Mar Biol (2015) 162:1779–1786
DOI 10.1007/s00227-015-2710-0

ORIGINAL PAPER

Refining the invertivore: diversity and specialisation in fish predation on coral reef crustaceans

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Received: 17 April 2015 / Accepted: 20 July 2015 / Published online: 4 August 2015

Abstract Crustaceans are one of the most influential groups in aquatic trophic networks by providing a major connection between primary production and higher consumers. Although coral reefs support a high diversity and abundance of crustaceans and crustacean predators, their trophic interrelationships remain unclear. Using predator gut content analyses, we investigated trophic relationships between Crustacea and adult fishes of the family Labridae, which are one of the most abundant and diverse families of marine crustacean predators. Crustaceans were present within the guts of 93 % of the 30 wrasse genera investigated. We found a distinct division between micro- and macro-crustacean predators: wrasses <80 mm standard length (SL) were predominantly micro-crustacean feeders, while wrasses >90 mm SL displayed a predominantly macro-Crustacea diet. Notably, micro-crustacean predators tended to specialise on certain crustacean taxa, whereas macro-crustacean predators consumed mostly brachyurans. Our findings highlight complex patterns of feeding diversity within crustacean predators that prompt a more nuanced approach to defining the role of crustacean-feeding fishes in coral reef trophodynamics.

Introduction

Coral reefs are considered to be one of the most productive (Reaka-Kudla 1997) and species-rich ecosystems in the world (Plaisance et al. 2009; Stella et al. 2011). To support such a diverse ecosystem, the organisms that inhabit coral reefs utilise a wide variety of nutritional resources such as algae (Choat and Clements 1998; Bellwood et al. 2004), detritus (Wilson et al. 2003), coral (Cole et al. 2008) and benthic invertebrates (Glynn and Enochs 2011). Fishes are one of the most important consumers on a coral reef, incorporating all major nutritional resources into their respective diets and, as a result, shaping ecosystem dynamics (Bellwood and Wainwright 2002; Wilson et al. 2003; Bellwood et al. 2006).

Fishes are widely considered to be major conduits for the movement of energy from benthic invertebrates to higher trophic levels in aquatic ecosystems (Marnane and Bellwood 2002; Pusey et al. 2004; Depczynski et al. 2007; Kramer et al. 2013). Of the 1460 species of fish on the Great Barrier Reef (GBR), approximately 70 % feed predominantly on invertebrates (Williams and Hatcher 1983; Randall et al. 1997; Froese and Pauly 2014). Of these invertivores, 60 % incorporate benthic Crustacea in their diet as a primary component (Randall et al. 1997; Froese and Pauly 2014). Furthermore, broad-scale studies on the diet of reef fish assemblages have found that the most important category is crustaceans, which are consumed by over 50 % of the investigated species (Hiatt and Strasburg 1960; Randall 1967; Hobson 1974). Although the number

Communicated by D. Goulet.

Reviewed by C.E.L. Ferreira and M. Depczynski.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-015-2710-0) contains supplementary material, which is available to authorized users.

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of fish species that feed on Crustacea appears to outnumber all other groups on coral reefs (e.g. Randall 1967; Ferry-Graham et al. 2002; Depczynski and Bellwood 2003; Cowman et al. 2009), information on this trophic group is scarce, even within well-studied families such as the Labridae (but see Bellwood et al. 2006; Ashworth et al. 2014).

Quantitative dietary information is essential in characterising the trophic level of predators, developing tractable trophodynamic models, and for ecosystem-based fishery models (Pauly et al. 1998; Stergiou and Karpouzi 2002; Smith et al. 2011). To explore the potential role of Crustacea in the diet of reef fishes, we concentrate on one of the most abundant, speciose and widespread marine fish families: the Labridae (Randall et al. 1997; Bellwood et al. 2006). We focus on adult specimens (i.e. above 50 % of the maximum adult size; cf. Bellwood and Choat 2011) to minimise the confounding effects of ontogenetic shifts in diet and habitat use (Fulton and Bellwood 2002a) and to focus on the larger individuals within a species that are likely to contribute most to reef trophodynamics (cf. Bonaldo and Bellwood 2008). Our goal was to quantitatively determine the extent and nature of Crustacea in the diets of adult labrids and to determine whether specialisation in crustacean feeding is apparent among labrid genera.

