by pre-emptive appeasement. *Animal Behaviour* **69**, 19-28.

Bergmüller, R., Heg, D. & Taborsky, M. 2005. Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints. *Proceedings of the Royal Society London B* **272**, 325-331.

Berumen, M.L. & Pratchett, M.S. 2006. Effects of resource availability on the competitive behaviour of butterflyfishes (Chaetodontidae). *Proceedings of the 10th International Coral Reef Symposium* 644–650

Berumen, M.L., Pratchett, M.S. & McCormick MI 2005. Within-reef differences in diet and condition of butterflyfishes (Chaetodontidae). *Marine Ecology Progress Series* **287**, 217–227

Beukers-Stewart, B.D. & Jones, G.P. 2004. The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish. *Journal of Experimental Marine Biology and Ecology* **299**,155–184.

Beukers, J. S. & Jones, G. P. 1998. Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* **114**, 50-59.

Beumer, J.P. 1978. Feeding ecology of four fishes from a mangrove creek in north Queensland, Australia. *Journal of Fish Biology* **12**, 475–490.

Biro, P.A., Beckmann, C. & Stamps J.A. 2009. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society London B* **277**, 71–78.

Birrell, C.L., McCook, L.J., Willis, B.L. & Diaz-Pulido, G.A. 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceanography and Marine Biology Annual Reviews* **46**, 25–63

Blaber, S.J.M. & Cyrus, D.P. 1983. The biology of Carangidae (Teleostei) in natal estuaries. *Journal of Fish Biology* **22**, 173–188.

Blaber, S.J.M. 1977. The feeding ecology and relative abundance of mullet (Mugilidae) in Natal and Pondoland estuaries. *Biological Journal of the Linnean Society* **9**, 259–275.

Blaber, S.J.M., Milton, D.A., Rawlinson, N.J.F., Tiroba, G. & Nichols, P.V. 1990. Diets of lagoon fishes of the Solomon Islands: predators of tuna baitfish and trophic effects of baitfishing on the subsistence fishery. *Fisheries Research* **8**, 263–286.

Black, J.M. 2001. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. *Behavioral Ecology* **12**, 640–645.

Boaden, A.E. & Kingsford, M.J. 2012. Diel behaviour and trophic ecology of *Scolopsis bilineatus* (Nemipteridae). *Coral Reefs* **31**, 871–883.

Boesch, C. & Boesch, H. 1989. Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology* **78**, 547-573.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* **161**, 1-28.

Bonaldo, R.M. & Bellwood, D.R. 2011. Parrotfish predation on massive *Porites* on the Great Barrier Reef. *Coral Reefs* **30**, 259–269

Bonaldo, R.M., Hoey, A.S. & Bellwood, D.R. 2014. The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology Annual Reviews* **52**, 81-132.

Bonaldo, R.M., Krajewski, J.P. & Sazima, I. 2005. Meals for two: foraging activity of the butterflyfish *Chaetodon striatus* (Perciformes) in southeast Brazil. *Brazilian Journal of Biology* **65**, 211–215

Bonaldo, R.M. & Bellwood, D.R. 2011. Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. *Coral Reefs* **30**, 381-390.

Bonin, M.C., Almany, G.R. & Jones, G.P. 2011. Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology* **92**, 1503-1512.

Borrell BJ. 2005 Long tongues and loose niches: evolution of euglossine bees and their nectar flowers. *Biotropica* **37**, 664-669.

Borsa, P., Lemer, S. & Aurell, D. 2007. Pattern of lineage diversification in rabbitfishes. *Molecular Phylogenetics and Evolution* **44**, 427–435.

Botton, M.L. & Loveland, R.E. 1992. Body size, morphological constraints, and mated pair-formation in four populations of horseshoe crabs (*Limulus polyphemus*) along a geographic cline. *Marine Biology* **112**, 409–415.

Bouton N, v. Os N, Witte F. 1998 Feeding performance of Lake Victoria rock cichlids: testing predictions from morphology. *Journal of Fish Biology* **53**, 118-127.

Box, S.J. & Mumby, P.J. 2007. Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Marine Ecology Progress Series* **342**, 139–149.

Brandl, S.J. & Bellwood, D.R. 2013a. Morphology, sociality, and ecology: can morphology predict pairing behaviour in coral reef fishes? *Coral Reefs* **32**, 835–846.

Brandl, S.J. & Bellwood, D.R. 2013b. Pair formation in the herbivorous rabbitfish *Siganus doliatus*. *Journal of Fish Biology* **82**, 2031–2044.

Brandl, S.J. & Bellwood, D.R. 2014a. Individual-based analyses reveal limited functional overlap in a coral reef fish community. *Journal of Animal Ecology* **83**, 661-670.

Brandl, S.J. & Bellwood, D.R. 2014b. Pair formation in coral reef fishes: an ecological perspective. *Oceanography and Marine Biology Annual Reviews* **52**, 1-80.

Brandl, S.J., Hoey, A.S. & Bellwood, D.R. (2014). Micro-topography mediates interactions between corals, algae, and herbivorous fishes on coral reefs. *Coral Reefs* **33**, 421-430.

Brewer, D.T., Blaber, S.J.M. & Salini, J.P. 1989. Feeding biology of *Caranx bucculentus* Alleyne and Macleay (Teleostei: Carangidae) in Albatross Bay, Gulf of Carpentaria, with special reference to predation on penaeid prawns. *Australian Journal of Marine and Freshwater Research* **40**, 657-668.

Brock, R. 1979. An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Marine Biology* **51**, 381–388

Brooker, R.M., Munday, P.L. & Ainsworth, T.D. 2010. Diets of coral-dwelling fishes of the genus *Gobiodon* with evidence of corallivory. *Journal of Fish Biology* **76**, 2578–2583.

Brosnan, S.F., Salwiczek, L. & Bshary, R. 2010. The interplay of cognition and cooperation. *Philosophical Transactions of the Royal Society London B* **365**, 2699-2710.

Brown, J.H. 1981. Two decades of homage to Santa Rosalia: toward a general theory of diversity. *American Zoologist* **21**, 877-888.

Brown, J.H. 2014. Why are there so many species in the tropics? *Journal of Biogeography* **41**, 8-22.

Brown, C. 2015. Fish intelligence, sentience and ethics. *Animal Cognition* **18**, 1-17.

Brown, C., Laland K. & Krause, J. *Fish cognition and behavior.* (Wiley-Blackwell, Oxford, UK).

Brown, G.E., Godin, J.J. & Pedersen, J. 1999. Fin-flicking behaviour: a visual antipredator alarm signal in a characin fish, *Hemigrammus erythrozonus*. *Animal Behaviour* **58**, 469-475.

Bruns, P.J. & Brussard, T.B. 1974. Pair-formation in *Tetrahymena pyriformis* - an inducible developmental system. *Journal of Experimental Zoology* **188**, 337-344.

Bshary, R. & Grutter, A.S. 2006. Image scoring and cooperation in a cleaner fish mutualism. *Nature* **441**, 975-978.

Bshary, R. & Grutter, A.S. 2005. Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biology Letters* **1**, 396-399.

Bshary, R. & Schäffer, D. 2002. Choosy reef fish select cleaner fish that provide high-quality service. *Animal Behaviour* **63**, 557-564.

Bshary, R., Hohner, A., Ait-el-Djoudi, K., & Fricke, H. 2006. Interspecific communicative and coordinated hunting between groupers and giant moray eels in the Red Sea. *PLoS Biology* **4**, e431.

Bshary, R., Gingins, S. & Vail, A.L. 2014. Social cognition in fishes. *Trends in Cognitive Science* **18**, 465-471.

Bshary, R., Grutter, A.S., Willener, A.S.T. & Leimar, O. 2008. Pairs of cooperating cleaner fish provide better service quality than singletons. *Nature* **455**, 964–966.

Bshary, R., Wickler, W. & Fricke, H. 2002. Fish cognition: a primate's eye view. *Animal Cognition* **5**, 1-13.

Bull, C.M. & Pamula, Y. 1998. Enhanced vigilance in monogamous pairs of the lizard *Tiliqua rugosa*. *Behavioral Ecology* **9**, 452–455.

Burchmore, J.J., Pollard, D.A. & Bell, J.D. 1984. Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia australis* seagrass habitat in Port Hacking, New South Wales. *Aquatic Botany* **18**, 71-87.

Burkepile, D.E. & Hay, M.E. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* **87**, 3128-3139.

Burkepile, D.E. & Hay, M.E. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences USA* **105**, 16201-16206.

Burkepile, D.E. & Hay, M.E. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS One* **5**, e8963.

Burkepile, D.E. & Hay, M.E. 2011. Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs* **30**, 351–362.

Burpee, D.M. & Sakaluk, S.K. 1993. The effect of pair-formation on diel calling patterns in two cricket species, *Gryllus veletis* and *Gryllodes sigillatus* (Orthoptera, Gryllidae). *Journal of Insect Behavior* **6**, 431–440.

Cable, R.M. & Hopp, R.M. 1954. Acanthocephalan parasites of the genus *Neoechinorhynchus* in North American turtles with the description of two new species. *Journal of Parasitology* **40**, 674–680.

Calenge C. 2006. The package ‘adehabitat’ for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modeling* **197**, 516-519.

Cardinale, B.J., Palmer, M.A., & Collins, S.L. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**, 426-429.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., et al. 2012. Biodiversity loss and its impact on humanity. *Nature* **486**, 59-67.

Cardoso, S.C., Soares, M.C., Oxenford, H.A. & Côté, I.M. 2006. Interspecific differences in foraging behavior and functional role of Caribbean parrotfish. *Marine Biodiversity Records* **2**, 1–6.

Carlon, D.B. 2001. Depth-related patterns of coral recruitment and cryptic suspension-feeding invertebrates on Guana Island, British Virgin Islands. *Bulletin of Marine Science* **68**, 525–541

Carlson, B.A. 2012. Feeding activity by the blenny *Exallias brevis* causes multifocal bleaching in corals: Comment on Zvuloni et al. (2011). *Marine Ecology Progress Series* **463**, 297–299.

Carter, G.G. & Wilkinson, G.S. 2013. Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proceedings of the Royal Society London B* **280**, 20122573.

Carter, G.G. 2014. The reciprocity controversy. *Animal Behaviour and Cognition* **1**, 368-386.

Ceccarelli, D.M., Jones, G.P. & McCook, L.J. 2005. Foragers versus farmers: contrasting effects of two behavioural groups of herbivores on coral reefs. *Oecologia* **145**, 445–453

Ceccarelli, D.M. 2007. Modification of benthic communities by territorial damselfish: a multi-species comparison. *Coral Reefs* **26**, 853–866.

Chapin, S.F., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. & Tilman, D. 1997. Biotic control over the functioning of ecosystems. *Science* **277**, 500–504.

Chase, J.M., & Leibold, M.A. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press.

Cheal, A.J., Emslie, M.J., Miller, I. & Sweatman, H. 2012. The distribution of herbivorous fishes on the Great Barrier Reef. *Marine Biology* **159**, 1143–1154.

Cheal, A.J., Emslie, M.J., MacNeil, M.A., Millar, I. & Sweatman, H. 2013. Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. *Ecological Applications* **23**, 174-188.

Cheal, A.J., MacNeil, M.A., Cripps, E., Emslie, M.J., Jonker, M., Schaffelke, B. & Sweatman, H. 2010. Coral-macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* **29**, 1005–1015.

Chen, T.C., Ormond, R.F.G. & Mok, H.K. 2001. Feeding and territorial behaviour in juveniles of three co-existing triggerfishes. *Journal of Fish Biology* **59**, 524–532.

Cheney, D.L., Moscovice, L.R., Heesen, M., Mundry, R. & Seyfarth, R.M. Contingent cooperation between wild female baboons. *Proceedings of the National Academy of Sciences USA* **107**, 9562-9566.

Choat, J.H., & Bellwood, D.R. 1985. Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. *Marine Biology* **89**, 221-234.

Choat, J.H., & Clements, K.D. 1993. Daily feeding rates in herbivorous labroid fishes. *Marine Biology* **117**, 205-211.

Choat, J.H. & Clements, K.D. 1998. Vertebrate herbivores in marine and terrestrial environments: a nutritional ecology perspective. *Annual Reviews of Ecology, Evolution and Systematics* **29**, 375-403.

Choat, J.H., Clements, K.D. & Robbins, W.D. 2002. The trophic status of herbivorous fishes on coral reefs. *Marine Biology* **140**, 613-623.

Choat, J.H., Klanten, O.S., van Herwerden, L., Robertson, D.R. & Clements, K.D. 2012. Patterns and processes in the evolutionary history of parrotfishes (Family Labridae). *Biological Journal of the Linnean Society* **107**, 529–557.

Choat, J.H., Robbins, W.D. & Clements, K.D. 2004. The trophic status of herbivorous fishes on coral reefs. *Marine Biology* **145**, 445–454.

Christy, J.H. & Salmon, M. 1991. Comparative studies of reproductive behavior in Mantis shrimps and fiddler crabs. *American Zoologist* **31**, 329–337.

Cinner, J.E., McClanahan, T.R., Daw, T.M., Graham, N.A.J., Maina, J., Wilson, S.K., & Hughes, T.P. 2009. Linking social and ecological systems to sustain coral reef fisheries. *Current Biology* **19**, 206-212.

Cinner, J.E., McClanahan, T.R., MacNeil, M.A., Graham, N.A.J., Daw, T.M., Mukminin, A., et al. 2012. Comanagement of coral reef social-ecological systems. *Proceedings of the National Academy of Sciences USA* **109**, 5219-5222.

Claisse, J.T., Clark, T.B., Schumacher, B.D., McTee, S.A., Bushnell, M.E., Callan, C.K., et al. 2011. Conventional tagging and acoustic telemetry of a small surgeonfish, *Zebrasoma flavescens*, in a structurally complex coral reef environment. *Environmental Biology of Fishes* **91**, 185-201.

Clark, C.J., Poulsen, J.R. & Parker, V.T. 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica* **33**, 606–620.

Clark, E. & Pohle, J.F. 1992. Monogamy in tilefish. *National Geographic Research and Exploration* **8**, 276–295.

Clark, E. & Pohle, M. 1996. *Trichonotus halstead*, a new sand-diving fish from Papua New Guinea. *Environmental Biology of Fishes* **45**, 1–11.

Clark, E., Pohle, J.F. & Halstead, B. 1998. Ecology and behaviour of tilefishes, *Hoplolatilus starki*, *H. fronticinctus* and related species (Malacanthidae): non-mound and mound builders. *Environmental Biology of Fishes* **52**, 395–417.

Clark, E., Rabin, J.S. & Holderman, S. 1988. Reproductive behavior and social organization in the sand tilefish, *Malacanthus plumieri*. *Environmental Biology of Fishes* **22**, 273–286.

Clark, E., Stoll, M.J., Alburn, T.K. & Petzold, R. 2000. Mound-building and feeding behaviour of the two-stripe goby *Valenciennea helsdingenii*, in the south Red Sea. *Environmental Biology of Fishes* **57**, 131–141.

Clarke, K.R. & Ainsworth, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**, 205–219

Clarke, K.R., Somerfield, P.J. & Gorley, R.N. 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* **366**, 56–69

Clarke, K.R. & Warwick R.M. 2001. *Change in marine communities: an approach to statistical analysis and interpretation*, 2nd edn. PRIMER-E, Plymouth

Clavel, J., Julliard, R. & Devictor, V. 2010. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* **9**, 222-228.

Claydon, J. 2004. Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. *Oceanography and Marine Biology Annual Reviews* **42**, 265–302.

Clemente, S., Hernández, J.C., Rodríguez, A. & Brito, A. 2010. Identifying keystone predators and the importance of preserving functional diversity in sublittoral rocky-bottom areas. *Marine Ecology Progress Series* **413**, 55–67.

Clements, K.C. & Stephens, D.W. 1995. Testing models of non-kin cooperation: mutualism and the Prisoner’s Dilemma. *Animal Behaviour* **50**, 527-535.

Clements, K.D. & Choat, J.H. 1995. Fermentation in tropical marine herbivorous fishes. *Physiological Zoology* **68**, 355-378.

Clements, K.D. & Choat, J.H. 1997. Comparison of herbivory in the closely-related marine fish genera *Girella* and *Kyphosus*. *Marine Biology* **127**, 579–586.

Clements, K.D., Raubenheimer, D. & Choat, J.H. 2009. Nutritional ecology of marine herbivorous fishes: ten years on. *Functional Ecology* **23**, 79-92.

Clutton-Brock, T.H., O'Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R., Griffin, A.S., Manser, M. 1999. Selfish sentinels in cooperative mammals. *Science* **284**, 1640-1644.

Clutton-Brock, T.H. Cooperation between non-kin in animal societies. *Nature* **462**, 51-57 2009.

Colin, P.L. & Bell, L.J. 1991. Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak Atoll, Marshall Islands (North Pacific Ocean) with notes on other families. *Environmental Biology of Fishes* **31**, 229–260.

Collar, D.C., Wainwright, P.C. & Alfaro, M.E. 2008. Integrated diversification of locomotion and feeding in labrid fishes. *Biology Letters* **4**, 84–86

Colwell, R.K. & Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. *Ecology* **52**, 567-576.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302-1310.

Connell, S.D. 1998. Patterns of pisciviory by resident predatory reef fish at One Tree Reef, Great Barrier Reef. *Marine and Freshwater Research* **49**, 25–30.

Connell, S.D., Foster, M.S. & Airoldi, L. 2014. What are algal turfs? Towards a better description of turfs. *Marine Ecology Progress Series* **495**, 299-307.

Connor, R.C. 1995. Altruism among non-relatives: alternatives to the ‘Prisoner's Dilemma’. *Trends in Ecology and Evolution* **10**, 84-86.

Connor, R.C. 2010. Cooperation beyond the dyad: on simple models and a complex society. *Philosophical Transactions of the Royal Society London B* **365**, 2687-2697.

Connor, R.C. 1992. Egg-trading in simultaneous hermaphrodites: an alternative to Tit-for-Tat. *Journal of Evolutionary Biology* **5**, 523-528.

Connor, R.C. 1996. Partner preferences in by-product mutualisms and the case of predator inspection in fish. *Animal Behaviour* **51**, 451-454.

Cornwell, W.K., Schwilk, D.W. & Ackerly, D.D. 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* **87**, 1465–1471.

Cowman, P.F. & Bellwood, D.R. 2013. The historical biogeography of coral reef fishes: global patterns of origination and dispersal. *Journal of Biogeography* **40**, 209-224. (doi:10.1111/jbi.12003).

Cox, C.R., Goldschmidt, V.I. & Engelhardt, H.R. 1993. Pair-formation in California condors. *American Zoologist* **33**, 126–138.

Craig, M.T. 2007. Preliminary observations on the life history of the white-streaked grouper, *Epinephelus ongus*, from Okinawa, Japan. *Ichthyological Research* **54**, 81–84.

Croft, D. et al. 2006. Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behavioural Ecology and Sociobiology* **59**, 644-650.

Cvitanovic, C. & Bellwood, D.R. 2009. Local variation in herbivore feeding activity on an inshore reef of the Great Barrier Reef. *Coral Reefs* **28**, 127–133.

Daly, J.M. 1973. Some relationships between the process of pair-formation and gamete maturation in *Harmothoe imbricata* (L.) (Annelida: Polychaeta). *Marine and Freshwater Behaviour and Physiology* **1**, 277–284.

Daroonchoo, L. 1991. Study on some biology of Mahidol smiling goby (*Mahidolia mystacina* Cuvier and Valenciennes) in Chanthaburi River. Bangkok (Thailand): *Seminar on Fisheries* 16-18 Sep 1991.

D’agata, S., Mouillot, D., Kulbicki, M., Andréfouët, S., Bellwood, D. R., Cinner, J. E., et al. 2014. Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Current Biology* **24**, 555-560.

Day RW 1983. Effects of benthic algae on sessile animals: observational evidence from coral reef habitats. *Bulletin of Marine Science* **33**, 597–605.

De Waal, F.B. & Brosnan, S.F. 2006. *Simple and complex reciprocity in primates.* In Cooperation in primates and humans: mechanisms and evolution, eds Kappeler, P. M., van Schaik, C. P., pp. 85–105. Springer, Berlin.

Debenay, J.P., Sigura, A. & Justine, J.L. 2011. Foraminifera in the diet of coral reef fish from the lagoon of New Caledonia: Predation, digestion, dispersion. *Revue de Micropaléontologie* **54**, 87–103.

Delmonte Corrado M.U., Locatelli, D., Paleari, L. & Bottiroli, G. 1997. Lectin-binding sites involved in *Paramecium primaurelia* mating pair-formation. *Journal of Eukaryotic Microbiology* **44**, 603–608.

DeMartini, E.E., Anderson, T.W., Friedlander, A.M. & Beets, J.P. 2011. Predator biomass, prey density, and species composition effects on group size in recruit coral reef fishes. *Marine Biology* **158**, 2437-2447.

Depczynski, M. & Bellwood, D.R. 2003. The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series* **256**, 183–191.

Depczynski, M. & Bellwood, D.R. 2004. Microhabitat utilization patterns in cryptobenthic reef fish communities. *Marine Biology* **145**, 455–463.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. & Mouquet N. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology* **47**, 15–25.

Díaz, S., & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646-655.

Diaz-Pulido, G., Harii, S., McCook, L.J., Hoegh-Guldberg, O. 2010. The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs* **29**, 203–208.

Diaz-Pulido, G. & McCook, L.J. 2003. Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. *Ecology* **84**, 2026–2033.

Diaz-Pulido, G. & McCook, L.J. 2004. Effects of live coral, epilithic algal communities and substrate type on algal recruitment. *Coral Reefs* **23**, 225–233.

Dickens, L.C., Goatley, C.H.R., Tanner, J.K., & Bellwood, D.R. 2011. Quantifying relative diver effects in underwater visual censuses. *PLoS ONE* **6**:e18965

Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 398–408.

DiSalvo, L.H., Randall, J.E. & Cea, A. 2007. Stomach contents and feeding observations of some Easter Island fishes. *Atoll Research Bulletin* **548**, 234–245.

Domeier, M.L. & Colin, P.L. 1997. Tropical reef spawning aggregations: defined and reviewed. *Bulletin of Marine Science* **60**, 698–726.

Donaldson, T.J. 1989. Facultative monogamy in obligate coral-dwelling hawkfishes (Cirrhitidae). *Environmental Biology of Fishes* **26**, 295–302.

Donaldson, T.J. 1990. Reproductive behavior and social organization of some Pacific hawkfishes (Cirrhitidae). *Japanese Journal of Ichthyology* **36**, 439–458.

Doropoulos, C., Hyndes, G.A., Abecasis, D. & Vergés, A. 2013. Herbivores strongly influence algal recruitment in both coral-and algal-dominated coral reef habitats. *Marine Ecology Progress Series* **486**, 153-164.

Douglas, M.E. & Matthews, W.J. 1992. Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. *Oikos* **65**, 213-224.

Dudley, T.L. & D'Antonio, C.M. 1991. The effects of substrate texture, grazing, and disturbance on macroalgal establishment in streams. *Ecology* **72**, 297-309.

Duffy, J.E. & Hay, M.E. 1990. Seaweed adaptations to herbivory. *Bioscience* **40**, 368-375.

Duffy, J.E., Richardson, J.P. & Canuel, E.A. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters* **6**, 637–645.

Dugatkin, L.A. & Alfieri, M. 1991. Tit-for-tat in guppies (*Poecilia reticulata*): the relative nature of cooperation and defection during predator inspection. *Evolutionary Ecology* **5**, 300-309.

Dugatkin, L.A. & Mesterton-Gibbons M. 1996. Cooperation among unrelated individuals: reciprocal altruism, by-product mutualism and group selection in fishes. *BioSystems* **37**, 19-30.

Dugatkin, L.A. 1997. *Cooperation Among Animals: An Evolutionary Perspective.* Oxford University Press, New York.

Dumay, O., Tari, P.S., Tomasini, J.A. & Mouillot, D. 2004. Functional groups of lagoon fish species in Languedoc Roussillon (South of France, Mediterranean Sea). Journal of Fish Biology **64**, 970-983

Edmunds, P.J., Bruno, J.F. & Carlon, D.B. 2004. Effects of depth and microhabitat on growth and survivorship of juvenile corals in the Florida Keys. *Marine Ecology Progress Series* **278**, 115–124

Edmunds, P.J., Nozawa, Y. & Villanueva, R.D. 2014. Refuges modulate coral recruitment in the Caribbean and the Pacific. *Journal of Experimental Marine Biology and Ecology* **454**, 78-84.

Edwards, C.B., Friedlander, A., Green, A., Hardt, M., Sala, E., Sweatman, H. et al. 2014. Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proceedings of the Royal Society London B* **281**, 20131835.

Elliott, J.P. & Bellwood, D.R. 2003. Alimentary tract morphology and diet in three coral reef fish families. *Journal of Fish Biology* **63**, 1598–1609.

Elton, C.S. 1927. *Animal Ecology*. Macmillan Co, New York.

Emery, N.C., Forrestel, E.J., Jui, G., Park, M.S., Baldwin, B.G. & Ackerly, D.D. 2012. Niche evolution across spatial scales: climate and habitat specialization in California Lasthenia (Asteraceae). *Ecology* **93**, 151-166.

Emlen, S.T. & Oring, L.W. 1977. Ecology, sexual selection, and the evolution of the mating systems. *Science* **197**, 215–223.

Evans, M.J., Coffrath, M.A. & Lasker HR 2013. Effects of predator exclusion on recruit survivorship in an octocoral (*Briareum asbestinum*) and a scleractinian coral (*Porites astreoides*). *Coral Reefs* **32**, 597-601.

Farmer, B.M. & Wilson, S.K. 2011. Diet of finfish targeted by fishers in North West Australia and the implications for trophic cascades. *Environmental Biology of Fishes* **91**, 71–85.

Fautin, D.G. & Allen, G.R. 1992. *Field guide to anemonefishes and their host sea anemones.* Perth, Australia: Western Australian Museum.

Favreau, F.R., Goldizen, A.W. & Pays, O. 2010. Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proceedings of the Royal Society London B*, rspb20092337.

Feeney, W.E., Lönnstedt, O.M., Bosiger, Y., Martin, J., Jones, G.P., Rowe, R.J. & McCormick, M.I. (2012). High rate of prey consumption in a small predatory fish on coral reefs. *Coral Reefs* **31**, 909–918.

Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* **126**, 1–25.

Fernald, R.D. 1991. Teleost vision: seeing while growing. *Journal of Experimental Zoology* **5**, 167–180

Fernández-Juricic, E., Erichsen, J. T. & Kacelnik, A. 2004. Visual perception and social foraging in birds. *Trends in Ecology and Evolution* **19**, 25-31.

Fernández-Juricic, E., Smith, R. & Kacelnik, A. 2005. Increasing the costs of conspecific scanning in socially foraging starlings affects vigilance and foraging behaviour. *Animal Behaviour* **69**, 73-81.

Ferry-Graham, L.A., Konow, N. 2010. The intramandibular joint in *Girella*: a mechanism for increased force production? *Journal of Morphology* **271**, 271-279.

Ferry-Graham, L.A., Wainwright, P.C., Hulsey, C.D. & Bellwood, D.R. 2001a. Evolution and mechanics of long jaws in butterflyfishes (family Chaetodontidae). *Journal of Morphology* **248**, 120–143.

Ferry-Graham, L.A., Wainwright, P.C. & Bellwood, D.R. 2001b. Prey capture in long-jawed butterflyfishes (Chaetodontidae): the functional basis of novel feeding habits. *Journal of Experimental Marine Biology and Ecology* **256**, 167-184.

Ferry-Graham, L.A., Wainwright, P.C., Westneat, M.W. & Bellwood DR 2002a. Mechanisms of benthic prey capture in wrasses (Labridae). *Marine Biology* **141**, 819–830.

Ferry-Graham, L.A., Bolnick, D.I. & Wainwright, P.C. 2002b. Using functional morphology to examine the ecology and evolution of specialization. *Integrative and Comparative Biology* **42**, 265–277.

Ferry-Graham, L.A., Gibb, A.C. & Hernandez, L.P. 2008. Premaxillary movements in cyprinodontiform fishes: An unusual protrusion mechanism facilitates "picking" prey capture. *Zoology* **111**, 455–466.

Fessler, J.L. & Westneat, M.W. 2007. Molecular phylogenetics of the butterflyfishes (Chaetodontidae): Taxonomy and biogeography of a global coral reef fish family. *Molecular Phylogenetics and Evolution* **45**, 50–68.

Fischer, E.A. 1984. Egg trading in the chalk bass, *Serranus tortugarum*, a simultaneous hermaphrodite. *Zeitschrift für Tierpsychologie* **66**, 143-151.

Fischer, E.A. 1988. Simultaneous hermaphroditism, tit-for-tat, and the evolutionary stability of social systems. *Ethology and Sociobiology* **9**, 119-136.

Fishelson, L. 1976. Spawning and larval development of the blenniid fish *Meiacanthus nigrolineatus* from the Red Sea. *Copeia* **4**, 798–800.

Fisher, R., O'Leary, R.A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R.E., & Caley, M.J. 2015. Species richness on coral reefs and the pursuit of convergent global estimates. *Current Biology* **25**, 500-505.

Fletcher, R.L. & Callow, M.E. 1992. The settlement, attachment and establishment of marine algal spores. *British Phycological Journal* **27**, 303–329.

Floeter, S.R., Behrens, M.D., Ferreira, C.E.L., Paddack, M.J., & Horn, M.H. 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. *Marine Biology* **147**, 1435-1447.

Flynn, D.F., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., et al. 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* **12**, 22-33.

Fontaine, C., Collin, C.L. & Dajoz, I. 2008. Generalist foraging of pollinators: diet expansion at high density. *Journal of Ecology* **96**, 1002-1010.

Ford, J.R. & Swearer, S.E. 2013a. Shoaling behavior enhances risk of predation from multiple predator guilds in a marine fish. *Oecologia* **172**, 387–397.

Ford, J.R., & Swearer, S.E. 2013b. Two's company, three's a crowd: Food and shelter limitation outweigh the benefits of group living in a shoaling fish. *Ecology* **94**, 1069–1077.

Forister, M., Dyer, L., Singer, M., Stireman, III J., Lill, J. 2012. Revisiting the evolution of ecological specialization, with emphasis on insect-plant interactions. *Ecology* **93**, 981-991.

Forrester, G.E. & Steele, M.A. 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. *Ecology* **85**, 1332–1342.

Foster, S.A. 1985. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. *Animal Behaviour* **33**, 782-792

Foster, S. & Vincent, A.C.J. 2004. The life history and ecology of seahorses, *Hippocampus spp.*: implications for conservation and management. *Journal of Fish Biology* **65**, 1–61.

Fouda, M.M., El-Sayed, A.M. (1994) Distribution and feeding habits of two surgeonfish *Zebrasoma xanthurum* and *Ctenochaetus striatus* in the Gulf of Aqaba, Red Sea. *J. KAU: Mar Sci 7 Spec Issue: Symp. on Red Sea Mar Environ,* Jeddah, pp 233–244

Fox, R.J., Sunderland, T.L., Hoey, A.S., Bellwood, D.R. 2009. Estimating ecosystem function: contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs. *Marine Ecology Progress Series* **385**, 261–269.

Fox, R.J. & Donelson, J.M. 2014. Rabbitfish sentinels: first report of coordinated vigilance in conspecific marine fishes. *Coral Reefs* **33**, 253-253.

Fox, R.J. & Bellwood, D.R. 2007. Quantifying herbivory across a coral reef depth gradient. *Marine Ecology Progress Series* **339**, 49–59.

Fox, R.J. & Bellwood, D.R. (2011) Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus*. *Functional Ecology* **25**, 1096–1105.

Fox, R.J. & Bellwood, D.R. (2013) Niche partitioning of feeding microhabitats produces a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. *Coral Reefs* **32**, 13-23.

Fox, R.J. & Bellwood, D.R. 2008. Remote video bioassays reveal the potential feeding impact of the rabbitfish *Siganus canaliculatus* (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs* **27**, 605–615.

Frédérich, B., Fabri, G., Lepoint, G., Vandewalle, P. & Parmentier, E. 2009. Trophic niches of thirteen damselfishes (Pomacentridae) at the Grand Récif of Toliara, Madagascar. *Ichthyological Research* **56**, 10–17.

Fricke, H.W. & Fricke, S. 1977. Monogamy and sex change by aggressive dominance in coral reef fish. *Nature* **266**, 830–832.

Fricke, H.W. 1980. Control of different mating systems in a coral reef fish by one environmental factor. *Animal Behaviour* **28**, 561–569.

Fricke, H.W. 1986. Pair swimming and mutual partner guarding in monogamous butterflyfish (Pisces, Chaetodontidae): a joint advertisement for territory. *Ethology* **73**, 307–333

Fricke, R. & Zaiser, M.J. 1982. Redescription of *Diplogrammus xenicus* (Teleostei: Callionymidae) from Miyake-jima, Japan, with ecological notes. *Japanese Journal of Ichthyology* **29**, 253–259.

Froese, R. & Pauly, D. 2013. *FishBase*. World Wide Web electronic publication. www.fishbase.org, version (04/2013).

Fukumori, K., Okuda, N., Hamaoka, H., Fukumoto, T. Takahashi, D. & Omori, K. 2008. Stable isotopes reveal life history polymorphism in the coastal fish *Apogon notatus*. *Marine Ecology Progress Series* **362**, 279–289.

Fulton, C.J. & Bellwood, D.R. 2002. Ontogenetic habitat use in labrid fishes: an ecomorphological perspective. *Marine Ecology Progress Series* **236**, 255–262.

Fulton, C.J. 2007. Swimming speed performance in coral reef fishes: field validations reveal distinct functional groups. *Coral Reefs* **26**, 217–228.

Futuyma, D.J. & Moreno, G. 1988. The evolution of ecological specialization. *Annual Reviews in Ecology, Evolution and Systematics* **19**, 207-233.

Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* **89**, 1223–1231.

Gardiner, N.M. & Jones, G.P. 2010. Synergistic effects of habitat preference and gregarious behaviour on habitat use in coral reef cardinalfish. *Coral Reefs* **29**, 845–856.

Gerstner, C.L. 1999. Maneuverabilty of four species of coral-reef fish that differ in body and pectoral-fin morphology. *Canadian Journal of Zoology* **77**, 1102–1110.

Getz, L.L. & Hofman, J.E. 1986. Social organization in free-living prairie voles, *Microtus ochrogaster*: field and laboratory evidence for pair-bonding. *Behavioral Ecology and Sociobiology* 8, 189–194.

Geyer, C.J. & Meeden, G.D. 2014. *R package rcdd (C Double Description for R).* R package version 1.1-8.

Ghoul, M., Griffin, A.S., & West, S.A. 2014. Towards an evolutionary definition of cheating. *Evolution* **68**, 318–331.

Gleason, M.G. 1996. Coral recruitment in Moorea, French Polynesia - the importance of patch type and temporal variation. *Journal of Experimental Marine Biology and Ecology* **207**, 79–101.

Gluckmann, I. & Vandewalle, P. 1998. Morphofunctional analysis of the feeding apparatus in four Pomacentridae species: *Dascyllus aruanus*, *Chromis retrofasciata*, *Chrysiptera biocellata* and *C. unimaculata*. *Italian Journal of Zoology* **65**, 421–424.

Goatley, C.H. & Bellwood, D.R. 2011. The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PLoS One* **6**, e27307.

Goatley, C.H.R. & Bellwood, D.R. 2009. Morphological structure in a reef fish assemblage. *Coral Reefs* **28**, 449–457.

Godard, R. 1991. Tit for tat among neighboring hooded warblers. *Behavioral Ecology and Sociobiology* **33**, 45-50.

Golani, D. & Galil, B. 1991. Trophic relationships of colonizing and indigenous goatfishes (Mullidae) in the eastern Mediterranean with special emphasis on decapod crustaceans. *Hydrobiologia* **218**, 27-33.

Gómez, J.M., Bosch, J., Perfectti, F., Fernández, J., Abdelaziz, M., Camacho, J.P.M. 2008. Spatial variation in selection on corolla shape in a generalist plant is promoted by the preference patterns of its local pollinators. *Proceedings of the Royal Society London B* **275**, 2241-2249.

Gore, M.A. 1983. The effect of a flexible spacing system on the social organization of a coral reef fish, *Chaetodon capistratus*. *Behaviour* **85**, 118–145.

Gower, J.C. (1966) Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* **53**, 325–338.

Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V., Bijoux, J.P., & Robinson, J. 2006. Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences USA* **103**, 8425-8429.

Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D. & Wilson, S.K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518**, 94-97.

Grandcourt, E.M., Al Abdessalaam, T.Z., Francis, F. & Al Shamsi, A. 2004. Population biology and assessment of representatives of the family Carangidae: *Carangoides bajad* and *Gnathanodon speciosus* (Forsskaal, 1775), in the Southern Arabian Gulf. *Fisheries Research* **69**, 331–341.

Grant, B.R. & Grant, P.R. 1996. High survival of Darwin's finch hybrids: effects of beak morphology and diets. *Ecology* **77**, 500-509.

Green, A.L. & Bellwood, D.R. 2009. *Monitoring functional groups of herbivorous fishes as indicators of coral reef resilience – A practical guide for coral reef managers in the Asia Pacific region*. IUCN working group on climate change and coral reefs. Gland, Switzerland: IUCN.

Gregson, M.A., Pratchett, M.S., Berumen, M.L. & Goodman, B.A. 2008. Relationships between butterflyfish (Chaetodontidae) feeding rates and coral consumption on the Great Barrier Reef. *Coral Reefs* **27**, 583–591

Grinnell, J. 1917. The niche-relationships of the California Thrasher. *The Auk*, 427-433.

Gronell, A.M. 1984. Courtship, spawning and social organization of the pipefish, *Corythoichthys intestinalis* (Pisces: Syngnathidae) with notes on two congeneric species. *Zeitschrift für Tierpsychologie* **65**, 1–24.

