NOTE

Foraging and microhabitat use by crustacean-feeding wrasses on coral reefs

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ABSTRACT: Crustaceans are an important component of coral reef ecosystems, occupying a broad range of microhabitats, but achieving the greatest biomass in dead coral and coral rubble. These 2 microhabitats are therefore hypothesised to be focal foraging locations for crustacean-feeding fishes. The present study investigated the relationship between foraging in wrasses (Labridae), a major group of crustacean predators, and 5 major microhabitats on a coral reef: live coral, dead coral, coral rubble, sand and the epilithic algal matrix (EAM). Although the greatest biomass of crustaceans typically occurs in dead coral and coral rubble, crustacean-feeding wrasses displayed positive selection for a more diverse range of microhabitats. In contrast, sand and live coral were not positively selected by any taxa. The relationships between crustacean predators and their prey appear to be more complicated than previously assumed, and may be mediated by habitat structure, preferred prey, predation risk and behavioural and morphological adaptations.

KEY WORDS: Crustacea · Labridae · Foraging · Dead coral · Coral rubble · Predation

INTRODUCTION

Crustaceans are one of the most widespread and abundant groups of marine invertebrates. On coral reefs, crustaceans are both diverse and abundant (Plaisance et al. 2009, Stella et al. 2011, Kramer et al. 2014), which enables them to perform a wide range of functional roles including scavenging dead material, predation, cleaning fishes, clearing sediments, parasitism and defending coral colonies (Keable 1995, Becker & Grutter 2004, Stewart et al. 2006, Pollock et al. 2013, Rouzé et al. 2014). However, their most influential role is arguably in trophic pathways, as prey for higher-level consumers (Glynn & Enochs 2011, Kramer et al. 2013, 2015).

Although crustaceans are common on coral reefs, recent work has indicated that their abundance and biomass vary greatly among microhabitats. Dead coral and coral rubble are particularly crustacean-rich, whereas live coral supports very low abundances (Kramer et al. 2014). As crustaceans are a valuable source of energy and nutrition for a wide range of fishes (Randall et al. 1997, Kramer et al. 2015) it is likely that their availability influences the trophic relationship between microhabitats and small benthic predators (Syms & Jones 2000, Berkström et al. 2012). Fish feeding on crustaceans, therefore, would be expected to forage primarily around dead corals, where the density and biomass of Crustacea is highest (Kramer et al. 2014). However, information on the re-

lationship between coral reef microhabitats and the foraging habits of crustacean predators is limited (but see Fulton & Bellwood 2002, Layton & Fulton 2014).

Benthic crustaceans are the dominant prey for approximately 50% of all fish species on the Great Barrier Reef (GBR) (Froese & Pauly 2014, Kramer et al. 2015). One family in particular, the wrasses (Labridae), contains one of the highest proportions of crustacean-feeding species, in addition to being one of the most diverse and abundant families of coral reef fishes (Randall et al. 1997, Bellwood et al. 2006). Wrasses exhibit unusual morphologies and behaviours that allow them to exploit resources from a wide range of microhabitats (Wainwright et al. 2004, Bellwood et al. 2006). Recent studies also indicate that there is a division between micro- and macro-crustacean feeding taxa, with separation related to a standard length greater or less than approximately 90 mm, respectively (Kramer et al. 2015). This trophic division within crustacean predators may influence their choice of microhabitat in which to forage. Foraging patterns of many fishes are governed largely by the capacity of specific microhabitats to yield their preferred prey (Berumen et al. 2005). The morphological and functional diversity within wrasses, therefore, provides an opportunity to investigate how these fishes utilise coral reef microhabitats in the context of the distribution of their crustacean prey.