Materials and Methods

Dietary data were collected from 1864 adult specimens of 107 species in 30 labrid genera (average ± SE of 17 ± 1 individuals per species, sample sizes are given in ESM Table 1). This represents 91 % of wrasse species (Labridae, excluding parrotfishes) and 88 % of wrasse genera found on the GBR (Randall et al. 1997; Froese and Pauly 2014). The vast majority of individuals were collected using barrier nets and hand spears from the northern section of the GBR, between Orpheus and Lizard Islands. Species/genera that were uncommon or unavailable on the GBR were represented by specimens from other GBR locations (*Pseudolabrus guentheri* from Heron Island), as well as French Polynesia (*Halichoeres ornatissimus*, *Pseudojuloides cerasinus*) and Papua New Guinea (*Diproctacanthus, Pseudocheilinops, Paracheilinus*). Specimens were placed on ice shortly after capture, and then, either the whole intestine or the whole fish (with the lateral abdominal wall removed) was fixed in 10 % buffered seawater formalin for a minimum of 4 weeks before being transferred to 70 % ethanol for storage and gut content analysis. The contents of the anterior section of the intestine (wrasses have no stomach) were carefully removed under a dissecting microscope, using irrigation to remove all particles, and evenly spread into a single layer of prey items, arranged in a square shape on a petri dish. Contents were then viewed under a dissection microscope (10–40× magnification) through an overlayed grid of 100 squares, of which 40 random squares were open to view. Dietary items nearest to the upper right corner of each random square (i.e. point intersect) were identified to the lowest practical taxonomic level and translated to proportions for data analysis. We subsequently allocated each of these taxa to functional prey types for graphical representation: micro-Crustacea, macro-Crustacea and non-Crustacea (see ESM Table 2 for specific prey items within each category). Micro- and macro-Crustacea are separated based on size and habitat associations: micro-crustaceans are small (<3 mm) and highly abundant in almost all habitats, whereas macro-crustaceans are large (>3 mm) and only found in particular habitats such as dead coral or coral rubble (Kramer et al. 2014). The standard length of each fish was recorded to the nearest mm. Collections and dissections were conducted under approval from the James Cook University Animal Ethics committee (A650).

Mean proportions (±SE) of all identified prey items found within the guts of species were assembled for each wrasse genus. Principal component analysis (PCA) (based on covariance with no pre-transformation) in conjunction with *K*-means cluster analysis was used to identify major feeding groups within the investigated wrasses (micro-Crustacea, macro-Crustacea and non-Crustacea) and the specific genera associated with each group. Locally weighted scatterplot smoothing (LOESS) regression models were conducted on the relationship between the standard length and the mean proportion of micro- and macro-Crustacea within the gut of each genus. A step function, using a tree model, was used to determine threshold values that separated genera into micro- and macro-crustacean groups (Crawley 2007). All analyses were conducted with the software R (version 3.1.0) and the package *tree.*

Results

Crustacea were found to be a significant dietary item in all labrid genera examined, except *Diproctacanthus*, *Labrichthys, Labropsis, Pseudodax, Pteragogus* and *Macropharyngodon* (Fig. 1). Crustaceans comprised more than 50 % of the diet in most (17 of 30) labrid genera (Fig. 1), with the diets of a further 7 labrid genera comprising, on average, at least 20 % Crustacea. While 8 labrid genera fed predominantly on macro-Crustacea, 14 genera fed predominantly on micro-Crustacea (Fig. 2). *Choerodon* and *Coris* consumed similar proportions of macro- and micro-Crustacea (Fig. 2). Limited among-species variation in the proportion of Crustacea within wrasse gut contents was apparent for most genera. *Gomphosus* and *Novaculichthys* were the greatest consumers of macro-Crustacea (69–85 % of prey items in the gut), whereas *Cirrhilabrus*, *Labroides*, *Pseudocoris*,