Grubich, J.R., Rice, A.N. & Westneat, M.W. 2008. Functional morphology of bite mechanics in the great barracuda (*Sphyraena barracuda*). *Zoology* **111**, 16–29.

Gruner, D.S., Smith, J.E., Seabloom, E.W., Sandin, S.A., Ngai, J.T., Hillebrand, H. et al. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecology Letters* **11**, 740-755.

Guillemain M, Martin GR, Fritz H (2002) Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). *Functional Ecology* **16**, 522–529.

Guisan, A., & Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993-1009.

Gwinner, E., Rödl, T. & Schwabl, H. 1994. Pair territoriality of wintering stonechats: behaviour, function and hormones. *Behavioral Ecology and Sociobiology* **34**, 321–327.

Habel, K., Grasman, R., Stahel, A., Sterratt, C. 2014. *geometry: Mesh generation and surface tesselation*. R package version 0.3-5.

Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1-22.

Hadley Hansen, P.E. 1986. Revision of the tripterygiid fish genus *Helcogramma*, including descriptions of four new species. *Bulletin of Marine Science* **38**, 313–354.

Hagiwara, K. & Winterbottom, R. 2007. Two new species of *Trimma* (Gobiidae) from the western Pacific. *Bulletin of National Museum of Nature and Science* **1**, 163–174.

Hajisamae, S. 2009. Trophic ecology of bottom fishes assemblage along coastal areas of Thailand. *Estuarine, Coastal and Shelf Science* **82**, 503–514.

Hajisamae, S., Chou, L.M. & Ibrahim, S. 2003. Feeding habits and trophic organization of the fish community in shallow waters of an impacted tropical habitat. *Estuarine, Coastal and Shelf Science* **58**, 89–98.

Halpern, B.S. & Floeter, S.R. 2008. Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series* **364**, 147–156.

Hamilton, I.M. & Dill, L.M. 2003. The use of territorial gardening versus kleptoparasitism by a subtropical reef fish (*Kyphosus cornelii*) is influenced by territory defendability. *Behavioral Ecology* **14**, 561–568.

Hamner, W.M., Jones, M.S., Carleton, J.H., Hauri, I.R. & Williams, D.M. 1988. Zooplankton, planktivorous fish and water currents on a windward reef face: Great Barrier Reef, Australia. *Bulletin of Marine Science* **42**, 459–479.

Hara, S., Duray, M.N., Parazo, M. & Taki, Y. 1986. Year-round spawning and seed production of the rabbitfish, *Siganus guttatus*. *Aquaculture* **59**, 259–272.

Harahap, A.P., Takemura, A., Nakamura, S., Rahman, M.S. & Takano, K. 2001. Histological evidence of lunar-synchronized ovarian development and spawning in the spiny rabbitfish *Siganus spinus* (Linnaeus) around the Ryukyus. *Fisheries Science* **67**, 888–893.

Harding, J.A., Almany, G.R., Houck, L.D. & Hixon, M.A. 2003. Experimental analysis of monogamy in the Caribbean cleaner goby, *Gobiosoma evelynae*. *Animal Behaviour* **65**, 865–874.

Harmelin-Vivien, M.L. & Bouchon, C. 1976. Feeding behavior of some carnivorous fishes (Serranidae and Scorpaenidae) from Tulear (Madagascar). *Marine Biology* **37**, 329–340.

Harmelin-Vivien, M.L. 1979. *Ichtyofaune des récifs coralliens de Tuléar (Madagascar): écologie et relations trophiques*. Thèse es sciences, University of Aix-Marseille II, France.

Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. 2008. *GEIGER: investigating evolutionary radiations*. Bioinformatics 24, 129-131.

Harrington, L., Fabricius, K., De'ath, G., Negri, A. 2004. Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* **85**, 3428–3437

Harriott, V.J. & Fisk, D.A. 1987. A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. *Marine Ecology Progress Series* **37**, 201–208.

Hartnoll, R.G. & Smith, S.M. 1978. Pair-formation and the reproductive cycle in Gammarus duebeni. *Journal of Natural History* **12**, 501–511.

Hastie, T.J. & Tibshirani, R.J. 1990. *Generalized Additive Models*. Chapman & Hall, New York.

Hauser, M.D., Chen, M.K., Chen, F. & Chuang, E. 2003. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society London B* **270**, 2363-2370.

Hay, M.E. 1981. Spatial patterns of agrazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquatic Botany* **11**, 97-109.

Hay, M.E. 1991. *Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey*. The ecology of fishes on coral reefs. Academic Press, San Diego, 96-119.

Hay, M.E., & Fenical, W. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. *Annual Review of Ecology and Systematics* **19**, 111-145.

Henderson, R.W., Pauers, M.J. & Colston, T.J. 2013. On the congruence of morphology, trophic ecology, and phylogeny in Neotropical treeboas (Squamata: Boidae: Corallus). *Biological Journal of the Linnean Society* **109**, 466-475.

Hensley, D.A. & Allen, G.R. 1977. A new species of *Abudefduf* (Pisces: Pomacentridae) from the Indo-Australian Archipelago. *Records of the Western Australian Museum* **6**, 107–118.

Herler, J., Munday, P.L. & Hernaman, V. 2011. *Gobies on coral reefs.* The biology of gobies. Saint Helier, United Kingdom: Science Publishers, 493–529.

Hernaman, V. & Munday, P. L. 2007. Evolution of mating systems in coral reef gobies and constraints on mating system plasticity. *Coral Reefs* **26**, 585–595.

Hernaman, V. & Munday, P.L. 2005. Life-history characteristics of coral reef gobies. II. Mortality rate, mating system and timing of maturation. *Marine Ecology Progress Series* **290**, 223–237.

Hernaman, V., Probert, P.K. & Robbins, W.D. 2009. Trophic ecology of coral reef gobies: interspecific, ontogenetic, and seasonal comparison of diet and feeding intensity. *Marine Biology* **156**, 317–330.

Hernandez, L.P., Gibb, A.C., Ferry-Graham, L.A. 2009. Trophic apparatus in Cyprinodontiform fishes: functional specializations for picking and scraping behaviors. *Journal of Morphology* **270**, 645–661.

Herold, D. & Clark, E. 1993. Monogamy, spawning and skin-shedding of the sea moth, *Eurypegasus draconis* (Pisces: Pegasidae). *Environmental Biology of Fishes* **37**, 219–236.

Hess, H.C. 1993. Male mouthbrooding in jawfishes (Opistognathidae): constraints on polygyny. *Bulletin of Marine Science* **52**, 806–818.

Hiatt, R.W. & Strasburg, D.W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs* **30**, 65–127.

Hirose, Y. 1995. Patterns of pair formation in protandrous anemonefishes, *Amphiprion clarkii*, *A. frenatus* and *A. perideraion*, on coral reefs of Okinawa, Japan. *Environmental Biology of Fishes* **43**, 153–161.

Hixon, M.A. 1991. *Predation as a process structuring coral reef fish communities.* In The Ecology of Fishes on Coral Reefs, P.F. Sale (ed.), San Diego, CA: Academic Press, 475–508.

Hixon, M.A. & Brostoff, W.N. 1985. Substrate characteristics, fish grazing, and epibenthic reef assemblages off Hawaii. *Bulletin of Marine Science* **37**, 200-213.

Hixon, M.A. & Brostoff, W.N. 1996. Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecological Monographs* **66**, 67-90.

Ho, C.T., Kao, S.J., Dai, C.F., Hsieh, H.L., Shiah, F.K. & Jan, R.Q. 2007. Dietary separation between two blennies and the Pacific gregory in northern Taiwan: evidence from stomach content and stable isotope analyses. *Marine Biology* **151**, 729–736.

Hobson, E.S. 1975. Feeding patterns among tropical reef fishes. *American Scientist* **63**, 382–392.

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

Hodgson, G. 1990. Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis. Coral Reefs* **9**, 41–43.

Hoey, A.S. & Bellwood, D.R. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* **27**, 37–47

Hoey, A.S. & Bellwood, D.R. 2010a. Damselfish territories as a refuge for macroalgae on coral reefs. *Coral Reefs* **29**,107-118.

Hoey, A.S. & Bellwood, D.R. 2010b. Among-habitat variation in herbivory on *Sargassum spp.* on a mid-shelf reef in the northern Great Barrier Reef. *Marine Biology* **157**, 189-200

Hoey, A.S. & Bellwood, D.R. 2009. Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* **12**, 1316–1328.

Hoey, A.S. & Bellwood, D.R. 2011. Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecology Letters* **14**, 267–273.

Hoey, A.S., Brandl, S.J. & Bellwood, D.R. 2013. Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. *Coral Reefs* **32**, 973-984.

Holbrook, S.J. & Schmitt, R.J. 1992. Causes and consequences of dietary specialization in surfperches: patch choice and intraspecific competition. *Ecology* **73**, 402-412.

Holbrook, S.J. & Schmitt R.J. 2004. Population dynamics of a damselfish: effects of a competitor that also is an indirect mutualist. *Ecology* **85**, 979–985.

Hollén, L.I., Bell, M.B. & Radford, A.N. 2008. Cooperative sentinel calling? Foragers gain increased biomass intake. *Current Biology* **18**, 576-579.

Holmes, T.H. & McCormick, M.I. 2011. Response across a gradient: behavioural reactions of newly settled fish to predation cues. *Animal Behaviour* **81**, 543–550.

Holt, R.D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences USA* **106**, 19659-19665.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D. M., Loreau, M., Naeem, S., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E., Hungate, B.A., Matulich, K.L., et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**, 105-108.

Hoque, M.M., Takemura, A., Matsuyama, M., Matsuura, S. & Takano, K. 1999. Lunar spawning in *Siganus canaliculatus*. *Journal of Fish Biology* **55**, 1213–1222.

Horinouchi, M., Tongnunui, P., Furumitsu, K., Nakamura, Y., Kanou, K., Yamaguchi, A., Okamoto, K. & Sano, M. 2012. Food habits of small fishes in seagrass habitats in Trang, southern Thailand. *Fisheries Science* **78**, 577–587.

Horn, M.H. 1989. Biology of marine herbivorous fishes. *Oceanography and Marine Biology Annual Reviews* **27**, 167–272.

Hourigan, T.F. 1989. Environmental determinants of butterflyfish social systems. *Environmental Biology of Fishes* **25**, 61–78.

Howard, R.D. & Kluge, A.H. 1985. Proximate mechanisms of sexual selection in wood frogs. *Evolution* **39**, 260–277.

Huckins, C.J.F. 1997. Functional linkages among morphology, feeding performance, diet, and competitive ability in molluscivorous sunfish. *Ecology* **78**, 2401-2414.

Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**, 1547–1551

Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschaniwskyj, N.A., Pratchett, M.S., Tanner, J.E. & Willis, B.L. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* **397**, 59–63.

Hughes, T.P. & Tanner, J.E. 2000. Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* **81**, 2250-2263.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C. & Kleypas J. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* **301**, 929– 933.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L. et al. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* **17**, 360-365.

Hughes, T.P., Graham, N.A.J., Jackson, J.B.C., Mumby, P.J., & Steneck, R.S. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution* **25**, 633-642.

Hulsey, C.D. & García de León, F. 2005. Cichlid jaw mechanics: linking morphology to feeding specialization. *Functional Ecology* **19**, 487-494.

Hunte, W. & Wittenberg, M. 1992. Effects of eutrophication and sedimentation on juvenile corals. II. Settlement. *Marine Biology* **114**, 625–631.

Huston, M.A. 1985. Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics* **16**, 149-177.

Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals. Am Nat 93:145-159

Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* **22**, 415-427.

Iyer, N. 2012. The effects of background adaptation and food availability on habitat preference of *Corythoichthys flavofasciatus*. http://escholarship.org/uc/item/5182x106

Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629-637.

Janovetz, J. 2005. Functional morphology of feeding in the scale-eating specialist Catoprion mento. *Journal of Experimental Biology* **208**, 4757-4768.

Job, S.D. & Bellwood, D.R. 1996. Visual acuity and feeding in larval *Premnas biaculeatus*. *Journal of Fish Biology* **48**, 952–963.

Job, S.D. & Shand, J. 2001. Spectral sensitivity of larval and juvenile coral reef fishes: implications for feeding in a variable light environment. *Marine Ecology Progress Series* **214**, 267-277.

Johannes, R.E. 1981. *Words of the Lagoon: fishing and marine lore in the Palau District of Micronesia*. Berkeley, CA: University of California Press.

Johansson, C.L., van de Leemput, I.A., Depczynski, M., Hoey, A.S. & Bellwood, D.R. 2013. Key herbivores reveal limited functional redundancy on inshore coral reefs. *Coral Reefs* **32**, 963-972.

Johnson, S.D. & Steiner, K.E. 2000. Generalization versus specialization in plant pollination systems. *Trends in Ecology and Evolution* **15**, 140-143.

Johnson, R.H. & Nelson, D.R. 1978. Copulation and possible olfaction-mediated pair-formation in two species of carcharhinid sharks. *Copeia* **3**, 76–84.

Jones, A.G. & Avise, J.C. 1997. Microsatellite analysis of maternity and the mating system in the Gulf pipefish *Syngnathus scovelli*, a species with male pregnancy and sex-role reversal. *Molecular Ecology* **6**, 203–213.

Jones, A.G., Kvarnemo, C., Moore, G.I., Simmons, L.W. & Avise, J.C. 1998. Microsatellite evidence for monogamy and sex-biased recombination in the Western Australian seahorse *Hippocampus angustus*. *Molecular Ecology* **7**, 1497–1505.

Jordano P, Bascompte J, Olesen JM. 2003 Invariant properties in coevolutionary networks of plant-animal interactions. *Ecology Letters* **1**, 69-81.

Kadota, T., Osato, J., Hashimoto, H. & Sakai, Y. 2011. Harem structure and female territoriality in the dwarf hawkfish *Cirrhitichthys falco* (Cirrhitidae). *Environmental Biology of Fishes* **92**, 79–88.

Kane, C.N., Brooks, A.J., Holbrook, S.J. & Schmitt, R.J. 2009. The role of microhabitat preference and social organization in determining the spatial distribution of a coral reef fish. *Environmental Biology of Fishes* **84**, 1–10.

Karplus, I. 1979. The tactile communication between *Cryptocentrus steinitzi* (Pisces, Gobiidae) and *Alpheus purpurilenticularis* (Crustacea, Alpheidae). *Zeitschrift für Tierpsychologie* **49**, 173–196.

Karplus, I. 1987. The association between gobiid fishes and burrowing alpheid shrimps. *Oceanography and Marine Biology Annual Reviews* **25**, 507–562.

Karplus, I., Szlep, R. & Tsurnamal, M. 1972. Associative behavior of the fish *Cryptocentrus cryptocentrus* (Gobiidae) and the pistol shrimp *Alpheus djiboutensis* (Alpheidae) in artificial burrows. *Marine Biology* **15**, 95–104.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., et al. 2011. TRY–a global database of plant traits. *Global Change Biology* **17**, 2905-2935.

Kawase, H. 2002. Simplicity and diversity in the reproductive ecology of triggerfish (Balistidae) and filefish (Monacanthidae). *Proceedings of the International Commemorative Symposium, 70th Anniversary of the Japanese Society of Fisheries Science*, 119–122.

Kei, K. 2010. Pair-formation and reproductive behavior in the egg cowry *Ovula ovum* (Gastropoda: Ovulidae) in Southern Kyushu, Japan. *Venus* **69**, 49–58.

Kelley, J.L., Fitzpatrick, J.L. & Merilaita, S. 2013. Spots and stripes: ecology and colour pattern evolution in butterflyfishes. *Proceedings of the Royal Society London B* **280**, 20122730. doi:10.1098/rspb.2012.2730

Kiso, K. & Mahyam, M.I. 2003. Distribution and feeding habits of juvenile and young John's snapper *Lutjanus johnii* in the Matang mangrove estuary, west coast of Peninsular Malaysia. *Fisheries Science* **69**, 563–568.

Kizhakudan, S.J. & Gomathy, S. 2007. Unusual landings of the bluntnose lizardfish *Trachinocephalus myops* (Forster, 1801) at Chennai, with a note on some aspects of biology. *Journal of the Marine Biological Association of India* **49**, 250–253.

Klumpp, D.W., McKinnon, A.D. & Mundy, C.N. 1988. Motile cryptofauna of a coral reef: abundance, distribution and trophic potential. *Marine Ecology Progress Series* **45**, 95–108.

Knowlton, N. 2012. Iconic coral reef degraded despite substantial protection. *Proceedings of the National Academy of Sciences USA* **109**, 17734-17735.

Kobayashi, D.R. 1986. Social organisation of the spotted sharpnose puffer, *Canthigaster punctatissima* (Tetradontidae). *Environmental Biology of Fishes* **15**, 141–145.

Kohda, M. 1988. Diurnal periodicity of spawning activity of permanently territorial damselfishes (Teleostei: Pomacentridae). *Environmental Biology of Fishes* **21**, 91–100.

Kokita, T. & Mizota, T. 2002. Male secondary sexual traits are hydrodynamic devices for enhancing swimming performance in a monogamous filefish *Paramonacanthus japonicus*. *Journal of Ethology* **20**, 35–42.

Konow N, Bellwood DR (2005) Prey-capture in *Pomacanthus semicirculatus* (Teleostei, Pomacanthidae): functional implications of intramandibular joints in marine angelfishes. *Journal of Experimental Biology* **208**, 1421–1433.

Konow N, Bellwood DR, Wainwright PG, Kerr AM (2008) Evolution of novel jaw joints promote trophic diversity in coral reef fishes. *Biological Journal of the Linnean Society* **93**, 545–555.

Kortlandt, A. 1995. Patterns of pair-formation and nest-building in the European Cormorant *Phalacrocorax carbo sinensis*. *Ardea* **83**, 11–25.

Krama, T. et al. 2012. You mob my owl, I'll mob yours: birds play tit-for-tat game. *Scientific Reports* **2**, 800.

Kramer, M.J., Bellwood D.R. & Bellwood O. 2012a. Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. *Coral Reefs* **31**, 1007-1015.

Kramer, M.J., Bellwood, O. & Bellwood, D.R. 2012b. The trophic importance of algal turfs for coral reef fishes: the crustacean link. *Coral Reefs* **32**, 575–583.

Krams, I., Krama, T., Igaune, K. & Mänd, R. Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology* **62**, 599-605.

Krause, J. & Godin, J.G.J. 1996. Influence of prey foraging posture on flight behavior and predation risk: predators take advantage of unwary prey. *Behavioral Ecology* **7**, 264-271.

Kuriiwa, K., Naoto, H., Tetsuo, Y., Seishi, K. & Mutsumi, N. 2007. Phylogenetic relationships and natural hybridization in rabbitfishes (Teleostei: Siganidae) inferred from mitochondrial and nuclear DNA analyses. *Molecular Phylogenetics and Evolution* **45**, 69–80.

Kuwamura, T. 1985. Social and reproductive behaviour of three mouthbrooding cardinalfishes, *Apogon doederleini*, *A. niger* and *A. notatus*. *Environmental Biology of Fishes* **13**, 17–24.

Kuwamura, T. 1991. Habitat segregation, coexistence or interspecific territoriality between two triggerfishes, *Rhinecanthus aculeatus* and *Sufflamen chrysopterus*, with notes on distribution of other balistids at Sesoko Island, Okinawa. *Galaxea* **10**, 65–78.

Kuwamura, T. 1997. Evolution of female egg care in haremic triggerfish, *Rhinecanthus aculeatus*. *Ethology* **103**, 1015-1023.

Kuwamura, T., Yugo, Y. & Nakashima, Y. (1993). Size-assortative monogamy and paternal egg care in a coral goby *Paragobiodon echinocephalus*. *Ethology* **95**, 65–75.

Kvarnemo, C., Moore, G.I., Jones, A.G., Nelson, W.S. & Avise, J.C. (2000). Monogamous pair bonds and mate switching in the Western Australian seahorse *Hippocampus subelongatus*. *Journal of Evolutionary Biology* **13**, 882–888.

Kwak, S.N., Huh, S.H. & Klumpp, D.W. 2004. Partitioning of food resources among *Sillago japonica*, *Ditremma temmincki*, *Tridentiger trigonocephalus*, *Hippocampus japonicus* and *Petroscirtes breviceps* in an eelgrass, *Zostera marina*, bed. *Environmental Biology of Fishes* **71**, 353–364.

Laliberté, E. & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299-305.

Laliberté, E., Zemunik, G., & Turner, B.L. 2014. Environmental filtering explains variation in plant diversity along resource gradients. *Science* **345**, 1602-1605.

Ledlie, M.H., Graham, N.A.J., Bythell, J.C., Wilson, S.K., Jennings, S., Polunin, N.V.C., & Hardcastle, J. 2007. Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* **26**, 641-653.

Lefcheck, J.S., Byrnes, J.E., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., et al. 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature Communications* **6**, 6936.

Legendre, P. & Legendre, L. 1998. *Numerical Ecology*. Elsevier, Amsterdam, The Netherlands.

Leibold, M.A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* **147**, 784-812.

Lek, E., Fairclough, D.V., Platell, M.E., Clarke, K.R., Tweedley, J.R. & Potter, I.C. 2011. To what extent are the dietary compositions of three abundant, co-occurring labrid species different and related to latitude, habitat, body size and season? *Journal of Fish Biology* **78**, 1913–1943.

Letourneur, Y. 1996. Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. I. Patterns of spatial distribution. *Journal of Experimental Marine Biology and Ecology* **195**, 1–30.

Leu, S.T., Kappeler, P.M. & Bull, C.M. 2011. Pair-living in the absence of obligate biparental care in a lizard: trading-off sex and food? *Ethology* **117**, 758–768.

Lewis, A.R. 1998. Effects of experimental coral disturbance on the population dynamics of fishes on large patch reefs. *Journal of Experimental Marine Biology and Ecology* **230**, 91–110.

Leysen, H., Christiaens, J., De Kegel, B., Boone, M.N., Van Hoorebeke, L. & Adriaens, D. 2011. Musculoskeletal structure of the feeding system and implications of snout elongation in *Hippocampus reidi* and *Dunckerocampus dactyliophorus*. *Journal of Fish Biology* **78**, 1799–1823.

Li, K.T., Wetterer, J.K., Hairston, N.G. 1985. Fish size, visual resolution and prey selectivity. *Ecology* **66**, 1729-1735

Liem, K.F. 1980. Adaptive significance of intra-and interspecific differences in the feeding repertoires of cichlid fishes. *American Zoologist* **20**, 295-314.

Linsenmair, K.E. & Linsenmair, C. 1971. Paarbildung und Paarzusammenhalt bei der monogamen Wüstenassel *Hemilepistus reaumuri* (Crustacea, Isopoda, Oniscoidea). *Zeitschrift für Tierpsychologie* **29**, 134–155.

Liske, E. & Davis, W.J. 1984. Sexual behaviour of the Chinese praying mantis. *Animal Behaviour* **32**, 916–917.

Littler, M.M., Taylor, P.R., Littler, D.S. 1986. Plant defense associations in the marine environment. *Coral Reefs* **5**, 63-71.

Lobel, P.S. 1989. Spawning behavior of *Chaetodon multicinctus* (Chaetodontidae): pairs and intruders. *Environmental Biology of Fishes* **25**, 125–130.

Loffler, Z., Bellwood, D.R., & Hoey, A.S. 2015. Among-habitat algal selectivity by browsing herbivores on an inshore coral reef. *Coral Reefs* **34**, 597-605.

Longenecker, K. & Langston, R. 2006. Life history characteristics of a small cardinalfish, *Ostorhinchus rubrimacula* (Percoidei: Apogonidae), from Koro, Fiji. *Pacific Science* **60**, 225–233.

Longenecker, K. 2007. Devil in the details: high-resolution dietary analysis contradicts a basic assumption of reef-fish diversity models. *Copeia* **3**, 543–555.

López-Peralta, R.H. & Arcila, C.A.T. 2002. Diet composition of fish species from the southern continental shelf of Colombia. *Naga WorldFish Center Quarterly* **25**, 23–29.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804-808.

Lotze HK, Worm B, Sommer U 2001. Strong bottom–up and top–down control of early life stages of macroalgae. *Limnological Oceanography* **46**, 749-757.

Lourie, S.A. & Randall, J.E. 2003. A new pygmy seahorse, *Hippocampus denise* (Teleostei Syngnathidae) from the Indo-Pacific. *Zoological Studies Taipei* **42**, 284–291.

Mackereth, R.W. & Keenleyside, M.H.A. 1993. Breeding territoriality and pair-formation in the convict cichlid (*Cichlasoma nigrofasciatum*; Pisces, Cichlidae). *Canadian Journal of Zoology* **71**, 960–967.

Madin, E.M.P., Gaines, S.D. & Warner, R.R. 2010. Field evidence for pervasive indirect effects of fishing on prey foraging behavior. *Ecology* **91**, 3563–3571.

Madin, J.S. & Connolly, S.R. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* **444**, 477–480.

Madin, E.M.P., Gaines, S.D., Madin, J.S., Link, A.K., Lubchenco, P.J., Selden, R.L., Warner, R.R. 2012. Do behavioral foraging responses of prey to predators function similarly in restored and pristine foodwebs? *PLoS ONE* **7**, 0032390.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. & Hornik, K. 2015. *cluster: cluster analysis basics and extensions.* R package version 2.0.1.

Maida, M., Coll, J.C. & Sammarco, P.W. 1994. Shedding new light on scleractinian coral recruitment. Journal of Experimental Marine Biology and Ecology **180**, 189–202.

Manly, B.F., McDonald, L., Thomas, D., McDonald, T.L. & Erickson, W.P. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Springer Netherlands.

Manly, B.F.J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*. 2nd edn. Chapman & Hall, Cornwall, United Kingdom.

Manser, M.B. 1999. Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. *Proceedings of the Royal Society London B* **266**, 1013-1019.

Mantyka, C.S. & Bellwood, D.R. 2007. Macroalgal grazing selectivity among herbivorous coral reef fishes. *Marine Ecology Progress Series* **352**, 177–185.

Marguillier, S., Van Der Velde, G., Dehairs, F., Hemminga, M.A. & Rajagopal, S. 1997. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by δ13C and δ15N. *Marine Ecology Progress Series* **151**, 115–121.

Marnane, M.J. & Bellwood, D.R. 2002. Diet and nocturnal foraging in cardinalfishes (Apogonidae) at One Tree Reef, Great Barrier Reef, Australia. *Marine Ecology Progress Series* **231**, 261-268.

Marshall, N.J., Jennings, K., McFarland, W.N., Loew, E.R. & Losey, G.S. 2003. Visual biology of Hawaiian coral reef fishes: III. Environmental light and an integrated approach to the ecology of reef fish vision. *Copeia* **3**, 467–480.

Marshell, A., Mumby, P.J. 2012. Revisiting the functional roles of the surgeonfish *Acanthurus nigrofuscus* and *Ctenochaetus striatus*. *Coral Reefs* **31**, 1093-1101.

Marshell, A., Mills, J.S., Rhodes, K.L., & McIlwain, J. 2011. Passive acoustic telemetry reveals highly variable home range and movement patterns among unicornfish within a marine reserve. *Coral Reefs* **30**, 631-642.

Martin, C.H. & Wainwright, P.C. 2011 Trophic novelty is linked to exceptional rates of morphological diversification in two adaptive radiations of Cyprinodon pupfish. *Evolution* **65**, 2197-2212.

Martin, G.R. & Katzir, G. 1999. *Visual fields, foraging and binocularity in birds.* In: Adams N, Slowtow R (eds) Proceedings of the 22nd International Ornithological Congress, Durban. Birdlife, Johannesburg, pp 2711–2728

Mathews, L.M. 2002. Territorial cooperation and social monogamy: factors affecting intersexual interactions in pair-living snapping shrimp. *Animal Behaviour* **63**, 767–777.

McClanahan, T., Muthiga, N., & Mangi, S. 2001. Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* **19**, 380-391.

McComb, D.M. & Kajiura, S.M. 2008. Visual fields of four batoid fishes: a comparative study. *Journal of Experimental Biology* **211**, 482–490.

McCook, L.J., Jompa, J., Diaz-Pulido, G. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* **19**, 400–417.

McCormick, M.I. 1995. Fish feeding on mobile benthic invertebrates: influence of spatial variability in habitat associations. *Marine Biology* **121**, 627–637.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**, 178–185.

McGowan, K.J. & Woolfenden, G.E.A 1989. A sentinel system in the Florida scrub jay. *Animal Behaviour* **37**, 1000-1006.

Mehta, R.S. 2009. Ecomorphology of the moray bite: relationship between dietary extremes and morphological diversity. *Physiological and Biochemical Zoology* **82**, 90–103.

Melis, A.P. & Semmann, D. 2010. How is human cooperation different? *Philosophical Transactions of the Royal Society London B* **365**, 2663-2674.

Menge, B.A. & Lubchenco, J. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monography* **51**, 429-450.

Mequila, A.T. & Campos, W. 2007. Feeding relationships of dominant fish species in the Visayan Sea. *Science Diliman* **19**, 35–46.

Messier, J., McGill, B.J. & Lechowicz M.J. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**, 838–848.

Mesterton-Gibbons M. & Dugatkin, L.A. 1992. Cooperation among unrelated individuals: evolutionary factors. *Quarterly Reviews in Biology* **67**, 267-281.

Metian, M., Warnau, M., Chouvelon, T., Pedraza, F., Rodriguez y Baena, A. & Bustamante, P. 2013. Trace element bioaccumulation in reef fish from New Caledonia: influence of trophic groups and risk assessment for consumers. *Marine Environmental Research* **87**, 26-36.

Meyer-Rochow, V.B. 1976. Some observations on spawning and fecundity in the luminescent fish *Photoblepharon palpebratus*. *Marine Biology* **37**, 325–328.

Meyer, C.G., Holland, K.N., Wetherbee, B.M. & Lowe, C.G. 2001. Diet, resource partitioning and gear vulnerability of Hawaiian jacks captured in fishing tournaments. *Fisheries Research* **53**, 105–113.

Micheli, F., Mumby, P.J., Brumbaugh, D.R., Broad, K., Dahlgren, C.P., Harborne, A.R., et al. 2014. High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs. *Biological Conservation* **171**, 186-194.

Milchunas, D.G. & Noy-Meir, I. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* **99**, 113-130.

Milinski, M. & Wedekind, C. 1998. Working memory constrains human cooperation in the Prisoner's Dilemma. *Proceedings of the National Academy of Sciences USA* **95**, 13755-13758.

Milinski, M. 1987. Tit for tat in sticklebacks and the evolution of cooperation. *Nature* **325**, 433-435.

Milinski, M., Pfluger, D., Külling, D. & Kettler, R. 1990. Do sticklebacks cooperate repeatedly in reciprocal pairs? *Behavioral Ecology and Sociobiology* **27**, 17-21.

Miller, T.J., Crowder, L.B., Rice, J.A. 1993. Ontogenetic changes in behavioural and histological measures of visual acuity in three species of fish. *Environmental Biology of Fishes* **37**, 1–8.

Mitamura, H., Arai, N., Mitsunaga, Y., Yokota, T., Takeuchi, H., Tsuzaki, T. & Itani M. 2005. Directed movements and diel burrow fidelity patterns of red tilefish *Branchiostegus japonicus* determined using ultrasonic telemetry. *Fisheries Science* **71**, 491–498.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* **65**, 499-513

Montgomery, W.L., Myrberg, A.A. & Fishelson, L. 1989. Feeding ecology of surgeonfishes (Acanthuridae) in the northern Red Sea, with particular reference to *Acanthurus nigrofuscus* (Forsskål). *Journal of Experimental Marine Biology and Ecology* **132**, 179–207.

Mooi, R.D. & Gill, A.C. 2004. Notograptidae, sister to Acanthoplesiops Regan (Teleostei: Plesiopidae: Acanthoclininae), with comments on biogeography, diet and morphological convergence with Congrogadinae (Teleostei: Pseudochromidae). *Zoological Journal of the Linnean Society* **141**, 179–205.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G., & Worm, B. 2011. How many species are there on Earth and in the ocean? *PLoS Biology*, e1001127.

Morgan, I.E. & Kramer, D.L. 2004. The social organization of adult blue tangs, *Acanthurus coeruleus*, on a fringing reef, Barbados, West Indies. *Environmental Biology of Fishes* **71**, 261–273.

Motta, P.J. 1988. Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): An ecomorphological approach. *Environmental Biology of Fishes* **22**, 39–67.

Motta, P.J. 1989. Dentition patterns among Pacific and Western Atlantic butterflyfishes (Perciformes, Chaetodontidae): relationship to feeding ecology and evolutionary history. *Environmental Biology of Fishes* **25**, 159–170.

Motta, P.J., Clifton, K.B., Hernandez, P., Eggold, B.T. 1995. Ecomorphological correlates in ten species of subtropical seagrass fishes: diet and microhabitat utilization. *Environmental Biology of Fishes* **44**, 37-60.

Mouillot, D., Dumay, O., Tomasini, J.A. 2007. Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Estuarine Coastal and Shelf Science* **71**, 443–456.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood D.R. 2012. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* **1621**, 1-11.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M. & Mason N.W.H. 2011. Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, **6**, e17476.

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J. E., Bender, M., et al. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences USA* **111**, 13757-13762.

Moyer, J.T. & Nakazono, A. 1978. Population structure, reproductive behavior and protogynous hermaphroditism in the angelfish *Centropyge interruptus* at Miyake-jima, Japan. *Japanese Journal of Ichthyology* **25**, 25–39.

Moyer, J.T. & Sano, M. 1987. Feeding habits of two sympatric ostraciid fishes at Miyake-jima, Japan. *Ichthyological Research* **34**, 108–112.

Munday, P.L., Pierce, S.J., Jones, G.P. & Larson, H.K. 2002. Habitat use, social organization and reproductive biology of the seawhip goby, *Bryaninops yongei*. *Marine and Freshwater Research* **53**, 769–775.

Mundy C.N. 2000. An appraisal of methods used in coral recruitment studies. *Coral Reefs* **19**, 124–131.

Mundy, C.N. & Babcock, R.C. 1998. Role of light intensity and spectral quality in coral settlement: implications for depth-dependent settlement? *Journal of Experimental Marine Biology and Ecology* **223**, 235–255.

Mundy, C.N. & Babcock, R.C. 2000. Are vertical distribution patterns of scleractinian corals maintained by pre-settlement or post-settlement processes? A case study of three contrasting species. *Marine Ecology Progress Series* **198**, 109–119.

Muñoz, G., Grutter, A.S. & Cribb, T.H. 2006. Endoparasite communities of five fish species (Labridae: Cheilininae) from Lizard Island: how important is the ecology and phylogeny of the hosts? *Parasitology* **132**, 363–374.

Muñoz, R.C., Currin, C.A. & Whitfield, P.E. 2011. Diet of invasive lionfish on hard bottom reefs of the Southeast USA: insights from stomach contents and stable isotopes. *Marine Ecology Progress Series* **432**, 181–193.

Murphy, K. E. & Pitcher, T. J. 1987. Predator attack motivation influences the inspection behaviour of European minnows. *Journal of Fish Biology* **50**, 407–417.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., & Woodfin, R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**, 734-737.

Naeem, S., Duffy, J.E., & Zavaleta, E. 2012. The functions of biological diversity in an age of extinction. *Science* **336**, 1401-1406.

Nakamura, Y., Horinouchi, M., Nakai, T. & Sano, M. 2003. Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan. *Ichthyological Research* **50**, 15–22.

Nakane, Y., Yusuke S. & Mitsuhiko S. 2011. Food habits of fishes on an exposed sandy beach at Fukiagehama, South-West Kyushu Island, Japan. *Helgoland Marine Research* **65**, 123–131.

Nanami, A. & Yamada, H. 2008. Size and spatial arrangement of home range of checkered snapper *Lutjanus decussatus* (Lutjanidae) in an Okinawan coral reef determined using a portable GPS receiver. *Marine Biology* **153**, 1103–1111.

Nanjo, K., Kohno, H. & Sano, M. 2008. Food habits of fishes in the mangrove estuary of Urauchi River, Iriomote Island, southern Japan. *Fisheries Science* **74**, 1024–1033.

Near, T.J., Eytan, R.I., Dornburg, A., Kuhn, K.L., Moore, J.A., Davis, M.P., Wainwright, P.C., Friedman, M. & Smith, W. L. 2012. Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences USA* **109**, 13698–13703.

Neudecker, S. & Lobel, P.S. 1982. Mating systems of chaetodontid and pomacanthid fishes at St. Croix. *Zeitschrift für Tierpsychologie* **59**, 299–318.

Noë, R. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour* **71**, 1-18.

Norström, A.V., Nyström, M., Lokrantz, J. & Folke, C. 2009. Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series* **376**, 295–306.

Nowak, M.A. & Sigmund, K. 1992. Tit for tat in heterogeneous populations. *Nature* **355**, 250-253.

Nowak, M.A. 2006. Five rules for the evolution of cooperation. *Science* **314**, 1560-1563.

Nozawa, Y. 2008. Micro-crevice structure enhances coral spat survivorship. *Journal of Experimental Marine Biology and Ecology* **367**, 127-130.

Nyström, M. 2006. Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *Ambio* **35**, 30–35

Nyström, M., Graham, N.A.J., Lokrantz, J. & Norström, A.V. 2008. Capturing the cornerstones of coral reef resilience: linking theory to practice. *Coral Reefs* **27**, 795-809.

Öhman, M.C., Munday, P.L., Jones, G.P. & Caley, M.J. 1998. Settlement strategies and distribution patterns of coral-reef fishes. *Journal of Experimental Marine Biology and Ecology* **225**, 219–238.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R. et al. (2013). *Vegan: Community Ecology Package*. R-package version 2.2-1.

Olff, H. & Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* **13**, 261-265.