MATERIALS AND METHODS

Observations were conducted in February 2014 at Lizard Island (14° 40′ 40″ S, 145° 26′ 55″ E), a mid-shelf island in the Northern Great Barrier Reef, Australia. Two locations on the fringing reef were selected for surveys: Mermaid Cove and Lagoon Entrance. The fringing reef at each location was a typical fringing reef with a reef flat, crest and slope that reached a sandy base at approximately 6 m depth. Microhabitats at each location included live coral (branching: primarily *Acropora* spp.; massive: primarily *Porites* spp.; other: assorted non-branching taxa), dead coral (intact *Acropora* spp. skeletons devoid of live coral tissue), coral rubble (accumulated fragments of dead coral), sand (soft calcareous sediment) and the EAM (epilithic algal matrix, sensu Wilson et al. 2003: flat areas dominated by short filamentous algae). Benthic composition, and hence habitat availability, was determined using planar photographic transects and the image analysis software ImageJ (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m548p277_supp.pdf for de-

tailed microhabitat cover data). This study was conducted at the same locations and sites as in Kramer et al. (2014), with no ecological disruption (e.g. cyclone or bleaching event) occurring between the 2 studies. For the purpose of the selectivity index, branching coral abundance was used for live coral since it is known to shelter prey, whereas other live coral morphologies (e.g. massive) are lacking in crustaceans.

As wrasses are diurnal predators, foraging surveys occurred between 09:00 and 16:00 h. Survey swims focussed on the crest region in an area that extended approximately 10 m onto the reef flat and down the slope, respectively. An area of approximately 3000 m^2 was surveyed at each location for 1 h and replicated over 6 non-consecutive days, resulting in 12 survey swims and 1145 individual observations. When a wrasse (Labridae, not including parrotfish) was sighted, the individual was identified to species level, and its activity and microhabitat association in the first 3 s of observation recorded. Activity was defined as either foraging (searching or feeding) or swimming. This was repeated daily until a minimum cumulative total of 10 foraging observations were recorded for each species (mean no. of foraging observations = 25 species^{-1}; see Table S2 in the Supplement). Juveniles were not recorded to avoid shifts in diet or habitat during ontogeny (Dahlgren & Eggleston 2000), and care was taken to avoid observing the same individual in a single survey swim by using a non-overlapping path, while independence was maximised by ensuring over 24 h had elapsed between observations at a location, and trying to avoid individuals of similar size and colour between successive observation periods.

Data were analysed using the 'sampling design 1 protocol A' procedure outlined by Manly et al. (2002) to determine habitat selectivity by each species. Confidence intervals (95% CI) were constructed by applying a Bonferroni inequality adjustment ($z_{\alpha/2I}$, where $\alpha = 0.05$ and I = number of microhabitats) to the standard error of the standardised selection ratio (Manly et al. 2002). CIs served to indicate the significance of positive or negative selection. A chi-squared test (df = 1) was also conducted to determine if the microhabitat utilisation patterns differed from random expectations based on microhabitat availability. A non-metric multidimensional scaling (nMDS) ordination was then conducted on a Bray-Curtis matrix of the standardised selection ratios (from the selection index of Manly et al. 2002) to graphically represent habitat selection. Ward's cluster analysis was used to determine clusters, of which 6 were identified based on a within-groups sum of squares by number of clusters scree plot (Everitt & Hothorn 2010).

RESULTS

A total of 24 wrasse species were observed foraging during the study period. The proportion of foraging time ranged from 27.5% in *Thalassoma lunare* to 83.6% in *Stethojulis bandanensis* (see Table S2 in the Supplement at www.int-res.com/articles/suppl/m548p277_supp.pdf).

In terms of habitat selection, 15 (62.5%) of the 24 species exhibited positive microhabitat selection when foraging. Of the available microhabitats, dead coral, the EAM and coral rubble were each selected for by 5, 6 and 5 species, respectively (Table 1). This is in marked contrast to live coral and sand, which were not selected for by any species, and were negatively selected by 21 species each (Table 1).