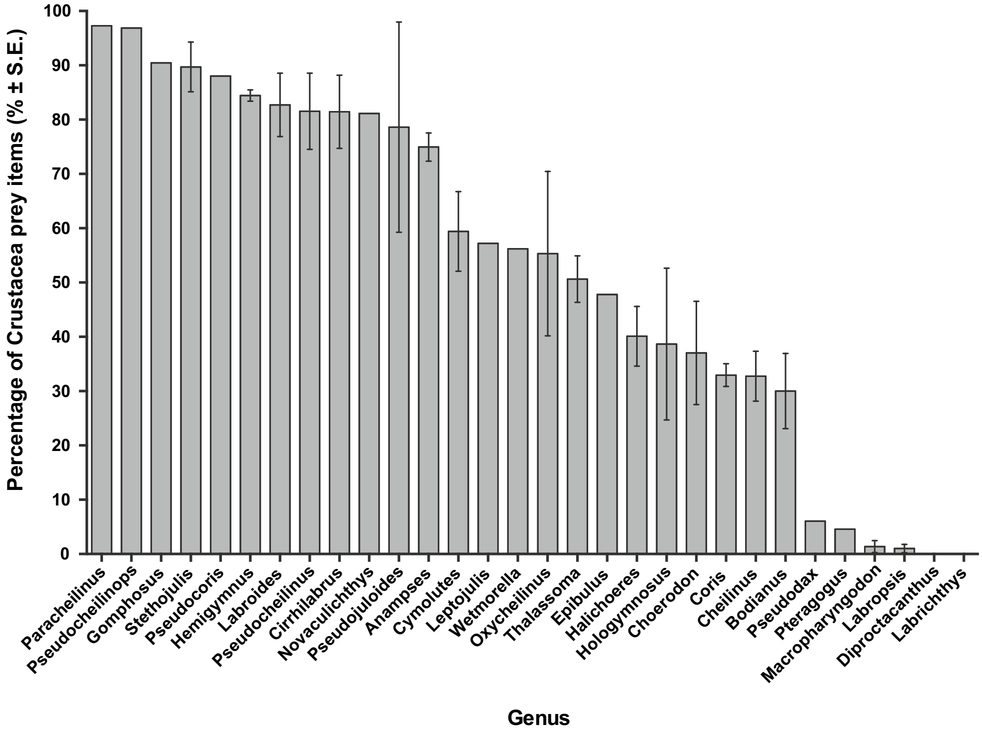

Fig. 1 Mean percentages (±SE) of crustacean prey items in the diet of wrasses. *Error bars* indicate among-species variation within genera (none for genera with only one species examined). Number of species and individuals within genera are given in ESM Table 1

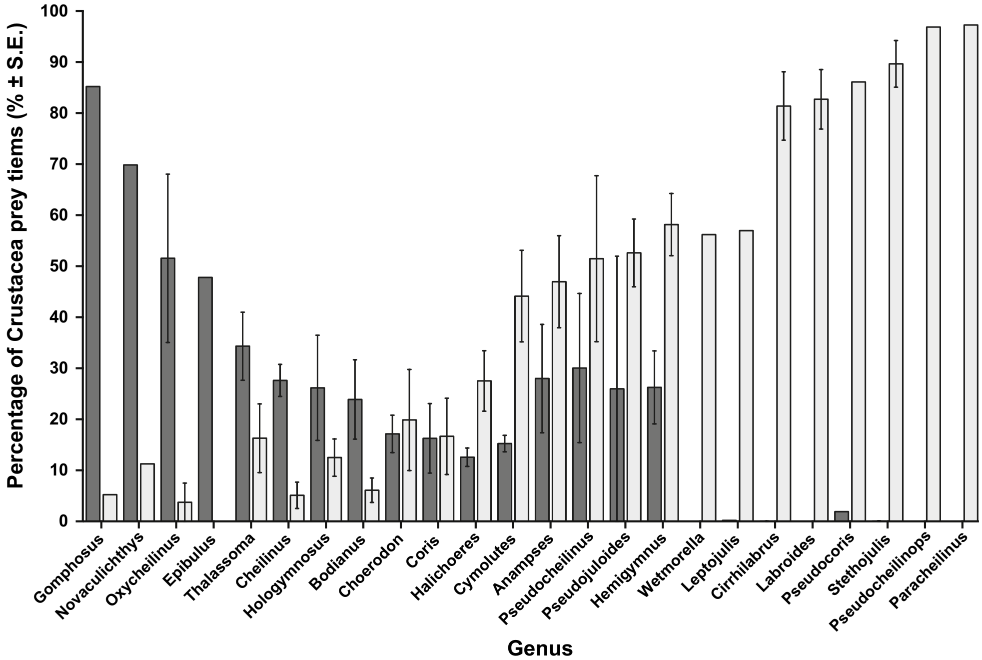

Fig. 2 Mean percentage (±SE) of macro- and micro-Crustacea prey items in the diet of wrasses. Macro-Crustacea are represented by *dark bars*, micro-Crustacea by *light bars*. Only genera with >10 % Crustacea in the diet are included (Fig. 1)