Orians, G.H. 1961. The ecology of blackbird (Agelaius) social systems. *Ecological Monographs* **31**, 285–312.

Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist* **103**, 589–603.

Osenberg, C.W., Mittelbach, G.G. & Wainwright, P.C. 1992. Two-stage life histories in fish - the interaction between juvenile competition and adult performance. *Ecology* **73**, 255-267

Overholtzer, K.L. & Motta, P.L. 2000. Effects of mixed-species foraging groups on the feeding and aggression of juvenile parrotfishes. *Environmental Biology of Fishes* **58**, 345–354.

Paine, R.T. 1966. Food web complexity and species diversity. *American Naturalist* **100**, 65-75.

Paradis, E., Claude, J., Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289-290.

Parmentier, E., Boyle, K. S., Berten, L., Brié, C. & Lecchini, D. 2011. Sound production and mechanism on *Heniochus chrysostomus* (Chaetodontidae). *Journal of Experimental Biology* **214**, 2702-2708.

Parrish, J.K. & Edelstein-Keshet, L. 1999. Complexity, pattern and evolutionary trade-offs in animal aggregation. *Science* **284**, 99–101.

Paul, V.J., Nelson, S.G. & Sanger, H.R. 1990. Feeding preferences of adult and juvenile rabbitfish *Siganus argenteus* in relation to chemical defenses of tropical seaweeds. *Marine Ecology Progress Series* **60**, 23–34.

Pays, O., Dubot, A.L., Jarman, P.J., Loisel, P. & Goldizen, A.W. 2009. Vigilance and its complex synchrony in the red-necked pademelon, *Thylogale thetis*. *Behavioral Ecology* **20**, 22-29.

Penin, L., Michonneau, F., Baird, A.H., Connolly, S.R., Pratchett, M.S., Kayal, M., Adjeroud, M. 2010. Early post-settlement mortality and the structure of coral assemblages. *Marine Ecology Progress Series* **408**, 55–64.

Penin, L., Michonneau, F., Carroll, A., Adjeroud, M. 2011. Effects of predators and grazers exclusion on early post-settlement coral mortality. *Hydrobiologia* **663**, 259–264.

Persson, A., Andersson, J., Wahlstrom, E. & Eklov, P. 1996. Size specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology* **77**, 900–911.

Petchey, O.L. & Gaston, K.J. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* **9**, 741–758.

Petchey, O.L., Evans, K.L., Fishburn, I.S., & Gaston, K.J. 2007. Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology* **76**, 977-985.

Pettigrew, J.D., Collin, S.P. & Fritsches, K. 2000. Prey capture and accommodation in the sandlance, *Limnichthytes fasciatus* (Creediidae; Teleostei). *Journal of Comparative Physiology* **186**, 247–260

Pfeiffer, T., Rutte, C., Killingback, T., Taborsky, M. & Bonhoeffer, S. 2005. Evolution of cooperation by generalized reciprocity. *Proceedings of the Royal Society London B* **272**, 1115-1120.

Pfister, C.A. & Hay, M.E. 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia* **77**, 118-129.

Pietsch, T.W. & Grobecker, D.B. 1987. *Frogfishes of the world: systematics, zoogeography, and behavioral ecology.* Stanford, CA: Stanford University Press.

Pink, J. & Fulton, C. 2014. Right tools for the task: intraspecific modality in the swimming behaviour of coral reef fishes. *Marine Biology* **161**, 1103-111.

Pitcher T.J. & Parrish J.K. 1993. *Functions of shoaling behaviour in teleosts.* In: Pitcher T.J. (ed.), Behaviour of Teleost Fishes. London, UK: Chapman and Hall, 363–439.

Poisot, T., Bever, J.D., Nemri, A., Thrall, P.H. & Hochberg, M.E. 2011. A conceptual framework for the evolution of ecological specialisation. *Ecology Letters* **14**, 841-851.

Poore, A.G., Campbell, A.H., Coleman, R.A., Edgar, G.J., Jormalainen, V., Reynolds, P.L. et al. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters* **15**, 912-922.

Popp, J.W. 1988. Effects of food-handling time on scanning rates in American goldfinches. *Auk* **105**, 384-385.

Pouilly, M., Lino, F., Bretenoux, J.G. & Rosales, C. 2003. Dietary–morphological relationships in a fish assemblage of the Bolivian Amazonian floodplain. *Journal of Fish Biology* **62**, 1137-1158.

Pratchett, M.S. 2005. Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Marine Biology* **148**, 373–382.

Pratchett, M.S., Gust, N., Goby, G. & Klanten, S.O. 2001. Consumption of coral propagules represents a significant trophic link between corals and reef fish. *Coral Reefs* **20**, 13–17.

Pratchett, M.S., Pradjakusuma, O.A. & Jones, G.P. 2006. Is there a reproductive basis to solitary living versus pair-formation in coral reef fishes? *Coral Reefs* **25**, 85–92.

Price, S.A., Wainwright, P.C., Bellwood, D.R., Kazancioglu, E., Collar, D.C. & Near, T.J. 2010. Functional innovations and morphological diversification in parrotfish. *Evolution* **64**, 3057–3068.

Pyle, R.L. 2003. *A systematic treatment of the reef-fish family Pomacanthidae (Pisces: Perciformes)*. PhD-Thesis, University of Hawaii, United States.

R Core Team (2012). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0

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

R Core Team (2015) *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0

Radford, A.N., Hollén, L.I. & Bell, M.B. 2009. The higher the better: sentinel height influences foraging success in a social bird. *Proceedings of the Royal Society London B* **276**, 2437-2442.

Raihani, N.J. & Bshary, R. 2011. Resolving the iterated prisoner's dilemma: theory and reality. *Journal of Evolutionary Biology* **24**, 1628-1639.

Raimondi, P.T., Morse, A.N.C. 2000. The consequences of complex larval behavior in a coral. *Ecology* **81**, 3193–3211.

Randall, J.E., Allen, G.R. & Steene, R.C. 1997. *Fishes of the Great Barrier Reef and Coral Sea.* Crawford House Publishing Pty. Ltd., Bathurst

Randall, H.A. & Allen, G.R. 1977. A revision of the damselfish genus Dascyllus (Pomacentridae) with the description of a new species. *Records of the Australian Museum* **31**, 349–385.

Randall, J.E. & Goren, M. 1993. A review of the gobioid fishes of the Maldives. *Ichthyological Bulletin of the J.L.B Smith Institute of Ichthyology* **58**, 1–37.

Randall, J.E. & Myers, R.F. 2002. *Parupeneus insularis,* a new central Pacific species of goatfish (Perciformes: Mullidae) of the *P. trifasciatus* complex. *Zoological Studies Taipei* **41**, 431–440.

Randall, J.E. & Struhsaker, P. 1981. *Naso maculatus,* a new species of acanthurid fish from the Hawaiian Islands and Japan. *Copeia* **3**, 553–558.

Randall, J.E. 1980. A survey of ciguatera at Eniwetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatoxic fishes. *Fishery Bulletin* **78**, 201–249.

Randall, J.E. 1998. Revision of the Indo-Pacific squirrelfishes (Beryciformes: Holocentridae: Holocentrinae) of the genus *Sargocentron*, with descriptions of four new species. *Indo-Pacific Fishes* **27**, 1–105.

Randall, J.E. 2005. *Reef and Shorefishes of the South Pacific*. Honolulu, HI: University of Hawaii Press.

Randall, J.E., Allen, G.R. & Steene, R.C. 1997. *Fishes of the Great Barrier Reef and Coral Sea*. Bathurst, Australia: Crawford House Publishing Pty. Ltd.

Rasher, D.B. & Hay, M.E. 2010. Chemically rich seaweeds poison corals when not controlled by herbivores. *Proceedings of the National Academy of Sciences USA* **107**, 9683–9688.

Rasher, D.B., Stout, E.P., Engel, S., Kubanek, J. & Hay, M.E. 2011. Macroalgal terpenes function as allelopathic agents against reef corals. *Proceedings of the National Academy of Sciences USA* **108**, 17726-17731.

Rasher, D.B., Engel, S., Bonito, V., Fraser, G.J., Montoya, J.P. & Hay, M.E. 2012. Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. *Oecologia* **169**, 187-198.

Rasher, D.B., Hoey, A.S. & Hay, M.E. 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* **94**, 1347-1358.

Reavis, R.H. & Barlow, G.W. 1998. Why is the coral reef fish *Valenciennea strigata* (Gobiidae) monogamous? *Behavioral Ecology and Sociobiology* **43**, 229–237

Reavis, R.H. & Copus, J.M. 2011. Monogamy in a feeding generalist, *Chaetodon trichrous*, the endemic Tahitian butterflyfish. *Environmental Biology of Fishes* **92**, 167–179.

Reavis, R.H. 1997a. The natural history of a monogamous coral-reef fish, *Valenciennea strigata* (Gobiidae): 1. Abundance, growth, survival and predation. *Environmental Biology of Fishes* **49**, 239–246.

Reavis, R.H. 1997b. The natural history of a monogamous coral reef fish, *Valenciennea strigata* (Gobiidae) 2. Behaviour, mate fidelity and reproductive success. *Environmental Biology of Fishes* **49**, 247–257.

Reece, J.S., Bowen, B.W., Smith, D.G. & Larson, A.F. 2010. Molecular phylogenetics of moray eels (Murenidae) demonstrates multiple origins of a shell-crushing jaw (Gymnomuraena, Echidna) and multiple colonizations of the Atlantic Ocean. *Molecular Phylogenetics and Evolution* **57**, 829–835.

Reese, E.S. 1975. A comparative field study of the social behaviour and related ecology of reef fishes of the family Chaetodontidae. *Zeitschrift für Tierpyschologie* **37**, 37–61.

Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217-223.

Reynolds, J.D. 1996. Animal breeding systems. *Trends in Ecology and Evolution* **11**, 68–72.

Rice, A.N. & Westneat, M.W. 2005. Coordination of feeding, locomotor, and visual systems in parrotfishes (Teleostei: Labridae). *Journal of Experimental Biology* **208**, 3503–3518.

Ridley, A.R., Nelson-Flower, M.J. & Thompson, A.M. 2013. Is sentinel behaviour safe? An experimental investigation. *Animal Behaviour* **85**, 137-142.

Rimmer, D.W. & Wiebe, W.J. 1987. Fermentative microbial digestion in herbivorous fishes. *Journal of Fish Biology* **31**, 229–236.

Ritson-Williams, R., Paul, V.J., Arnold, S.N. & Steneck, R.S. 2010. Larval settlement preferences and post-settlement survival of the threatened Caribbean corals *Acropora palmata* and *A. cervicornis*. *Coral Reefs* **29**, 71–81.

Roberts, C.M. & Ormond, R.G.F. 1992. Butterflyfish social behaviour, with special reference to the incidence of territoriality: a review. *Environmental Biology of Fishes* **34**, 79–93.

Roberts, C.M. 1987. Experimental analysis of resource sharing between herbivorous damselfish and blennies on the Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* **111**, 61–75.

Roberts, G. 2005. Cooperation through interdependence. *Animal Behaviour* **70**, 901-908.

Robertson DR (1987) Responses of two coral reef toadfishes (Batrachoididae) to the demise of their primary prey, the sea urchin *Diadema antillarum*. *Copeia* **1987**, 637-642.

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

Robertson, D.R. & Hoffman, S.G. 1977. The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. *Zeitschrift für Tierpsychologie* **45**, 298–320.

Robertson, D.R. 1973. Field observation on the reproductive behaviour of a pomacentrid fish, *Acanthochromis polyacanthus*. *Zeitschrift für Tierpsychologie* **32**, 319–24.

Robertson, D.R. 1983. On the spawning behavior and spawning cycles of eight surgeonfishes (Acanthuridae) from the Indo-Pacific. *Environmental Biology of Fishes* **9**, 193–223.

Robertson, D.R., Polunin, N.V.C. & Leighton, K. 1979. The behavioural ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus, A. leucosternon* and *Zebrasoma scopas*): their feeding strategies, and social and mating systems. *Environmental Biology of Fishes* **4**, 125–170.

Robertson, D.R., Sweatman, H.P.A., Fletcher, E.A. & Cleland, M.G. 1976. Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology* **57**, 1208–1220.

Robinson B.W., Wilson, D.S., Margosian, A.S., Lotito, P.T. 1993. Ecological and morphological differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. *Evolutionary Ecology* **7**, 451–464.

Robinson, B.W., Wilson DS. 1998 Optimal foraging, specialization, and a solution to Liem's paradox. *American Naturalist* **151**, 223-235.

Roff, G. & Mumby, P.J. 2012. Global disparity in the resilience of coral reefs. *Trends in Ecology and Evolution* **27**, 404-413.

Roff, G., Doropoulos, C., Zupan, M., Rogers, A., Steneck, R.S., Golbuu, Y., & Mumby, P.J. 2015. Phase shift facilitation following cyclone disturbance on coral reefs. *Oecologia*, 1-11.

Rosenfeld, J.S. 2002. Functional redundancy in ecology and conservation. *Oikos* **98**, 156–162.

Ross, J.L. 1982. Feeding habits of the gray tilefish, *Caulolatilus microps* (Goode and Bean, 1878) from North Carolina and South Carolina waters. *Bulletin of Marine Science* **32**, 448–454.

Roth, M.S. & Knowlton, N. 2009. Distribution, abundance, and microhabitat characterization of small juvenile coral at Palmyra Atoll. *Marine Ecology Progress Series* **376**, 133-142.

Russ, G.R. 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Marine Ecology Progress Series* **20**, 35–44.

Russ, G.R. 1984, Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Marine Ecology Progress Series* **20**, 23–34.

Russ, G.R. 1987. Is rate of removal of algae by grazers reduced inside territories of tropical damselfishes? *Journal of Experimental Marine Biology and Ecology* **110**, 1–17.

Russell, A. F. & Wright, J. 2009. Avian mobbing: byproduct mutualism not reciprocal altruism. *Trends in Ecology and Evolution* **24**, 3-5.

Rutte, C. & Taborsky, M. 2008. The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): direct vs generalised reciprocity. *Behavioral Ecology and Sociobiology* **62**, 499-505.

Ryer, C.H. & Olla, B.L. 1998. Shifting the balance between foraging and predator avoidance: the importance of food distribution for a schooling pelagic forager. Environmental Biology of Fishes **52**, 467–475.

Rylaarsdam, K.W. 1983. Life histories and abundance patterns of colonial corals on Jamaican reefs. *Marine Ecology Progress Series* **13**, 249-260.

Sabrah, M.M. & El-Ganainy, A. 2009. Observation on biological traits of striped goatfish (*Upeneus vittatus*) and freckled goatfish (*Upeneus tragula*) from the Gulf of Suez, Egypt. *World Journal of Fish and Marine Sciences* **1**, 121–128.

Sabrah, M.M. El-Ganainy, A.A. & Zaky, M.A. 2006. Biology and toxicity of the pufferfish *Lagocephalus sceleratus* (Gmelin, 1789) from the Gulf of Suez. *Egyptian Journal of Aquatic Research* **32**, 283–97.

Sackley, P.G. & Kaufman, L.S. 1996. Effect of predation on foraging height in a planktivorous coral reef fish, *Chromis nitida*. *Copeia* **3**, 726–729.

Sadovy de Mitcheson, Y. & Colin, P.L. (eds) 2012. Reef fish spawning aggregations: biology, research and management. *Fish and Fisheries Series* **35**.

Sadovy De Mitcheson, Y., Cornish, A., Domeier, M., Colin, P.L., Russel, M. & Lindeman, K.C. 2008. A global baseline for spawning aggregations of reef fishes. *Conservation Biology* **22**, 1233–1244.

Sakashita, H. 1992. Sexual dimorphism and food habits of the clingfish, *Diademichthys lineatus*, and its dependence on host sea urchin. *Environmental Biology of Fishes* **34**, 95–101.

Salini, J.P., Blaber, S.J.M. & Brewer, D.T. 1990. Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. *Marine Biology* **105**, 363–374.

Salini, J.P., Blaber, S.J.M. & Brewer, D.T. 1994. Diets of trawled predatory fish of the Gulf of Carpentaria, Australia, with particular reference to predation on prawns. *Marine and Freshwater Research* **45**, 397–411.

Sammarco, P.W. 1980. Diadema and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *Journal of Experimental Marine Biology and Ecology* **45**, 245-272.

Samoilys, M.A. & Squire, L.C. 1994. Preliminary observations on the spawning behaviour of coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on the Great Barrier Reef. *Bulletin of Marine Science* **54**, 332–342.

Sancho, G., Petersen, C.W. & Lobel, P.S. 2000. Predator-prey relations at a spawning aggregation site of coral reef fishes. *Marine Ecology Progress Series* **203**, 275–288.

Sanderson SL. 1990 Versatility and specialization in labrid fishes: ecomorphological implications. *Oecologia* **84**, 272-279.

Sandin, S.A. & Williams, I. 2010. *Trophic classifications of reef fishes from the tropical US Pacific (Version 1.0).* UC San Diego: Scripps Institution of Oceanography. Retrieved from: http://escholarship.org/uc/item/5394f7m3.

Sano, M. 1989. Feeding habits of Japanese butterfyfishes (Chaetodontidae). *Environmental Biology of Fishes* **25**, 195–203.

Sano, M., Shimizu, M. & Nose, Y. 1984. Food habits of teleostean reef fishes in Okinawa Island, southern Japan. *The University of Tokyo Bulletin* **25**, 1–128.

Schino, G. & Aureli, F. 2010. A few misunderstandings about reciprocal altruism. *Communicative and Integrative Biology* **3**, 561–563.

Schleuter, D., Daufresne, M., Massol, F., & Argillier, C. 2010. A user's guide to functional diversity indices. *Ecological Monographs* **80**, 469-484.

Schluter D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.

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

Schmitz, L. & Wainwright, P.C. 2011b. Nocturnality constrains morphological and functional diversity in the eyes of reef fishes. *BMC Evolutionary Biology* 11:338

Şekercioğlu, Ç. 2006. Increasing awareness of avian ecological function. *Trends in Ecology and Evolution* **221**, 464–471.

Shallenberger, R.J. & Madden, W.D. 1973. Luring behavior in the scorpionfish, *Iracundus signifer*. *Behaviour* **47**, 1–2.

Shitzer, D., Noy-Meir, I. & Milchunas, D.G. 2008. The role of geologic grazing refuges in structuring Mediterranean grassland plant communities. *Plant Ecology* **198**, 135-147.

Sikkel, P.C. & Sikkel, N.M. 2012. First report of spawning and social organization in Hawai'ian Ambon Toby, *Canthigaster amboinensis. Ichthyological Research* **59**, 394–395.

Sikkel, P.C. 1990. Social organisation and spawning in the Atlantic sharpnose puffer, *Canthigaster rostrata* (Tetraodontidae). *Environmental Biology of Fishes* **27**, 243–254.

Silberschneider, V. & Booth, D.J. 2001. Resource use by *Enneapterygius rufopileus* and other rockpool fishes. *Environmental Biology of Fishes* **61**, 195–204.

Sirot, E. & Touzalin, F. 2009. Coordination and synchronization of vigilance in groups of prey: the role of collective detection and predators’ preference for stragglers. *American Naturalist* **173**, 47-59.

Sirot, E. 2012. Negotiation may lead selfish individuals to cooperate: the example of the collective vigilance game. *Proceedings of the Royal Society London B* **279**, 2862-2867.

Sivakumar, R. & Ramaiyan, V. 1987. The morphology of the alimentary tract in relation to food of platycephalids of Porto Novo Coast (Order: Scorpaeniformes). *Kochi: CMFRI Bulletin National Symposium on Research and Development in Marine Fisheries Sessions I & II* 44, 262–266.

Slade, E.M., Mann, D.J., Villanueva, J.F., & Lewis, O.T. 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology* **76**, 1094-1104.

Smith, G.C., & Parrish, J.D. 2002. Estuaries as nurseries for the jacks *Caranx ignobilis* and *Caranx melampygus* (Carangidae) in Hawaii. *Estuarine, Coastal and Shelf Science* **55**, 347–359.

Snorrason, S.S., Skùlason, S., Jonsson, B., Malmquist, H.J., Jónasson, P.M., Sandlund, O.T. & Lindem, T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. *Biological Journal of the Linnean Society* **52**, 1-18.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* **10**, 1115-1123.

Sogabe, A. & Yanagisawa, Y. 2008. Maintenance of pair bond during the non-reproductive season in a monogamous pipefish *Corythoichthys haematopterus*. *Journal of Ethology* **26**, 195–199.

Sogabe, A., Matsumoto, K. & Yanagisawa, Y. 2007. Mate change reduces the reproductive rate of males in a monogamous pipefish *Corythoichthys haematopterus*. *Ethology* **113**, 764–771.

Sommer, U. 1999. The impact of herbivore type and grazing pressure on benthic microalgal diversity. *Ecology Letters* **2**, 65-69.

Sorenson, L., Santini, F., Carnevale, G. & Alfaro, M.E. 2013. A multi-locus timetree of surgeonfishes (Acanthuridae, Percomorpha), with revised family taxonomy. *Molecular Phylogenetics and Evolution* **68**, 150-160.

Sotka, E.E. & Hay, M.E. 2009. Effects of herbivores, nutrient enrichment, and their interactions on macroalgal proliferation and coral growth. *Coral Reefs* **28**, 555–568.

Sreenivasan, P.V. 1978. Observations on the fishery and biology of *Megalaspis cordyla* (Linnaeus) at Vizhinjam. *Indian Journal of Fisheries* **25**, 122–140.

St-Pierre, A., Larose, K. & Dubois, F. 2009. Long-term social bonds promote cooperation in the iterated Prisoner's Dilemma. *Proceedings of the Royal Society London B* **276**, 4223-4228.

Stachowicz, J.J. 2001. Mutualism, Facilitation, and the Structure of Ecological Communities: Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. *BioScience* **51**, 235-246.

Stella, J.S., Pratchett, M.S., Hutchings, P.A. & Jones, G.P. 2011. Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. *Oceanography and Marine Biology Annual Reviews* **49**, 43–104.

Steneck R. 1988 Herbivory on coral reefs: a synthesis. *Proceedings of the 6th International Coral Reef Symposium* (pp. 37-49). 1 (ed. J. H. Choat et al.), pp. 37 – 49. Townsville, Queensland: James Cook University.

Steneck RS. 1983 Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* **9**, 44-61.

Steneck, R.S. & Dethier, M.N. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* **69**, 476-498.

Steneck, R.S., Arnold, S.N. & Mumby, P.J. 2014. Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternative attractors. *Marine Ecology Progress Series* **506**, 115-127.

Stephens, D.W., Anderson, J.P. & Benson, K.E. 1997. On the spurious occurrence of Tit for Tat in pairs of predator-approaching fish. *Animal Behaviour* **53**, 113-131.

Stevens, J.R. & Hauser, M.D. 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Science* **8**, 60-65.

Stewart, B.D. & Jones, G.P. 2001. Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. *Marine Biology* **138**, 383–397.

Stiger, V. & Payri, C.E. 2005. Natural settlement dynamics of a young population of *Turbinaria ornata* and phonological comparisons with older populations. *Aquatic Botany* **81**, 225–243.

Stork, N.E., McBroom, J., Gely, C., & Hamilton, A.J. 2015. New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences USA* **112**, 7519-7523.

Streelman, J.T., Alfaro, M., Westneat, M.W., Bellwood, D.R. & Karl, S.A. 2002. Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. *Evolution* **56**, 961–971.

Sturmbauer C, Mark W, Dallinger R. 1992 Ecophysiology of Aufwuchs-eating cichlids in Lake Tanganyika: niche separation by trophic specialization. *Environmental Biology of Fishes* **35**, 283-290.

Suzuki, K., Tanaka, Y. & Hioki, S. 1980. Spawning behaviour, eggs, and larvae of the butterflyfish, *Chaetodon nippon*, in an aquarium. *Japanese Journal of Ichthyology* **26**, 334–341.

Sweatman, H.P.A. 1993. Tropical snapper (Lutjanidae) that is piscivorous at settlement. *Copeia* **4**, 1137–1139.

Taborsky, M. 1984. Broodcare helpers in the cichlid fish Lamprologus brichardi: their costs and benefits. *Animal Behaviour* **32**, 1236-1252.

Taborsky, M. 2013. Social evolution: reciprocity there is. *Current Biology* **23**, 486-488.

Takegaki, T. & Nakazono, A. 1999. Division of labour in the monogamous goby, Valenciennea longipinnis, in relation to burrowing behaviour. *Ichthyological Research* **46**, 125–129.

Takegaki, T. 2000. Monogamous mating system and spawning cycle in the gobiid fish, *Amblygobius phalaena* (Gobiidae). *Environmental Biology of Fishes* **59**, 61–67.

Tamaki, A., Miyamoto, S., Yamazaki, T. & Nojima, S. 1992. Abundance pattern of the ghost shrimp *Callianassa japonica* Ortmann (Thalassinidea) and the snake eel *Pisodonophis cancrivorus* Richardson (Pisces, Ophichthidae) and their possible interaction on an intertidal sand flat. *Plankton and Benthos Research* **43**, 11–22.

Tamura, T. 1957. A study of visual perception in fish, especially on resolving power and accommodation. *Bulletin of the Japanese Society of Scientific Fisheries* **22**, 536-557.

Tandon, K.K. 1960. The food and feeding habits of Selaroides leptolepis (Cuvier and Valenciennes). *Current Science* **29**, 62–63.

Taquet, M., Sancho, G., Dagorn, L., Gaertner, J.C., Itano, D., Aumeeruddy, R. & Peignon, C. 2007. Characterizing fish communities associated with drifting fish aggregating devices (FADs) in the Western Indian Ocean using underwater visual surveys. *Aquatic Living Resources* **20**, 331–341.

Temeles, E.J., Koulouris, C.R., Sander, S.E. & Kress, W.J. 2009. Effect of flower shape and size on foraging performance and trade-offs in a tropical hummingbird. *Ecology* **90**, 1147-1161.

Thompson, A.R. 2004. Habitat and mutualism affect the distribution and abundance of a shrimp-associated goby. *Marine and Freshwater Research* **55**, 105–113.

Thompson, A.R. 2005. Dynamics of demographically open mutualists: immigration, intraspecific competition, and predation impact goby populations. *Oecologia* **143**, 61–69.

Thomson, J.D., McKenna, M.A. & Cruzan, M.B. 1989. Temporal patterns of nectar and pollen production in *Aralia hispida*: implications for reproductive success. *Ecology* **70**, 1061-1068.

Thornhill, R. 1979. Male pair-formation pheromones in *Panorpa* scorpionflies (Mecoptera: Panorpidae). *Environmental Entomology* **8**, 886–888.

Thresher, R.E. 1984. *Reproduction in reef fishes.* Neptune City, NJ: T.F.H. Publications.

Tilman, D., Isbell, F., & Cowles, J.M. 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* **45**, 471-493.

Tilman, D., & Downing, J.A. 1996. Biodiversity and stability in grasslands. In *Ecosystem Management* (pp. 3-7). Springer New York.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300-1302.

Townsend, K.A. & Tibbetts, I.R. 2000. Biomass and distribution of herbivorous blennies in the southern Great Barrier Reef. *Journal of Fish Biology* **56**, 774–791.

Trapon, M.L., Pratchett, M.S. & Hoey, A.S. 2013a. Spatial variation in abundance, size and orientation of juvenile corals related to the biomass of parrotfishes on the Great Barrier Reef, Australia. *PLoS ONE* **8**:e57788

Trapon, M.L., Pratchett, M.S., Hoey, A.S. & Baird, A.H. 2013b. Influence of fish grazing and sedimentation on the early post-settlement survival of the tabular coral *Acropora cytherea*. *Coral Reefs* **32**, 1051-1059.

Tribble, G.W. & Nishikawa, H. 1982. An analysis of the diets of four spatially overlapping damselfishes of the genus *Chromis*. *Japanese Journal of Ichthyology* **29**, 267–271.

Tricas, T.C., Kajiura, S.M. & Kosaki, R.K. 2006. Acoustic communication in territorial butterflyfishes: test of the sound production hypothesis. *Journal of Experimental Biology* **209**, 4994-5004.

Trivers, R.L. 1971. The evolution of reciprocal altruism. *Quarterly Reviews in Biology* **46**, 35-57.

Ungar, P.S., Grine, F.E. & Teaford, M.F. 2008 Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS one* **3**, e2044.

Unsworth, R.K.F., Garrard, S.L., Salinas De León, P., Cullen, L.C., Smith, D.J., Sloman, K.A. & Bell, J.J. 2009. Structuring of Indo-Pacific fish assemblages along the mangrove-seagrass continuum. *Aquatic Biology* **5**, 85–95.

Unsworth, R.K.F., Wylie, E., Smith, D.J. & Bell, J.J. 2007. Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. *Estuarine, Coastal and Shelf Science* **72**, 81–88.

Vadas, R.L., Johnson, S., Norton, T.A. 1992. Recruitment and mortality of early post-settlement stages of benthic algae. *British Phycological Journal* **27**, 331-351.

Vail, A.L., Manica, A., & Bshary, R. 2013. Referential gestures in fish collaborative hunting. *Nature Communications* **4**, 1765.

van Doorn, G. S., Riebli, T. & Taborsky, M. 2014. Coaction versus reciprocity in continuous-time models of cooperation. *Journal of Theoretical Biology* **356**, 1-10.

Vermeij, M.J.A. 2005. Substrate characteristics and adult density determine recruitment patterns in a Caribbean brooding coral. *Marine Ecology Progress Series* **295**, 123–133.

Vermeij MJA (2006) Early life-history dynamics of Caribbean coral species on artificial substratum: the importance of competition, growth and variation in life-history strategy. Coral Reefs 25:59–71

Vermeij, M.J.A., Smith, J.E., Smith, C.M., Vega Thurber, R. & Sandin, S.A. 2009. Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes. *Oecologia* **159**, 325–336.

Villéger, S., Grenouillet G. & Brosse, S. 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography* **22**, 671-681.

Villéger, S., Mason, N.W.H. & Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301.

Villéger, S., Novack-Gottshall, P.M. & Mouillot, D. 2011. The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecology Letters* **14**, 561–568.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* **27**, 244–252.

Vitousek, P. M., Mooney, H.A., Lubchenco, J. & Melillo J.M. 1997. Human domination of Earth's ecosystems. *Science* **277**, 494–499.

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

Wainwright, P.C. 1991. Ecomorphology: experimental functional anatomy for ecological problems. *American Zoologist* **31**, 680–693.

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

Wainwright, P.C. & Bellwood, D.R. 2002. *Ecomorphology of feeding in coral reef fishes*. In Coral reef fishes: dynamics and diversity in a complex ecosystem (ed. PE Sale), pp. 33-55. San Diego, CA: Academic Press.

Wainwright, P.C. & Reilly, S.M. 1994. *Ecological Morphology.* Chicago, US: University of Chicago Press.

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

Wainwright, P.C. 1996. Ecological explanation through functional morphology: the feeding biology of sunfishes. *Ecology* **77**, 1336-1343.

Wantiez, L. & Kulbicki, M. 1995. Main fish populations and their relation to the benthos in a silted Bay of New Caledonia, as determined by visual censuses. *Cybium* **19**, 223–240.

Ward, A.J.W., Herbert-Read, J.E., Sumpter, D.J., Krause, J. 2011. Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences USA* **108**, 2312-2315.

Ward, A.J.W., Sumpter, D.J., Couzin, I.D., Hart, P.J. & Krause, J. 2008. Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences USA* **105**, 6948-6953.

Warren, D.L., Glor, R.E., & Turelli, M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**, 2868-2883.

Webb, P.W. 1997. *Swimming.* In: Evans (ed) The physiology of fishes, 2nd ed. CRC Press, Marine Science Series, Boca Raton, pp3-24

Welsh, J.Q. & Bellwood, D.R. 2012a. Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. *Coral Reefs* **31**, 55–65.

Welsh, J.Q. & Bellwood, D.R. 2012b. How far do schools of roving herbivores rove? A case study using *Scarus rivulatus*. *Coral Reefs* **31**, 991–1003.

Wenger, A.S., Johansen, J.L. & Jones, G.P. 2012. Increasing suspended sediment reduces foraging, growth and condition of a planktivorous damselfish. *Journal of Experimental Marine Biology and Ecology* **428**, 43–48.

Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64**, 1540-1548.

Westneat, D.F. & Stewart, I.R. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Annual Review of Ecology, Evolution, and Systematics* **34**, 365–396.

Westneat, M.W., Alfaro, M.E., Wainwright, P.C., Bellwood, D.R., Grubich, J.R., Fessler, J.L., Clements, K.D. & Smith, L.L. 2005. Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. *Proceedings of the Royal Society London B* **272**, 993–1000.

Wetterer, J.K. 1989. Mechanisms of prey choice by planktivorous fish: perceptual constraints and rules of thumb. *Animal Behaviour* **37**, 955-967.

White, G.E. & Brown, C. 2013. Site fidelity and homing behaviour in intertidal fishes. *Marine Biology* **160**, 1365-1372.

White, J.W. & Warner, R.R. 2007a. Behavioral and energetic costs of group membership in a coral reef fish. *Oecologia* **154**, 423–433.

White, J.W. & Warner, R.R. 2007b. Safety in numbers and the spatial scaling of density-dependent mortality in a coral reef fish. *Ecology* **88**, 3044–3054.

Whiteman, E.A. & Côté, I.M. 2003. Social monogamy in the cleaning goby Elacatinus evelynae: ecological constraints or net benefit? *Animal Behaviour* **66**, 281–291.

Whiteman, E.A. & Côté, I.M. 2004. Monogamy in marine fishes. *Biological Reviews* **79**, 351–375.

Whittaker, R.H., Levin, S.A. & Root R.B. (1973) Niche, habitat, ecotope. *American Naturalist* **955**, 321–338.

Wickler, W. 1985. Coordination of vigilance in bird groups. The “Watchman's Song” Hypothesis. *Zeitschrift für Tierpsychologie* **69**, 250-253.

Wilcox, R.S. 1984. Male copulatory guarding enhances female foraging in a water strider. *Behavioral Ecology and Sociobiology* **15**, 171–174.

Wilkinson, G.S. 1984. Reciprocal food sharing in the vampire bat. *Nature* 308, 181-184.

Williams, D.M. & Hatcher, A.I. 1983. Structure of fish communities on outer slopes of inshore, mid shelf and outer shelf reefs of the Great Barrier Reef. *Marine Ecology Progress Series* **10**, 239–250.

Williams, L.B. & Williams Jr, E.H. 1986. Icthyological notes about fishes collected for parasite examination around Sesoko Island, Okinawa. *Galaxea* **5**, 217–221.

Wilson, S.K. 2000. Trophic status and feeding selectivity of blennies (Blenniidae: Salariini). *Marine Biology* **136**, 431–437.

Wilson, S.K., Bellwood, D.R., Choat, J.H. & Furnas, M.J. 2003. Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology Annual Reviews* **41**, 279-310.

Wilson, S.K., Graham, N.A.J., Polunin, N.V.C. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology* **151**, 1069-1076.

Winterbottom, R. 1984. A review of the gobiid fish genus *Trimma* from the Chagos Archipelago, central Indian Ocean, with the description of seven new species. *Canadian Journal of Zoology* **62**, 695–715.

Wismer, S., Hoey, A.S. & Bellwood, D.R. 2009. Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Marine Ecology Progress Series* **376**, 45-54.

Wittenberger, J.F. & Tilson, R.L. 1980. The evolution of monogamy. *Annual Review of Ecology, Evolution, and Systematics* **11**, 197–232.

Wong, M.Y.L., Munday, P.L. & Jones, G.P. 2005. Habitat patch size, facultative monogamy and sex change in a coral-dwelling fish, *Caracanthus unipinna*. *Environmental Biology of Fishes* **74**, 141–150.

Woodland, D.J. 1990. *Revision of the fish family Siganidae with descriptions of two new species and comments on distribution and biology*. Honolulu, HI: Bishop Museum.

Worm, B. & Duffy, J.E. 2003. Biodiversity, productivity and stability in real food webs. *Trends in Ecology and Evolution* **18**, 628-632.

Worm, B., Lotze, H.K., Hillebrand, H. & Sommer, U. 2002. Consumer versus resource control of species diversity and ecosystem functioning. **Nature** *417*, 848-851.

Wright, J.T. & Steinberg, P.D. 2001. Effect of variable recruitment and post-recruitment herbivory on local abundance of a marine alga. *Ecology* **82**, 2200–2215.

Wright, J., Berg, E., De Kort, S., Khazin, V. & Maklakov, A.A. 2001. Safe selfish sentinels in a cooperative bird. *Journal of Animal Ecology* **70**, 1070-1079.

Wright, J.P., Naeem, S., Hector, A., Lehman, C., Reich, P.B., Schmid, B. & Tilman D. 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters* **9**, 111–120.

Yabuta, S. 1997. Spawning migrations of the monogamous butterflyfish *Chaetodon trifasciatus*. *Ichthyological Research* **44**, 177–182.

Yabuta, S. 2007. Social groupings in 18 species of butterflyfish and pair bond weakening during the nonreproductive season. *Ichthyological Research* **54**, 207–210.

Yabuta, S., & Kawashima, M. 1997. Spawning behavior and haremic mating system in the corallivorous butterflyfish, *Chaetodon trifascialis*, at Kuroshima Island, Okinawa. *Ichthyological Research* **44**, 183–188.

Yahner, R.H. 1978. The adaptive nature of the social system and behavior in the eastern chipmunk, *Tamias striatus*. *Behavioral Ecology and Sociobiology* **3**, 397–427.

Young, L.C., Zaun, B.J. & Van der Werf, E.A. 2008. Successful same-sex pairing in Laysan albatross. *Biology Letters* **4**, 323–325.

Zagars, M., Ikejima, K., Arai, N. & Tongnunui P. 2013. Trophic characteristics of a mangrove fish community in Southwest Thailand: Important mangrove contribution and intraspecies feeding variability. *Estuarine, Coastal and Shelf Science* **119**, 145-152.

