REPORT

The trophic importance of algal turfs for coral reef fishes: the crustacean link

M. J. Kramer · O. Bellwood · D. R. Bellwood

Abstract On coral reefs, the epilithic algal matrix (EAM) is widely recognised as an important resource for herbivorous and detritivorous fishes. In comparison, little is known of the interaction between benthic carnivores and the EAM, despite the abundance of Crustacea within the EAM. The trophic importance of the EAM to fishes was investigated in Pioneer Bay, Orpheus Island, Great Barrier Reef. Fish densities were quantified using visual and clove oil censuses, and gut content analyses conducted on abundant fish species. Crustaceans were found to be an important dietary category, contributing between 49.5 and 100 % of the gut contents, with harpacticoid copepods being the dominant component. Of the benthic carnivores, the goby *Eviota zebrina* was found to consume the most harpacticoids with a mean of 249 copepods m^{-2} day^{-1}. This represents approximately 0.1 % of the available harpacticoid population in the EAM. In a striking comparison, herbivorous parrotfishes were estimated to consume over 12,000 harpacticoids m^{-2} day^{-1}, over 27 times more than all benthic carnivores surveyed, representing approximately 5.3 % of the available harpacticoid copepod population each day. The high consumption of harpacticoid copepods by benthic carnivores and parrotfishes indicates that harpacticoids form an important trophic link between the EAM and higher trophic levels on coral reefs.

Keywords Crustacea · Harpacticoid copepods · Epilithic algal matrix · Cryptobenthic fish · Parrotfish · Benthic carnivory

M. J. Kramer (✉) · O. Bellwood · D. R. Bellwood
School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia
e-mail: michael.kramer@my.jcu.edu.au

M. J. Kramer · D. R. Bellwood
Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

Introduction

On coral reefs, a major source of primary productivity is derived from algal turfs, or more broadly, the epilithic algal matrix (EAM) which includes filamentous algae and loose detrital and non-algal components such as inorganic sediments (Purcell and Bellwood 2001; Wilson et al. 2003). The EAM is the most abundant microhabitat on coral reefs, comprising between 30–80 % of the total surface area (Klumpp and McKinnon 1992; Wismer et al. 2009; Vermeij et al. 2010; Fricke et al. 2011; Goatley and Bellwood 2011). It is widely recognised that the EAM supports both the algal and detrital trophic pathways (Scott and Russ 1987; Wilson et al. 2003; Fox and Bellwood 2007; Bonaldo and Bellwood 2011) and that fishes which feed directly on the EAM provide a vital trophic link between primary production and secondary consumers (Choat et al. 2002; Depczynski and Bellwood 2003).

However, recent research has indicated that the EAM also contains high numbers of benthic crustaceans, particularly harpacticoid copepods, which may play a substantial role to the trophic structure of a coral reef (Kramer et al. 2012). The widespread availability of the EAM, combined with an abundant cryptofaunal component within the EAM itself, presents a potentially valuable nutrient source for

predators on small, benthic motile invertebrates such as copepods, amphipods and tanaidaceans. Yet, little is known of the links between the EAM cryptofauna and the fishes that feed on them.

The most numerous and speciose trophic category of fishes on coral reefs are those species that consume mobile benthic invertebrates, hereafter referred to as benthic carnivores (Hiatt and Strasburg 1960; Williams and Hatcher 1983; Jones et al. 1991). Previous studies on the diet of benthic carnivores have shown crustaceans to be a major prey item (Williams and Hatcher 1983; Jones et al. 1991; Randall et al. 1997). This is not surprising as a large proportion of the mobile benthic invertebrate coral reef fauna is composed of a highly abundant and diverse variety of crustacean taxa (Peyrot-Clausade 1980; Preston and Doherty 1994; Logan et al. 2008; Kramer et al. 2012). Crustacean communities form distinct assemblages favouring specific microhabitats such as dead coral (Preston and Doherty 1994), live coral (Stella et al. 2010), and lagoonal soft sediments (Carleton and Hamner 2007). However, whilst the interactions between the crustacean fauna and benthic carnivores of macro-algal-dominated temperate ecosystems are relatively well understood (Choat and Kingett 1982; Edgar and Shaw 1995; Denny and Schiel 2001), this information is noticeably lacking for coral reefs (but see Wolf et al. 1983; Jones et al. 1991). The aim of the present study, therefore, is to investigate the potential trophic relationship between the EAM, its crustacean inhabitants, and the associated fish fauna on an inner-shelf fringing reef of the Great Barrier Reef, including both benthic carnivores and EAM feeding parrotfishes. These data will be used to evaluate the role of Crustacea in linking primary production in the EAM and with higher trophic levels.