Stethojulis, *Pseudocheilinops* and *Paracheilinus* contained the highest proportion (over 70 % of prey items in the gut) of micro-Crustacea (Fig. 2). Molluscs, coral tissue and fish were the dominant food items in the guts of non-crustacean-feeding genera. Non-identifiable material was predominantly amorphous organic matter and comprised 15.6 ± 3.5 % (mean ± SE) of the diet of all genera.

Groups of micro-, macro- and non-Crustacea predators were confirmed by *K*-means clustering (Fig. 3a), against which the prey vectors provided detail of the characteristic crustaceans consumed by each group (Fig. 3b). The only overlap that occurred between groupings was observed in *Bodianus*, which consumed a slightly greater proportion of non-Crustacea (principally molluscs) than Crustacea

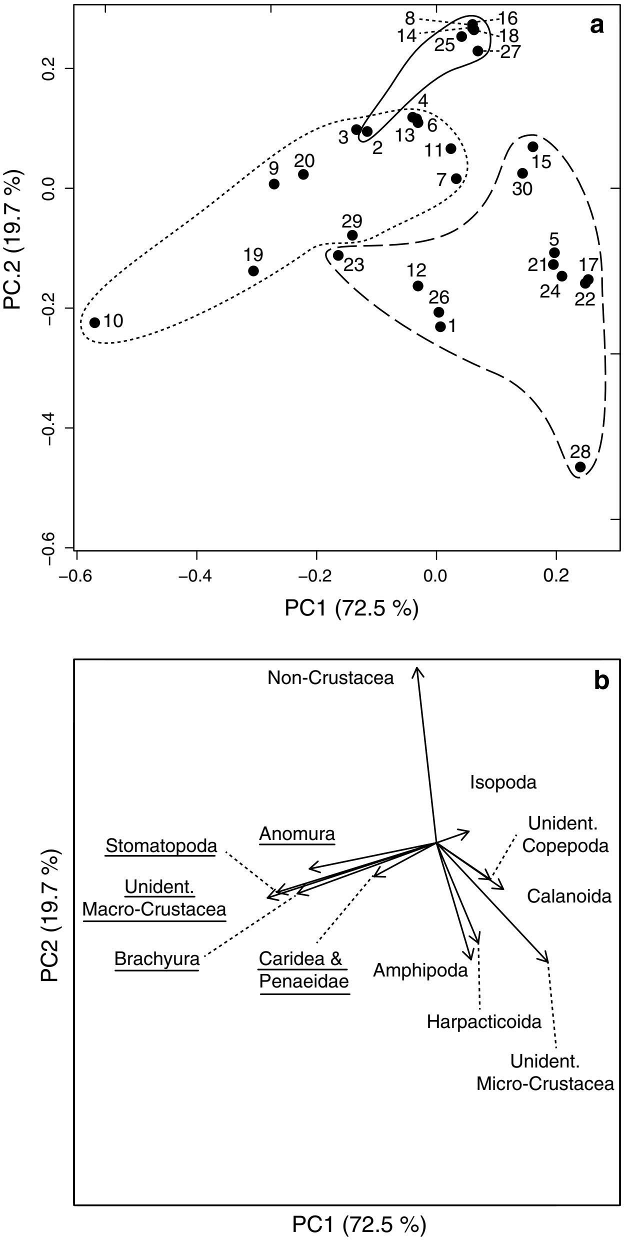

Fig. 3 Principal components analysis (PCA) of prey items within wrasse genera indicating **a** three major groups based on cluster analysis (*K*-means clustering) and **b** identifying the major prey items (n species and n individuals are given in ESM Table 1). Non-Crustacea, macro-Crustacea and micro-Crustacea feeders are indicated by *solid*, *dotted* and *dashed lines*, respectively. Macro-Crustacea are *underlined*. *1. Anampses*, *2. Bodianus*, *3. Cheilinus*, *4. Choerodon*, *5. Cirrhilabrus*, *6. Coris*, *7. Cymolutes*, *8. Diproctacanthus*, *9. Epibulus*, *10. Gomphosus*, *11. Halichoeres*, *12. Hemigymnus*, *13. Hologymnosus*, *14. Labrichthys*, *15. Labroides*, *16. Labropsis*, *17. Leptojulis*, *18. Macropharyngodon*, *19. Novaculichthys*, *20. Oxycheilinus*, *21. Paracheilinus*, *22. Pseudocheilinops*, *23. Pseudocheilinus*, *24. Pseudocoris*, *25. Pseudodax*, *26. Pseudojuloides*, *27. Pteragogus*, *28. Stethojulis*, *29. Thalassoma* and *30. Wetmorella*