Zak, D. R., Holmes, W. E., White, D. C., Peacock, A. D., & Tilman, D. 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? *Ecology* **84**, 2042-2050.

Zöttl, M., Heg, D., Chervet, N., & Taborsky, M. 2013. Kinship reduces alloparental care in cooperative cichlids where helpers pay-to-stay. *Nature Communications* **4**, 1341.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. Springer.

Appendix A

Publications arising from this thesis:

1. Brandl SJ, Bellwood DR (2014). Pair-formation in coral reef fishes: an ecological perspective. *Oceanogr Mar Biol Annu Rev* 52, 1-80 (doi: 10.1201/b17143-2).
2. Brandl SJ, Bellwood DR (2013). Morphology, ecology, and sociality: can morphology predict pair-forming behaviour in coral reef fishes. *Coral Reefs* 32, 835-846 (doi: 10.1007/s00338-013-1042-0).
3. Brandl SJ, Bellwood DR. Coordinated, cooperative vigilance in pairing coral reef fishes permits the exploitation of cryptic resources. *Sci Rep* 5, 14556 (doi:10.1038/srep14556).
4. Brandl SJ, Bellwood DR (2014). Individual-based analyses reveal limited functional overlap in a coral reef fish community. *J Anim Ecol* 83, 661-670 (doi: 10.1111/1365-2656.12171).
5. Brandl SJ, Robbins WR, Bellwood DR. Exploring the nature of ecological specialization in a coral reef fish community: morphology, diet, and foraging microhabitat use. *Proc R Soc B* 20151147 (doi: 10.1098/rspb.2015.1147).
6. Brandl SJ, Hoey AS, Bellwood DR. (2014) Micro-topography mediates interactions between corals, algae, and herbivorous fishes on coral reefs. *Coral Reefs* 33, 421-430 (doi: 10.1007/s00338-013-1110-5).
7. Brandl SJ, Bellwood DR. Micro-topographic refuges drive consumer-producer dynamics by mediating consumer functional diversity (under review).

Appendix B

Publications during candidature not arising from this thesis:

1. Hoey AS, Brandl SJ, Bellwood DR (2013). Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. *Coral Reefs* 32, 973-982 (doi: 10.1007/s00338-013-1043-z).
2. Bellwood DR, Goatley CHR, Brandl SJ, Bellwood O (2014). Fifty million years of herbivory: fossils, fishes and functional innovations. *Proc R Soc B* 281, 20133046 (doi: 10.1098/rspb.2013.3046).
3. Brooker RM, Munday PL, Brandl SJ, Jones GP (2014). Local extinction of a coral reef fish explained by inflexible prey choice. *Coral Reefs* 33, 891-896 (doi: 10.1007/s00338-014-1197-3).
4. Rocker MM, Brandl SJ (2015). Transplantation of corals into a new environment results in substantial skeletal loss in *Acropora tenuis*. Mar Biodiv (doi: 10.1007/s12526-014-0239-y).
5. Heinrich DDU, Watson SA. Rummer JL, Brandl, SJ, Simpfendorfer CA, Heupel MR, Munday PL (2015) Foraging behaviour of the epaulette shark *Hemiscyllium ocellatum* is not affected by elevated CO2. ICES (in press, doi: 10.1093/icesjms/fsv085).
6. Brooker RM, Brandl SJ, Dixson DL. Cryptic effects of habitat declines: coral-associated fishes avoid coral-seaweed interactions due to visual and chemical cues. *Sci Rep* 6, 18842 (doi:10.1038/srep18842).
7. Brandl SJ, Emslie MJ, Ceccarelli DM. Functional redundancy buffers trait-specific susceptibility to disturbance in a high-diversity system (under review).

8. Mirbach CE, Brandl SJ. The ontogeny of pairing in coral reef rabbitfishes (f. Siganidae) (under review).
9. Casey JM, Baird AH, Brandl SJ, Hoogenboom MO, Rizzari JR, Mirbach CE, Frisch AJ, Connolly SR. A test of trophic cascade theory: fish and benthic assemblages across a predator density gradient on coral reefs (under review).

Appendix C

Supplemental table for **Chapter 2:** Pair-formation in coral reef fishes: an ecological perspective

List of Indo-Pacific reef fishes and their social system, trophic affiliation, burrowing behaviour, activity patterns, size and reproductive traits. Troph. = trophic group; Ca = carnivore; Co = corallivore; De = detritivore; He = herbivore; Ma = macroinvertevore; Mi = microinvertevore; Om = omnivore; Pl = planktivore; Pi = Piscivore; Sp = spongivore; Burr. = burrowing; Act. = activity period; D = diurnal; N = nocturnal; Spa. = spawning mode; G = group; P = pair; B = both; Gam. = gamete release; Br = broadcast; Dm = demersal; Gel = gelatinous egg mass; Es = egg-scattering; Mo = mouthbrooding; Po = pouchbrooding; Mon. = monogamy; Refs. = references. N/A = no available information. *Asterisks* mark burrowing species that associate with alpheid shrimps. References are listed numerically at the end of the table.

Family	Species	Pairs	Troph.	Burr.	Act.	Size (mm)	Spa.	Gam.	Mon.	Refs.
Acanthuridae	*Acanthurus achilles*	Yes	He	No	D	200	G	Br	Yes	5
	Acanthurus albipectoralis	No	Pl	No	D	330	G	Br	No	6
	Acanthurus auranticavus	No	De	No	D	350	G	Br	No	6
	Acanthurus bariene	Yes	De	No	D	500	G	Br	No	6
	Acanthurus blochii	No	De	No	D	420	G	Br	No	6
	Acanthurus dussumieri	No	De	No	D	500	G	Br	No	7
	Acanthurus fowleri	Yes	He	No	D	450	G	Br	No	2
	Acanthurus grammoptilus	No	De	No	D	350	G	Br	No	6
	Acanthurus guttatus	No	He	No	D	280	B	Br	No	1;3
	Acanthurus japonicus	No	He	No	D	210	G	Br	No	2
	Acanthurus leucocheilus	No	De	No	D	200	G	Br	No	2
	Acanthurus leucopareius	No	He	No	D	200	G	Br	No	1;3
	Acanthurus leucosternon	Yes	He	No	D	380	G	Br	Yes	8
	Acanthurus lineatus	No	He	No	D	380	G	Br	No	6
	Acanthurus maculiceps	No	He	No	D	200	G	Br	No	6
	Acanthurus mata	No	Pl	No	D	500	G	Br	No	1;2;3
	Acanthurus nigricans	Yes	He	No	D	210	G	Br	Yes	5

	Acanthurus nigricauda	No	De	No	D	400	G	Br	No	7;6
	Acanthurus nigrofuscus	No	He	No	D	210	B	Br	No	8;9
	Acanthurus nigroris	No	He	No	D	250	G	Br	No	1;2;3
	Acanthurus nubilus	No	Pl	No	D	450	G	Br	No	2;3;4
	Acanthurus olivaceus	No	De	No	D	350	G	Br	No	7
	Acanthurus pyroferus	No	He	No	D	250	G	Br	No	6
	Acanthurus reversus	No	De	No	D	340	G	Br	No	3
	Acanthurus tennenti	Yes	He	No	D	310	G	Br	No	8
	Acanthurus thompsoni	No	Pl	No	D	270	G	Br	No	1;2;3
	Acanthurus triostegus	Yes	He	No	D	260	G	Br	No	8;6
	Acanthurus tristis	No	He	No	D	250	G	Br	No	2
	Acanthurus xanthopterus	No	De	No	D	560	G	Br	No	1;2;3
	Ctenochaetus binotatus	No	De	No	D	220	G	Br	No	2;3;4
	Ctenochaetus cyanocheilus	No	He	No	D	200	G	Br	No	2;3
	Ctenochaetus flavicauda	No	De	No	D	130	G	Br	No	2
	Ctenochaetus hawaiiensis	No	De	No	D	250	G	Br	No	2;3
	Ctenochaetus marginatus	No	De	No	D	220	G	Br	No	2;3
	Ctenochaetus striatus	No	De	No	D	260	B	Br	No	8;6
	Ctenochaetus strigosus	No	De	No	D	180	P	Br	No	8;1
	Ctenochaetus tomiensis	No	De	No	D	150	G	Br	No	2;3
	Naso annulatus	No	Pl	No	D	1000	G	Br	No	1;2;3
	Naso brachycentron	No	He	No	D	600	G	Br	No	1;2;3;4
	Naso brevirostris	No	Pl	No	D	500	G	Br	No	1;2;3
	Naso caeruleacauda	No	Pl	No	D	300	G	Br	No	2;3
	Naso caesius	No	Pl	No	D	600	G	Br	No	1;2;3
	Naso hexacanthus	No	Pl	No	D	750	G	Br	No	1;2;3
	Naso lituratus	Yes	He	No	D	300	G	Br	No	8;6;9
	Naso lopezi	No	Pl	No	D	650	G	Br	No	1;2;3
	Naso maculatus	No	Pl	No	D	600	G	Br	No	3;10
	Naso minor	No	Pl	No	D	190	G	Br	No	2;4
	Naso thynnoides	No	Pl	No	D	300	G	Br	No	1;2;3
	Naso tonganus	No	He	No	D	600	G	Br	No	2;3;4
	Naso tuberosus	No	He	No	D	600	G	Br	No	1;2;3;6
	Naso unicornis	No	He	No	D	700	G	Br	No	8;1;2;3;6
	Naso vlamingii	No	Pl	No	D	500	G	Br	No	1;2;3
	Paracanthurus hepatus	No	Pl	No	D	310	G	Br	No	1;2;3;6
	Prionurus maculatus	No	He	No	D	435	G	Br	No	1;3
	Prionurus microlepidotus	No	He	No	D	700	P	Br	No	1
	Zebrasoma desjardinii	Yes	He	No	D	400	P	Br	No	2;4
	Zebrasoma flavescens	No	He	No	D	200	B	Br	No	2;4
	Zebrasoma rostratum	No	He	No	D	210	P	Br	No	2;3
	Zebrasoma scopas	Yes	He	No	D	200	B	Br	Yes	8;6;9
	Zebrasoma veliferum	Yes	He	No	D	400	P	Br	No	8;6;9
Anomalopidae	*Anomalops katoptron*	No	Pl	No	N	350	P	Br	No	4;11
	Photoblepharon palpebratus	No	Pl	No	N	120	P	Br	No	4
Antennariidae	*Antennarius biocellatus*	No	Pi	No	D	150	P	Gel	No	2;4
	Antennarius coccineus	No	Pi	No	D	120	P	Gel	No	1;2;3;12
	Antennarius commersoni	No	Pi	No	D	300	P	Gel	No	1;2;3;4
	Antennarius dorehensis	No	Pi	No	D	50	P	Gel	No	2
	Antennarius maculatus	No	Pi	No	D	90	P	Gel	No	1;2;3;13
	Antennarius nummifer	No	Pi	No	D	100	P	Gel	No	1;2;3
	Antennarius pictus	No	Pi	No	D	160	P	Gel	No	1;2;3
	Antennarius randalli	No	Pi	No	D	45	P	Gel	No	1;2;3

	Antennarius striatus	No	Pi	No	D	220	P	Gel	No	1;2;3
	Antennatus rosaceus	No	Pi	No	D	58	P	Gel	No	3
	Antennatus tuberosus	No	Pi	No	D	80	P	Gel	No	2
	Histiophryne cryptacanthus	No	Pi	No	D	85	P	Gel	No	1;2;3
	Histrio histrio	No	Ca	No	D	140	P	Gel	No	1;2;3;4
	Lophiocharon trisignatus	No	Pi	No	D	180	P	Gel	No	1;2;4
	Tathicarpus butleri	No	Pi	No	D	120	P	Gel	No	2
Apistidae	*Apistus carinatus*	No	Pl	No	D	88	N/A	N/A	No	2;14
Aploactinidae	*Paraploactis kagoshimensis*	No	N/A	No	D	120	N/A	N/A	No	2
Apogonidae	*Apogon amboinensis*	No	Ca	No	D	100	P	Mo	No	2;15
	Apogon exostigma	No	Ca	No	N	110	P	Mo	No	1;2;16
	Apogon guamensis	Yes	Pl	No	N	110	P	Mo	No	1;2;3;16
	Apogon hyalosoma	No	Ca	No	N	200	P	Mo	No	2;17
	Apogon norfolcensis	No	Ca	No	N	100	P	Mo	No	2;3;4
	Apogon sangiensis	No	Ca	No	N	80	P	Mo	No	1;4
	Apogon semiornatus	No	Ca	No	N	70	P	Mo	No	1;3;4
	Apogonichthyoides melas	No	Ca	No	D	130	P	Mo	No	2;4
	Apogonichthyoides timorensis	No	Ca	No	N	80	P	Mo	No	2;4
	Apogonichthyoides uninotatus	No	Ca	No	D	60	P	Mo	No	2
	Apogonichthys ocellatus	No	Ca	No	N	35	P	Mo	No	2;4
	Archamia biguttata	No	Pl	No	N	90	P	Mo	No	1;2;3;12
	Archamia bleekeri	No	Pl	No	N	90	P	Mo	No	2;4
	Archamia fucata	No	Pl	No	N	90	P	Mo	No	1;2;3;18
	Archamia leai	No	Pl	No	N	80	P	Mo	No	1;2;3;16
	Archamia macroptera	No	Pl	No	D	90	P	Mo	No	2;3;
	Archamia zosterophora	No	Pl	No	N	80	P	Mo	No	1;2;4
	Cercamia cladara	No	N/A	No	N	40	P	Mo	No	3;4
	Cercamia eremia	No	N/A	No	N	40	P	Mo	No	2
	Cheilodipterus alleni	No	N/A	No	N	40	P	Mo	No	2;4
	Cheilodipterus artus	No	Ca	No	D	120	P	Mo	No	1;2;3;18
	Cheilodipterus intermedius	No	N/A	No	D	110	P	Mo	No	2;4
	Cheilodipterus isostigmus	No	Pi	No	D	100	P	Mo	No	2;3;4
	Cheilodipterus macrodon	No	Pi	No	D	200	P	Mo	Yes	1;2;3;18
	Cheilodipterus nigrotaeniatus	Yes	Ma	No	D	80	P	Mo	No	2;12
	Cheilodipterus parazonatus	Yes	Ma	No	D	70	P	Mo	No	1;2;12
	Cheilodipterus quinquelineatus	No	Ca	No	N	120	P	Mo	No	1;2;3;18
	Cheilodipterus singapurensis	No	N/A	No	N	175	P	Mo	No	2
	Cheilodipterus zonatus	Yes	Ma	No	D	70	P	Mo	No	2;12
	Foa brachygramma	No	Pl	No	D	60	P	Mo	No	1;4
	Foa fo	No	Pl	No	D	35	P	Mo	No	1;2;3
	Foa hyalina	No	Pl	No	D	50	P	Mo	No	1;2;3
	Fowleria marmorata	No	N/A	No	D	45	P	Mo	No	1;2;3
	Fowleria punctulata	No	N/A	No	N	60	P	Mo	No	1;4
	Fowleria vaiulae	No	N/A	No	D	50	P	Mo	No	1;2;3
	Fowleria variegata	No	N/A	No	D	50	P	Mo	No	1;2;3
	Nectamia bandanensis	No	Pl	No	N	90	P	Mo	No	2;3;4
	Nectamia fusca	No	Pl	No	N	100	P	Mo	No	2;3;4
	Nectamia octospina	No	Pl	No	D	50	P	Mo	No	1;2;3
	Nectamia savayensis	No	Ma	No	D	110	P	Mo	No	1;4
	Ostorhinchus angustatus	No	Mi	No	N	90	P	Mo	No	1;2;3;4
	Ostorhinchus apogonides	No	Pl	No	D	100	P	Mo	No	1;2;3;12
	Ostorhinchus aureus	No	N/A	No	D	120	P	Mo	No	1;2;3
	Ostorhinchus capricornis	Yes	N/A	No	D	100	P	Mo	No	2

Ostorhinchus cavitiensis	No	N/A	No	D	80	P	Mo	No	2
Ostorhinchus chrysopomus	No	N/A	No	D	90	P	Mo	No	2
Ostorhinchus chrysotaenia	No	N/A	No	N	100	P	Mo	No	2;4
Ostorhinchus compressus	No	Pl	No	N	120	P	Mo	No	1;2;3;19
Ostorhinchus cookii	No	N/A	No	N	100	P	Mo	No	1;2;3;4
Ostorhinchus crassiceps	No	Ma	No	N	60	P	Mo	No	1;2;3;4
Ostorhinchus cyanosoma	Yes	Ma	No	D	80	P	Mo	No	1;2;3;16
Ostorhinchus dispar	No	N/A	No	N	50	P	Mo	No	2;4
Ostorhinchus doederleini	Yes	Ca	No	N	120	P	Mo	No	1;2;3;16
Ostorhinchus endekataenia	No	N/A	No	N	140	P	Mo	No	2;4
Ostorhinchus evermanni	Yes	N/A	No	N	120	P	Mo	No	2;4
Ostorhinchus fleurieu	No	N/A	No	D	110	P	Mo	No	2
Ostorhinchus franssedai	No	N/A	No	D	75	P	Mo	No	2
Ostorhinchus griffini	Yes	N/A	No	D	140	P	Mo	No	2;4
Ostorhinchus hartzfeldii	No	Ma	No	N	120	P	Mo	No	2;20
Ostorhinchus hoevenii	No	Ma	No	D	50	P	Mo	No	2;20
Ostorhinchus holotaenia	No	N/A	No	D	80	P	Mo	No	1;2;3
Ostorhinchus kiensis	No	N/A	No	D	90	P	Mo	No	2;3
Ostorhinchus komodoensis	No	Pl	No	D	70	P	Mo	No	2;4
Ostorhinchus lateralis	No	Ma	No	N	80	P	Mo	No	2;21
Ostorhinchus lineomaculatus	No	N/A	No	N	65	P	Mo	No	2
Ostorhinchus luteus	No	Pl	No	D	50	P	Mo	No	1;2;3;12
Ostorhinchus margaritophorus	No	N/A	No	N	55	P	Mo	No	2;22
Ostorhinchus moluccensis	No	N/A	No	N	90	P	Mo	No	2
Ostorhinchus monospilus	Yes	N/A	No	N	80	P	Mo	No	2;4
Ostorhinchus multilineatus	No	N/A	No	D	100	P	Mo	No	2;4
Ostorhinchus nanus	No	N/A	No	D	35	P	Mo	No	2;4
Ostorhinchus neotes	No	N/A	No	D	30	P	Mo	No	2
Ostorhinchus nigrofasciatus	Yes	Mi	No	N	80	P	Mo	No	1;2;3;4
Ostorhinchus notatus	No	Pl	No	N	100	P	Mo	Yes	1;2;23
Ostorhinchus novemfasciatus	Yes	Ca	No	N	90	P	Mo	No	1;2;3;4
Ostorhinchus ocellicaudus	Yes	N/A	No	D	60	P	Mo	No	2
Ostorhinchus parvulus	No	N/A	No	D	80	P	Mo	No	2;4
Ostorhinchus properupta	Yes	N/A	No	D	75	P	Mo	No	2
Ostorhinchus quadrifasciatus	No	Ma	No	N	100	P	Mo	No	2;24
Ostorhinchus rubrimacula	No	Ma	No	D	80	P	Mo	No	2;3;25
Ostorhinchus ruepellii	No	N/A	No	N	120	P	Mo	No	2;4
Ostorhinchus sealei	No	N/A	No	D	90	P	Mo	No	2
Ostorhinchus selas	No	N/A	No	D	55	P	Mo	No	2
Ostorhinchus semiornatus	No	N/A	No	N	70	P	Mo	No	2;3
Ostorhinchus taeniophorus	N/A	N/A	No	N	100	P	Mo	No	1;2;3;4
Ostorhinchus talboti	No	N/A	No	N	100	P	Mo	No	1;2;3
Ostorhinchus thermalis	No	N/A	No	D	80	P	Mo	No	2
Ostorhinchus wassinki	Yes	N/A	No	D	70	P	Mo	No	2
Pristiapogon fraenatus	No	N/A	No	N	110	P	Mo	No	1;2;4
Pristiapogon kallopterus	No	Pl	No	N	150	P	Mo	No	2;12
Pristicon rhodopterus	No	N/A	No	N	150	P	Mo	No	2
Pristicon trimaculatus	Yes	Pl	No	N	150	P	Mo	No	2;3;12
Pseudamia gelatinosa	No	N/A	No	N	100	P	Mo	No	1;2;3
Pseudamia hayashii	No	N/A	No	N	75	P	Mo	No	2
Pseudamia zonata	No	N/A	No	N	90	P	Mo	No	2;3
Pseudamiops gracilicauda	No	Pl	No	N	50	P	Mo	No	3
Pseudamiops phasma	N/A	N/A	No	D	47	P	Mo	No	3

	Pterapogon kauderni	No	Pl	No	N	65	P	Mo	No	2;4
	Pterapogon mirifica	No	N/A	No	N	140	P	Mo	No	2;4
	Rhabdamia cypselurus	No	Pl	No	N	60	P	Mo	No	1;2;3;4
	Rhabdamia gracilis	No	Pl	No	N	60	P	Mo	No	1;2;3;4
	Rhabdamia spilota	No	Pl	No	D	60	P	Mo	No	2;4
	Siphamia corallicola	No	N/A	No	D	38	P	Mo	No	2;4
	Siphamia elongata	No	N/A	No	D	38	P	Mo	No	2
	Siphamia fuscolineata	No	N/A	No	D	35	P	Mo	No	2
	Siphamia majimai	N/A	N/A	No	N	35	P	Mo	No	1;4
	Siphamia tubifer	No	N/A	No	D	40	P	Mo	No	2
	Siphamia versicolor	No	N/A	No	D	40	P	Mo	No	2;3
	Sphaeramia nematoptera	No	Pl	No	N	80	P	Mo	No	1;2;3;26
	Sphaeramia orbicularis	No	Pl	No	N	115	P	Mo	No	2;3;4
	Zoramia fragilis	Yes	Mi	No	N	55	P	Mo	No	1;2;3;18
	Zoramia gilberti	No	N/A	No	D	55	P	Mo	No	2;4
	Zoramia leptacanthus	No	N/A	No	N	60	P	Mo	No	2;3;4
	Zoramia perlita	No	N/A	No	N	55	P	Mo	No	2;4
Aulostomidae	*Aulostomus chinensis*	No	Ca	No	D	800	P	Br	No	4
Balistidae	*Abalistes stellatus*	No	N/A	No	D	600	P	Dm	No	1;2;3
	Balistapus undulatus	No	Om	No	D	300	P	Dm	No	1;2;3
	Balistes polylepis	No	Ma	No	D	760	G	Dm	No	4
	Balistoides conspicillum	No	Ma	No	D	500	G	Dm	No	4
	Balistoides viridescens	No	Ma	No	D	750	G	Dm	No	1;2;3
	Canthidermis maculata	No	Pl	No	D	300	P	Dm	No	12
	Melichthys indicus	No	Om	No	D	240	P	Dm	No	4
	Melichthys niger	No	Om	No	D	350	P	Dm	No	1;2;3
	Melichthys vidua	No	Om	No	D	300	P	Dm	No	1;2;3
	Odonus niger	No	Pl	No	D	400	P	Dm	No	1;2;3
	Pseudobalistes flavimarginatus	No	Ma	No	D	600	G	Dm	No	4
	Pseudobalistes fuscus	No	Ma	No	D	550	G	Dm	Yes	1;2;3
	Rhinecanthus aculeatus	No	Om	No	D	250	P	Dm	No	27
	Rhinecanthus lunula	No	Om	No	D	280	P	Dm	No	1;2;3
	Rhinecanthus rectangulus	No	Om	No	D	250	P	Dm	No	4
	Rhinecanthus verrucosus	No	Om	No	D	230	P	Dm	No	28
	Sufflamen bursa	No	Om	No	D	240	P	Dm	No	4
	Sufflamen chrysopterum	No	Ma	No	D	220	P	Dm	Yes	4
	Sufflamen fraenatum	No	Om	No	D	380	P	Dm	No	4
	Xanthichthys auromarginatus	No	Pl	No	D	220	P	Dm	No	12
	Xanthichthys caeruleolineatus	No	Pl	No	D	350	P	Dm	No	12
	Xanthichthys mento	No	Pl	No	D	220	P	Dm	No	12
Batrachoididae	*Halophyrne diemensis*	No	Ca	No	D	260	N/A	N/A	No	1;2;3;4
Belonidae	*Platybelone argalus*	No	Pi	No	D	370	N/A	Es	No	1;2;3
	Strongylura incisa	No	Pi	No	D	700	N/A	Es	No	1;2;3
	Tylosurus acus	No	Pi	No	D	1000	N/A	Es	No	3
	Tylosurus crocodilus	No	Pi	No	D	1500	N/A	Es	No	1;2;4
Blenniidae	*Andamia tetradactylus*	N/A	N/A	No	D	65	P	Dm	No	2
	Aspidontus dussumieri	No	Om	No	D	120	P	Dm	No	3
	Aspidontus taeniatus	No	Ca	No	D	115	P	Dm	No	1;2;3;4
	Atrosalarias fuscus	No	De	No	D	145	P	Dm	No	1;2;3;29
	Blenniella caudolineata	N/A	N/A	No	D	100	P	Dm	No	3
	Blenniella chrysospilos	No	Om	No	D	140	P	Dm	No	1;2;3;4
	Blenniella gibbifrons	No	N/A	No	D	100	P	Dm	No	2;3
	Blenniella interrupta	No	N/A	No	D	80	P	Dm	No	2

Blenniella paula	No	Om	No	D	130	P	Dm	No	1;2;3;4
Cirripectes auritus	No	Om	No	D	90	P	Dm	No	2;3
Cirripectes chelomatus	No	De	No	D	120	P	Dm	No	1;2;3;29
Cirripectes filamentosus	No	De	No	D	90	P	Dm	No	1;2;3
Cirripectes polyzona	No	De	No	D	85	P	Dm	No	1;2;3;4
Cirripectes springeri	No	Om	No	D	80	P	Dm	No	2
Cirripectes stigmaticus	No	De	No	D	130	P	Dm	No	2
Cirripectes variolosus	No	De	No	D	80	P	Dm	No	2
Cirripectus castaneus	Yes	Om	No	D	125	P	Dm	No	1;2;3;4
Crossosalarias macrospilus	No	N/A	No	D	85	P	Dm	No	1;2;3
Ecsenius alleni	No	De	No	D	85	P	Dm	No	2
Ecsenius australianus	No	De	No	D	50	P	Dm	No	1;2
Ecsenius axelrodi	No	De	No	D	50	P	Dm	No	2
Ecsenius bathi	No	De	No	D	40	P	Dm	No	2
Ecsenius bicolor	No	De	No	D	100	P	Dm	No	1;2;3;29
Ecsenius bimaculatus	No	De	No	D	50	P	Dm	No	2;3
Ecsenius caeruliventris	No	De	No	D	30	P	Dm	No	2
Ecsenius collettei	No	De	No	D	40	P	Dm	No	2
Ecsenius dilemma	No	De	No	D	50	P	Dm	No	2
Ecsenius fijiensis	No	De	No	D	40	P	Dm	No	2;3
Ecsenius fourmanoiri	N/A	De	No	D	62	P	Dm	No	3
Ecsenius isos	N/A	De	No	D	40	P	Dm	No	3
Ecsenius kurti	No	De	No	D	45	P	Dm	No	2
Ecsenius lineatus	No	De	No	D	70	P	Dm	No	2;30
Ecsenius lividanalis	No	De	No	D	50	P	Dm	No	2
Ecsenius lubbocki	Yes	De	No	D	40	P	Dm	No	2
Ecsenius mandibularis	No	De	No	D	72	P	Dm	No	29;4
Ecsenius melarchus	No	De	No	D	60	P	Dm	No	2;3
Ecsenius midas	No	Pl	No	D	130	P	Dm	No	1;2;3;4
Ecsenius monoculus	No	De	No	D	60	P	Dm	No	2
Ecsenius namiyei	No	De	No	D	100	P	Dm	No	2;30
Ecsenius oculus	No	De	No	D	60	P	Dm	No	2
Ecsenius ops	No	De	No	D	55	P	Dm	No	2
Ecsenius pardus	N/A	De	No	D	62	P	Dm	No	3
Ecsenius pictus	Yes	De	No	D	50	P	Dm	No	2
Ecsenius portenoyi	N/A	De	No	D	58	P	Dm	No	3
Ecsenius prooculis	No	De	No	D	50	P	Dm	No	2
Ecsenius schroederi	No	De	No	D	50	P	Dm	No	2
Ecsenius sellifer	No	De	No	D	45	P	Dm	No	2
Ecsenius shirleyae	No	De	No	D	40	P	Dm	No	2
Ecsenius stictus	No	De	No	D	55	P	Dm	No	2;29
Ecsenius stigmatura	No	De	No	D	55	P	Dm	No	2
Ecsenius taeniatus	No	De	No	D	40	P	Dm	No	2
Ecsenius tessera	N/A	De	No	D	40	P	Dm	No	3
Ecsenius tigris	No	De	No	D	40	P	Dm	No	1;2
Ecsenius tricolor	No	De	No	D	50	P	Dm	No	2;3
Ecsenius trilineatus	No	De	No	D	35	P	Dm	No	2;3
Ecsenius yaeyamaensis	No	De	No	D	60	P	Dm	No	2
Enchelyurus ater	N/A	N/A	No	D	53	P	Dm	No	3
Enchelyurus kraussii	N/A	N/A	No	D	50	P	Dm	No	3
Entomacrodus caudofasciatus	N/A	N/A	No	D	66	P	Dm	No	3
Entomacrodus corneliae	N/A	N/A	No	D	50	P	Dm	No	3
Entomacrodus decussatus	N/A	N/A	No	D	190	P	Dm	No	3

Entomacrodus epalzeocheilos	N/A	N/A	No	D	128	P	Dm	No	3
Entomacrodus macrospilus	N/A	N/A	No	D	42	P	Dm	No	3
Entomacrodus randalli	N/A	N/A	No	D	109	P	Dm	No	3
Entomacrodus sealei	N/A	N/A	No	D	109	P	Dm	No	3
Entomacrodus striatus	N/A	N/A	No	D	118	P	Dm	No	3
Entomacrodus thalassinus	N/A	N/A	No	D	60	P	Dm	No	3
Exallias brevis	No	Co	No	D	145	P	Dm	No	1;2;3;31
Glyptoparus delicatulus	Yes	Om	No	D	50	P	Dm	No	1;2;3;29
Istiblennius bellus	No	N/A	No	D	150	P	Dm	No	2
Istiblennius dussumieri	No	N/A	No	D	125	P	Dm	No	2
Istiblennius edentulus	No	He	No	D	170	P	Dm	No	1;2;3;32
Istiblennius lineatus	No	He	No	D	140	P	Dm	No	2
Meiacanthus abditus	No	Pl	No	D	65	P	Dm	No	2
Meiacanthus anema	Yes	N/A	No	D	65	P	Dm	No	2;4
Meiacanthus atrodorsalis	Yes	Mi	No	D	110	P	Dm	No	1;2;3
Meiacanthus bundoon	Yes	Pl	No	D	80	P	Dm	No	2;3
Meiacanthus crinitus	Yes	N/A	No	D	65	P	Dm	No	2
Meiacanthus ditrema	No	Pl	No	D	65	P	Dm	No	1;2;3;4
Meiacanthus geminatus	No	N/A	No	D	65	P	Dm	No	2
Meiacanthus grammistes	Yes	N/A	No	D	100	P	Dm	No	1;2;3
Meiacanthus kamoharai	Yes	Om	No	D	85	P	Dm	No	2;4
Meiacanthus lineatus	Yes	N/A	No	D	95	P	Dm	No	1;2
Meiacanthus oualanensis	No	N/A	No	D	100	P	Dm	No	2
Meiacanthus smithi	Yes	Mi	No	D	80	P	Dm	No	2;4
Meiacanthus urostigma	No	N/A	No	D	55	P	Dm	No	2
Meiacanthus vicinus	Yes	N/A	No	D	65	P	Dm	No	2
Meiacanthus vittatus	No	N/A	No	D	65	P	Dm	No	2
Omobranchus elongatus	No	N/A	No	D	55	P	Dm	No	2
Omobranchus germaini	No	Om	No	D	78	P	Dm	No	3
Omobranchus obliquus	No	N/A	No	D	70	P	Dm	No	2
Paralticus amboinensis	No	N/A	No	D	150	P	Dm	No	2
Petroscirtes breviceps	Yes	Om	No	D	130	P	Dm	No	1;2;33
Petroscirtes fallax	Yes	Om	No	D	95	P	Dm	No	1;2
Petroscirtes lupus	No	He	No	D	130	P	Dm	No	3;34
Petroscirtes mitratus	No	Om	No	D	150	P	Dm	No	1;2;3;26
Petroscirtes variabilis	No	Om	No	D	75	P	Dm	No	1;2;3;26
Petroscirtes xestus	No	N/A	No	D	95	P	Dm	No	2
Plagiotremus flavus	No	Ca	No	D	70	P	Dm	No	2
Plagiotremus laudandus	No	Ca	No	D	130	P	Dm	No	1;2;3;4
Plagiotremus rhinorhynchos	No	Ca	No	D	130	P	Dm	No	1;2;3;4
Plagiotremus tapeinosoma	No	Ca	No	D	130	P	Dm	No	1;2;3;4
Salarias alboguttatus	No	N/A	No	D	65	P	Dm	No	1;2;3
Salarias ceramensis	No	He	No	D	140	P	Dm	No	2;34
Salarias fasciatus	No	De	No	D	140	P	Dm	No	1;2;3;29
Salarias guttatus	No	De	No	D	140	P	Dm	No	2;29
Salarias nigrocinctus	No	De	No	D	53	P	Dm	No	3
Salarias obscurus	No	De	No	D	130	P	Dm	No	2
Salarias patzneri	No	De	No	D	50	P	Dm	No	2;29
Salarias ramosus	No	De	No	D	50	P	Dm	No	2
Salarias segmentatus	No	He	No	D	75	P	Dm	No	2;4
Salarias sinuosus	No	De	No	D	60	P	Dm	No	1;2;3
Stanulus seychellensis	Yes	N/A	No	D	33	P	Dm	No	2
Stanulus talboti	No	N/A	No	D	48	P	Dm	No	3

	Xiphasia matsubarai	No	Ca	No	N	300	P	Dm	No	3;4
	Xiphasia setifer	No	Ca	No	N	530	P	Dm	No	2;3;4
Bothidae	*Asterorhombus fijiensis*	No	Ca	No	D	150	P	Br	No	2
	Asterorhombus filifer	No	Ca	No	D	130	P	Br	No	3
	Asterorhombus intermedius	No	Ca	No	D	160	P	Br	No	4
	Bothus mancus	No	Pi	No	N	420	P	Br	No	1;2;3;4
	Bothus pantherinus	No	Ca	No	D	390	P	Br	No	4
	Engyprosopon grandisquama	No	Ma	No	D	110	P	Br	No	4
Caesionidae	*Caesio caerulaurea*	No	Pl	No	D	400	G	Br	No	2;4
	Caesio cuning	No	Pl	No	D	500	G	Br	No	1;2;3;35;12
	Caesio lunaris	No	Pl	No	D	400	G	Br	No	2;4
	Caesio teres	No	Pl	No	D	400	G	Br	No	1;2;3;12
	Caesio varilineata	No	Pl	No	D	400	G	Br	No	2;4
	Caesio xanthonota	No	Pl	No	D	400	G	Br	No	2;4
	Dipterygonotus balteatus	No	Pl	No	D	140	G	Br	No	2;3;4
	Gymnocaesio gymnoptera	No	Pl	No	D	180	G	Br	No	2;3;4
	Pterocaesio chrysozona	No	Pl	No	D	210	G	Br	No	2;4
	Pterocaesio digramma	No	Pl	No	D	210	G	Br	No	2;3;35
	Pterocaesio lativittata	No	Pl	No	D	200	G	Br	No	2;4
	Pterocaesio marri	No	Pl	No	D	350	G	Br	No	1;2;3;12
	Pterocaesio pisang	No	Pl	No	D	210	G	Br	No	2;3;4
	Pterocaesio randalli	No	Pl	No	D	250	G	Br	No	2;4
	Pterocaesio tessellata	No	Pl	No	D	250	G	Br	No	2;4
	Pterocaesio tile	No	Pl	No	D	250	G	Br	No	1;2;3;12
	Pterocaesio trilineata	No	Pl	No	D	200	G	Br	No	1;2;3;12
Callionymidae	*Anaora tentaculata*	No	Mi	No	D	45	P	Br	No	2;26
	Calionymus enneactis	Yes	Mi	No	D	45	P	Br	No	2;12
	Callionymus filamentosus	No	Mi	No	D	165	P	Br	No	3;4
	Callionymus keeleyi	No	Mi	No	D	60	P	Br	No	2;12
	Callionymus marquesensis	No	Mi	No	D	55	P	Br	No	3
	Callionymus simplicicornis	No	Mi	No	D	60	P	Br	No	3
	Callionymus superbus	Yes	Mi	No	D	150	P	Br	No	2;12
	Dactylopus dactylopus	Yes	Mi	No	D	150	P	Br	No	2;24
	Dactylopus kuiteri	Yes	Mi	No	D	150	P	Br	No	2
	Diplogrammus goramensis	No	Mi	No	D	80	P	Br	No	1;2;4
	Diplogrammus xenicus	Yes	Mi	No	D	70	P	Br	No	2;36
	Synchiropus bartelsi	Yes	Mi	No	D	45	P	Br	No	2
	Synchiropus morrisoni	Yes	Mi	No	D	45	P	Br	No	1;2;3;4
	Synchiropus moyeri	No	Pl	No	D	75	P	Br	No	2;12
	Synchiropus ocellatus	No	Mi	No	D	70	P	Br	No	1;2;3;12
	Synchiropus picturatus	No	Mi	No	D	60	P	Br	No	2;4
	Synchiropus splendidus	No	Mi	No	D	60	P	Br	No	1;2;3;4
	Synchiropus stellatus	No	Mi	No	D	60	P	Br	No	2;12
Caracanthidae	*Caracanthus maculatus*	No	Ma	No	D	50	P	Gel	No	2;12
Carangidae	*Alectis ciliaris*	No	Ca	No	D	1300	G	Br	No	1;2;3
	Carangoides bajad	No	Ca	No	D	610	G	Br	No	2;37
	Carangoides chrysophrys	No	Pi	No	D	600	G	Br	No	38;4
	Carangoides coeruleopinnatus	No	N/A	No	D	400	G	Br	No	1;3
	Carangoides dinema	No	N/A	No	D	580	G	Br	No	3
	Carangoides equula	No	N/A	No	D	370	G	Br	No	3
	Carangoides ferdau	No	Ca	No	D	700	G	Br	No	1;2;3
	Carangoides fulvoguttatus	No	Pi	No	D	1300	G	Br	No	1;2;3;39
	Carangoides gymnostethus	No	Ca	No	D	900	G	Br	No	1;2;3;4