Ward's clustering method identified 6 clusters, represented in the nMDS, which were largely associated with particular microhabitats (Fig. 1). Notably, *Novaculichthys taeniourus* was the only single-species group, associating solely with coral rubble. Three species (*Coris batuensis*, *Halichoeres chloropterus* and *H. trimaculatus*) were grouped in a region of the ordination correlated with both sand and coral rubble, while *Anampses neoguinaicus*, *Epibulus insidiator*, *Hemigymnus fasciatus* and *Pseudocheilinus hexataenia* were all associated strongly with dead coral (Fig. 1). The remaining 2 groups included species that appeared to have relatively general habitat preferences, but with a tendency to associate with both EAM and coral rubble (*Coris gaimard*, *Halichoeres margaritaceus*, *H. marginatus*, *H. nebulosus*, *Stethojulis bandanensis*, *S. trilineata* and *Thalassoma lunare*), and those that were generally associated with dead coral (*Anampses geographicus*, *Cheilinus chlorourus*, *C. fasciatus*, *Gomphosus varius*, *Halichoeres hortulanus*, *H. melanurus*, *Hemigymnus melapterus*, *Thalassoma hardwicke* and *T. jansenii*) (Fig. 1).

Notably, a number of taxa were not associated with any particular microhabitat, either being part of the 3 central clusters on the nMDS (16 species) or displaying no positive microhabitat selection in the selection index (9 species). The 8 taxa that were present in the central clusters and also exhibited neutral selection indices included *A. geographicus*, *C. fasciatus*, *C. gaimard*, *G. varius*, *H. hortulanus*, *H. melanurus*, *S. trilineata* and *T. lunare*.

Table 1. Selection of foraging microhabitats by species of Labridae indicating (+) positive, (−) negative, and (o) neutral selection, based on the foraging index of Manly et al. (2002). EAM: epilithic algal matrix. Significant p-values (p ≤ 0.05) from the chi-squared test (df = 1) indicate whether the species' habitat use differed from random based on the abundance of microhabitats; ns: not significant. Species are ordered based on their microhabitat selection. Potential macro-crustacean predators (species with mean standard length > 90 mm; cf. Kramer et al. 2015) are indicated with (M)

	Dead coral	Coral rubble	EAM	Sand	Live coral	Chi-squared p-value
Epibulus insidiator (M)	+	o	o	−	−	< 0.001
Anampses neoguinaicus (M)	+	o	o	−	−	< 0.001
Hemigymnus fasciatus (M)	+	o	o	−	−	< 0.001
Pseudocheilinus hexataenia	+	−	−	−	o	< 0.001
Hemigymnus melapterus (M)	+	−	+	−	−	< 0.001
Cheilinus chlorourus (M)	o	+	−	−	−	< 0.05
Coris batuensis	o	+	o	o	−	< 0.001
Halichoeres chloropterus	o	+	o	o	−	< 0.02
Novaculichthys taeniourus (M)	−	+	−	−	−	< 0.001
Stethojulis bandanensis	o	+	o	−	−	< 0.002
Halichoeres marginatus	o	o	+	−	−	< 0.001
Halichoeres nebulosus	−	o	+	−	−	< 0.02
Thalassoma hardwicke (M)	o	−	+	−	−	< 0.001
Thalassoma jansenii (M)	o	o	+	−	−	< 0.01
Halichoeres hortulanus (M)	o	o	o	−	−	< 0.005
Halichoeres melanurus	o	o	o	−	−	< 0.001
Halichoeres trimaculatus	−	o	o	o	−	< 0.001
Halichoeres margaritaceus	o	o	+	−	−	ns
Anampses geographicus (M)	o	o	o	−	−	ns
Cheilinus fasciatus (M)	o	o	o	−	o	ns
Coris gaimard (M)	−	o	o	−	−	ns
Gomphosus varius (M)	o	−	o	−	o	ns
Thalassoma lunare (M)	o	o	o	−	−	ns
Stethojulis trilineata	o	o	−	−	−	ns