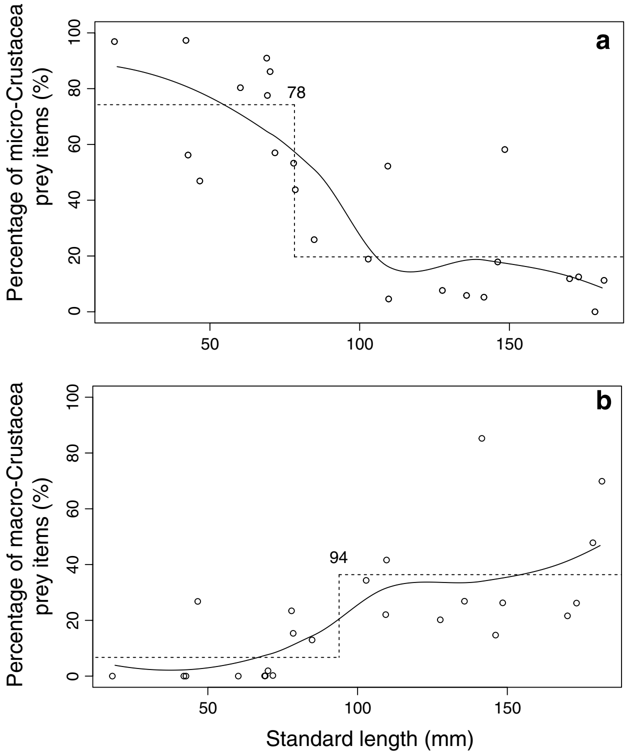

Fig. 4 Mean percentage of prey items in the gut contents of 24 wrasse genera, separated into **a** micro-crustacean and **b** macro-crustacean prey items. The LOESS regression smoothing model is indicated by the *solid line*. The *dashed line* and associated number indicate the step threshold at which the data are split between high and low sections of mean percentage. *Numbers* indicate standard length (mm) at which the step occurs

(Fig. 3). Amphipoda and Harpacticoida were characteristic of micro-Crustacea predators, while Brachyura and Stomatopoda were characteristic of macro-Crustacea predators (Fig. 3b). Fish body size appeared to play a role in these consumption patterns, with a distinct division between consumption of micro-Crustacea and macro-Crustacea below and above a standard length threshold of 78–94 mm, respectively (Fig. 4).

Crustaceans consumed by micro-crustacean feeders varied from predominantly Amphipoda (*Anampses*, *Halichoeres*, *Pseudojuloides* and *Stethojulis*), Harpacticoida (*Anampses*, *Hemigymnus* and *Stethojulis*) and Calanoida (*Cirrhilabrus*, *Paracheilinus*, *Leptojulis*, *Pseudocoris* and *Thalassoma*) to Isopoda (*Labroides*) (Fig. 5). Of the identifiable items for macro-crustacean predators, Brachyura was the major prey item in almost all genera. Notably, over 40 % of the prey items consumed by *Gomphosus* and *Novaculichthys* were Brachyura (Fig. 6).