	Carangoides hedlandensis	No	Pi	No	D	320	G	Br	No	1;3
	Carangoides humerosus	No	Ca	No	D	250	G	Br	No	1;38
	Carangoides malabricus	No	Ca	No	D	280	G	Br	No	1;38
	Carangoides oblongus	No	Ca	No	D	460	G	Br	No	2;3;40
	Carangoides orthogrammus	No	Ca	No	D	700	G	Br	No	2;3;41
	Carangoides plagiotaenia	No	N/A	No	D	420	G	Br	No	2;3
	Carangoides talamparoides	No	Pi	No	D	320	G	Br	No	1;38
	Caranx bucculentus	No	Ca	No	D	660	G	Br	No	42;3
	Caranx ignobilis	No	Ca	No	D	1650	G	Br	No	1;2;3;43
	Caranx lugubris	No	Pi	No	N	740	G	Br	No	2;4
	Caranx melampygus	No	Pi	No	D	1000	G	Br	No	44;1;2;3;41
	Caranx papuensis	No	Pi	No	D	800	G	Br	No	45;1;2;3
	Caranx sexfasciatus	No	Ca	No	N	1000	G	Br	No	2;3
	Caranx tille	No	Ca	No	D	690	G	Br	No	3;4
	Decapterus kurroides	No	Pl	No	D	500	G	Br	No	1;4
	Decapterus macarellus	No	Pl	No	D	350	G	Br	No	1;2;3;4
	Decapterus macrosoma	No	Pl	No	D	320	G	Br	No	3;4
	Decapterus muroadsi	No	Pl	No	D	450	G	Br	No	3
	Decapterus russelli	No	Pl	No	D	380	G	Br	No	1;4
	Decapterus tabl	No	Pl	No	D	500	G	Br	No	1;4
	Elagatis bipinnulatus	No	Ca	No	D	1200	G	Br	No	1;2;4
	Gnathodon speciosus	No	Ca	No	D	1400	G	Br	No	1;2;3
	Megalaspis cordyla	No	Ca	No	D	800	G	Br	No	3;46
	Naucrates ductor	No	Ca	No	D	750	G	Br	No	2;4
	Pseudocaranx dentex	No	Ca	No	D	940	G	Br	No	1;2;3
	Scomberoides commersonnianus	No	Pi	No	D	1200	G	Br	No	1;2;3;39
	Scomberoides lysan	No	Ca	No	D	700	G	Br	No	1;2;3;4
	Scomberoides tol	No	Ca	No	D	510	G	Br	No	1;3;4
	Selar boops	No	Ca	No	N	220	G	Br	No	1;2;3;4
	Selar crumenophthalmus	No	Ca	No	N	300	G	Br	No	1;2;3;4
	Selaroides leptolepis	No	Ca	No	D	220	G	Br	No	2;47
	Seriola dumerili	No	Pi	No	D	1880	G	Br	No	1;2;3
	Seriola lalandi	No	Ca	No	D	1930	G	Br	No	1;2;3
	Seriola rivoliana	No	Pi	No	D	900	G	Br	No	1;2;3;48
	Trachinotus baillonii	No	Pi	No	D	540	G	Br	No	1;2;3;4
	Trachinotus blochii	No	Ma	No	D	650	G	Br	No	1;2;3;4
	Trachinotus botla	No	Ma	No	D	610	G	Br	No	1;4
	Uraspis helvola	No	N/A	No	N	500	G	Br	No	2;4
Centriscidae	*Aeoliscus strigatus*	No	Pl	No	D	150	N/A	N/A	No	4
	Centriscus scutatus	No	Pl	No	D	140	N/A	N/A	No	4
Chaetodontidae	*Amphichaetodon howensis*	No	Ma	No	D	180	P	Br	No	2;4
	Chaetodon adiergastos	Yes	N/A	No	D	160	P	Br	No	2
	Chaetodon andamanensis	Yes	Co	No	D	150	P	Br	No	49;1;2;3
	Chaetodon argentatus	Yes	Om	No	D	200	P	Br	Yes	49;2
	Chaetodon assarius	No	Pl	No	D	130	P	Br	No	2;49
	Chaetodon aureofasciatus	Yes	Co	No	D	125	P	Br	Yes	49;2;50
	Chaetodon auriga	Yes	Om	No	D	230	G	Br	Yes	51;49
	Chaetodon auripes	Yes	Om	No	D	200	P	Br	Yes	52;2
	Chaetodon baronessa	Yes	Co	No	D	150	P	Br	Yes	1;2;49
	Chaetodon bennetti	Yes	Co	No	D	180	P	Br	No	52;1;2
	Chaetodon burgessi	Yes	N/A	No	D	140	P	Br	No	2
	Chaetodon citrinellus	Yes	Om	No	D	130	P	Br	Yes	52;2;3
	Chaetodon collare	Yes	Om	No	D	160	P	Br	Yes	53;2

Chaetodon daedalma	No	Om	No	D	150	P	Br	No	52;2
Chaetodon declivis	No	N/A	No	D	150	P	Br	No	4
Chaetodon decussatus	Yes	Om	No	D	200	P	Br	No	2
Chaetodon ephippium	Yes	Om	No	D	230	G	Br	Yes	49;1;2;3
Chaetodon falcula	Yes	Mi	No	D	200	P	Br	Yes	2;4
Chaetodon flavirostris	Yes	Om	No	D	200	P	Br	Yes	49;2
Chaetodon flavocoronatus	Yes	N/A	No	D	120	P	Br	No	2
Chaetodon guentheri	No	N/A	No	D	130	P	Br	No	2;4
Chaetodon guttatissimus	Yes	N/A	No	D	120	P	Br	No	2
Chaetodon interruptus	No	N/A	No	D	200	P	Br	No	2
Chaetodon kleinii	Yes	Om	No	D	140	G	Br	Yes	49;1;2;3
Chaetodon lineolatus	Yes	Om	No	D	300	G	Br	Yes	49;1;2;3
Chaetodon litus	No	N/A	No	D	150	P	Br	No	2;
Chaetodon lunula	Yes	Om	No	D	210	G	Br	Yes	49;1;2;3
Chaetodon lunulatus	Yes	Co	No	D	150	P	Br	Yes	49;1;2;3
Chaetodon melannotus	Yes	Co	No	D	150	G	Br	Yes	2;50;54
Chaetodon mertensii	Yes	Om	No	D	125	P	Br	No	1;2
Chaetodon meyeri	Yes	Co	No	D	180	P	Br	Yes	2;3
Chaetodon modestus	No	N/A	No	D	170	P	Br	No	4
Chaetodon nippon	Yes	Om	No	D	150	P	Br	No	52;2
Chaetodon ocellicaudus	Yes	Co	No	D	140	P	Br	No	2;4
Chaetodon octofasciatus	Yes	Co	No	D	120	P	Br	Yes	4
Chaetodon ornatissimus	Yes	Co	No	D	180	P	Br	Yes	49;2
Chaetodon oxycephalus	Yes	Co	No	D	250	P	Br	No	1;2
Chaetodon pelewensis	Yes	Mi	No	D	125	P	Br	Yes	49;1;2;3
Chaetodon plebeius	Yes	Co	No	D	150	P	Br	Yes	49;1;2;3
Chaetodon punctofasciatus	Yes	Om	No	D	120	P	Br	Yes	49;1;2;3
Chaetodon quadrimaculatus	Yes	Om	No	D	160	P	Br	Yes	49;2
Chaetodon rafflesi	Yes	Mi	No	D	150	G	Br	No	2;55;3
Chaetodon rainfordi	Yes	Om	No	D	150	P	Br	Yes	49;1;2;55
Chaetodon reticulatus	Yes	Om	No	D	160	P	Br	Yes	2;3
Chaetodon selene	Yes	Mi	No	D	160	P	Br	No	2;4
Chaetodon semeion	Yes	Mi	No	D	240	G	Br	No	2;55
Chaetodon smithi	No	Pl	No	D	170	P	Br	No	53;2
Chaetodon speculum	Yes	Om	No	D	180	P	Br	Yes	49;2;3
Chaetodon tinkeri	Yes	Om	No	D	150	P	Br	No	53;2
Chaetodon triangulum	Yes	Co	No	D	150	P	Br	Yes	51;2
Chaetodon trichrous	Yes	Om	No	D	120	P	Br	Yes	2;56
Chaetodon tricinctus	Yes	N/A	No	D	150	P	Br	Yes	2
Chaetodon trifascialis	No	Co	No	D	180	P	Br	No	51;57
Chaetodon ulietensis	Yes	Om	No	D	150	P	Br	Yes	49;2;3
Chaetodon unimaculatus	Yes	Om	No	D	200	P	Br	Yes	49;1;2;3
Chaetodon vagabundus	Yes	Om	No	D	230	P	Br	Yes	51;2;54
Chaetodon wiebeli	Yes	He	No	D	180	P	Br	Yes	2;4
Chaetodon xanthurus	Yes	Om	No	D	140	P	Br	Yes	2;3
Chelmon marginalis	Yes	Mi	No	D	180	P	Br	No	58;2
Chelmon muelleri	Yes	Mi	No	D	180	P	Br	No	1;58;2
Chelmon rostratus	Yes	Mi	No	D	200	P	Br	Yes	49;58;2
Coradion altivelis	No	N/A	No	D	200	P	Br	No	2;4
Coradion chrysozonus	Yes	Sp	No	D	150	P	Br	No	2;4
Coradion melanopus	Yes	Sp	No	D	150	P	Br	No	2;4
Forcipiger flavissimus	Yes	Mi	No	D	220	P	Br	Yes	1;2;3
Forcipiger longirostris	Yes	Mi	No	D	220	P	Br	Yes	49;1;2;3

	Hemitaurichthys multispinosus	No	Pl	No	D	208	P	Br	No	3;4
	Hemitaurichthys polylepis	Yes	Pl	No	D	180	P	Br	No	49;1;2;3
	Hemitaurichthys thompsoni	Yes	Pl	No	D	180	P	Br	No	49;1;2;3
	Hemitaurichthys zoster	Yes	Pl	No	D	160	P	Br	No	49;1;2;3
	Heniochus acuminatus	Yes	Om	No	D	250	G	Br	No	49;1;2;3
	Heniochus chrysostomus	Yes	Co	No	D	180	G	Br	No	1;2;3
	Heniochus diphreutis	No	Pl	No	D	210	G	Br	No	1;2;3
	Heniochus monocerus	Yes	Om	No	D	230	G	Br	No	1;2;3;4
	Heniochus pleurotaenia	Yes	N/A	No	D	170	G	Br	No	2
	Heniochus singularius	Yes	Om	No	D	230	G	Br	No	1;2;3
	Heniochus varius	Yes	Mi	No	D	190	G	Br	No	2;3
	Parachaetodon ocellatus	Yes	Mi	No	D	180	P	Br	No	1;2;59
Chanidae	*Chanos chanos*	No	Om	No	D	1800	G	Br	No	1;2;3;4
Cirrhitidae	*Amblycirrhitus bimacula*	Yes	Ma	No	D	85	P	Br	No	1;2;3;60;12
	Amblycirrhitus unimacula	N/A	N/A	No	D	110	P	Br	No	3
	Cirrhitichthys aprinus	No	Ca	No	D	100	P	Br	No	1;2;3;61
	Cirrhitichthys aureus	No	Ca	No	D	150	P	Br	No	1;2;3
	Cirrhitichthys falco	Yes	Mi	No	D	70	P	Br	No	1;2;3;60;12
	Cirrhitichthys oxycephalus	No	Ca	No	D	95	P	Br	No	1;2;3;60;4
	Cirrhitichthys splendens	No	Ca	No	D	230	P	Br	No	2
	Cirrhitops hubbardi	N/A	Ca	No	D	75	P	Br	No	3
	Cirrhitus pinnulatus	No	Ca	No	D	280	P	Br	No	1;2;3;4
	Cyprinocirrhites polyactis	No	Pl	No	D	150	P	Br	No	1;2;3
	Isocirrhitus sexfasciatus	N/A	N/A	No	D	75	P	Br	No	3
	Itycirrhitus wilhelmi	N/A	N/A	No	D	75	P	Br	No	3
	Neocirrhitus armatus	Yes	Ma	No	D	90	P	Br	Yes	1;2;3;62
	Oxycirrhites typus	Yes	Mi	No	D	130	P	Br	Yes	1;2;3;62
	Paracirrhites arcatus	No	Ca	No	D	130	P	Br	No	1;2;3;63
	Paracirrhites forsteri	Yes	Ca	No	D	220	P	Br	No	1;2;3;62
	Paracirrhites hemistictus	No	Ma	No	D	280	P	Br	No	1;2;3;62
	Paracirrhites nisus	Yes	Ma	No	D	100	P	Br	No	2;3;4
	Paracirrhites xanthus	No	Ma	No	D	110	P	Br	No	1;2;3;4;12
Congridae	*Ariosoma anagoides*	No	N/A	No	N	400	G	Br	No	1;2;3
	Ariosoma scheelei	No	N/A	No	N	200	G	Br	No	1;2;3
	Conger cinereus	No	Ca	No	N	1300	G	Br	No	4
	Gorgasia maculata	No	Pl	No	D	550	P	Br	No	1;2;3
	Gorgasia preclara	No	Pl	No	D	400	P	Br	No	4
	Heteroconger enigmaticus	No	N/A	No	D	450	G	Br	No	1;2;3
	Heteroconger perissodon	No	N/A	No	D	600	G	Br	No	1;2;3
	Heteroconger polyzona	Yes	N/A	No	D	700	G	Br	No	4
	Heteroconger taylori	No	N/A	No	D	400	G	Br	No	1;2;3
	Poeciloconger fasciatus	No	N/A	No	D	600	G	Br	No	1;2;3
Coryphaenidae	*Coryphaena hippurus*	No	Ca	No	D	1620	G	Br	No	4
Dactylopteridae	*Dactyloptena orientalis*	No	Ca	No	D	380	N/A	Br	No	1;2;3;4
Diodontidae	*Chilomycterus reticularis*	No	Ma	No	D	550	P	Br	No	4;64
	Cyclichthys orbicularis	No	Ma	No	N	150	P	Br	No	4
	Cyclichthys spilostylus	No	Ma	No	N	340	P	Br	No	4
	Diodon holocanthus	No	Ma	No	N	290	P	Br	No	4
	Diodon hystrix	No	Ma	No	N	710	P	Br	No	4
	Diodon liturosus	No	Ma	No	N	500	P	Br	No	4
	Lophodiodon calori	No	Ma	No	N	300	P	Br	No	4
Echeneidae	*Echeneis naucrates*	No	Ca	No	D	1000	N/A	N/A	No	4
Ephippidae	*Platax batavianus*	Yes	Om	No	D	500	G	Br	No	2;4

	Platax boersii	No	Om	No	D	470	G	Br	No	2
	Platax orbicularis	Yes	Om	No	D	280	G	Br	No	2;3
	Platax pinnatus	No	Om	No	D	370	G	Br	No	2;65
	Platax teira	No	Om	No	D	410	G	Br	No	1;2;3;66
	Zabidius novemaculeatus	No	N/A	No	D	450	G	Br	No	2
Fistulariidae	*Fistularia commersonii*	No	Ca	No	D	1500	P	Br	No	4
Gobiesocidae	*Diademichthys lineatus*	No	Mi	No	D	50	P	Dm	No	1;2;3;67
	Lepadichthys crinophilum	Yes	Mi	No	D	30	P	Dm	No	1;2;3
	Lepadichthys lineatus	Yes	Mi	No	D	30	P	Dm	No	1;2;3;4
Gobiidae	*Acentrogobius janthinopterus*	No	N/A	No	D	70	P	Dm	No	2
	Amblyeleotris arcupinna	No	Pl	Yes*	D	85	P	Dm	No	2
	Amblyeleotris aurora	No	Pl	Yes*	D	90	P	Dm	No	2
	Amblyeleotris bellicauda	No	Pl	Yes*	D	70	P	Dm	No	3;12
	Amblyeleotris biguttata	No	Pl	Yes*	D	104	P	Dm	No	3;12
	Amblyeleotris diagonalis	No	Pl	Yes*	D	90	P	Dm	No	2;3
	Amblyeleotris ellipse	No	Pl	Yes*	D	73	P	Dm	No	3;12
	Amblyeleotris fasciata	Yes	Pl	Yes*	D	80	P	Dm	No	1;2;3;4
	Amblyeleotris fontanesii	No	Pl	Yes*	D	170	P	Dm	No	2;3
	Amblyeleotris guttata	No	Pl	Yes*	D	90	P	Dm	No	1;2;3;12
	Amblyeleotris gymnocephala	No	Pl	Yes*	D	100	P	Dm	No	2
	Amblyeleotris katherine	Yes	Pl	Yes*	D	60	P	Dm	No	3;12;4
	Amblyeleotris latifasciata	No	Pl	Yes*	D	100	P	Dm	No	2
	Amblyeleotris marquesas	No	Pl	Yes*	D	85	P	Dm	No	3;12
	Amblyeleotris novaecaledoniae	No	Pl	Yes*	D	100	P	Dm	No	3;12
	Amblyeleotris ogasawarensis	No	Pl	Yes*	D	110	P	Dm	No	3;12
	Amblyeleotris periophthalma	No	Pl	Yes*	D	80	P	Dm	No	1;2;3
	Amblyeleotris randalli	No	Pl	Yes*	D	90	P	Dm	No	2;3
	Amblyeleotris rhyax	No	Pl	Yes*	D	80	P	Dm	No	1;2
	Amblyeleotris rubrimarginata	No	Pl	Yes*	D	90	P	Dm	No	2;3
	Amblyeleotris steinitzi	No	Pl	Yes*	D	80	P	Dm	No	1;2;3;12
	Amblyeleotris stenotaeniata	No	Pl	Yes*	D	95	P	Dm	No	3;12
	Amblyeleotris wheeleri	No	Pl	Yes*	D	80	P	Dm	No	1;2
	Amblyeleotris yanoi	No	Pl	Yes*	D	120	P	Dm	No	2
	Amblygobius buanensis	Yes	Om	No	D	60	P	Dm	No	2;4
	Amblygobius bynoensis	Yes	He	Yes	D	80	P	Dm	No	1;2;3;68
	Amblygobius decussatus	No	Om	No	D	60	P	Dm	No	1;2;3;69
	Amblygobius esakiae	Yes	He	No	D	65	P	Dm	No	2
	Amblygobius nocturnis	Yes	De	Yes	D	50	P	Dm	Yes	1;2;3;70
	Amblygobius phalaena	Yes	He	Yes	D	135	P	Dm	Yes	1;2;3;68
	Amblygobius semicinctus	Yes	Om	Yes	D	140	P	Dm	Yes	2;4
	Amblygobius sphynx	Yes	Mi	No	D	165	P	Dm	No	1;2;3
	Asterropteryx bipunctatus	No	De	Yes	D	40	P	Dm	No	2;71;4
	Asterropteryx ensifera	No	Pl	No	D	35	P	Dm	No	1;2;3;4
	Asterropteryx semipunctatus	No	De	Yes	D	60	P	Dm	No	1;2;3;70
	Asterropteryx spinosa	No	De	No	D	35	P	Dm	No	3;71
	Asterropteryx striata	No	Pl	No	D	35	P	Dm	No	2;72
	Bathygobius coalitus	No	De	No	D	120	P	Dm	No	1;3;71
	Bathygobius cocosensis	Yes	Mi	No	D	50	P	Dm	No	1;2;3;73
	Bathygobius cotticeps	No	De	No	D	110	P	Dm	No	3;71
	Bathygobius cyclopterus	No	De	No	D	70	P	Dm	No	3;71
	Bathygobius fuscus	No	De	No	D	80	P	Dm	No	1;3;70
	Bathygobius laddi	No	De	No	D	50	P	Dm	No	1;3;71
	Bathygobius padangensis	No	De	No	D	50	P	Dm	No	2;71

Bryaninops amplus	N/A	N/A	No	D	50	P	Dm	No	2
Bryaninops dianneae	N/A	N/A	No	D	24	P	Dm	No	3
Bryaninops erythrops	N/A	N/A	No	D	20	P	Dm	No	2
Bryaninops loki	N/A	N/A	No	D	30	P	Dm	No	1;2;3
Bryaninops natans	No	N/A	No	D	25	P	Dm	No	1;2;3
Bryaninops tigris	No	Pl	No	D	55	P	Dm	No	2;4
Bryaninops yongei	Yes	Pl	No	D	35	P	Dm	No	2;74
Callogobius clitellus	No	N/A	No	D	45	P	Dm	No	2
Callogobius hasseltii	No	N/A	No	D	60	P	Dm	No	1;2;3
Callogobius maculipinnis	No	N/A	No	D	90	P	Dm	No	1;3
Callogobius sclateri	No	N/A	No	D	45	P	Dm	No	3
Calumia profunda	No	N/A	No	D	23	P	Dm	No	2
Cristatogobius lophius	No	N/A	Yes*	D	75	P	Dm	No	2;4
Cryptocentrus caeruleopunctatus	No	Mi	Yes*	D	80	P	Dm	No	1;2;75
Cryptocentrus cinctus	Yes	Mi	Yes*	D	70	P	Dm	No	1;2;75
Cryptocentrus cyanotaenia	Yes	Mi	Yes*	D	70	P	Dm	No	1;2;75;4
Cryptocentrus fasciatus	Yes	Mi	Yes*	D	80	P	Dm	No	1;2;3;75;4
Cryptocentrus inexplicatus	No	Mi	Yes*	D	75	P	Dm	No	2;75
Cryptocentrus insignitus	No	Mi	Yes*	D	80	P	Dm	No	1;2;75
Cryptocentrus leptocephalus	No	Mi	Yes*	D	100	P	Dm	No	2;75
Cryptocentrus leucostictus	No	Mi	Yes*	D	90	P	Dm	No	1;2;3;75
Cryptocentrus pavaninoides	No	Mi	Yes*	D	140	P	Dm	No	2;75
Cryptocentrus polyophthalmus	No	Mi	Yes*	D	90	P	Dm	No	2;75
Cryptocentrus strigilliceps	No	Mi	Yes*	D	60	P	Dm	No	2;75
Ctenogobiops aurocingulus	No	N/A	Yes*	D	55	P	Dm	No	2;3
Ctenogobiops crocineus	No	N/A	Yes*	D	50	P	Dm	No	2
Ctenogobiops feroculus	Yes	N/A	Yes*	D	55	P	Dm	No	2;3;4
Ctenogobiops pomastictus	No	N/A	Yes*	D	50	P	Dm	No	1;2;3
Ctenogobiops tangaroai	No	N/A	Yes*	D	50	P	Dm	No	1;2;3
Ctenogobiops tongaensis	No	N/A	Yes*	D	55	P	Dm	No	3
Discordipinna griessingeri	No	N/A	No	D	25	P	Dm	No	1;2;3
Echinogobius hayashi	No	N/A	Yes	D	120	P	Dm	No	2;4
Eviota afelei	No	N/A	No	D	23	P	Dm	No	1;3
Eviota albolineata	No	Mi	No	D	35	P	Dm	No	1;2;3;12
Eviota bifasciata	No	Pl	No	D	30	P	Dm	No	1;2;4
Eviota cometa	No	N/A	No	D	24	P	Dm	No	3
Eviota distigma	No	N/A	No	D	27	P	Dm	No	3
Eviota fasciola	No	N/A	No	D	24	P	Dm	No	3
Eviota guttata	No	Mi	No	D	25	P	Dm	No	1;2;3;12
Eviota infulata	No	N/A	No	D	24	P	Dm	No	3
Eviota lachdeberi	No	N/A	No	D	25	P	Dm	No	2
Eviota latifasciata	No	N/A	No	D	20	P	Dm	No	1;2;3
Eviota melasma	No	N/A	No	D	32	P	Dm	No	1;2;3
Eviota mikiae	No	N/A	No	D	25	P	Dm	No	2
Eviota monostigma	No	N/A	No	D	33	P	Dm	No	3
Eviota nebulosa	No	N/A	No	D	24	P	Dm	No	3
Eviota nigriventris	No	N/A	No	D	25	P	Dm	No	1;2;3
Eviota pellucida	No	N/A	No	D	25	P	Dm	No	1;2;3
Eviota prasina	No	N/A	No	D	30	P	Dm	No	1;2
Eviota prasites	No	Mi	No	D	25	P	Dm	No	1;2;3;12
Eviota punctulata	No	N/A	No	D	20	P	Dm	No	1;2;3
Eviota queenslandica	No	Om	No	D	30	P	Dm	No	1;2;70
Eviota sebreei	No	N/A	No	D	25	P	Dm	No	1;2;3

Eviota sigillata	No	N/A	No	D	25	P	Dm	No	1;2
Eviota smaragdus	No	N/A	No	D	24	P	Dm	No	2;3
Eviota storthynx	No	N/A	No	D	25	P	Dm	No	2
Eviota zebrina	No	Om	No	D	24	P	Dm	No	1;3;69
Exyrias bellissimus	No	Om	No	D	130	P	Dm	No	1;2;3
Exyrias ferrarisi	Yes	N/A	No	D	95	P	Dm	No	2
Exyrias puntang	No	Om	No	D	135	P	Dm	No	1;2;3;15
Favonigobius reichei	No	Ma	No	D	45	P	Dm	No	2;15
Fusigobius aureus	No	N/A	No	D	75	P	Dm	No	2
Fusigobius duospilus	No	Ma	No	D	55	P	Dm	No	1;2;3;12
Fusigobius inframaculatus	No	N/A	No	D	75	P	Dm	No	2
Fusigobius neophytus	No	Ma	No	D	70	P	Dm	No	1;2;3;12
Fusigobius signipinnis	No	N/A	No	D	30	P	Dm	No	2
Gnatholepis anjerensis	No	N/A	No	D	55	P	Dm	No	1;2;3
Gnatholepis cauerensis	No	N/A	No	D	45	P	Dm	No	1;2;3
Gobiodon acicularis	No	Om	No	D	38	P	Dm	No	2;71
Gobiodon axillaris	N/A	N/A	No	D	40	P	Dm	No	3
Gobiodon brochus	Yes	Om	No	D	34	P	Dm	No	1;3;76
Gobiodon ceramensis	Yes	N/A	No	D	35	P	Dm	No	2
Gobiodon citrinus	No	Co	No	D	55	P	Dm	No	1;2;3;77
Gobiodon histrio	No	Om	No	D	35	P	Dm	No	1;3;76
Gobiodon okinawae	No	Om	No	D	35	P	Dm	No	1;2;3;76
Gobiodon quinquestrigatus	Yes	Om	No	D	35	P	Dm	Yes	1;2;3;76
Gobiodon spilophthalmus	No	N/A	No	D	35	P	Dm	No	2
Gobiopsis exigua	No	N/A	No	D	50	P	Dm	No	2
Heteroplopomus barbatus	No	N/A	No	D	25	P	Dm	No	2
Istigobius decoratus	No	De	No	D	90	P	Dm	No	1;2;3;70
Istigobius goldmanni	No	De	No	D	62	P	Dm	No	3;70
Istigobius ornatus	No	Mi	No	D	90	P	Dm	No	1;2;3;4
Istigobius rigilius	No	Om	No	D	90	P	Dm	No	1;2;3;69
Koumansetta hectori	No	Om	No	D	50	P	Dm	No	2;78
Koumansetta rainfordi	No	He	No	D	55	P	Dm	No	1;2;3;70
Lotilia graciliosa	No	N/A	Yes*	D	45	P	Dm	No	1;2;3
Luposicya lupus	No	N/A	No	D	35	P	Dm	No	2
Macrodontogobius wilburi	No	Om	No	D	65	P	Dm	No	1;2;3;26
Mahidolia mystacina	No	Mi	Yes*	D	70	P	Dm	No	1;2;3;79
Myersina lachneri	No	N/A	Yes*	D	50	P	Dm	No	2
Myersina nigrivirgata	No	N/A	Yes*	D	100	P	Dm	No	2
Oplopomus caninoides	No	N/A	No	D	60	P	Dm	No	2
Oplopomus oplopomus	Yes	Mi	No	D	75	P	Dm	No	1;2;3;80
Oxyurichthys notonema	N/A	N/A	Yes	D	160	P	Dm	No	3
Oxyurichthys papuensis	No	N/A	Yes	D	200	P	Dm	No	1;2;3
Pandaka pusilila	No	N/A	No	D	12	P	Dm	No	2
Paragobiodon echinocephalus	No	N/A	No	D	35	P	Dm	Yes	1;2;3
Paragobiodon lacunicolus	No	N/A	No	D	35	P	Dm	No	1;2;3
Paragobiodon modestus	No	N/A	No	D	35	P	Dm	No	1;2;3
Paragobiodon xanthosomus	No	N/A	No	D	40	P	Dm	Yes	1;2;3
Phyllogobius platycephalops	No	N/A	No	D	25	P	Dm	No	2
Pleurosicya bilobata	No	Mi	No	D	28	P	Dm	No	3;4
Pleurosicya boldinghi	Yes	N/A	No	D	35	P	Dm	No	2
Pleurosicya coerulea	N/A	N/A	No	D	22	P	Dm	No	3
Pleurosicya elongata	N/A	N/A	No	D	35	P	Dm	No	2
Pleurosicya fringilla	N/A	N/A	No	D	22	P	Dm	No	3

Pleurosicya labiata	No	N/A	No	D	35	P	Dm	No	2
Pleurosicya micheli	No	N/A	No	D	25	P	Dm	No	2;3
Pleurosicya mossambica	No	N/A	No	D	35	P	Dm	No	1;2;3
Priolepis aureoviridis	No	N/A	No	D	65	P	Dm	No	2;
Priolepis cincta	No	N/A	No	D	50	P	Dm	Yes	1;2;3
Priolepis compita	No	Mi	No	D	17	P	Dm	No	3
Priolepis fallacincta	N/A	N/A	No	D	32	P	Dm	No	3
Priolepis inhaca	No	N/A	No	D	35	P	Dm	No	1;2;3
Priolepis kappa	N/A	N/A	No	D	26	P	Dm	No	3
Priolepis nocturna	No	N/A	No	D	35	P	Dm	No	1;2;3;
Priolepis nuchifasciata	Yes	Mi	No	D	40	P	Dm	No	1;70
Priolepis pallidicincta	N/A	N/A	No	D	36	P	Dm	No	3
Priolepis semidoliata	N/A	N/A	No	D	36	P	Dm	No	3
Priolepis squamogena	N/A	N/A	No	D	54	P	Dm	No	3
Priolepis triops	N/A	N/A	No	D	26	P	Dm	No	3
Signigobius biocellatus	Yes	Mi	Yes	D	65	P	Dm	Yes	1;2;4
Stonogobiops larsonae	No	N/A	Yes*	D	60	P	Dm	No	2
Stonogobiops medon	No	N/A	Yes*	D	60	P	Dm	No	2
Stonogobiops nematodes	Yes	N/A	Yes*	D	60	P	Dm	No	1;2 4
Stonogobiops xanthorhinica	Yes	N/A	Yes*	D	60	P	Dm	No	1;2;3 4
Stonogobiops yasha	Yes	N/A	Yes*	D	60	P	Dm	No	1;2;3;4
Tomiyamichthys lanceolata	No	N/A	Yes*	D	50	P	Dm	No	2;4
Tomiyamichthys oni	No	N/A	Yes*	D	100	P	Dm	No	2
Trimma anaima	No	N/A	No	D	20	P	Dm	No	2
Trimma annosum	No	N/A	No	D	25	P	Dm	No	2
Trimma benjamini	No	Pl	No	D	25	P	Dm	No	1;2;3;4
Trimma caesiura	No	Om	No	D	25	P	Dm	No	1;2;3;70
Trimma cana	No	N/A	No	D	25	P	Dm	No	2
Trimma emeryi	N/A	N/A	No	D	24	P	Dm	No	3
Trimma griffithsi	No	Pl	No	D	23	P	Dm	No	2;81
Trimma halonevum	No	N/A	No	D	28	P	Dm	No	2
Trimma hoesei	Yes	N/A	No	D	25	P	Dm	No	25
Trimma macrophthalma	No	N/A	No	D	25	P	Dm	No	1;2;3
Trimma milta	N/A	N/A	No	D	30	P	Dm	No	3
Trimma naudei	No	Mi	No	D	30	P	Dm	No	2;4
Trimma okinawae	No	N/A	No	D	28	P	Dm	No	1;2;3
Trimma rubromaculatus	No	N/A	No	D	22	P	Dm	No	2
Trimma stobbsi	No	N/A	No	D	20	P	Dm	No	2
Trimma striata	No	Mi	No	D	35	P	Dm	No	1;2;3;70
Trimma taylori	No	Pl	No	D	25	P	Dm	No	1;2;3;82
Trimma tevegae	No	Pl	No	D	40	P	Dm	No	1;2;3;4
Tryssogobius colini	No	N/A	No	D	50	P	Dm	No	2
Valenciennea alleni	Yes	Mi	Yes	D	65	P	Dm	No	2;4
Valenciennea bella	Yes	Mi	Yes	D	90	P	Dm	No	2;4
Valenciennea decora	Yes	Mi	Yes	D	140	P	Dm	No	1;2;3
Valenciennea helsdingenii	Yes	Mi	Yes	D	145	P	Dm	Yes	1;2;3;83
Valenciennea immaculata	Yes	Mi	Yes	D	105	P	Dm	No	1;2;3;4
Valenciennea limicola	Yes	Mi	Yes	D	80	P	Dm	No	2
Valenciennea longipinnis	Yes	Mi	Yes	D	150	P	Dm	Yes	1;2;3;4
Valenciennea muralis	Yes	Mi	Yes	D	115	P	Dm	Yes	1;2;3;50;4
Valenciennea parva	Yes	Mi	Yes	D	65	P	Dm	Yes	1;2;3
Valenciennea puellaris	Yes	Mi	Yes	D	155	P	Dm	Yes	1;2;3;4
Valenciennea randalli	No	Mi	Yes	D	90	P	Dm	No	1;2;3

	Valenciennea sexguttata	Yes	Mi	Yes	D	115	P	Dm	Yes	1;2;3
	Valenciennea strigata	Yes	Mi	Yes	D	155	P	Dm	Yes	1;2;3;84
	Valenciennea wardii	Yes	Mi	Yes	D	100	P	Dm	No	1;2;3
	Vanderhorstia ambanoro	No	N/A	Yes*	D	120	P	Dm	No	2;3
	Vanderhorstia flavilineata	No	N/A	Yes*	D	40	P	Dm	No	2;4
	Vanderhorstia macropteryx	No	N/A	Yes*	D	60	P	Dm	No	2
	Vanderhorstia ornatissima	No	N/A	Yes*	D	60	P	Dm	No	2;4
	Yongeichthys nebulosus	No	Pl	No	D	160	P	Dm	No	2;17
Haemulidae	*Diagramma melanacrum*	No	Ma	No	N	500	G	Br	No	2
	Diagramma pictum	No	Ca	No	N	940	G	Br	No	1;2;3;4
	Plectorhinchus albovittatus	No	Ma	No	N	1000	G	Br	No	1;2;3
	Plectorhinchus chaetodonoides	No	Ca	No	N	720	G	Br	No	1;2;3;4
	Plectorhinchus chrysotaenia	No	Ma	No	N	500	G	Br	No	2;3
	Plectorhinchus flavomaculatus	No	Ca	No	N	600	G	Br	No	1;2;3
	Plectorhinchus gibbosus	No	Ma	No	N	600	G	Br	No	1;2;3
	Plectorhinchus lessonii	No	Ma	No	N	480	G	Br	No	1;2;3
	Plectorhinchus lineatus	No	Ma	No	N	480	G	Br	No	1;2;3;4
	Plectorhinchus multivittatum	No	Ma	No	N	500	G	Br	No	2;3
	Plectorhinchus picus	No	Ma	No	N	850	G	Br	No	1;2;3;4
	Plectorhinchus polytaenia	No	Mi	No	N	400	G	Br	No	2
	Plectorhinchus unicolor	No	Ma	No	N	800	G	Br	No	1;2;3
	Plectorhinchus vittatus	No	Ma	No	N	850	G	Br	No	1;2;3
	Pomadasys argenteus	N/A	N/A	No	D	520	G	Br	No	1
Holocentridae	*Myripristis adusta*	No	Pl	No	N	320	G	Br	No	4
	Myripristis amaena	No	Pl	No	N	320	G	Br	No	4
	Myripristis berndti	No	Pl	No	N	300	G	Br	No	4
	Myripristis botche	Yes	Pl	No	N	300	G	Br	No	4
	Myripristis chryseres	No	Pl	No	N	250	G	Br	No	4
	Myripristis earlei	No	Ma	No	N	300	G	Br	No	12
	Myripristis hexagona	No	Pl	No	N	200	G	Br	No	4
	Myripristis kuntee	No	Pl	No	N	200	G	Br	No	4
	Myripristis murdjan	No	Pl	No	N	270	G	Br	No	4
	Myripristis pralinia	No	Pl	No	N	200	G	Br	No	4
	Myripristis trachyacron	No	Pl	No	N	150	G	Br	No	12
	Myripristis violacea	No	Pl	No	N	200	G	Br	No	4
	Myripristis vittata	No	Pl	No	N	200	G	Br	No	4
	Myripristis woodsi	No	Pl	No	N	210	G	Br	No	4
	Neoniphon argenteus	No	Ma	No	N	190	G	Br	No	4
	Neoniphon aurolineatus	No	Ma	No	N	250	G	Br	No	12
	Neoniphon opercularis	No	Ma	No	N	350	G	Br	No	4
	Neoniphon sammara	No	Ca	No	N	320	G	Br	No	4
	Plectrypops lima	No	Ca	No	N	160	G	Br	No	4
	Sargocentron caudimaculatum	No	Ma	No	N	250	G	Br	No	4
	Sargocentron cornutum	No	Ma	No	N	180	G	Br	No	4
	Sargocentron diadema	No	Ma	No	N	170	G	Br	No	85
	Sargocentron ensiferum	No	Ma	No	N	250	G	Br	No	1;2;3
	Sargocentron iota	No	Ma	No	N	80	G	Br	No	1;2;3
	Sargocentron ittodai	No	Ma	No	N	170	G	Br	No	85
	Sargocentron melanospilos	No	Ma	No	N	250	G	Br	No	4
	Sargocentron microstoma	No	Ma	No	N	190	G	Br	No	3
	Sargocentron punctatissimum	No	Ma	No	N	200	G	Br	No	4
	Sargocentron rubrum	No	Ma	No	N	270	G	Br	No	4
	Sargocentron spiniferum	Yes	Ca	No	N	450	G	Br	No	4