Methods

Study site

This study was conducted in June and July 2011, in Pioneer Bay, Orpheus Island (18°35'S, 146°20'E), on the inner-shelf region of the Great Barrier Reef. Pioneer Bay exhibits an extensive fringing reef, comprised of a reef flat that extends approximately 150 m from the shoreline to the reef crest, from which it gradually slopes down to approximately 15 m depth (details in Fox and Bellwood 2007). The EAM in Pioneer Bay is the dominant benthic constituent in the outer flat and crest, with low particulate loads, and is relatively heavily grazed by fishes. Details of the EAM and the major grazing species at this location are given in Fox and Bellwood (2007) and Bonaldo and Bellwood (2011).

Sampling procedure

Ten fish species (Gobiidae: *Amblygobius decussatus*, *Asterropteryx semipunctatus*, *Eviota zebrina*, *Istigobius rigilis*; Labridae: *Halichoeres melanurus*, *Stethojulis strigiventer*, *Thalassoma lunare*; Pomacentridae: *Neopomacentrus bankieri*, *Pomacentrus adelus*, *Pomacentrus moluccensis*) were selected for gut content analysis based on high local abundance (Ackerman and Bellwood 2000), or if they were suspected to feed on EAM components based on observations or published data (Depczynski and Bellwood 2003; Ceccarelli 2007). Specimens for gut content analysis were collected between 1000 h and 1600 h to ensure that the guts contained prey items consumed during the day. Ten specimens were collected per species from the combined inner flat and outer crest zone using clove oil or barrier net techniques, euthanised with clove oil, placed into perforated click-seal bags and immersed in ice-chilled phosphate-buffered 4 % formalin within 10 min of capture. Mean standard lengths and maturity status for each species are given in the Electronic Supplementary Material (ESM Table S1).

To provide site-specific fish abundances, surveys were conducted across two habitats (the inner crest and outer flat, as this region encompasses two very similar, yet narrow habitats) at four sites. In each site, five 10 × 1 m transects were surveyed for visible (i.e., non-cryptobenthic) fishes, and five clove oil samples for cryptobenthic fishes (species that are too small, or too well camouflaged, to be observed in visual transects following Ackerman and Bellwood 2000). To minimise diver effects, fish were counted as the transect line was deployed (after Dickens et al. 2011). Following the visual transects, the abundance of cryptobenthic species was measured using clove oil and a fine mesh net (1 mm mesh) that sampled a basal area of 0.4 m^2, following Depczynski and Bellwood (2004).

Gut content analysis

For all species (excluding fishes from the Pomacentridae), the entire length of the gut was examined for gut contents. Only the stomach and anterior section of the gut from members of Pomacentridae were investigated, as the contents of the posterior section were subject to extensive digestion and were not indicative of the ingested material (Wilson and Bellwood 1997). Gut contents were removed and spread as evenly as possible across a square grid fixed to the bottom of a glass petri dish following Depczynski and Bellwood (2003). Because of the range of gut volumes across taxa, four square sizes were constructed: 30 × 30, 20 × 20, 10 × 10, and 5 × 5 mm. The grids contained 100 squares, of which 60 were randomly blacked out. Dietary items that were observed in the bottom-right corner

of each of the 40 non-blacked out squares were identified using an Olympus SZ40 binocular dissection microscope under 4× magnification. The data were subsequently converted into proportions. Following grid analysis, the gut contents of species containing high abundances of crustaceans were retained on the petri dish and examined at 4× magnification to count and identify all of the ingested crustaceans using Boxshall and Halsey (2004) and Forest and von Vaupel Klein (2004). Species of fish were assigned to trophic categories based on the dominant contents (Depczynski and Bellwood 2003) and the origin of the contents.

Estimating rates of predation on EAM Crustacea

The relative importance of EAM Crustacea to benthic carnivores was estimated based on the consumption rates of the harpacticoid copepods, the dominant crustacean found in the EAM (Kramer et al. 2012). This can be summarised by the formula:

$$C_H = 2.6 \times (H_a \times D_a)$$

where C_H is the consumption of harpacticoid copepods m^{-2} day^{-1} for fish species 'a'; H_a is the mean number of harpacticoid copepods in the gut of species 'a' at a single point in time; D_a is the density of species 'a' m^{-2} (from census data); and 2.6 is a conservative estimate of the mean gut throughput rate per day (following Polunin et al. 1995; Marnane and Bellwood 1997).