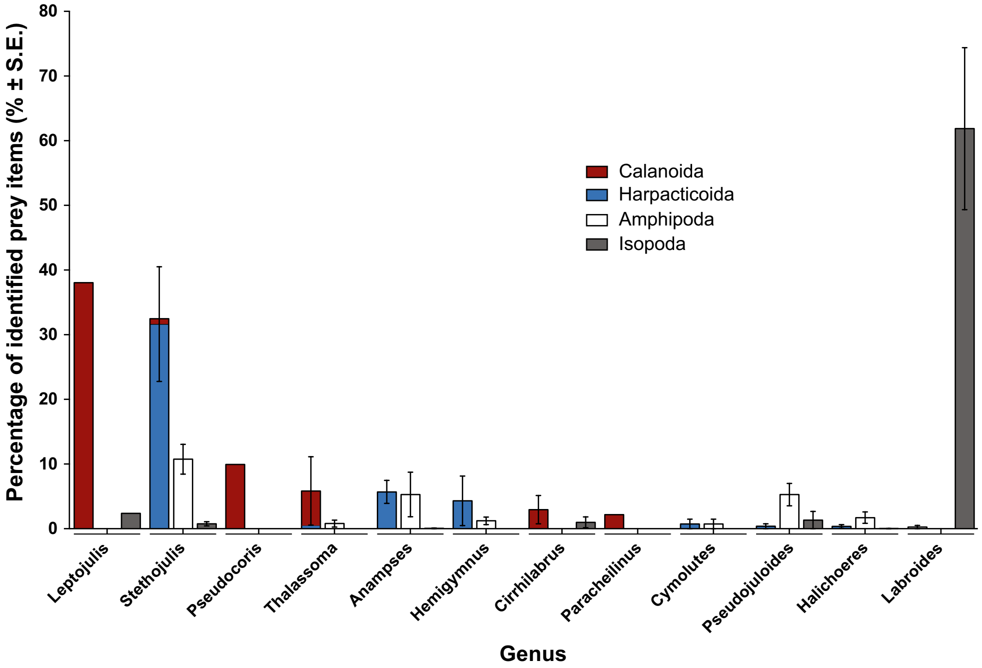

Fig. 5 Mean percentage (±SE) of micro-Crustacea prey items identified in the gut contents of different wrasse genera. Only genera with >20 % micro-Crustacea prey are included. The dietary category 'unidentified fragments' was excluded to emphasise identifiable prey items

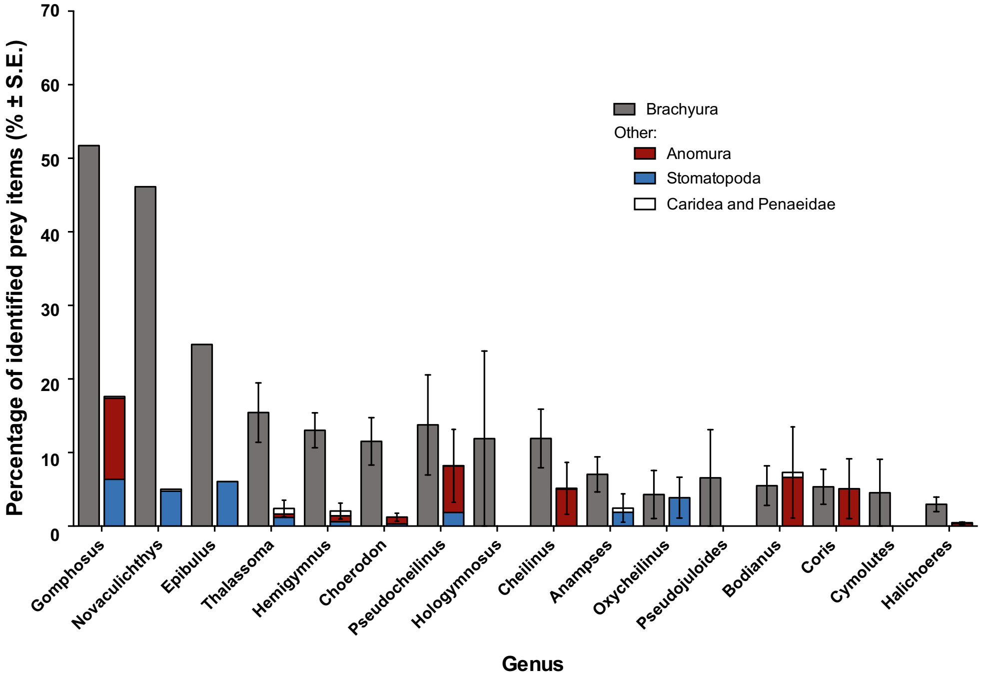

Fig. 6 Mean percentage (±SE) of macro-Crustacea prey items identified in the gut contents of different wrasse genera. Only genera with >10 % macro-Crustacea are included. The dietary category 'unidentified fragments' was excluded to emphasise identifiable prey items