	Sargocentron tiere	No	Ca	No	N	330	G	Br	No	4
	Sargocentron tiereoides	No	Ma	No	N	160	G	Br	No	4
	Sargocentron violaceum	No	Ma	No	N	250	G	Br	No	4
Kyphosidae	*Kyphosus bigibbus*	No	He	No	D	700	G	Br	No	1;2;3;86
	Kyphosus cinerascens	No	He	No	D	450	G	Br	No	1;2;3;86
	Kyphosus cornelii	No	He	No	D	600	G	Br	No	2;3;87
	Kyphosus pacificus	No	He	No	D	650	G	Br	No	3
	Kyphosus sydneyanus	No	He	No	D	600	G	Br	No	3;86
	Kyphosus vaigiensis	No	He	No	D	450	G	Br	No	1;2;3;86
	Sectator ocyurus	No	He	No	D	380	G	Br	No	3;12
Labridae	*Anampses caeruleopunctatus*	Yes	Ma	No	D	420	G	Br	No	1;2;3;4
	Anampses elegans	No	Ma	No	D	300	P	Br	No	2;4
	Anampses femininus	No	Mi	No	D	240	P	Br	No	1;2;3;87
	Anampses geographicus	No	Pl	No	D	200	P	Br	No	1;2;3;4
	Anampses lennardi	Yes	Mi	No	D	280	P	Br	No	2;4
	Anampses lineatus	No	Ma	No	D	120	P	Br	No	2;12
	Anampses melanurus	Yes	Mi	No	D	120	P	Br	No	1;2;3
	Anampses meleagrides	No	Ma	No	D	220	P	Br	No	1;2;3;12
	Anampses neoguinaicus	No	Ma	No	D	170	P	Br	No	2;4
	Anampses twistii	Yes	Ma	No	D	180	P	Br	No	1;2;3;4
	Bodianus anthioides	No	Ma	No	D	210	P	Br	No	1;2;3
	Bodianus axillaris	No	Ma	No	D	200	P	Br	No	1;2;3;88
	Bodianus bilunulatus	No	Ma	No	D	550	P	Br	No	2;3
	Bodianus bimaculatus	No	Ma	No	D	100	P	Br	No	1;2;12
	Bodianus diana	Yes	Ma	No	D	250	P	Br	No	1;2;12
	Bodianus loxozonus	No	Ma	No	D	400	P	Br	No	1;2;3;4
	Bodianus mesothorax	No	Ma	No	D	190	P	Br	No	1;2;3;4;12
	Bodianus neilli	No	Ma	No	D	200	P	Br	No	2;4
	Bodianus opercularis	No	Ma	No	D	150	P	Br	No	2
	Bodianus perditio	No	Ma	No	D	150	P	Br	No	1;2;3
	Bodianus prognathus	No	Ma	No	D	200	P	Br	No	1;2;12
	Bolbometopon muricatum	No	Co	No	D	1260	B	Br	No	1;2;3;89
	Calotomus carolinus	No	He	No	D	500	B	Br	No	1;2;3;4
	Calotomus spinidens	No	He	No	D	190	B	Br	No	1;2;3;4
	Cetoscarus bicolor	No	De	No	D	800	B	Br	No	1;2;3
	Cheilinus chlorourus	No	Ma	No	D	360	P	Br	No	2;90
	Cheilinus fasciatus	No	Ma	No	D	360	P	Br	No	1;2;3;90
	Cheilinus oxycephalus	Yes	Mi	No	D	170	P	Br	No	1;2;3;91
	Cheilinus trilobatus	No	Ma	No	D	450	P	Br	No	1;2;3;90
	Cheilinus undulatus	No	Ca	No	D	2290	G	Br	No	1;2;3
	Cheilio inermis	No	Ca	No	D	500	P	Br	No	1;2;3
	Chlorurus bleekeri	No	De	No	D	480	B	Br	No	1;2;3;92
	Chlorurus bowersi	No	De	No	D	300	B	Br	No	2
	Chlorurus capistratoides	No	De	No	D	550	B	Br	No	2
	Chlorurus frontalis	No	De	No	D	500	B	Br	No	1;2;3
	Chlorurus japanensis	No	De	No	D	300	B	Br	No	2;3
	Chlorurus microrhinos	No	De	No	D	800	B	Br	No	1;2;3;92
	Chlorurus sordidus	No	De	No	D	400	B	Br	No	1;2;3
	Chlorurus strongycephalus	No	De	No	D	700	B	Br	No	2
	Chlorurus troschelii	No	De	No	D	350	B	Br	No	2
	Choerodon anchorago	No	Ma	No	D	380	P	Br	No	1;2;3;26
	Choerodon cephalotes	No	Ma	No	D	380	P	Br	No	1;4
	Choerodon cyanodus	No	Ma	No	D	700	P	Br	No	1;2

Choerodon fasciatus	No	Ma	No	D	300	P	Br	Yes	1;2;3
Choerodon graphicus	No	Ma	No	D	460	P	Br	No	1;2;3;4
Choerodon jordani	No	Ma	No	D	170	P	Br	No	2;3
Choerodon monostigma	No	Ma	No	D	250	P	Br	No	2
Choerodon oligacanthus	Yes	Ma	No	D	350	P	Br	No	2
Choerodon rubescens	No	Ma	No	D	900	P	Br	No	2;39
Choerodon schoenleinii	No	Ma	No	D	900	P	Br	No	1;2
Choerodon vitta	No	Ma	No	D	200	P	Br	No	2
Choerodon zosterophorus	No	Ma	No	D	250	P	Br	No	2
Cirrhilabrus aurantidorsalis	No	Pl	No	D	100	G	Br	No	2;12
Cirrhilabrus bathyphilus	No	Pl	No	D	110	G	Br	No	2;12
Cirrhilabrus condei	No	Pl	No	D	100	G	Br	No	2;12
Cirrhilabrus cyanopleura	No	Pl	No	D	100	G	Br	No	2;4
Cirrhilabrus exquisitus	No	Pl	No	D	120	G	Br	No	1;2;3;12
Cirrhilabrus filamentosus	No	Pl	No	D	120	G	Br	No	2;4
Cirrhilabrus flavidorsalis	No	Pl	No	D	65	G	Br	No	2;12
Cirrhilabrus joanallenae	No	Pl	No	D	60	G	Br	No	2;12
Cirrhilabrus katherinae	No	Pl	No	D	90	G	Br	No	2;12
Cirrhilabrus laboutei	No	Pl	No	D	110	G	Br	No	1;2;3;12
Cirrhilabrus lineatus	No	Pl	No	D	120	G	Br	No	1;2;3;4
Cirrhilabrus lubbocki	No	Pl	No	D	80	G	Br	No	2;12;4
Cirrhilabrus luteovittatus	No	Pl	No	D	120	G	Br	No	2;12
Cirrhilabrus marjorie	No	Pl	No	D	70	G	Br	No	2;12
Cirrhilabrus morrisoni	No	Pl	No	D	80	G	Br	No	2;12
Cirrhilabrus punctatus	No	Ca	No	D	130	G	Br	No	1;2;3;12
Cirrhilabrus randalli	No	Pl	No	D	85	G	Br	No	2;12
Cirrhilabrus rhomboidalis	No	Pl	No	D	85	G	Br	No	2;12
Cirrhilabrus rubripinnis	No	Pl	No	D	80	G	Br	No	2;12
Cirrhilabrus rubrmarginatus	No	Pl	No	D	150	G	Br	No	1;2;3;12
Cirrhilabrus scottorum	No	Pl	No	D	120	G	Br	No	1;2;3;4
Cirrhilabrus solorensis	No	Pl	No	D	120	G	Br	No	2
Cirrhilabrus temminckii	No	Pl	No	D	100	G	Br	No	2;12;4
Cirrhilabrus tonozukai	No	Pl	No	D	70	G	Br	No	2;4;12
Cirrhilabrus walindi	No	Pl	No	D	70	G	Br	No	2;12
Cirrhilabrus walshi	No	Pl	No	D	100	G	Br	No	2;12
Coris auricularis	No	Ma	No	D	400	P	Br	No	2;93
Coris aurilineata	No	Om	No	D	115	P	Br	No	2;4;94
Coris aygula	No	Ma	No	D	400	P	Br	No	1;2;3
Coris batuensis	No	Ma	No	D	170	P	Br	No	2;3;4;12
Coris bulbifrons	No	Ma	No	D	1400	P	Br	No	2;4
Coris caudimacula	No	Ma	No	D	200	P	Br	No	2;3
Coris centralis	No	Ma	No	D	300	P	Br	No	2;3;4;12
Coris dorsomacula	No	Ma	No	D	200	P	Br	No	1;2;3;12
Coris gaimard	No	Ma	No	D	380	P	Br	No	1;2;3
Coris pictoides	No	Ma	No	D	120	P	Br	No	1;2;12
Cymolutes praetextatus	No	Ma	No	D	200	P	Br	No	1;2;3;12
Cymolutes torquatus	No	N/A	No	D	120	P	Br	No	1;2;3
Diprocatacanthus xanthurus	No	Mi	No	D	80	P	Br	No	1;2;12
Epibulus insidiator	No	Ca	No	D	350	P	Br	No	1;2;3
Gomphosus varius	No	Mi	No	D	280	P	Br	No	1;2;3
Halichoeres argus	No	N/A	No	D	110	P	Br	No	1;2
Halichoeres binotopsis	No	N/A	No	D	120	P	Br	No	2;4
Halichoeres biocellatus	No	N/A	No	D	120	P	Br	No	1;2;3

Halichoeres chlorocephalus	No	N/A	No	D	90	P	Br	No	2
Halichoeres chloropterus	No	Ma	No	D	190	P	Br	No	1;2;4
Halichoeres chrysus	No	Mi	No	D	120	P	Br	No	1;2;3;12
Halichoeres cosmetus	No	N/A	No	D	130	P	Br	No	2
Halichoeres hortulanus	No	Ma	No	D	270	P	Br	No	1;2;3;4
Halichoeres leucoxanthus	No	N/A	No	D	110	P	Br	No	2
Halichoeres leucurus	Yes	N/A	No	D	120	P	Br	No	2
Halichoeres margaritaceus	No	Ma	No	D	130	P	Br	No	1;2;3;4
Halichoeres marginatus	No	Ma	No	D	170	P	Br	No	1;2;3
Halichoeres melanochir	Yes	N/A	No	D	100	P	Br	No	2
Halichoeres melanurus	No	Mi	No	D	120	P	Br	No	1;2;3 4
Halichoeres melasmapomus	No	Mi	No	D	140	P	Br	No	1;2;3
Halichoeres nebulosus	No	N/A	No	D	120	P	Br	No	2;3
Halichoeres nigrescens	No	N/A	No	D	140	P	Br	No	2
Halichoeres ornatissimus	No	Mi	No	D	150	P	Br	No	1;2;3;4
Halichoeres pallidus	No	Mi	No	D	80	P	Br	No	1;2;12
Halichoeres papilionaceus	No	N/A	No	D	100	P	Br	No	2
Halichoeres podostigma	No	N/A	No	D	190	P	Br	No	2
Halichoeres prosopeion	No	N/A	No	D	130	P	Br	No	1;2;3
Halichoeres richmondi	No	Mi	No	D	190	P	Br	No	2
Halichoeres rubricephalus	No	N/A	No	D	100	P	Br	No	2
Halichoeres scapularis	No	Mi	No	D	200	P	Br	No	1;2;4
Halichoeres solorensis	No	Ma	No	D	180	P	Br	No	2;4
Halichoeres trimaculatus	No	Ma	No	D	270	P	Br	No	1;2;3 4
Halichoeres trispilus	No	N/A	No	D	90	P	Br	No	2
Halichoeres vrolikii	No	N/A	No	D	130	P	Br	No	2
Halichoeres zeylonicus	No	N/A	No	D	150	P	Br	No	2
Hemigymnus fasciatus	No	Ma	No	D	500	P	Br	No	1;2;3
Hemigymnus melanopterus	No	Ma	No	D	600	P	Br	No	1;2;3
Hipposcarus harid	No	De	No	D	750	B	Br	No	2
Hipposcarus longiceps	No	De	No	D	600	B	Br	No	1;2;3
Hologymnosus annulatus	No	Pi	No	D	400	P	Br	No	1;2;3
Hologymnosus doliatus	No	Ca	No	D	400	P	Br	No	1;2;3
Hologymnosus longipes	No	N/A	No	D	400	P	Br	No	1;3
Hologymnosus rhodonotus	No	N/A	No	D	320	P	Br	No	2
Iniistius aneitensis	No	Ma	No	D	240	P	Br	No	2;3;12
Iniistius celebicus	No	Ma	No	D	250	P	Br	No	2;3;12
Iniistius pavo	No	Ma	No	D	350	P	Br	No	2;3;4
Iniistius pentadactylus	No	Ma	No	D	250	P	Br	No	2;4
Iniistius tetrazona	No	Ma	No	D	250	P	Br	No	2
Labrichthys unilineatus	No	Co	No	D	160	P	Br	No	77
Labroides bicolor	Yes	Mi	No	D	140	P	Br	No	1;2;3;4
Labroides dimidiatus	Yes	Mi	No	D	115	P	Br	Yes	1;2;3;4
Labroides pectoralis	No	Mi	No	D	80	P	Br	No	1;2;3;4
Labroides rubrolabiatus	Yes	Mi	No	D	90	P	Br	No	2;3;12
Labropsis alleni	Yes	Co	No	D	100	P	Br	No	2;4
Labropsis manabei	No	Co	No	D	130	P	Br	No	77
Labropsis micronesica	No	Mi	No	D	130	P	Br	No	2;4;12
Labropsis xanthonota	No	Co	No	D	140	P	Br	No	1;2;3;12
Leptojulis cyanopleura	No	Pl	No	D	130	P	Br	No	2
Leptoscarus vaigiensis	No	He	No	D	350	P	Br	No	1;2;3;4
Macropharyngodon choati	No	Ma	No	D	100	P	Br	No	2
Macropharyngodon kuiteri	No	Ma	No	D	100	P	Br	No	1;2;3

Macropharyngodon meleagris	No	Ma	No	D	150	P	Br	No	1;2;3;4
Macropharyngodon negrosensis	No	Ma	No	D	150	P	Br	No	1;2;3;4
Macropharyngodon ornatus	No	Ma	No	D	120	P	Br	No	2
Novaculichthys macrolepidotus	No	Ma	No	D	150	P	Br	No	2;3
Novaculichthys taeniourus	No	Ma	No	D	270	P	Br	No	1;2;3
Oxycheilinus arenatus	No	Ca	No	D	190	P	Br	No	2;1;4
Oxycheilinus bimaculatus	No	Ca	No	D	150	P	Br	No	2;1;12
Oxycheilinus celebicus	No	N/A	No	D	240	P	Br	No	2;1
Oxycheilinus digrammus	No	Pi	No	D	300	P	Br	No	2;1;12
Oxycheilinus orientalis	No	Ca	No	D	170	P	Br	No	2;4
Oxycheilinus rhodochrous	No	Ca	No	D	200	P	Br	No	2;4
Oxycheilinus sp.	No	Ca	No	D	140	P	Br	No	2;12
Oxycheilinus unifasciatus	No	Ca	No	D	460	P	Br	No	2;1;4
Paracheilinus angulatus	No	Pl	No	D	70	P	Br	No	2
Paracheilinus carpenteri	No	Pl	No	D	80	P	Br	No	2
Paracheilinus filamentosus	No	Pl	No	D	80	P	Br	No	2;4
Paracheilinus flavianalis	No	Pl	No	D	70	P	Br	No	2
Paracheilinus mccoskeri	No	Pl	No	D	70	P	Br	No	2
Paracheilinus rubricaudalis	No	Pl	No	D	80	P	Br	No	2;3
Paracheilinus togeanensis	No	Pl	No	D	80	P	Br	No	2
Pseudocheilinus ataenia	No	Mi	No	D	50	P	Br	No	2;4
Pseudocheilinus evanidus	No	Mi	No	D	80	P	Br	No	1;2;3;4
Pseudocheilinus hexataenia	No	Mi	No	D	75	P	Br	No	1;2;3;4
Pseudocheilinus ocellatus	No	Mi	No	D	85	P	Br	No	2;1
Pseudocheilinus octotaenia	No	Mi	No	D	135	P	Br	No	1;2;3;4
Pseudocheilinus tetrataenia	No	Mi	No	D	75	P	Br	No	2;3;4
Pseudocoris aurantiofasciatus	No	Pl	No	D	200	G	Br	No	2;3
Pseudocoris bleekeri	No	Pl	No	D	150	G	Br	No	2;4
Pseudocoris heteroptera	No	Pl	No	D	200	G	Br	No	2;4
Pseudocoris yamashiroi	No	Pl	No	D	150	G	Br	No	2;3
Pseudodax moluccanus	No	Ma	No	D	250	P	Br	No	1;2;3;12
Pseudojuloides atavai	No	Ma	No	D	130	P	Br	No	2;3;12
Pseudojuloides cerasinus	No	Ma	No	D	120	P	Br	No	1;2;3;12
Pseudojuloides kaleidios	No	N/A	No	D	100	P	Br	No	2
Pseudojuloides severnsi	No	Om	No	D	100	P	Br	No	2;4
Pteragogus cryptus	No	Mi	No	D	95	P	Br	Yes	1;2;3;4
Pteragogus enneacanthus	No	Ma	No	D	120	P	Br	No	2;3;12
Pteragogus flagellifer	No	N/A	No	D	200	P	Br	No	2
Scarus altipinnis	No	De	No	D	600	B	Br	No	1;2;3
Scarus chameleon	No	De	No	D	310	B	Br	No	1;2;3
Scarus dimidiatus	No	De	No	D	300	B	Br	No	1;2;3
Scarus festivus	No	De	No	D	430	B	Br	No	2;3
Scarus flavipectoralis	No	De	No	D	410	B	Br	No	1;2;3
Scarus forsteni	No	De	No	D	550	B	Br	No	1;2;3
Scarus frenatus	No	De	No	D	470	B	Br	No	1;2;3
Scarus ghobban	No	De	No	D	750	B	Br	No	1;2;3
Scarus globiceps	No	De	No	D	270	B	Br	No	1;2;3
Scarus hypselopterus	No	De	No	D	310	B	Br	No	2;3
Scarus koputea	N/A	De	No	D	310	B	Br	No	2;3
Scarus longipinnis	No	De	No	D	400	B	Br	No	1;2;3
Scarus niger	No	De	No	D	350	B	Br	No	1;2;3
Scarus oviceps	No	De	No	D	310	B	Br	No	1;2;3
Scarus prasiognathus	No	De	No	D	700	B	Br	No	2

	Scarus psittacus	No	De	No	D	300	B	Br	No	1;2;3
	Scarus quoyi	No	De	No	D	210	B	Br	No	2
	Scarus rivulatus	No	De	No	D	400	B	Br	No	1;2;3
	Scarus rubroviolaceus	Yes	De	No	D	700	B	Br	No	1;2;3
	Scarus russellii	No	De	No	D	510	B	Br	No	2
	Scarus schlegeli	No	De	No	D	380	B	Br	No	1;2;3
	Scarus spinus	No	De	No	D	300	B	Br	No	1;2;3
	Scarus tricolor	No	De	No	D	550	B	Br	No	1;2;3
	Scarus virdifucatus	No	De	No	D	320	B	Br	No	2
	Scarus xanthopleura	No	De	No	D	550	B	Br	No	2;3
	Stethojulis bandanensis	No	Mi	No	D	160	G	Br	No	1;2;3;4
	Stethojulis interrupta	No	Mi	No	D	130	G	Br	No	2;3;4
	Stethojulis notialis	No	Mi	No	D	100	G	Br	No	2;1
	Stethojulis strigiventer	No	Mi	No	D	140	G	Br	No	1;2;3
	Stethojulis trilineata	No	Mi	No	D	140	G	Br	No	2;3
	Thalassoma amblycephalum	No	Pl	No	D	140	G	Br	No	1;2;3;4
	Thalassoma hardwicke	No	Om	No	D	200	G	Br	No	1;2;3;4
	Thalassoma jansenii	No	N/A	No	D	200	G	Br	No	2;3
	Thalassoma lunare	No	Pi	No	D	250	G	Br	No	1;2;3
	Thalassoma lutescens	No	Ma	No	D	250	G	Br	No	1;2;3;4
	Thalassoma purpureum	No	Ma	No	D	430	G	Br	No	1;2;3;4
	Thalassoma quinquevittatum	No	Ma	No	D	250	G	Br	No	1;2;3;4
	Thalassoma trilobatum	No	Ma	No	D	300	G	Br	No	1;2;3;4
	Wetmorella albofasciata	No	Ma	No	D	60	P	Br	No	1;2;3
	Wetmorella nigropinnata	No	Ma	No	D	80	P	Br	No	1;2;3;4
Lethrinidae	*Gnathodentex aureolineatus*	No	Ma	No	N	300	G	Br	No	2;3;4
	Gymnocranius euanus	No	Ma	No	D	450	G	Br	No	2;3
	Gymnocranius frenatus	No	Ma	No	D	350	G	Br	No	2;4
	Gymnocranius grandoculis	No	Ca	No	D	800	G	Br	No	1;2;3;4
	Gymnocranius griseus	No	Ma	No	D	350	G	Br	No	2;4
	Gymnocranius microdon	No	Ma	No	D	410	G	Br	No	2;4
	Lethrinus amboinensis	No	Ca	No	D	570	G	Br	No	2;4
	Lethrinus atkinsoni	No	Ca	No	D	410	G	Br	No	1;2;3
	Lethrinus erythracanthus	No	Ma	No	D	700	G	Br	No	44;1;2;3
	Lethrinus erythropterus	No	Ca	No	D	500	G	Br	No	2;4
	Lethrinus genivittatus	No	Ma	No	D	200	G	Br	No	1;2;3;95
	Lethrinus harak	No	Ca	No	D	500	G	Br	No	1;2;3;4
	Lethrinus laticaudis	No	Ca	No	D	560	G	Br	No	1;2;3;4
	Lethrinus lentjan	No	Ma	No	D	500	G	Br	No	1;2;3
	Lethrinus microdon	No	Ca	No	D	700	G	Br	No	2;4
	Lethrinus miniatus	No	Ca	No	D	900	G	Br	No	1;2;3
	Lethrinus nebulosus	No	Ca	No	D	800	G	Br	No	1;2;3
	Lethrinus obsoletus	No	Ma	No	D	500	G	Br	No	1;2;3
	Lethrinus olivaceus	No	Ca	No	D	1000	G	Br	No	44;1;2;3
	Lethrinus ornatus	No	Ca	No	D	400	G	Br	No	1;2;4
	Lethrinus ravus	No	N/A	No	D	320	G	Br	No	3
	Lethrinus rubrioperculatus	No	Ca	No	D	500	G	Br	No	1;2;3
	Lethrinus semicinctus	No	Ca	No	D	290	G	Br	No	2;4
	Lethrinus variegatus	No	Ma	No	D	200	G	Br	No	2;3
	Lethrinus xanthochilus	No	Ca	No	D	600	G	Br	No	44;1;2;3
	Monotaxis grandoculis	No	Ma	No	N	600	G	Br	No	44;1;2;3
Lutjanidae	*Aphareus furca*	No	Ca	No	D	400	G	Br	No	1;2;3
	Aphareus rutilans	No	Ca	No	D	1100	G	Br	No	3;4

	Aprion virescens	No	Ca	No	D	1000	G	Br	No	44;1;2;3
	Lutjanus adetii	No	Ca	No	N	500	G	Br	No	3;4
	Lutjanus argentimaculatus	No	Ca	No	D	1200	G	Br	No	1;2;3
	Lutjanus bengalensis	No	Ca	No	D	300	G	Br	No	2
	Lutjanus biguttatus	No	Ca	No	D	200	G	Br	No	2;3;4
	Lutjanus bohar	No	Pi	No	D	750	G	Br	No	44;1;2;3
	Lutjanus boutton	No	Ca	No	D	280	G	Br	No	2;4
	Lutjanus carponotatus	No	Ca	No	D	400	G	Br	No	1;96;2;3
	Lutjanus decussatus	No	Ca	No	D	300	G	Br	No	1;2;97
	Lutjanus ehrenbergii	No	Ca	No	D	350	G	Br	No	1;2;3
	Lutjanus fulviflamma	No	Ca	No	N	350	G	Br	No	1;96;2;3;
	Lutjanus fulvus	No	Ca	No	D	400	G	Br	No	44;1;2;3
	Lutjanus gibbus	No	Ca	No	N	500	G	Br	No	1;2;3
	Lutjanus johnii	No	Ca	No	D	700	G	Br	No	98;3;4
	Lutjanus kasmira	No	Ca	No	D	350	G	Br	No	1;2;3
	Lutjanus lemniscatus	No	Ca	No	D	650	G	Br	No	1;2;4
	Lutjanus lunulatus	No	Ca	No	D	350	G	Br	No	2
	Lutjanus lutjanus	No	Ca	No	D	300	G	Br	No	1;2;3;4
	Lutjanus madras	No	Ca	No	D	300	G	Br	No	2;24
	Lutjanus malabaricus	No	Ca	No	N	1000	G	Br	No	2;4
	Lutjanus maxweberi	No	Ca	No	D	800	G	Br	No	2
	Lutjanus monostigma	No	Pi	No	D	600	G	Br	No	44;1;2;3
	Lutjanus quinquelineatus	No	Ca	No	D	390	G	Br	No	99;1;2;3
	Lutjanus rivulatus	No	Pi	No	D	800	G	Br	No	3
	Lutjanus rufolineatus	No	Ca	No	D	280	G	Br	No	2;3;4
	Lutjanus russelli	No	Ca	No	D	280	G	Br	No	100;1;2;3
	Lutjanus sebae	No	Ca	No	D	600	G	Br	No	1;2;3;4
	Lutjanus semicinctus	No	Pi	No	D	350	G	Br	No	1;2;4
	Lutjanus timorensis	No	Pi	No	D	500	G	Br	No	2;101;4
	Lutjanus vitta	No	Ca	No	D	400	G	Br	No	1;2;3;39
	Macolor macularis	No	Pl	No	N	600	G	Br	No	1;2;3;4
	Macolor niger	No	Ca	No	D	600	G	Br	No	1;2;3;4
	Paracaesio sordida	No	Pl	No	D	400	G	Br	No	2;3;4
	Paracaesio xanthura	No	Pl	No	D	400	G	Br	No	2;3
	Pinjalo lewisi	No	Ma	No	D	500	G	Br	No	2;3;4
	Pinjalo pinjalo	No	Ma	No	D	500	G	Br	No	2;3;4
	Symphorichthys spilurus	No	Ma	No	D	600	G	Br	No	1;2;3
	Symphorus nematophorus	No	Pi	No	D	800	G	Br	No	1;2;3
Malacanthidae	*Hoplolatilus chlupatyi*	Yes	Pl	Yes	D	150	P	Br	Yes	2;102
	Hoplolatilus cuniculus	Yes	Pl	Yes	D	150	P	Br	Yes	1;2;3;102
	Hoplolatilus fronticinctus	Yes	Pl	Yes	D	170	P	Br	Yes	2;102
	Hoplolatilus luteus	Yes	Pl	Yes	D	110	P	Br	Yes	2;102
	Hoplolatilus marcosi	Yes	Pl	Yes	D	150	P	Br	Yes	2;102
	Hoplolatilus purpureus	Yes	Pl	Yes	D	120	P	Br	Yes	2;102
	Hoplolatilus starcki	Yes	Pl	Yes	D	150	P	Br	Yes	1;2;102
	Malacanthus brevirostris	Yes	Ma	Yes	D	300	P	Br	No	1;2;3;103
	Malacanthus latovittatus	Yes	Ma	Yes	D	350	P	Br	Yes	1;2;3;103
Microcanthidae	*Microcanthus strigatus*	No	Om	No	D	160	N/A	Br	No	1;2;3
	Gunnelichthys curiosus	Yes	Mi	Yes	D	120	N/A	Br	No	1;2;3;4
	Gunnelichthys monostigma	Yes	Mi	Yes	D	110	N/A	Br	No	1;2;3;4
	Gunnelichthys pleurotaenia	Yes	Mi	Yes	D	90	N/A	Br	No	1;2;3;4
	Gunnelichthys viridescens	Yes	Mi	Yes	D	100	N/A	Br	No	1;2;3;4
Molidae	*Mola mola*	No	Ca	No	D	3080	N/A	Br	No	4

Monacanthidae	*Acreichthys radiatus*	No	Co	No	D	70	P	Dm	No	4
	Acreichthys tomentosus	No	Ma	No	D	100	P	Dm	No	4
	Aluterus monoceros	No	Om	No	D	750	P	Dm	No	104
	Aluterus scriptus	No	Om	No	D	750	P	Dm	No	1;2;3
	Amanses scopas	Yes	Co	No	D	200	G	Br	No	105
	Anacanthus barbatus	No	N/A	No	D	350	P	Dm	No	1;2;3
	Cantherhines dumerili	Yes	Co	No	D	350	P	Dm	No	77
	Cantherhines fronticinctus	No	Ma	No	D	230	P	Dm	No	4
	Cantherhines pardalis	No	Ma	No	D	250	P	Dm	No	4
	Cantherhines sandwichiensis	No	Om	No	D	194	P	Dm	No	1;2;3
	Chaetodermis penicilligera	No	N/A	No	D	310	P	Dm	No	1;2;3
	Monacanthus chinensis	No	Om	No	D	380	P	Dm	No	4
	Oxymonacanthus longirostris	Yes	Co	No	D	90	P	Dm	Yes	77
	Paraluteres arqat	No	N/A	No	D	80	P	Dm	No	1;2;3
	Paraluteres prionurus	Yes	Om	No	D	100	P	Dm	No	4
	Paramonacanthus choirocephalus	No	Om	No	D	130	P	Dm	No	24
	Paramonacanthus japonicus	Yes	Mi	No	D	100	P	Dm	Yes	106
	Pervagor alternans	No	Mi	No	D	160	P	Dm	No	12
	Pervagor aspricaudus	No	Mi	No	D	120	P	Dm	No	12
	Pervagor janthinosoma	Yes	Mi	No	D	140	P	Dm	No	4
	Pervagor melanocephalus	Yes	Mi	No	D	100	P	Dm	No	12
	Pervagor nigrolineatus	No	Mi	No	D	100	P	Dm	No	12
	Pseudalutarius nasicornis	Yes	Mi	No	D	180	P	Dm	No	107
	Pseudomonacanthus macrurus	Yes	Om	No	D	240	P	Dm	No	21
	Rudarias excelsus	N/A	N/A	No	D	25	G	Dm	No	1;2;3
	Rudarias minutus	No	N/A	No	D	30	G	Dm	No	1;2;3
Monocentridae	*Cleidopus gloriamaris*	Yes	N/A	No	D	220	N/A	Br	No	1;2;3
	Monocentris japonica	Yes	N/A	No	D	170	N/A	Br	No	1;2;3
Mugilidae	*Chelon macrolepis*	No	De	No	D	400	G	Br	No	3;15
	Chelon melinopterus	No	De	No	D	300	G	Br	No	3;15
	Chelon subviridis	No	De	No	D	400	G	Br	No	3;4
	Crenimugil crenilabis	No	De	No	D	400	G	Br	No	2;3;108
	Ellochelon vaigiensis	No	Om	No	D	520	G	Br	No	2;3;15
	Moolgarda engeli	No	De	No	D	150	G	Br	No	2;108
	Moolgarda seheli	No	De	No	D	500	G	Br	No	3;4
	Mugil cephalus	No	De	No	D	300	G	Br	No	3;15
	Neomyxus leuciscus	No	Om	No	D	460	G	Br	No	2;3;4
Mullidae	*Mulloidichthys flavolineatus*	No	Ma	No	N	400	G	Br	No	1;2;3;4
	Mulloidichthys mimicus	No	Ma	No	N	300	G	Br	No	1;2;3
	Mulloidichthys pflugeri	Yes	Ma	No	D	480	G	Br	No	1;2;3;
	Mulloidichthys vanicolensis	No	Ma	No	N	380	G	Br	No	1;2;3;4
	Parupeneus barberinoides	No	Ma	No	D	250	G	Br	No	1;2;3;4
	Parupeneus barberinus	No	Ma	No	D	500	G	Br	No	1;2;3;4
	Parupeneus ciliatus	No	Ma	No	N	380	G	Br	No	1;2;3;4
	Parupeneus crassilabris	No	Ma	No	D	350	G	Br	No	1;2;3
	Parupeneus cyclostomus	Yes	Ca	No	D	500	P	Br	No	1;2;3;4
	Parupeneus heptacanthus	No	Ma	No	D	360	P	Br	No	1;2;3;109
	Parupeneus indicus	No	Ma	No	N	350	P	Br	No	1;2;3;4
	Parupeneus insularis	No	Ma	No	D	330	P	Br	No	1;2;3;110
	Parupeneus macronemus	No	Ma	No	D	320	P	Br	No	1;2;3;111
	Parupeneus multifasciatus	No	Ma	No	D	300	P	Br	No	1;2;3;109
	Parupeneus pleurostigma	No	Ma	No	D	330	P	Br	No	1;2;3;109
	Parupeneus rubescens	No	Ma	No	D	430	P	Br	No	1;2;3;112

	Parupeneus spilurus	No	Ma	No	N	350	P	Br	No	1;2;3
	Parupeneus trifasciatus	No	Ca	No	N	350	P	Br	No	1;2;3;4
	Upeneus moluccensis	No	Ca	No	D	200	P	Br	No	113
	Upeneus taeniopterus	No	Ca	No	D	360	P	Br	No	2
	Upeneus tragula	No	Ca	No	D	300	P	Br	No	114
	Upeneus vittatus	No	Ca	No	D	280	P	Br	No	114
Muraenidae	*Channomuraena vittata*	No	N/A	No	N	1500	P	Br	No	4
	Echidna delicatula	No	Ma	No	N	650	P	Br	No	115
	Echidna nebulosa	No	Ma	No	N	750	P	Br	No	115
	Echidna polyzona	No	Ma	No	N	600	P	Br	No	115
	Enchelycore bayeri	No	Pi	No	N	600	P	Br	No	115
	Enchelycore lichenosa	No	Pi	No	N	925	P	Br	No	4
	Enchelycore pardalis	No	Pi	No	N	800	P	Br	No	12
	Enchelycore schismatorhynchus	No	Pi	No	N	1200	P	Br	No	4
	Enchelynassa canina	No	Ca	No	N	1540	P	Br	No	4
	Gymnomuraena zebra	No	Ma	No	D	1540	P	Br	No	116
	Gymnothorax albimarginatus	No	N/A	No	N	1000	P	Br	No	4
	Gymnothorax breedeni	No	Pi	No	N	750	P	Br	No	115
	Gymnothorax buroensis	No	N/A	No	N	330	P	Br	No	1;2;3
	Gymnothorax chilospilus	No	N/A	No	D	500	P	Br	No	1;2;3
	Gymnothorax chlamydatus	No	N/A	No	D	800	P	Br	No	1;2;3
	Gymnothorax cribroris	No	N/A	No	N	470	P	Br	No	1;2;3
	Gymnothorax enigmaticus	No	N/A	No	N	580	P	Br	No	1;2;3
	Gymnothorax eurostus	No	Ca	No	D	650	P	Br	No	3
	Gymnothorax favagineus	No	Ca	No	D	1800	P	Br	No	4
	Gymnothorax fimbriatus	No	Ca	No	N	800	P	Br	No	4
	Gymnothorax flavimarginatus	No	Ca	No	N	1500	P	Br	No	3
	Gymnothorax gracilicauda	No	N/A	No	N	320	P	Br	No	1;2;3
	Gymnothorax herrei	No	N/A	No	D	300	G	Br	No	1;2;3
	Gymnothorax isingteena	No	N/A	No	D	1800	P	Br	No	1;2;3
	Gymnothorax javanicus	No	Pi	No	N	2390	P	Br	No	3
	Gymnothorax melatremus	No	Ma	No	N	200	P	Br	No	12
	Gymnothorax meleagris	No	Pi	No	N	1200	P	Br	No	3
	Gymnothorax minor	No	N/A	No	D	600	P	Br	No	1;2;3
	Gymnothorax nudivomer	No	N/A	No	D	1800	P	Br	No	1;2;3
	Gymnothorax picta	No	Ca	No	D	1200	P	Br	No	4
	Gymnothorax richardsoni	No	N/A	No	D	320	P	Br	No	1;2;3
	Gymnothorax rueppelliae	No	Ca	No	N	800	P	Br	No	12
	Gymnothorax tile	No	N/A	No	D	530	P	Br	No	1;2;3
	Gymnothorax undulatus	No	Ca	No	N	1500	P	Br	No	4
	Gymnothorax zonipectis	No	N/A	No	N	800	P	Br	No	1;2;3
	Pseudechidna brummeri	No	N/A	No	N	1030	P	Br	No	1;2;3
	Rhinomuraena quaesita	Yes	Pi	No	D	850	P	Br	No	115
	Scuticaria okinawae	No	N/A	No	D	930	P	Br	No	1;2;3
	Scuticaria tigrina	No	N/A	No	N	1200	P	Br	No	1;2;3
	Siderea thysoidea	Yes	N/A	No	D	650	P	Br	No	4
	Strophidon sathete	No	Ca	No	D	3750	P	Br	No	4
	Uropterygius fasciolatus	No	Pi	No	D	530	P	Br	No	116
	Uropterygius macrocephalus	No	Pi	No	D	400	P	Br	No	116
Nemipteridae	*Nemipterus furcosus*	No	Ca	No	D	300	G	Br	No	100;2;3
	Nemipterus peronii	No	Ca	No	D	280	G	Br	No	3;4
	Nemipterus zysron	No	Ca	No	D	250	G	Br	No	3;4
	Pentapodus aureofasciatus	Yes	Ca	No	D	250	G	Br	No	2;3