DISCUSSION

Given that dead coral and coral rubble may contain 2 to 3 orders of magnitude higher abundance and biomass of crustaceans than other reef substrata, and that branching live coral also supports a relatively high biomass of crustaceans (Kramer et al. 2014), one would expect that crustacean-feeding fishes, regardless of size, would forage preferentially in these 3 microhabitats. However, our results showed that less than half of the crustacean-feeding wrasses exhibited positive selection for dead coral and coral rubble combined, and that sand and live coral were strongly negatively selected. Interestingly, macro-crustacean predators that were expected to
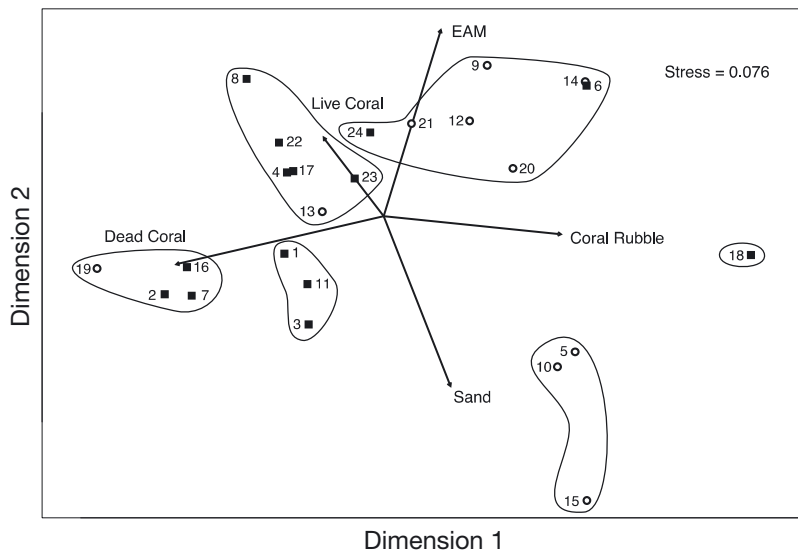
Fig. 1. Non-metric multidimensional scaling (nMDS) ordination of the microhabitat foraging exhibited by wrasse species based on the standardised selection ratio of Manly et al. (2002). Squares: likely macro-crustacean predators; open circles: micro-crustacean predators. EAM: epilithic algal matrix. Numbers correspond to the following species: 1: *Anampses geographicus*; 2: *A. neoguinaicus*; 3: *Cheilinus chlorourus*; 4: *C. fasciatus*; 5: *Coris batuensis*; 6: *C. gaimard*; 7: *Epibulus insidiator*; 8: *Gomphosus varius*; 9: *Halichoeres marginatus*; 10: *H. chloropterus*; 11: *H. hortulanus*; 12: *H. margaritaceus*; 13: *H. melanurus*; 14: *H. nebulosus*; 15: *H. trimaculatus*; 16: *Hemigymnus fasciatus*; 17: *H. melapterus*; 18: *Novaculichthys taeniourus*; 19: *Pseudocheilinus hexataenia*; 20: *Stethojulis bandanensis*; 21: *S. trilineata*; 22: *Thalassoma hardwicke*; 23: *T. jansenii*; 24: *T. lunare*

forage in microhabitats of high crustacean abundance and biomass did not necessarily do so. There was, therefore, a mismatch between the microhabitats where crustaceans were most abundant and the foraging locations of their potential fish predators.

Crustacean-feeding wrasses appear to forage in a manner that does not reflect the densities of their prey, and may be influenced by other factors such as energy expenditure, prey accessibility and predation risk. For example, taxa such as *Gomphosus varius* and *Hemigymnus melapterus* are known to swim to patches of dead coral in a very direct manner, maximising their foraging yield and the likelihood of encountering prey for the energy expended (Fulton & Bellwood 2002). In contrast, *Halichoeres* spp. and *Thalassoma* spp. swim haphazardly across a variety of microhabitats that potentially yield prey items (Fulton & Bellwood 2002, Kramer et al. 2015). These observations are consistent with the microhabitat preferences presented herein. It appears that those species that forage in a haphazard manner, across a variety of microhabitats, tend to feed opportunistically on a wide variety of available prey and seldom exhibit positive selection for any single microhabitat (Fulton & Bellwood 2002, Kramer et al. 2014).