Discussion

Crustaceans are abundant, widespread and diverse members of marine faunas (Ruppert et al. 2004; Stella et al. 2011; Kramer et al. 2014). They support a diverse group of predators, including the majority of fish species and genera within the diverse and abundant group of fishes in the family Labridae. In exploring the crustaceans consumed by each wrasse genus, we found three different trophic groups, with consequences for broader trophic pathways within reef ecosystems. Predator body size appears to be linked to these patterns: wrasse genera with a mean standard length above 94 mm or below 78 mm predominantly consuming brachyuran crabs or micro-Crustacea, respectively. Nuanced differences in micro-crustacean feeding were also apparent, with different wrasses tending to specialise towards the Amphipoda, Calanoida, Harpacticoida and/or Isopoda. This suggests that there are at least two distinct crustacean-based trophic pathways on reefs and that care is needed when assessing the role of crustacean-feeding fishes in coral reef trophodynamics (Depczynski and Bellwood 2003; Graham et al. 2003; Ashworth et al. 2014).

Allometric trends in prey consumption are common in predatory animals, including fishes, where crustaceans appear to be the foundational diet of small fishes (e.g. Alheit and Scheibel 1982; Bellwood 1988; Wen et al. 2012). Throughout the ontogeny of predatory fish species, prey sizes have been found to correlate strongly with body size. Prey items will often progress from copepods to small shrimps, then to crabs and finally to fishes (Wainwright and Richard 1995; Morton et al. 2008; Fukuoka and Yamada 2015). Previous research of fishes from the Haemulidae, Labridae, Lutjanidae, Serranidae and Centrarchidae has found major shifts in prey type at standard lengths of approximately 70–100 mm (Wainwright 1988; Wainwright and Richard 1995; de la Morinière et al. 2003). However, these size thresholds have overwhelmingly been associated with ontogenetic shifts within species, rather than the dietary differences we find here in labrid adults of different mean sizes. Nonetheless, such congruence in predator size with prey relationships suggests that an overarching mechanism is at work, such as limitations in the feeding morphology for consumption of larger prey. This may involve the gape of the oral and pharyngeal jaws, or the crushing capability of the levator posterior muscle and the pharyngeal apparatus (Wainwright 1988; Wainwright and Richard 1995). Combined with the trade-off between costs of foraging and prey consumption, and the value of larger prey (Osenberg and Mittelbach 1989; Wainwright and Bellwood 2002), there appears to be powerful selection for size-related divisions in prey consumption. Thus, most predatory species will likely to progress through size-appropriate diet shifts until reaching maturity, where the adult body size will be a good indication of the predominant prey items.

Micro-crustaceans were of particularly high importance for small wrasses. The consumption of small Crustacea (i.e. amphipods, copepods and isopods) likely requires minimal foraging effort, as these prey items are highly abundant across all reef substrata, except live corals (Kramer et al. 2014). It is important to note, however, that the wrasse genera that feed on these items differ in their preferred micro-crustacean prey. For more demersal wrasses such as *Anampses, Hemigymnus, Pseudojuloides* and *Stethojulis*, benthic amphipods and harpacticoid copepods are the dominant identifiable prey item, while water column users such as *Cirrhilabrus*, *Leptojulis, Paracheilinus* and *Pseudocoris* prey on planktonic copepods (Fulton et al. 2001; Fulton and Bellwood 2002b). *Labroides* functions as a cleaner, feeding primarily on parasitic isopods located on other fishes (as previously noted by Grutter 2000). These specialisations are likely to be due, at least in part, to the extensive morphological disparity among crustacean-consuming wrasses, which is broader than corallivorous or piscivorous wrasses (Wainwright et al. 2004). Moreover, wrasses often display different patterns of foraging behaviour and micro-habitat preferences, which are likely to influence the micro-crustaceans they encounter (Bellwood and Wainwright 2001; Fulton et al. 2001; Fulton and Bellwood 2002a).