	Pentapodus bifasciatus	No	Ca	No	D	200	G	Br	No	2;4
	Pentapodus caninus	No	Ca	No	D	250	G	Br	No	2;3
	Pentapodus emeryii	No	Ca	No	D	350	G	Br	No	2;4
	Pentapodus nagasakiensis	No	Ma	No	D	250	G	Br	No	2;4
	Pentapodus paradiseus	No	Ca	No	D	350	G	Br	No	1;2;3
	Pentapodus porosus	No	Ca	No	D	300	G	Br	No	2
	Pentapodus setosus	No	Ma	No	D	250	G	Br	No	2;4
	Pentapodus trivittatus	Yes	Ca	No	D	300	G	Br	No	2;4
	Scaevius milii	No	Ca	No	D	300	G	Br	No	2;4
	Scaevius vitta	No	Ca	No	D	400	G	Br	No	2;3
	Scolopsis affinis	No	Ma	No	D	300	G	Br	No	2;117
	Scolopsis auratus	No	N/A	No	D	300	G	Br	No	2
	Scolopsis bilineatus	No	Ma	No	N	250	G	Br	No	1;2;3;118
	Scolopsis ciliatus	No	Ca	No	D	250	G	Br	No	2;3;4
	Scolopsis ghanam	No	Ca	No	D	250	G	Br	No	2;4
	Scolopsis lineatus	No	Ca	No	D	250	G	Br	No	1;2;3;4
	Scolopsis margaritifer	No	Ca	No	D	250	G	Br	No	1;119;2
	Scolopsis monogramma	No	Ca	No	D	380	G	Br	No	2;4
	Scolopsis taeniopterus	No	Ca	No	D	300	G	Br	No	2;4
	Scolopsis trilineatus	No	Ma	No	D	250	G	Br	No	1;2;3;20
	Scolopsis vosmeri	No	Ma	No	D	250	G	Br	No	2;4
	Scolopsis xenochrous	No	Ma	No	D	250	G	Br	No	2;4
Ophichthidae	*Apterichtus klazingai*	No	Ca	No	D	400	G	Br	No	4
	Brachysomophis cirrocheilos	No	Ca	No	D	1250	G	Br	No	4
	Brachysomophis crocodilinus	No	Ca	No	N	820	G	Br	No	120
	Brachysomophis henshawi	No	Ca	No	N	1060	G	Br	No	4
	Callechelys catostoma	No	Ca	No	D	850	G	Br	No	1;2;3
	Callechelys marmorata	No	Ca	No	D	900	G	Br	No	1;2;3
	Leiuranus semicinctus	No	Ca	No	N	600	G	Br	No	4
	Leiuranus versicolor	No	N/A	No	D	520	G	Br	No	1;2;3
	Myrichthys colubrinus	No	N/A	No	D	900	G	Br	No	1;2;3
	Myrichthys maculosus	No	N/A	No	N	1000	G	Br	No	4
	Ophichthus bonaparti	No	N/A	No	N	750	G	Br	No	4
	Ophichthus cephalozona	No	N/A	No	N	1080	G	Br	No	1;2;3
	Ophichthus melanochir	No	N/A	No	D	800	G	Br	No	4
	Ophichthus polyophthalmus	No	N/A	No	D	350	G	Br	No	4
	Pisodonophis cancrivorus	Yes	Ma	No	D	750	G	Br	No	121
Opistognathidae	*Opistognathus darwiniensis*	No	Pl	No	D	450	P	Mo	No	2
	Opistognathus dendriticus	No	Pl	No	D	450	P	Mo	No	1;2
	Opistognathus papuensis	No	Pl	No	D	450	P	Mo	No	1;2
	Opistognathus solorensis	No	Pl	No	D	450	P	Mo	No	1;2
Ostraciidae	*Lactoria cornuta*	No	Ma	No	D	460	P	Br	No	1;2;3;4
	Lactoria diaphana	No	Ma	No	D	250	P	Br	No	2;122
	Lactoria fornasini	No	Ma	No	D	150	P	Br	No	1;2;3;122
	Ostracion cubicus	No	Om	No	D	450	P	Br	No	1;2;3;4
	Ostracion meleagris	Yes	Om	No	D	180	P	Br	No	1;2;3;4
	Ostracion rhinorhynchus	Yes	Ma	No	D	300	P	Br	No	2;4
	Ostracion solorensis	Yes	N/A	No	D	110	P	Br	No	1;2;3
	Ostracion whitleyi	Yes	Ma	No	D	155	P	Br	No	1;2;3;12
	Rhynchostracion nasus	No	N/A	No	D	300	P	Br	No	2
	Tetrosomus concatenatus	No	N/A	No	D	300	P	Br	No	2
	Tetrosomus gibbosus	No	Ma	No	D	300	P	Br	No	1;2;3;4
Pegasidae	*Eurypegasus draconis*	Yes	Mi	No	D	70	P	Br	Yes	1;2;3;4

	Pegasus volitans	Yes	Mi	No	D	110	P	Br	No	1;2;3;4
Pempheridae	*Parapriacanthus ransonneti*	No	Pl	No	N	100	G	Br	No	4
	Pempheris adusta	No	Pl	No	N	170	G	Br	No	4
	Pempheris oualensis	No	Pl	No	N	220	G	Br	No	4
	Pempheris schwenkii	No	Pl	No	N	150	G	Br	No	4
	Pempheris vanicolensis	No	Pl	No	N	200	G	Br	No	4
Pinguipedidae	*Parapercis clathrata*	No	Ma	No	D	175	P	Br	No	1;2;3;12
	Parapercis cylindrica	No	Ma	No	D	230	P	Br	No	2;88
	Parapercis hexophthalma	No	Ma	No	D	280	P	Br	No	1;2;3
	Parapercis lata	No	Ma	No	D	260	P	Br	No	2;3;
	Parapercis lineopunctata	No	Ma	No	D	120	P	Br	No	2
	Parapercis maculatus	No	Ma	No	D	200	P	Br	No	2
	Parapercis millipunctata	No	Ma	No	D	260	P	Br	No	1;2;3
	Parapercis multiplicata	No	Ma	No	D	120	P	Br	No	1;2;3
	Parapercis schauinslandi	No	Pl	No	D	130	P	Br	No	1;2;3;4
	Parapercis snyderi	No	Ma	No	D	110	P	Br	No	1;2;3
	Parapercis tetracantha	No	Ma	No	D	260	P	Br	No	2
	Parapercis xanthozona	No	Ma	No	D	230	P	Br	No	1;2;3
Platycephalidae	*Cociella punctata*	No	Pl	No	D	350	P	Br	No	2;14
	Cymbacephalus beauforti	No	Pi	No	D	470	P	Br	No	2;123
	Inegocia japonica	No	N/A	No	D	250	P	Br	No	2
	Onigocia spinosa	No	N/A	No	N	130	P	Br	No	2
	Rogadius patriciae	No	N/A	No	D	270	P	Br	No	2
	Rogadius pristiger	No	N/A	No	D	210	P	Br	No	2
	Rogadius welanderi	No	N/A	No	D	130	P	Br	No	2
	Thysanophrys arenicola	No	Ca	No	D	370	P	Br	No	1;2;3;4
	Thysanophrys carbunculus	No	Pi	No	D	400	P	Br	No	2;124
	Thysanophrys chiltonae	No	Ca	No	D	220	P	Br	No	1;2;3;4
	Thysanophrys otaitensis	No	Ca	No	D	250	P	Br	No	1;2;3
Plesiopidae	*Assessor flavissimus*	No	Pl	No	D	55	G	Mo	No	1;2
	Assessor macneilli	No	Om	No	D	60	G	Mo	No	1;2;3;70
	Assessor randalli	No	Pl	No	D	60	G	Mo	No	2
	Belonopterygium fasciolatum	No	N/A	No	D	50	G	Dm	No	2
	Calloplesiops altivelis	No	N/A	No	D	130	G	Dm	No	1;2;3
	Paraplesiops poweri	No	Ma	No	D	149	G	Dm	No	1;125
	Plesiops coeruleolineatus	No	Ca	No	N	80	G	Dm	No	1;2;3;4
	Plesiops corallicola	No	Ma	No	N	160	G	Dm	No	1;2;3;125
	Plesiops insularis	No	Ma	No	D	149	G	Dm	No	1;125
	Plesiops verecundus	No	Ma	No	D	149	G	Dm	No	1;125
Pleuronectidae	*Pseudorhombus dupliciocellatus*	No	Ca	No	D	400	P	Br	No	2
	Samaris cristatus	No	Ma	No	D	220	P	Br	No	1;2;3;4
	Samariscus triocellatus	No	Ma	No	N	90	P	Br	No	1;2;3;4
Plotosidae	*Paraplotosus albilabris*	No	Ma	No	N	1300	P	Dm	No	4
	Plotosus lineatus	No	Ca	No	N	320	P	Dm	No	4
Pomacanthidae	*Apolemichthys griffisi*	Yes	Sp	No	D	250	P	Dm	No	2;4
	Apolemichthys trimaculatus	Yes	Sp	No	D	250	P	Br	No	1;2;3
	Apolemichthys xanthopunctatus	No	Sp	No	D	250	P	Br	No	2;4
	Centropyge aurantius	No	N/A	No	D	100	P	Br	No	2
	Centropyge bicolor	Yes	Om	No	D	150	P	Br	No	2;126
	Centropyge bispinosus	No	He	No	D	100	P	Br	No	53;2;4
	Centropyge boylei	N/A	He	No	D	70	P	Br	No	3;4
	Centropyge colini	No	He	No	D	90	P	Br	No	1;2;3
	Centropyge eibli	Yes	He	No	D	110	P	Br	No	2;4

	Centropyge ferrugatus	No	He	No	D	100	P	Br	No	53;2
	Centropyge fisheri	No	He	No	D	76	P	Br	No	2
	Centropyge flavipectoralis	No	He	No	D	100	P	Br	No	2
	Centropyge flavissimus	No	He	No	D	100	P	Br	No	127;2
	Centropyge heraldi	No	He	No	D	100	P	Br	No	127;2
	Centropyge hotumatua	No	He	No	D	80	P	Br	No	2;3
	Centropyge interruptus	No	He	No	D	150	P	Br	Yes	127
	Centropyge loriculus	No	He	No	D	100	P	Br	No	2;3;4
	Centropyge multicolor	No	He	No	D	90	P	Br	No	2
	Centropyge multifasciata	No	He	No	D	100	P	Br	No	1;2;3
	Centropyge multispinis	No	He	No	D	100	P	Br	No	2
	Centropyge narcosis	Yes	He	No	D	72	P	Br	No	3;4
	Centropyge nigriocellus	No	He	No	D	60	P	Br	No	2;4
	Centropyge nox	Yes	He	No	D	90	P	Br	No	2;4
	Centropyge shepardi	No	He	No	D	120	P	Br	No	53;2;4
	Centropyge tibicen	No	He	No	D	180	P	Br	No	127;2
	Centropyge venusta	Yes	He	No	D	120	P	Br	No	128
	Centropyge vrolikii	No	Om	No	D	120	P	Br	Yes	53;2
	Chaetodontoplus ballinae	No	Sp	No	D	200	P	Br	No	53;2
	Chaetodontoplus chrysocephalus	No	Sp	No	D	220	P	Br	No	53;2;4
	Chaetodontoplus conspicillatus	Yes	Sp	No	D	250	P	Br	No	1;53;2;3
	Chaetodontoplus dimidiatus	Yes	Sp	No	D	200	P	Br	No	2
	Chaetodontoplus duboulayi	Yes	Sp	No	D	250	P	Br	No	53;2
	Chaetodontoplus melanosoma	Yes	Sp	No	D	200	P	Br	No	53;2;4
	Chaetodontoplus meredithi	Yes	Sp	No	D	250	P	Br	No	53;2
	Chaetodontoplus mesoleucus	Yes	Om	No	D	180	P	Br	No	53;2
	Chaetodontoplus personifer	N/A	N/A	No	D	350	P	Br	No	2
	Chaetodontoplus septentrionalis	No	Sp	No	D	200	P	Br	No	53;2;4
	Genicanthus bellus	No	Pl	No	D	180	P	Br	No	1;53;2;3
	Genicanthus caudovittatus	No	Pl	No	D	200	P	Br	No	53;2;3
	Genicanthus lamarck	No	Pl	No	D	230	P	Br	No	53;2
	Genicanthus melanospilos	Yes	Pl	No	D	180	P	Br	No	53;2;3
	Genicanthus semicinctus	No	Pl	No	D	250	P	Br	No	53;2
	Genicanthus semifasciatus	No	Pl	No	D	210	P	Br	No	53;2
	Genicanthus spinus	No	Pl	No	D	375	P	Br	No	53;3
	Genicanthus watanabei	No	Pl	No	D	150	P	Br	No	53;2
	Pomacanthus annularis	Yes	Sp	No	D	450	P	Br	No	53;128;2
	Pomacanthus imperator	Yes	Sp	No	D	380	P	Br	No	53;2;3
	Pomacanthus navarchus	No	Sp	No	D	380	P	Br	No	53;2
	Pomacanthus semicirculatus	No	Om	No	D	350	P	Br	No	53;2;3
	Pomacanthus sexstriatus	Yes	Om	No	D	460	P	Br	No	53;2;129
	Pomacanthus xanthometopon	No	Sp	No	D	380	P	Br	No	53;2
	Pygoplites diacanthus	Yes	Sp	No	D	250	P	Br	No	53;2;3
Pomacentridae	*Abudefduf bengalensis*	No	Om	No	D	170	G	Dm	No	1;2;4
	Abudefduf conformis	N/A	N/A	No	D	170	G	Dm	No	3
	Abudefduf lorenzi	No	He	No	D	150	G	Dm	No	130;2
	Abudefduf notatus	No	N/A	No	D	150	G	Dm	No	2;4
	Abudefduf septemfasciatus	No	Om	No	D	190	G	Dm	No	1;2;3
	Abudefduf sexfasciatus	No	Pl	No	D	150	G	Dm	No	1;2;3;131
	Abudefduf sordidus	No	Om	No	D	190	G	Dm	No	1;2;3
	Abudefduf vaigiensis	No	Pl	No	D	190	G	Dm	No	1;2;3;131
	Abudefduf whitleyi	No	Pl	No	D	150	G	Dm	No	132;1;2;3
	Acanthochromis polyacanthus	Yes	Pl	No	D	130	P	Dm	Yes	1;2;137

Altrichthys azurelineatus	Yes	Pl	No	D	60	P	Dm	No	2;4
Altrichthys curatus	Yes	Pl	No	D	60	P	Dm	No	2;4
Amblyglyphidodon aureus	Yes	Pl	No	D	150	P	Dm	No	1;2;3
Amblyglyphidodon batunai	Yes	Om	No	D	100	P	Dm	No	2;4
Amblyglyphidodon curacao	No	Pl	No	D	115	P	Dm	No	132;1;2;3
Amblyglyphidodon leucogaster	No	Om	No	D	130	P	Dm	No	1;2;4
Amblyglyphidodon melanopterus	No	Om	No	D	140	P	Dm	No	3
Amblyglyphidodon orbicularis	Yes	Om	No	D	130	P	Dm	No	2;3
Amblyglyphidodon ternatensis	No	Om	No	D	120	P	Dm	No	2
Amblypomacentrus breviceps	No	N/A	No	D	80	P	Dm	No	1;2;4
Amphiprion akallopisos	No	Pl	No	D	100	P	Dm	No	133;2;131;4
Amphiprion akindynos	No	Pl	No	D	120	P	Dm	No	133;3
Amphiprion chrysopterus	No	Om	No	D	170	P	Dm	No	1;2;3;4
Amphiprion clarkii	No	Om	No	D	120	P	Dm	Yes	1;2;3;4
Amphiprion ephippium	Yes	Pl	No	D	120	P	Dm	No	2;4
Amphiprion frenatus	No	Pl	No	D	60	P	Dm	Yes	133;2;4
Amphiprion latezonatus	No	Pl	No	D	140	P	Dm	No	133;2;4
Amphiprion leucokranos	No	Pl	No	D	130	P	Dm	No	133;2;4
Amphiprion mccullochi	No	Pl	No	D	120	P	Dm	No	133;2;4
Amphiprion melanopus	Yes	Om	No	D	130	P	Dm	No	1;2;3;4
Amphiprion ocellaris	No	Pl	No	D	90	P	Dm	No	134;2
Amphiprion percula	No	Pl	No	D	90	P	Dm	No	1;2;4
Amphiprion perideraion	No	Pl	No	D	100	P	Dm	Yes	1;133;2;3;4
Amphiprion polymnus	No	Pl	No	D	120	P	Dm	No	133;2;4
Amphiprion rubrocinctus	No	Pl	No	D	120	P	Dm	No	2;4
Amphiprion sandaracinos	Yes	Pl	No	D	130	P	Dm	No	133;2;4
Amphiprion sebae	No	Pl	No	D	140	P	Dm	No	133;2;4
Amphiprion tricinctus	No	Om	No	D	130	P	Dm	No	2;4
Cheiloprion labiatus	No	Co	No	D	80	P	Dm	No	1;2
Chromis abrupta	No	Pl	No	D	80	P	Dm	No	3
Chromis acares	No	Pl	No	D	55	P	Dm	No	1;2;3
Chromis agilis	No	Pl	No	D	90	P	Dm	No	135;1;2;3
Chromis albomaculata	No	Pl	No	D	180	P	Dm	No	2
Chromis alleni	No	Pl	No	D	80	P	Dm	No	2
Chromis alpha	No	Pl	No	D	100	P	Dm	No	2
Chromis amboinensis	No	Pl	No	D	75	P	Dm	No	1;2;3
Chromis analis	No	Pl	No	D	150	P	Dm	No	1;2;3
Chromis atripectoralis	No	Pl	No	D	100	P	Dm	No	1;2;3
Chromis atripes	No	Pl	No	D	70	G	Dm	No	1;2
Chromis bami	No	Pl	No	D	85	P	Dm	No	3
Chromis caudalis	No	Pl	No	D	90	P	Dm	No	2
Chromis chrysura	No	Pl	No	D	160	P	Dm	No	1;2;3
Chromis cinerascens	No	Pl	No	D	130	P	Dm	No	2
Chromis delta	No	Pl	No	D	65	P	Dm	No	1;2;3
Chromis dimidiatus	No	Pl	No	D	70	P	Dm	No	2
Chromis elerae	No	Pl	No	D	70	P	Dm	No	1;2;3
Chromis fatuhivae	No	Pl	No	D	67	P	Dm	No	3
Chromis flavapicis	No	Pl	No	D	135	P	Dm	No	3
Chromis flavipectoralis	No	Pl	No	D	70	P	Dm	No	2
Chromis flavomaculata	No	Pl	No	D	150	P	Dm	No	136;2
Chromis fumea	No	Pl	No	D	130	P	Dm	No	1;2;3
Chromis iomelas	No	Pl	No	D	70	P	Dm	No	1;2;3
Chromis lepidolepis	No	Pl	No	D	80	P	Dm	No	138;1;2;3

Chromis leucura	No	Pl	No	D	55	P	Dm	No	2;3
Chromis lineata	No	Pl	No	D	50	P	Dm	No	2
Chromis margaritifer	No	Pl	No	D	80	P	Dm	No	2;4
Chromis nitida	No	Pl	No	D	90	P	Dm	No	139;1;2;3
Chromis notata	No	Pl	No	D	160	P	Dm	No	2
Chromis opercularis	No	Pl	No	D	160	P	Dm	No	2
Chromis ovatiformes	No	Pl	No	D	90	P	Dm	No	2
Chromis pamae	No	Pl	No	D	137	P	Dm	No	3
Chromis retrofasciata	No	Pl	No	D	55	P	Dm	No	1;140;2;3
Chromis scotochiloptera	No	Pl	No	D	150	P	Dm	No	2;4
Chromis ternatensis	No	Pl	No	D	70	P	Dm	No	1;2;3;131
Chromis vanderbilti	No	Pl	No	D	60	P	Dm	No	1;2;3
Chromis viridis	No	Pl	No	D	80	P	Dm	No	1;2;3
Chromis weberi	No	Pl	No	D	120	P	Dm	No	1;2;3
Chromis westaustralis	No	Pl	No	D	100	P	Dm	No	2
Chromis xanthochira	No	Pl	No	D	140	P	Dm	No	138;1;2
Chromis xanthura	No	Pl	No	D	150	P	Dm	No	1;2;3
Chrysiptera albata	No	N/A	No	D	46	P	Dm	No	3
Chrysiptera bioellata	No	Om	No	D	70	P	Dm	No	1;2;3
Chrysiptera bleekeri	Yes	N/A	Yes	D	80	P	Dm	No	2;4
Chrysiptera brownriggii	No	Om	No	D	85	P	Dm	No	2;3;4
Chrysiptera caeruleolineata	No	Pl	No	D	55	P	Dm	No	1;2;3
Chrysiptera cyanea	No	Pl	No	D	80	P	Dm	No	1;2;4
Chrysiptera cymatilis	No	Pl	No	D	60	P	Dm	No	2
Chrysiptera flavipinnis	No	N/A	No	D	80	P	Dm	No	1;2
Chrysiptera galba	No	N/A	No	D	95	P	Dm	No	3
Chrysiptera glauca	No	He	No	D	80	P	Dm	No	1;2;3
Chrysiptera hemicyanea	No	Pl	No	D	60	P	Dm	No	2;4
Chrysiptera kuiteri	Yes	Pl	Yes	D	60	P	Dm	No	141;2
Chrysiptera oxycephala	Yes	Pl	No	D	80	P	Dm	No	2;4
Chrysiptera parasema	No	N/A	No	D	60	P	Dm	No	2;4
Chrysiptera rex	No	He	No	D	80	P	Dm	No	1;2;3;4
Chrysiptera rollandi	No	Pl	No	D	50	P	Dm	No	1;2;3;4
Chrysiptera sinclairi	No	N/A	No	D	60	P	Dm	No	2
Chrysiptera springeri	No	Om	No	D	60	P	Dm	No	138;2
Chrysiptera starcki	No	N/A	No	D	90	P	Dm	No	1;2;3
Chrysiptera talboti	No	Pl	No	D	60	P	Dm	No	1;2;3;4
Chrysiptera taupou	No	N/A	No	D	80	P	Dm	No	1;2;3
Chrysiptera traceyi	No	Om	No	D	60	P	Dm	No	2;4
Chrysiptera tricincta	Yes	N/A	No	D	60	P	Dm	No	141;2
Chrysiptera unimaculata	No	He	No	D	80	P	Dm	No	1;2;3;131
Dascyllus aruanus	No	Pl	No	D	80	P	Dm	No	1;2;3
Dascyllus auripinnis	No	Pl	No	D	140	P	Dm	No	138;2;3
Dascyllus carneus	No	Pl	No	D	70	P	Dm	No	2;4
Dascyllus flavicaudus	No	Pl	No	D	110	P	Dm	No	138;2;3
Dascyllus melanurus	No	Pl	No	D	80	P	Dm	No	142;1;2;3
Dascyllus reticulatus	No	Pl	No	D	80	P	Dm	No	142;1;2;3
Dascyllus strasburgi	No	Om	No	D	105	P	Dm	No	142;3
Dascyllus trimaculatus	No	Om	No	D	140	P	Dm	No	142;1;2;3;4
Dischistodus chrysopoecilus	No	De	No	D	150	P	Dm	No	1;2
Dischistodus darwiniensis	No	De	No	D	130	P	Dm	No	2
Dischistodus fasciatus	No	De	No	D	130	P	Dm	No	2
Dischistodus melanotus	No	De	No	D	150	P	Dm	No	1;2;143

Dischistodus perspicillatus	No	De	No	D	190	P	Dm	No	1;2
Dischistodus prosopotaenia	No	De	No	D	180	P	Dm	No	1;2
Dischistodus pseudochrysopoecilus	No	De	No	D	160	P	Dm	No	1;2
Hemiglyphidodon plagiometopon	No	De	No	D	180	P	Dm	No	1;2;144
Lepidozygus tapeinosoma	No	Pl	No	D	90	P	Dm	No	1;2;3
Neoglyphidodon bonang	No	N/A	No	D	130	P	Dm	No	2;4
Neoglyphidodon carlsoni	No	N/A	No	D	120	P	Dm	No	2;3
Neoglyphidodon crossi	No	N/A	No	D	130	P	Dm	No	2;4
Neoglyphidodon melas	Yes	Co	No	D	150	P	Dm	No	1;2;4;143
Neoglyphidodon nigroris	No	Pl	No	D	110	P	Dm	No	1;2;3;4
Neoglyphidodon oxyodon	No	N/A	No	D	140	P	Dm	No	2;4
Neoglyphidodon polyacanthus	No	N/A	No	D	140	P	Dm	No	1;2;3
Neoglyphidodon thoracotaenatus	No	Pl	No	D	100	P	Dm	No	2;4
Neopomacentrus aquadulcis	No	Pl	No	D	100	P	Dm	No	2
Neopomacentrus azysron	No	Pl	No	D	80	G	Dm	No	35;1;2
Neopomacentrus bankieri	No	Pl	No	D	70	G	Dm	No	1;2;145
Neopomacentrus cyanomos	No	Pl	No	D	90	G	Dm	No	132;1;2
Neopomacentrus filamentosus	No	Pl	No	D	80	G	Dm	No	2;3;117
Neopomacentrus metallicus	No	Pl	No	D	80	G	Dm	No	3;4
Neopomacentrus nemurus	No	Pl	No	D	80	G	Dm	No	2;3;4
Neopomacentrus taeniurus	No	Pl	No	D	100	G	Dm	No	2
Neopomacentrus violascens	No	Pl	No	D	70	G	Dm	No	2;4
Parma oligolepis	No	N/A	No	D	200	P	Dm	No	1
Parma polylepis	No	De	No	D	220	P	Dm	No	146;1
Plectroglyphidodon dickii	No	Om	No	D	110	P	Dm	No	1;2;3;4
Plectroglyphidodon flaviventris	No	N/A	No	D	80	P	Dm	No	3;4
Plectroglyphidodon imparipennis	No	Om	No	D	60	P	Dm	No	1;2;3;4
Plectroglyphidodon johnstonianus	No	Co	No	D	90	P	Dm	No	1;2;3;4
Plectroglyphidodon lacrymatus	No	Om	No	D	100	P	Dm	No	1;2;3;144
Plectroglyphidodon leucozonus	No	He	No	D	100	P	Dm	No	1;2;3;4
Plectroglyphidodon phoenixensis	No	De	No	D	90	P	Dm	No	1;2;3;4
Plectroglyphidodon sagmarius	No	N/A	No	D	64	P	Dm	No	3
Pomacentrus adelus	No	De	No	D	85	P	Dm	No	2;3;144
Pomacentrus albimaculus	No	He	No	D	90	P	Dm	No	2;4
Pomacentrus alexanderae	No	Om	No	D	100	P	Dm	No	2;4
Pomacentrus alleni	No	N/A	No	D	65	P	Dm	No	2
Pomacentrus amboinensis	No	Om	No	D	100	P	Dm	No	1;147;2;3
Pomacentrus armillatus	No	N/A	No	D	70	P	Dm	No	2
Pomacentrus aurifrons	No	Pl	No	D	70	P	Dm	No	2;3
Pomacentrus auriventris	No	N/A	No	D	70	P	Dm	No	2
Pomacentrus australis	No	He	No	D	80	P	Dm	No	138;1;2
Pomacentrus azuremaculatus	No	N/A	No	D	100	P	Dm	No	2
Pomacentrus bankanensis	No	De	No	D	100	P	Dm	No	138;1;2;3;144
Pomacentrus bipunctatus	No	N/A	No	D	100	P	Dm	No	2
Pomacentrus brachialis	No	Om	No	D	100	P	Dm	No	138;2;3
Pomacentrus burroughi	No	De	No	D	80	P	Dm	No	2;144
Pomacentrus callainus	No	N/A	No	D	95	P	Dm	No	3
Pomacentrus chrysurus	No	De	No	D	90	P	Dm	No	1;2;3;144
Pomacentrus coelestis	No	Pl	No	D	70	P	Dm	No	1;2;3;4
Pomacentrus colini	No	N/A	No	D	90	P	Dm	No	2
Pomacentrus cuneatus	No	N/A	No	D	90	P	Dm	No	2
Pomacentrus geminospilos	No	N/A	No	D	75	P	Dm	No	2
Pomacentrus grammorhynchus	No	De	No	D	120	P	Dm	No	1;148;2

	Pomacentrus imitator	No	Pl	No	D	100	P	Dm	No	1;2;3
	Pomacentrus javanicus	No	N/A	No	D	80	P	Dm	No	2
	Pomacentrus komodoensis	No	N/A	No	D	80	P	Dm	No	2
	Pomacentrus lepidogenys	No	Pl	No	D	90	P	Dm	No	138;1;2
	Pomacentrus limosus	No	N/A	No	D	70	P	Dm	No	2
	Pomacentrus littoralis	No	N/A	No	D	100	P	Dm	No	2
	Pomacentrus melanochir	No	Pl	No	D	70	P	Dm	No	2;4
	Pomacentrus milleri	No	De	No	D	90	P	Dm	No	2;149
	Pomacentrus moluccensis	No	Om	No	D	70	P	Dm	No	138;1;2;3;69
	Pomacentrus nagasakiensis	No	Pl	No	D	120	P	Dm	No	1;2;3;4
	Pomacentrus nigromanus	No	Om	No	D	90	P	Dm	No	2;4
	Pomacentrus nigromarginatus	No	Om	No	D	90	P	Dm	No	138;1;2;3
	Pomacentrus optisthostigma	No	N/A	No	D	80	P	Dm	No	2
	Pomacentrus pavo	No	Pl	No	D	110	P	Dm	No	1;2;3
	Pomacentrus philippinus	No	Pl	No	D	100	P	Dm	No	1;2;3
	Pomacentrus polyspinus	No	N/A	No	D	100	P	Dm	No	2
	Pomacentrus proteus	No	N/A	No	D	100	P	Dm	No	2
	Pomacentrus reidi	No	N/A	No	D	110	P	Dm	No	2
	Pomacentrus saksonoi	No	N/A	No	D	90	P	Dm	No	2
	Pomacentrus similis	No	Om	No	D	70	P	Dm	No	147;2
	Pomacentrus simsiang	No	De	No	D	90	P	Dm	No	138;2
	Pomacentrus smithi	No	Pl	No	D	70	P	Dm	No	138;2
	Pomacentrus spilotoceps	No	N/A	No	D	80	P	Dm	No	2
	Pomacentrus stigma	No	N/A	No	D	120	P	Dm	No	2
	Pomacentrus taeniometopon	No	De	No	D	100	P	Dm	No	2;4
	Pomacentrus tripunctatus	No	De	No	D	100	P	Dm	No	1;2;144
	Pomacentrus vaiuli	No	Om	No	D	100	P	Dm	No	2;3
	Pomacentrus wardi	No	De	No	D	100	P	Dm	No	138;1;2;144
	Pomacentrus yoshii	No	N/A	No	D	80	P	Dm	No	2;3
	Pomachromis fuscidorsalis	No	Pl	No	D	85	P	Dm	No	3
	Pomachromis guamensis	No	Pl	No	D	55	P	Dm	No	2
	Pomachromis richardsoni	No	N/A	No	D	55	P	Dm	No	1;2;3
	Premnas biaculeatus	Yes	Om	No	D	80	P	Dm	No	2;4
	Pristotis obtusirostris	No	Pl	No	D	100	P	Dm	No	2;3
	Stegastes albifasciatus	No	De	No	D	110	P	Dm	No	1;2;3
	Stegastes altus	No	De	No	D	150	P	Dm	No	150;2
	Stegastes apicalis	No	De	No	D	130	P	Dm	No	1;2;144
	Stegastes aureus	No	De	No	D	110	P	Dm	No	1;2;3;4
	Stegastes emeryi	No	N/A	No	D	90	P	Dm	No	3
	Stegastes fasciolatus	No	De	No	D	110	P	Dm	Yes	151;1;2;3
	Stegastes gascoynei	No	De	No	D	150	P	Dm	No	1;2;3;4
	Stegastes lividus	No	De	No	D	150	P	Dm	No	1;2;3
	Stegastes nigricans	No	De	No	D	140	P	Dm	No	1;2;3
	Stegastes obreptus	No	De	No	D	150	P	Dm	No	2;149
	Stegastes punctatus	No	De	No	D	150	P	Dm	No	3
Priacanthidae	*Heteropriacanthus cruentatus*	No	Ca	No	N	320	G	Br	No	4
	Priacanthus blochii	No	Pl	No	N	350	G	Br	No	12
	Priacanthus hamrur	No	Ca	No	N	400	G	Br	No	4
	Pristigenys niphonia	No	N/A	No	N	350	G	Br	No	1;2;3
Pseudochromidae	*Amsichthys knighti*	No	N/A	No	D	45	P	Dm	No	1
	Congrogadus subducens	No	Ca	No	D	450	P	Dm	No	1;2;3;125
	Cypho purparescens	Yes	N/A	No	D	75	P	Dm	No	1;2
	Labracinus cyclyphthalmus	Yes	Ca	No	D	200	P	Dm	No	1;2;88

	Labracinus lineatus	No	N/A	No	D	250	P	Dm	No	2
	Lubbockichthys multisquamatus	No	Mi	No	D	75	P	Dm	No	1;2;152
	Manonichthys polynemus	No	N/A	No	D	120	P	Dm	No	2;4
	Manonichthys splendens	Yes	N/A	No	D	130	P	Dm	No	2;4
	Ogilbyina novaehollandiae	Yes	N/A	No	D	100	P	Dm	No	1;2
	Ogilbyina queenslandiae	No	N/A	No	D	150	P	Dm	No	1;2
	Ogilbyina salvati	N/A	N/A	No	D	80	P	Dm	No	3
	Ogilbyina velifera	No	N/A	No	D	120	P	Dm	No	1;2
	Pictichromis coralensis	No	N/A	No	D	70	P	Dm	No	3
	Pictichromis paccagnellae	No	N/A	No	D	70	P	Dm	No	1;2
	Pictichromis porphyrea	No	Ma	No	D	70	P	Dm	No	2;3
	Pseudochromis andamanensis	No	N/A	No	D	70	P	Dm	No	2
	Pseudochromis bitaeniatus	No	Ma	No	D	70	P	Dm	No	1;2
	Pseudochromis cyanotaenia	Yes	Mi	No	D	60	P	Dm	No	1;2;4
	Pseudochromis diadema	No	N/A	No	D	60	P	Dm	No	2
	Pseudochromis elongatus	No	Ma	No	D	35	P	Dm	No	2
	Pseudochromis flammicauda	Yes	Ma	No	D	55	P	Dm	No	1;2
	Pseudochromis fuscus	No	Ca	No	D	90	P	Dm	No	1;2;3;153
	Pseudochromis jamesi	No	Ma	No	D	55	P	Dm	No	1;3
	Pseudochromis marshallensis	No	Ma	No	D	70	P	Dm	No	2
	Pseudochromis moorei	Yes	Ma	No	D	100	P	Dm	No	2;4
	Pseudochromis paranox	No	Ma	No	D	70	P	Dm	No	1;2
	Pseudochromis perspicillatus	No	Ma	No	D	120	P	Dm	No	1;2
	Pseudochromis quinquedentatus	No	Ma	No	D	95	P	Dm	No	1
	Pseudochromis ransonneti	No	Ma	No	D	120	P	Dm	No	2
	Pseudochromis steenei	Yes	Ma	No	D	120	P	Dm	No	2
	Pseudochromis wilsoni	No	Ma	No	D	80	P	Dm	No	1;2
	Pseudoplesiops immaculatus	No	N/A	No	D	50	P	Dm	No	1;2
	Pseudoplesiops rosae	No	Ma	No	D	23	P	Dm	No	1;4
	Pseudoplesiops typus	No	N/A	No	D	70	P	Dm	No	1
Ptereleotridae	*Aioliops megastigma*	No	N/A	No	D	30	P	Dm	No	2
	Nemateleotris decora	Yes	Pl	Yes	D	85	P	Dm	Yes	1;2;3;4
	Nemateleotris helfrichi	Yes	Pl	Yes	D	65	P	Dm	Yes	2;3
	Nemateleotris magnifica	Yes	Pl	Yes	D	80	P	Dm	Yes	1;2;3;4
	Oxymetopon compressus	No	N/A	No	D	200	P	Dm	No	2
	Oxymetopon cyanoctenosum	Yes	N/A	Yes	D	200	P	Dm	No	2;4
	Parioglossus formosus	No	N/A	No	D	40	P	Dm	No	2
	Parioglossus interruptus	No	N/A	No	D	30	P	Dm	No	2
	Parioglossus nudus	No	N/A	No	D	20	P	Dm	No	2
	Parioglossus raoi	No	N/A	No	D	30	P	Dm	No	2
	Ptereleotris evides	Yes	Pl	Yes	D	135	P	Dm	Yes	1;2;3;12
	Ptereleotris grammica	Yes	Pl	Yes	D	100	P	Dm	No	1;2;12
	Ptereleotris hanae	Yes	Pl	Yes	D	120	P	Dm	No	1;2;3;12
	Ptereleotris heteroptera	Yes	Pl	Yes	D	120	P	Dm	Yes	1;2;3;4
	Ptereleotris microlepis	Yes	Pl	Yes	D	150	P	Dm	Yes	1;2;3;4
	Ptereleotris monoptera	Yes	Pl	Yes	D	150	P	Dm	Yes	1;2;3;4
	Ptereleotris uroditaenia	No	Pl	No	D	100	P	Dm	No	1;2
	Ptereleotris zebra	No	Pl	No	D	120	P	Dm	No	1;2;3;4
Rachycentridae	*Rachycentron canadum*	No	Ca	No	D	2000	G	Br	No	4
Scatophagidae	*Scatophagus argus*	No	Om	No	D	300	N/A	Dm	No	2;3
	Selenotoca multifasciata	No	N/A	No	D	280	N/A	Dm	No	2
Scombridae	*Acanthocybium solandri*	No	Pi	No	D	2100	G	Br	No	2
	Grammatorcynus bilineatus	No	Ca	No	D	1000	G	Br	No	1;2;3