The relationship between predator and prey may also be moderated by the complexity of the substrata: live and dead corals are often composed of highly complex branching skeletons with relatively deep interstices (Stella et al. 2010, Enochs & Manzello 2012). Although live corals support a relatively high biomass of crustaceans, particularly macro-Crustacea (Kramer et al. 2014), no crustacean-feeding wrasses showed selection for this microhabitat. It is likely that the complex structural morphology of corals prevents predators from extracting prey (Hixon & Jones 2005). Large crustaceans may therefore be present in high abundance within live or dead coral simply because wrasse predators are unable to capture them, except for those species that have specialized morphologies (e.g. *G. varius*; Wainwright et al. 2004). The distribution of large Crustacea in reef microhabitats may reflect realized variation in predation pressure, with the highest crustacean abundance and biomass found in areas where predation is least effective. The results of this study suggest that fish forage where predation events are likely to be more successful, not necessarily where prey items are most abundant. This has also been demonstrated in freshwater systems, where predators are most successful at an intermediate level of habitat complexity (Crowder & Cooper 1982, Warfe & Barmuta 2004).

The risk of predation may also determine where an organism forages (Lima et al. 1985, Cowlishaw 1997). Exposed areas such as bare EAM or open sand provide minimal shelter, and thus may represent a dangerous location in which to feed (Hay 1981, Fox & Bellwood 2007). Predation risk in open areas has been suggested as a potential limitation to herbivory (Fox & Bellwood 2007), and predator-avoidance responses amongst a range of herbivores are well documented (Nomikou et al. 2003, Heithaus et al. 2008, Valeix et al. 2009). To counter this, group formation in order to increase vigilance against predation has been suggested in mammals, birds and fishes (Elgar 1989, Magurran 1990, White & Warner 2007). In the present study, this grouping behaviour was most apparent in the taxa that positively selected EAM and were relatively small (e.g. *Halichoeres* spp.; Nunes et al. 2013).

Conversely, in complex microhabitats such as dead coral, the structural complexity (and therefore shelter) may permit solitary or pairing behaviour, particularly for small fishes (Hixon & Beets 1993, Munday & Jones 1998, Brandl & Bellwood 2014). Complex microhabitats in the form of live and dead corals have been identified as vital refuges for recruiting fishes in order to evade predation (Beukers & Jones 1998, Jones et al. 2004, Hixon & Jones 2005, Graham et al. 2006, Wilson et al. 2008); this may also apply to small wrasses. Thus, for species such as *Pseudocheilinus hexataenia* and *Coris batuensis*, microhabitat complexity may provide both profitable foraging and protection from larger predators. Interestingly, the shelter afforded by complex microhabitats also applies to the protection of crustaceans from their fish predators. The high abundance and biomass of crustaceans in dead corals and other complex microhabitats may reflect this process. Complex microhabitats are, therefore, a refuge for both fish and Crustacea.

Although macro-crustaceans, particularly decapods, are most abundant in dead coral and coral rubble, obtaining these crustaceans appears to be limited to those wrasses with highly modified behavioural or morphological adaptations. Specifically, the overturning of coral rubble by *Novaculichthys taeniourus* and the extended jaw structure of *G. varius*, respectively (Ferry-Graham et al. 2002, Wainwright et al. 2004), which allow them to extract prey items from the interstices of complex microhabitats. Notably, these 2 taxa have been shown to have the highest proportions of macro-crustacean prey in their gut (>45%; Kramer et al. 2015), indicating that these adaptations are effective in targeting prey that inhabit complex microhabitats. However, for other wrasse taxa, consuming macro-crustaceans may be a result of nuclear-follower foraging behaviour (Sazima et al. 2007) or simply opportunistically foraging when a vulnerable prey item is encountered.

In conclusion, foraging behaviour in wrasses is far more complex than one might expect given the distribution of their potential prey. In this regard, high diversity coral reef systems appear to reflect their freshwater and temperate counterparts, in that foraging behaviour is influenced by prey availability, the accessibility of microhabitats and predation risk to the predators themselves. With changing habitat complexities on coral reefs (Graham et al. 2006, Wilson et al. 2006), therefore, it is important to understand the subtleties of interactions between predators, prey and their habitats.

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