A relatively narrow group of macro-crustaceans appear to be targeted by larger wrasse genera. Although fewer wrasse genera utilise macro-crustaceans as a resource, the major predators (*Gomphosus*, *Novaculichthys* and *Epibulus*) all appear to feed predominantly on brachyurans. These genera have particular morphological or behavioural adaptations that enable them to target elusive Crustacea in crevices, coral heads or under coral rubble (Wainwright 1988; Ferry-Graham et al. 2002; Fulton and Bellwood 2002b; Wainwright et al. 2004). For example, *Gomphosus* has a prominent snout that enables it to extract prey from crevices (Fulton and Bellwood 2002b; Wainwright et al. 2004), while *Novaculichthys* is renowned for its ability to move pieces of coral rubble to uncover large, cryptic animals hiding underneath (Randall et al. 1997). Although macro-crustaceans are relatively scarce in comparison with micro-crustaceans (Kramer et al. 2014), it is likely that the effort exerted in order to capture macro-crustaceans is justified by the relatively high nutritional and energetic return. Additionally, wrasses that prey on larger crustaceans have the mechanical ability to obtain and process a wide range of hard-shelled prey items, including molluscs. Indeed, the crushing strength of the pharyngeal jaw has been suggested to be an excellent predictor for feeding abilities on hard-shelled prey; fishes with a crushing strength >3–5 N consume a higher proportion of gastropods and hard decapods

(Wainwright 1988). Although the relationship between standard length and pharyngeal jaw crushing strength varies between species of *Halichoeres*, it is important to note that the change in diet occurs between 65 and 120 mm (Wainwright 1988). This range is consistent with the size-related step threshold between micro- and macro-Crustacea predators observed in the present study.

Coral reef fishes are often grouped into distinct trophic categories, such as herbivores, planktivores and carnivores. The present study suggests that fishes previously classed as invertivores may contain representatives from at least two separate functional pathways: micro- and macro-crustacean predators. Macro-crustacean predators have the ability to feed on a variety of resources as a result of the mechanical advantage obtained with size (e.g. raptorial dentition and large levator posterior muscles for crushing). Although some species predominantly consume micro-crustaceans as a juvenile, upon reaching adult size (>80 mm) they are likely to feed on other large, shelled invertebrates such as gastropods (Wainwright 1987) and echinoderms (Young and Bellwood 2012) in addition to macro-Crustacea. The present study provides a differentiation within the invertivore group, not unlike the separation of grazers, browsers and excavators within coral reef herbivores (Green and Bellwood 2009). Some finer division of trophic categories is also apparent within micro-crustacean feeders where major prey items reflect feeding modes, for example, harpacticoids and amphipods in *Stethojulis* spp., isopods in *Labroides* spp. and calanoids in *Cirrhilabrus* spp. The predominant type of Crustacea consumed reflects the morphological or behavioural modifications in each genus. *Stethojulis* spp., for example, feed by taking bites from dead substrata and filtering material in the branchial basket, while *Cirrhilabrus* spp. swim above the reef, capturing pelagic copepods using well-developed eyes and a fast, low-strength jaw, and *Labroides* spp. are characteristic cleaners that remove parasitic isopods from fish hosts (Grutter 2000; Wainwright and Bellwood 2002; Wainwright et al. 2004).

Although crustaceans have been generally recognised as a major dietary category for fishes on coral reefs, the present study provides a new perspective with regard to the importance and diversity in consumption of Crustacea by fishes. Notably, there appears to be a substantial division between crustacean predators within the Labridae, with two separate trophic pathways based on micro-Crustacea and macro-Crustacea. Given an underlying connection to predator size (threshold around approximately 85 mm SL), there is potential for this division to be broadly relevant among and within a range of reef fish species. Accordingly, our understanding of invertivore trophic pathways requires a more detailed appreciation of the distinct contributions of invertivores, whereby crustacean-feeding fishes can provide very different contributions to flow of trophic biomass and energy on coral reefs.

Acknowledgments We wish to thank J. H. Choat, M. Marnane, I. Stobutzki and F. Walsh for assistance in obtaining specimens, and S. J. Brandl and two anonymous reviewers for helpful comments. This work was supported by the Australian Research Council (DRB).

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