	Gymnosarda unicolor	No	Pi	No	D	1800	G	Br	No	44;2;3
	Rastrelliger kanagurta	No	Pl	No	D	380	G	Br	No	3
	Sarda orientalis	No	Ca	No	D	1020	G	Br	No	2;4
	Scomberomorus commerson	No	Pi	No	D	2350	G	Br	No	1;2;3
	Thunnus albacares	No	Ca	No	D	2100	G	Br	No	2;4
Scorpaenidae	*Brachypterois serrulata*	No	N/A	No	N	120	P	Gel	No	2
	Dendrochirus biocellatus	No	Pi	No	N	100	P	Gel	No	2;12
	Dendrochirus brachypterus	No	Ma	No	N	170	P	Gel	No	1;2;3;154
	Dendrochirus zebra	No	Ma	No	N	180	P	Gel	No	1;2;3;154
	Ebosia bleekeri	No	N/A	No	N	220	P	Gel	No	2
	Iracundus signifer	No	Pi	No	D	130	P	Gel	No	2;4;155
	Parapterois heterura	No	N/A	No	N	230	P	Gel	No	2
	Parascorpaena mossambica	No	Ma	No	N	100	P	Gel	No	1;2;3;156
	Parascorpaena picta	No	Ma	No	N	150	P	Gel	No	2;154
	Pteroidichthys amboinensis	No	N/A	No	N	120	P	Gel	No	2
	Pterois antennata	No	Ma	No	N	200	P	Gel	No	1;2;3;4
	Pterois kodipungi	No	N/A	No	N	350	P	Gel	No	2
	Pterois miles	No	Ca	No	N	380	P	Gel	No	1;2;3;157
	Pterois mombasae	No	Ma	No	N	160	P	Gel	No	2;154
	Pterois radiata	No	Ma	No	N	240	P	Gel	No	2;154
	Pterois volitans	No	Ca	No	N	380	P	Gel	No	1;2;3;157
	Rhinopias aphanes	No	N/A	No	D	240	P	Gel	No	2
	Rhinopias eschmeyeri	No	N/A	No	D	190	P	Gel	No	2
	Rhinopias frondosa	No	Ca	No	N	230	P	Gel	No	2;4
	Scorpaenodes guamensis	No	Ma	No	N	140	P	Gel	No	1;2;3;154
	Scorpaenodes hirsutus	No	Ma	No	N	70	P	Gel	No	1;2;3;154
	Scorpaenodes kelloggi	No	Ma	No	D	48	P	Gel	No	3;158
	Scorpaenodes littoralis	No	Ma	No	N	80	P	Gel	No	2
	Scorpaenodes minor	N/A	Ma	No	D	52	P	Gel	No	3
	Scorpaenodes parvipinnis	No	Ma	No	N	130	P	Gel	No	1;2;3;154
	Scorpaenodes quadrispinosus	N/A	Ma	No	D	97	P	Gel	No	3
	Scorpaenodes varipinnis	No	Ma	No	N	70	P	Gel	No	2;154
	Scorpaenopsis diabolus	Yes	Pi	No	D	280	P	Gel	No	1;2;3;12
	Scorpaenopsis macrochir	Yes	N/A	No	D	150	P	Gel	No	2;3;4
	Scorpaenopsis neglecta	No	Pi	No	D	150	P	Gel	No	2;159
	Scorpaenopsis oxycephala	No	Ma	No	D	360	P	Gel	No	2;12
	Scorpaenopsis papuensis	No	N/A	No	D	220	P	Gel	No	2
	Scorpaenopsis possi	No	N/A	No	D	220	P	Gel	No	2;3
	Scorpaenopsis venosa	No	N/A	No	D	200	P	Gel	No	2
	Sebastapistes cyanostigma	No	Ma	No	N	80	P	Gel	No	1;2;3;4
	Sebastapistes mauritiana	No	Pi	No	N	80	P	Gel	No	2
	Sebastapistes strongia	No	Pi	No	N	95	P	Gel	No	3;4
	Taenianotus triacanthus	Yes	Ca	No	D	100	P	Gel	No	1;2;3;4
Serranidae	*Aethaloperca rogaa*	No	Pi	No	D	600	P	Br	No	1;3;154
	Anyperodon leucogrammicus	No	Pi	No	D	520	P	Br	No	1;2;3
	Aporops bilinearis	N/A	N/A	No	D	115	P	Br	No	1;3
	Belonoperca chabanaudi	No	Ma	No	D	150	P	Br	No	1;2;3;12
	Belonoperca pylei	N/A	N/A	No	D	80	P	Br	No	1;3
	Cephalopholis argus	No	Pi	No	D	550	G	Br	No	1;2;3;154
	Cephalopholis boenak	No	Ca	No	D	260	P	Br	No	1;2;3;4
	Cephalopholis cyanostigma	No	Ca	No	D	300	P	Br	No	1;2;4
	Cephalopholis formosa	No	N/A	No	D	340	P	Br	No	1;2
	Cephalopholis leopardus	No	Pi	No	D	200	P	Br	No	1;2;3;12

Cephalopholis microprion	No	Ca	No	D	240	P	Br	No	1;2;3;40;160
Cephalopholis miniata	No	Pi	No	D	410	G	Br	No	1;2;3;12
Cephalopholis polleni	No	N/A	No	D	430	P	Br	No	2;3
Cephalopholis sexmaculata	No	Pi	No	D	480	G	Br	No	1;2;3;12
Cephalopholis sonnerati	No	Ma	No	D	570	G	Br	No	1;2;3;154
Cephalopholis spiloparaea	No	Pi	No	D	220	P	Br	No	1;2;3;12
Cephalopholis urodeta	No	Pi	No	D	270	G	Br	No	1;2;3;12
Cromileptes altivelis	No	Ca	No	D	700	P	Br	No	1;2;3;4
Diploprion bifasciatum	No	Ca	No	D	250	P	Br	No	1;2;3;88;161
Epinephelus areolatus	No	Ca	No	D	400	G	Br	No	1;2;3;4
Epinephelus bilobatus	No	N/A	No	D	330	G	Br	No	2
Epinephelus bleekeri	No	Ca	No	D	750	G	Br	No	2;24
Epinephelus bontoides	No	N/A	No	D	300	G	Br	No	2
Epinephelus caerulopunctatus	No	Ca	No	D	600	G	Br	No	1;2;3;4
Epinephelus chlorostigma	No	Ca	No	D	750	G	Br	No	2;4
Epinephelus coioides	No	Ca	No	D	950	G	Br	No	1;2;3;4
Epinephelus corallicola	No	N/A	No	D	490	G	Br	No	1;2
Epinephelus cyanopodus	No	Pi	No	D	120	G	Br	No	1;2;3;12
Epinephelus erythrurus	No	N/A	No	D	430	G	Br	No	2
Epinephelus fasciatus	No	Ca	No	D	400	G	Br	No	1;2;3;154
Epinephelus fuscoguttatus	No	Ca	No	D	1000	G	Br	No	1;2;3;154;44
Epinephelus hexagonatus	No	Ca	No	D	260	G	Br	No	1;2;3;154
Epinephelus howlandi	No	Pi	No	D	440	G	Br	No	1;2;3;12
Epinephelus irroratus	No	N/A	No	D	340	G	Br	No	3
Epinephelus lanceolatus	No	Ca	No	D	2340	G	Br	No	1;2;3;4
Epinephelus longispinis	No	Ma	No	D	500	G	Br	No	2;4
Epinephelus macrospilos	No	Ca	No	D	430	G	Br	No	1;2;3;154
Epinephelus maculatus	No	Ca	No	D	600	G	Br	No	1;2;3;4
Epinephelus malabricus	No	Ca	No	D	2340	G	Br	No	1;2;3;4
Epinephelus melanostigma	No	Pi	No	D	330	G	Br	No	2;3;12
Epinephelus merra	No	Ca	No	D	320	G	Br	No	1;2;3
Epinephelus miliaris	No	Ma	No	D	530	G	Br	No	2;3;4
Epinephelus multinotatus	No	Ca	No	D	1000	G	Br	No	2;4
Epinephelus ongus	No	Ca	No	D	350	G	Br	No	1;2;3;162
Epinephelus polyphekadion	No	Ca	No	D	610	G	Br	No	1;2;3
Epinephelus quoyanus	No	Ca	No	D	380	G	Br	No	1;2;4
Epinephelus retouti	No	N/A	No	D	470	G	Br	No	3
Epinephelus rivulatus	No	Ca	No	D	450	G	Br	No	1;2;3;4
Epinephelus socialis	No	Pi	No	D	420	G	Br	No	2;3;12
Epinephelus spilotoceps	No	Ca	No	D	310	G	Br	No	2;4
Epinephelus tauvina	No	Pi	No	D	330	G	Br	No	1;2;3;12
Epinephelus tukula	No	Ca	No	D	2000	G	Br	No	1;2;3;4
Epinephelus undulosus	No	Ca	No	D	500	G	Br	No	2;4
Epinephelus waandersi	No	N/A	No	D	600	G	Br	No	2
Gracilo albomarginata	No	Pi	No	D	500	N/A	Br	No	1;2;3;12
Grammistes sexlineatus	No	Pi	No	D	270	N/A	Br	No	1;2;3;4
Grammistops ocellatus	Yes	N/A	No	D	130	N/A	Gel	No	1;2;3
Liopropoma flavidum	N/A	N/A	No	D	61	N/A	Br	No	3
Liopropoma latifasciatum	N/A	N/A	No	D	160	N/A	Br	No	2
Liopropoma mitratum	N/A	N/A	No	D	82	N/A	Br	No	3
Liopropoma multilineatum	N/A	N/A	No	D	77	N/A	Br	No	3
Liopropoma pallidum	N/A	N/A	No	D	78	N/A	Br	No	3
Liopropoma susumi	N/A	N/A	No	D	91	N/A	Br	No	3

Liopropoma tonstrinum	N/A	N/A	No	D	80	N/A	Br	No	3
Luzonichthys earlei	No	Pl	No	D	44	N/A	Br	No	2
Luzonichthys waitei	No	Pl	No	D	70	N/A	Br	No	1;2;3;12
Luzonichthys whitleyi	No	Pl	No	D	60	N/A	Br	No	2;3
Luzonichthys williamsi	No	N/A	No	D	58	N/A	Br	No	3
Plectranthias inermis	No	N/A	No	D	350	N/A	Br	No	2;4
Plectranthias longimanus	No	N/A	No	D	350	N/A	Br	No	1;2;3
Plectranthias nanus	No	N/A	No	D	50	N/A	Br	No	1;2;3
Plectranthias winniensis	No	N/A	No	D	350	N/A	Br	No	1;2;3
Plectropomus areolatus	No	Pi	No	D	800	G	Br	No	1;2;3;12
Plectropomus laevis	No	Pi	No	D	1250	G	Br	No	1;2;3;12
Plectropomus leopardus	No	Pi	No	D	700	G	Br	No	1;2;3;12
Plectropomus maculatus	No	Pi	No	D	1250	G	Br	No	1;2;3
Plectropomus oligacanthus	No	Ca	No	D	750	G	Br	No	1;2;3;4
Plectropomus pessuliferus	No	Pi	No	D	1200	G	Br	No	1;2;3;12
Pogonoperca punctata	Yes	Pi	No	D	350	N/A	Gel	No	1;2;3;12
Pseudanthias aurulentus	No	Pl	No	D	60	P	Br	No	2
Pseudanthias bartlettorum	No	Pl	No	D	90	P	Br	No	2;3
Pseudanthias bicolor	No	Pl	No	D	130	P	Br	No	1;2;3;12
Pseudanthias bimaculatus	No	Pl	No	D	90	P	Br	No	2
Pseudanthias carlsoni	No	Pl	No	D	100	P	Br	No	3
Pseudanthias cooperi	No	Pl	No	D	140	P	Br	No	1;2;3
Pseudanthias dispar	No	Pl	No	D	95	P	Br	No	1;2;3
Pseudanthias engelhardi	No	Pl	No	D	100	P	Br	No	1;2;3
Pseudanthias evansi	No	Pl	No	D	100	P	Br	No	2
Pseudanthias fasciatus	No	Pl	No	D	210	P	Br	No	1;2
Pseudanthias flavoguttatus	No	Pl	No	D	110	P	Br	No	2
Pseudanthias hiva	No	Pl	No	D	140	P	Br	No	3
Pseudanthias huchti	No	Pl	No	D	120	P	Br	No	1;2
Pseudanthias hutomoi	No	Pl	No	D	120	P	Br	No	2
Pseudanthias hypselosoma	No	Pl	No	D	70	P	Br	No	1;2
Pseudanthias ignitus	No	Pl	No	D	80	P	Br	No	2;4
Pseudanthias lori	No	Pl	No	D	120	P	Br	No	1;2;3
Pseudanthias luzonensis	No	Pl	No	D	145	P	Br	No	1;2
Pseudanthias mooreanus	N/A	Pl	No	D	72	P	Br	No	3
Pseudanthias olivaceus	No	Pl	No	D	120	P	Br	No	2;3
Pseudanthias parvirostris	No	Pl	No	D	100	P	Br	No	2;4
Pseudanthias pascalus	No	Pl	No	D	170	P	Br	No	2;3
Pseudanthias pictilis	No	Pl	No	D	135	P	Br	No	2
Pseudanthias pleurotaenia	No	Pl	No	D	200	P	Br	No	1;2;3;12
Pseudanthias randalli	No	Pl	No	D	70	P	Br	No	2
Pseudanthias regalis	No	Pl	No	D	62	P	Br	No	3
Pseudanthias rubrizonatus	No	Pl	No	D	100	P	Br	No	2;4
Pseudanthias sheni	No	Pl	No	D	200	P	Br	No	2
Pseudanthias smithvanizi	No	Pl	No	D	95	P	Br	No	1;2
Pseudanthias squamipinnis	No	Pl	No	D	150	P	Br	No	1;2;3
Pseudanthias tuka	No	Pl	No	D	120	P	Br	No	1;2
Pseudanthias venator	No	Pl	No	D	70	P	Br	No	2
Pseudanthias ventralis	No	Pl	No	D	70	P	Br	No	1;2;3;12
Pseudogramma polyacanthum	No	Mi	No	D	75	N/A	Br	No	1;2;3
Serranocirrhitus latus	No	N/A	No	D	350	N/A	Br	No	1;2;3
Suttonia lineata	N/A	N/A	No	D	96	N/A	Br	No	3
Variola albimarginata	No	Pi	No	D	550	G	Br	No	1;2;3

	Variola louti	No	Pi	No	D	550	G	Br	No	1;2;3;44
Siganidae	*Siganus argenteus*	No	He	No	D	420	G	Es	No	163;1;2;3;6
	Siganus canaliculatus	No	He	No	D	290	G	Es	No	163;1;2;3;164
	Siganus corallinus	Yes	He	No	D	250	G	Es	No	163;1;2;3;6
	Siganus doliatus	Yes	He	No	D	250	G	Es	No	1;2;3
	Siganus guttatus	No	He	No	D	350	G	Es	No	163;1;2;3
	Siganus javus	Yes	He	No	D	530	G	Es	No	163;1;2;3;165
	Siganus lineatus	No	De	No	D	350	G	Es	No	163;1;2;3;166
	Siganus magnificus	Yes	He	No	D	230	G	Es	No	163;2;4
	Siganus puelloides	Yes	He	No	D	310	G	Es	No	163;2
	Siganus puellus	Yes	Sp	No	D	380	G	Es	No	163;167
	Siganus punctatissimus	Yes	He	No	D	280	G	Es	No	163;2;6
	Siganus punctatus	Yes	He	No	D	300	G	Es	No	163;1;2;3;6
	Siganus randalli	No	He	No	D	250	G	Es	No	163;2
	Siganus spinus	No	He	No	D	200	G	Es	No	163;1;2;3
	Siganus stellatus	Yes	He	No	D	350	G	Es	No	163;2
	Siganus unimaculatus	Yes	He	No	D	240	G	Es	No	163;2;4
	Siganus uspi	Yes	He	No	D	220	G	Es	No	163;2;4
	Siganus vermiculatus	No	He	No	D	370	G	Es	No	163;1;2;3
	Siganus virgatus	No	He	No	D	300	G	Es	No	163;2
	Siganus vulpinus	Yes	He	No	D	240	G	Es	No	163;1;2;3
Soleidae	*Aseraggodes kaianus*	No	Ma	No	D	140	N/A	Br	No	1;2;3;4
	Aseraggodes melanostictus	No	Ma	No	D	40	N/A	Br	No	2
	Liachirus melanospilus	No	Ma	No	D	150	N/A	Br	No	2
	Pardachirus pavoninus	No	Ma	No	N	220	N/A	Br	No	2
	Soleichthys heterorhinos	No	Ma	No	N	150	N/A	Br	No	2
	Synaptura marginata	No	Ma	No	N	300	N/A	Br	No	1;2;3;4
	Zebrias fasciatus	No	Ma	No	N	250	N/A	Br	No	2
Solenostomidae	*Solenostomus cyanopterus*	Yes	Mi	No	D	160	P	Po	Yes	4
	Solenostomus halimeda	Yes	Mi	No	D	70	P	Po	No	1;2;3
	Solenostomus paegnius	Yes	Mi	No	D	120	P	Po	No	4
	Solenostomus paradoxus	Yes	Mi	No	D	110	P	Po	No	1;2;3
Sparidae	*Acanthopagrus berda*	No	Ca	No	D	500	G	Br	No	2;4
Sphyraenidae	*Sphyraena barracuda*	No	Pi	No	D	1800	G	Br	No	1;2;3;168
	Sphyraena flavicauda	No	N/A	No	N	500	G	Br	No	1;2;3;4
	Sphyraena forsteri	No	Ca	No	N	650	G	Br	No	1;2;3;4
	Sphyraena helleri	No	N/A	No	N	850	G	Br	No	1;2;3;4
	Sphyraena jello	No	Ca	No	D	1500	G	Br	No	1;2;3;169
	Sphyraena qenie	No	Pi	No	N	1000	G	Br	No	1;2;3;40
Synanceiidae	*Choridactylus multibarbus*	No	N/A	No	D	120	P	Gel	No	2
	Dampierosa daruma	No	N/A	No	D	130	P	Gel	No	2
	Inimicus caledonicus	No	N/A	No	D	250	P	Gel	No	2;3
	Inimicus didactylus	Yes	Ca	No	D	180	P	Gel	No	1;2;3;4
	Inimicus sinensis	No	N/A	No	D	180	P	Gel	No	2
	Minous trachycephalus	No	N/A	No	N	90	P	Gel	No	2;4
	Synanceia horridas	No	Ca	No	N	300	P	Gel	No	1;2;3
	Synanceia verrucosa	No	Ca	No	D	350	P	Gel	No	2;4
Syngnathidae	*Acentronura breviperula*	Yes	Mi	No	D	50	P	Po	No	1;2;3
	Choeroichthys brachysoma	No	Mi	No	D	65	P	Po	No	1;2;3
	Choeroichthys cinctus	No	Mi	No	D	80	P	Po	No	1;2;3
	Corythoichthys amplexus	Yes	Mi	No	D	95	P	Po	Yes	170
	Corythoichthys flavofasciatus	Yes	Mi	No	D	180	P	Po	Yes	171
	Corythoichthys haematopterus	Yes	Mi	No	D	180	P	Po	Yes	1;2;3

	Corythoichthys intestinalis	Yes	Mi	No	D	180	P	Po	Yes	170
	Corythoichthys nigripectus	Yes	Mi	No	D	110	P	Po	Yes	1;2;3
	Corythoichthys ocellatus	Yes	Mi	No	D	110	P	Po	No	1;2;3
	Corythoichthys polynotatus	Yes	Mi	No	D	160	P	Po	No	1;2;3
	Corythoichthys schultzi	Yes	Mi	No	D	160	P	Po	Yes	1;2;3
	Doryrhamphus excisus	Yes	Mi	No	D	70	P	Po	Yes	4
	Doryrhamphus janssi	Yes	Mi	No	D	130	P	Po	No	4
	Doryrhamphus japonicus	Yes	Mi	No	D	70	P	Po	Yes	4
	Doryrhamphus negrosensis	Yes	Mi	No	D	55	P	Po	No	1;2;3
	Dunckerocampus boylei	Yes	Mi	No	D	160	P	Po	No	1;2;3
	Dunckerocampus dactyliophorus	Yes	Mi	No	D	180	P	Po	No	172
	Dunckerocampus multiannulatus	Yes	Mi	No	D	180	P	Po	No	1;2;3
	Dunckerocampus pessuliferus	Yes	Mi	No	D	160	P	Po	No	172
	Halicampus brocki	No	N/A	No	D	115	P	Po	No	1;2;3
	Halicampus macrorhynchus	Yes	N/A	No	D	160	P	Po	No	4
	Halicampus mataafae	No	N/A	No	D	150	P	Po	No	1;2;3
	Halicampus nitidus	No	N/A	No	D	75	P	Po	No	1;2;3
	Hippichthys cyanospilos	No	N/A	No	D	160	P	Po	No	1;2;3
	Hippocampus barbouri	No	N/A	No	D	150	P	Po	No	1;2;3
	Hippocampus bargibanti	Yes	Mi	No	D	20	P	Po	No	173;174
	Hippocampus colemani	No	Mi	No	D	10	P	Po	No	1;2;3
	Hippocampus comes	Yes	Mi	No	N	160	P	Po	Yes	4
	Hippocampus denise	No	Mi	No	D	15	P	Po	No	174
	Hippocampus hystrix	No	Mi	No	D	150	P	Po	Yes	174
	Hippocampus kuda	Yes	Mi	No	D	150	P	Po	No	4
	Hippocampus trimaculatus	No	Mi	No	D	220	P	Po	No	174
	Micrognathus andersonii	No	N/A	No	D	60	P	Po	No	1;2;3
	Micrognathus pygmaeus	No	N/A	No	D	60	P	Po	No	1;2;3
	Phoxocampus tetrophthalmus	No	N/A	No	D	80	P	Po	No	1;2;3
	Siokunichthys nigrolineatus	No	N/A	No	D	400	P	Po	No	1;2;3
	Syngnathoides biaculeatus	Yes	Mi	No	D	280	P	Po	No	175
	Trachyrhamphus bicoarctatus	No	N/A	No	D	400	P	Po	No	1;2;3
	Trachyrhamphus longirostris	No	N/A	No	D	400	P	Po	No	1;2;3
Synodontidae	*Saurida gracilis*	No	Pi	No	N	280	P	Br	No	1;2;3;4
	Saurida nebulosa	No	Pi	No	D	200	P	Br	No	1;2;3
	Synodus binotatus	Yes	Pi	No	D	170	P	Br	No	1;2;3;12
	Synodus dermatogenys	Yes	Pi	No	D	200	P	Br	No	1;2;3;160
	Synodus jaculum	Yes	Pi	No	D	140	P	Br	No	1;2;3;12
	Synodus rubromarmoratus	No	Pi	No	D	85	P	Br	No	1;2;3
	Synodus variegatus	Yes	Pi	No	D	240	P	Br	No	1;2;3;12
	Trachinocephalus myops	No	Ca	No	D	250	P	Br	No	1;2;3;176
Tetraodontidae	*Arothron caeruleopunctatus*	No	Om	No	D	700	G	Es	No	1;2;3
	Arothron hispidus	No	Om	No	D	480	G	Es	No	4
	Arothron immaculatus	No	Om	No	D	280	G	Es	No	175
	Arothron manilensis	No	Om	No	D	310	G	Es	No	15
	Arothron mappa	No	Om	No	D	600	G	Es	No	1;2;3
	Arothron meleagris	No	Co	No	D	500	G	Es	No	77
	Arothron nigropunctatus	Yes	Co	No	D	330	G	Es	No	77
	Arothron reticularis	No	Ma	No	D	300	G	Es	No	4
	Arothron stellatus	No	Om	No	D	900	G	Es	No	1;2;3
	Canthigaster amboinensis	No	Om	No	D	140	P	Dm	No	177
	Canthigaster bennetti	Yes	He	No	D	100	P	Dm	Yes	4;178
	Canthigaster callisterna	Yes	N/A	No	D	240	P	Dm	No	1;2;3

	Canthigaster compressa	Yes	Mi	No	D	100	P	Dm	No	107;4
	Canthigaster coronata	No	Om	No	D	135	P	Dm	No	4
	Canthigaster epilampra	Yes	Om	No	D	110	P	Dm	No	4
	Canthigaster janthinoptera	Yes	Om	No	D	90	P	Dm	No	4
	Canthigaster leoparda	Yes	N/A	No	D	70	P	Dm	No	1;2;3
	Canthigaster ocellicincta	Yes	N/A	No	D	65	P	Dm	No	4
	Canthigaster papua	Yes	Mi	No	D	90	P	Dm	No	107
	Canthigaster rivulata	No	N/A	No	D	180	P	Dm	No	1;2;3
	Canthigaster smithae	No	N/A	No	D	130	P	Dm	No	1;2;3
	Canthigaster solandri	Yes	Om	No	D	105	P	Dm	No	4;178
	Canthigaster tyleri	No	Om	No	D	80	P	Dm	No	4
	Canthigaster valentini	Yes	Om	No	D	90	P	Dm	Yes	4;178
	Chelonodon patoca	No	Om	No	D	330	P	Dm	No	179
	Lagocephalus sceleratus	No	Ca	No	D	850	P	Dm	No	180;181
	Torquigener brevipinnis	No	N/A	No	D	140	P	Dm	No	1;2;3
Tetrarogidae	*Ablabys macracanthus*	Yes	N/A	No	D	150	P	Br	No	2
	Ablabys taenianotus	Yes	Ca	No	N	150	P	Br	No	1;2;3;20
	Paracentropogon longispinus	No	N/A	No	D	120	P	Br	No	2
	Richardsonichthys leucogaster	No	N/A	No	N	100	P	Br	No	2;4
	Tetraroge barbata	Yes	Ca	No	D	110	P	Br	No	2;4
	Tetraroge niger	Yes	N/A	No	D	135	P	Br	No	2
Trichonotidae	*Trichonotus elegans*	No	Ma	No	D	180	N/A	N/A	No	1;2;3;182
	Trichonotus halsteadi	No	Ma	No	D	150	N/A	N/A	No	2;182
	Trichonotus setiger	No	Ma	No	D	180	N/A	N/A	No	1;2;3;182
Tripterygiidae	*Ceratobregma helenae*	No	N/A	No	D	45	P	Dm	No	1;2;3
	Enneapterygius atrogulare	Yes	Om	No	D	53	P	Dm	No	3;73
	Enneapterygius elegans	N/A	N/A	No	D	35	P	Dm	No	3
	Enneapterygius flavoccipitis	Yes	N/A	No	D	35	P	Dm	No	2
	Enneapterygius hemimelas	N/A	N/A	No	D	48	P	Dm	No	3
	Enneapterygius mirabilis	No	N/A	No	D	35	P	Dm	No	1;2
	Enneapterygius nanus	N/A	N/A	No	D	28	P	Dm	No	3
	Enneapterygius niger	N/A	N/A	No	D	35	P	Dm	No	3
	Enneapterygius nigricauda	N/A	N/A	No	D	35	P	Dm	No	3
	Enneapterygius pallidoserialis	Yes	N/A	No	D	35	P	Dm	No	2
	Enneapterygius paucifasciatus	N/A	N/A	No	D	35	P	Dm	No	3
	Enneapterygius philippinus	Yes	N/A	No	D	35	P	Dm	No	2
	Enneapterygius pyramis	N/A	N/A	No	D	34	P	Dm	No	3
	Enneapterygius randalli	N/A	N/A	No	D	34	P	Dm	No	3
	Enneapterygius rhabdotus	N/A	N/A	No	D	32	P	Dm	No	3
	Enneapterygius rhothion	N/A	N/A	No	D	37	P	Dm	No	3
	Enneapterygius rufopileus	No	Mi	No	D	45	P	Dm	No	3;183
	Enneapterygius similis	N/A	N/A	No	D	39	P	Dm	No	3
	Enneapterygius triserialis	N/A	N/A	No	D	45	P	Dm	No	3
	Enneapterygius williamsi	N/A	N/A	No	D	33	P	Dm	No	3
	Helcogramma capidatum	No	N/A	No	D	41	P	Dm	No	3
	Helcogramma chica	No	Om	No	D	40	P	Dm	No	3;184
	Helcogramma rhinoceros	Yes	N/A	No	D	40	P	Dm	No	2
	Helcogramma striatum	No	Pl	No	D	50	P	Dm	No	1;2;3;4
	Helcogramma vulcanum	Yes	N/A	No	D	40	P	Dm	No	2
	Norfolkia brachylepis	N/A	N/A	No	D	73	P	Dm	No	3
	Norfolkia squamiceps	N/A	N/A	No	D	66	P	Dm	No	3
	Norfolkia thomasi	N/A	N/A	No	D	50	P	Dm	No	3
	Springerichthys kulbickii	N/A	N/A	No	D	35	P	Dm	No	3

	Ucla xenogrammus	No	N/A	No	D	45	P	Dm	No	1;2;3
Uranoscopidae	*Uranoscopus sulphureus*	No	N/A	No	D	350	N/A	N/A	No	2
Zanclidae	*Zanclus cornutus*	Yes	Om	No	D	160	G	Br	No	1;2;3

1: Randall et al. 1997; 2: Allen et al. 2003; 3: Randall 2005; 4: Froese & Pauly 2012; 5: Barlow 1974; 6: Cheal et al. 2012; 7: Russ 1984; 8: Robertson et al. 1979; 9: Brandl & Bellwood 2013b; 10: Randall & Struhsacker 1981; 11: Meyer-Rochow 1976; 12: Sandin & Williams 2010; 13: Pietsch & Grobecker 1987; 14: Nakane et al. 2011; 15: Nanjo et al. 2008; 16: Marnane & Bellwood 2002; 17: Zagars et al. 2013; 18: Barnett & Bellwood 2006; 19: Job & Shand 2001; 20: Unsworth et al. 2007; 21: Unsworth et al. 2009; 22: Schmitz & Wainwright 2011; 23: Fukumori et al. 2008; 24: Hajisamae 2009; 25: Longenecker & Langston 2006; 26: Nakamura et al. 2006; 27: Kuwamura 1991; 28: Chen et al. 2005; 29: Wilson 2000; 30: Ho et al. 2007; 31: Carlson 2012; 32: Roberts 1987; 33: Kwak et al. 2004; 34: Townsend & Tibbetts 2000; 35: Hamner et al. 1988; 36: Fricke & Zaiser 1982; 37: Grandcourt et al. 2004; 38: Salini et al. 1994; 39: Farmer & Wilson 2011; 40: Blaber et al. 1990; 41: Meyer et al. 2001; 42: Brewer et al. 1989; 43: Smith & Parrish 2002; 44: Randall 1980; 45: Blaber & Cyrus 1983; 46: Sreenivasan 1974; 47: Tandon 1960; 48: Barreiros et al. 2003; 49: Roberts & Ormond 1992; 50: Pratchett et al. 2006; 51: Reese 1975; 52: Sano 1989; 53: Allen et al. 1998; 54: Claydon 2004; 55: Pratchett 2005; 56: Reavis & Copus 2011; 57: Yabuta & Kawashima 1997; 58: Ferry-Graham et al. 2001; 59: Bellwood et al. 2010; 60: Donaldson 1990; 61: Kadota et al. 2011; 62: Donaldson 1989; 63: Kane et al. 2009; 64: Clemente et al. 2010; 65: Bellwood et al. 2006a; 66: Taquet et al. 2007; 67: Sakashita 1992; 68: Hernaman et al. 2009; 69: Kramer et al. 2012b; 70: Depczynski & Bellwood 2003; 71: Herler et al. 2011; 72: Allen & Munday 1995; 73: White & Brown 2013; 74: Munday et al. 2002; 75: Karplus 1979; 76: Brooker et al. 2010; 77: Cole et al. 2008; 78: Randall & Goren 1993; 79: Daroonchoo 1991; 80: Sano et al. 1984; 81: Hagiwara & Winterbottom 2007; 82: Winterbottom 1984; 83: Clark et al. 2000; 84: Reavis & Barlow 1998; 85: Randall 1998; 86: Clements & Choat 1997; 86: Rimmer & Wiebe 1987; 87: DiSalvo et al. 2007; 88: Williams & Williams 1986; 89: Bellwood et al. 2003; 90: Muñoz et al. 2006; 91: Ferry-Graham et al. 2002; 92: Choat et al. 2004; 93: Lek et al. 2011; 94: Pratchett et al. 2001; 95: Debenay et al. 2011; 96: Connell 1998; 97: Nanami & Yamada 2008; 98: Kiso & Mahyam 2003; 99: Sweatman 1992: 100: Salini et al. 1990; 101: Bonin et al. 2011; 102: Clark et al. 1998; 103: Clark & Pohle 1992; 104: López-Peralta & Arcilla 2002; 105: Harmelin-Vivien 1979; 106: Kokita & Mizota 2002; 107: Wantiez & Kulbicki 1995; 108: Blaber 1977; 109: McCormick

1995; 110: Randall & Myers 2002; 111: Randall 2004; 112: Letourneur 1996; 113: Golani & Galil 1991; 114: Sabrah & El-Ganainy 2009; 115: Mehta 2008; 116: Reece et al. 2010; 117: Mequila & Campos 2007; 118: Boaden & Kingsford 2012; 119: Russell 1997; 120: Hiatt & Strasburg 1960; 121: Tamaki et al. 1992; 122: Moyer & Sano 1987; 123: Metian et al. 2013; 124: Sivakumar & Ramaiyan 1987; 125: Mooi & Gill 2004; 126: Ang & Manica 2010; 127: Moyer & Nakazono 1978; 128: Pyle 2003; 129: Mantyka & Bellwood 2007; 130: Hensley & Allen 1977; 131: Frédérich et al. 2009: 132: Williams & Hatcher 1983; 133: Fautin & Allen 1992; 134: Fricke & Fricke 1977; 135: Hobson 1991; 136: Tribble & Nishikawa 1982; 137: Wenger et al. 2012; 138: Allen 1991; 139: Sackley & Kaufman 1996; 140: Gluckmann & Vandewalle 1998; 141: Allen & Rajasuriya 1995; 142: Randall & Allen 1977; 143: Elliot & Bellwood 2003; 144: Ceccarelli 2007; 145: Bellwood et al. 2006b; 146: Horn 1989; 147: Öhmann et al. 1998; 148: Lewis 1998; 149: Hamilton & Dill 2003; 150: Kohda 1981; 151: Russ 1987; 152: Allen 1987; 153: Feeney et al. 2012; 154: Harmelin-Vivien & Bouchon 1976; 155: Shallenberger & Madden 1973; 156: Marguillier et al. 1997; 157: Muñoz et al. 2011; 158: Longenecker 2007; 159: Barros et al. 2008; 160: Holmes & McCormick 2011; 161: Stewart & Jones 2001; 162: Craig 2007; 163: Woodland 1990; 164: Fox & Bellwood 2008; 165: Cvitanovic & Bellwood 2009; 166: Fox et al. 2009; 167: Hoey et al. 2013; 168: Grubich et al. 2008; 169: Hajisamae et al. 2003; 170: Gronell 1984; 171: Iyer 2012; 172: Leysen et al. 2011; 173: Lourie & Randall 2003; 174: Foster & Vincent 2004; 175: Horinouchi et al. 2012; 176: Kizhakudan & Gomathy 2007; 177: Sikkel & Sikkel 2012; 178: Sikkel 1990; 179: Beumer 1978; 180: Sabrah et al. 2006; 181: Aydin 2011; 182: Clark & Pohle 1996; 183: Silberschneider & Booth 2001; 184: Hadley Hansen 1986