In addition, two methods were used to estimate the consumption of harpacticoid copepods from the EAM by parrotfishes. Calculations were based on the data from the reef crest at Orpheus Island, where the most abundant parrotfishes (*Scarus rivulatus* and *Chlorurus microrhinos*) have the highest grazing impact on the reef (Fox and Bellwood 2007; Bonaldo and Bellwood 2011; Welsh and Bellwood 2012). Firstly, removal rates were based on values from the published literature, by multiplying the area of EAM removed by parrotfishes each day (Fox and Bellwood 2008), and the number of harpacticoid copepods per unit area of EAM on the reef crest (Kramer et al. 2012). The result was then divided by the number of harpacticoid copepods per square metre on the reef crest (2397.3 100 cm^{-2}; Kramer et al. 2012) to estimate the proportion of harpacticoids consumed per square metre each day.

Secondly, a submersible vacuum sampler (from Kramer et al. 2012) was modified to incorporate an artificial parrotfish premaxilla. The premaxilla was constructed from rigid plastic, cut in such a manner to replicate the size and shape of the upper jaw of a parrotfish. This was then secured to the inhalant tube of the vacuum sampler to 'bite' the EAM. Ten replicate 'bites', each 5 cm^2, were collected immediately adjacent to recent parrotfish feeding scars from

two sites on the reef crest of Pioneer Bay. The algae, detritus and cryptofauna removed by the 'bite' was drawn into the filter mechanism of the vacuum sampler, sealed and placed in phosphate-buffered 4 % formaldehyde. Samples were stained with Young's eosin erythrosin to aid in distinguishing the harpacticoid copepods, which were counted to give an abundance of harpacticoid copepods per unit bite area. This was then multiplied by the known bite area of three size classes of *S. rivulatus* (5–10; 11–25 and >25 cm) and one size class of *C. microrhinos* (>30 cm; following Fox and Bellwood 2007) to estimate the number of harpacticoids removed per bite. The number of bites per day for each size class for the two species (Fox and Bellwood 2007) was then used to estimate how many harpacticoids were consumed by an individual fish each day and then multiplied by the abundance of each size class (Bellwood et al. 2006; Fox and Bellwood 2007), to calculate the number of harpacticoid copepods consumed by the local population of *S. rivulatus* and *C. microrhinos* each day. This value was then divided by the number of harpacticoid copepods m^{-2} (Kramer et al. 2012) to estimate the proportion of the harpacticoid population consumed (m^{-2} day^{-1}).

Results

Gut content analysis

Gut content analysis of the ten fish species revealed a wide variety of dietary preferences (Fig. 1). The most conspicuous components included Crustacea, benthic filamentous algae and amorphous organic matter (AOM). *P. adelus* and *Asterropteryx semipunctatus* contained a particularly low proportion of crustaceans in their diet, with a mean ± SE of 7.5 ± 3.3 and 8.0 ± 1.6 %, respectively (Fig. 1). The dominant dietary component of these two species is algae (*P. adelus*) and AOM (*A. semipunctatus*) (Fig. 1). In contrast, *N. bankieri* contained the highest proportion of crustaceans at 100 % (Fig. 1) and crustaceans dominated the gut contents of all other species, ranging between 49.5 ± 8.3 % (*P. moluccensis*) and 85.3 ± 1.6 % (*Stethojulis strigiventer*) (Fig. 1).

Further investigations of the crustacean component of the gut contents revealed a diversity of taxa. Calanoid copepods were a major component of the diet of *N. bankieri* (93.3 ± 1.2 %) and, to a lesser extent, *P. moluccensis* (23.8 ± 6.3 %) (ESM Table S2). Crustacean fragments were defined as assorted appendages and pieces of exoskeleton from relatively large crustaceans such as decapods. This dietary category was prominent in the diet of *T. lunare* and *H. melanurus*, contributing to 38.0 ± 3.9 % and 22.5 ± 1.8 % of their total gut contents, respectively (ESM Table S2). Harpacticoid copepods were the dominant

Fig. 1 Composition of the gut
contents of 10 species of fish
(each species *n* = 10) as mean
proportion ± standard error of
major dietary items. *AOM*
amorphous organic matter. Note
y-axis varies with species
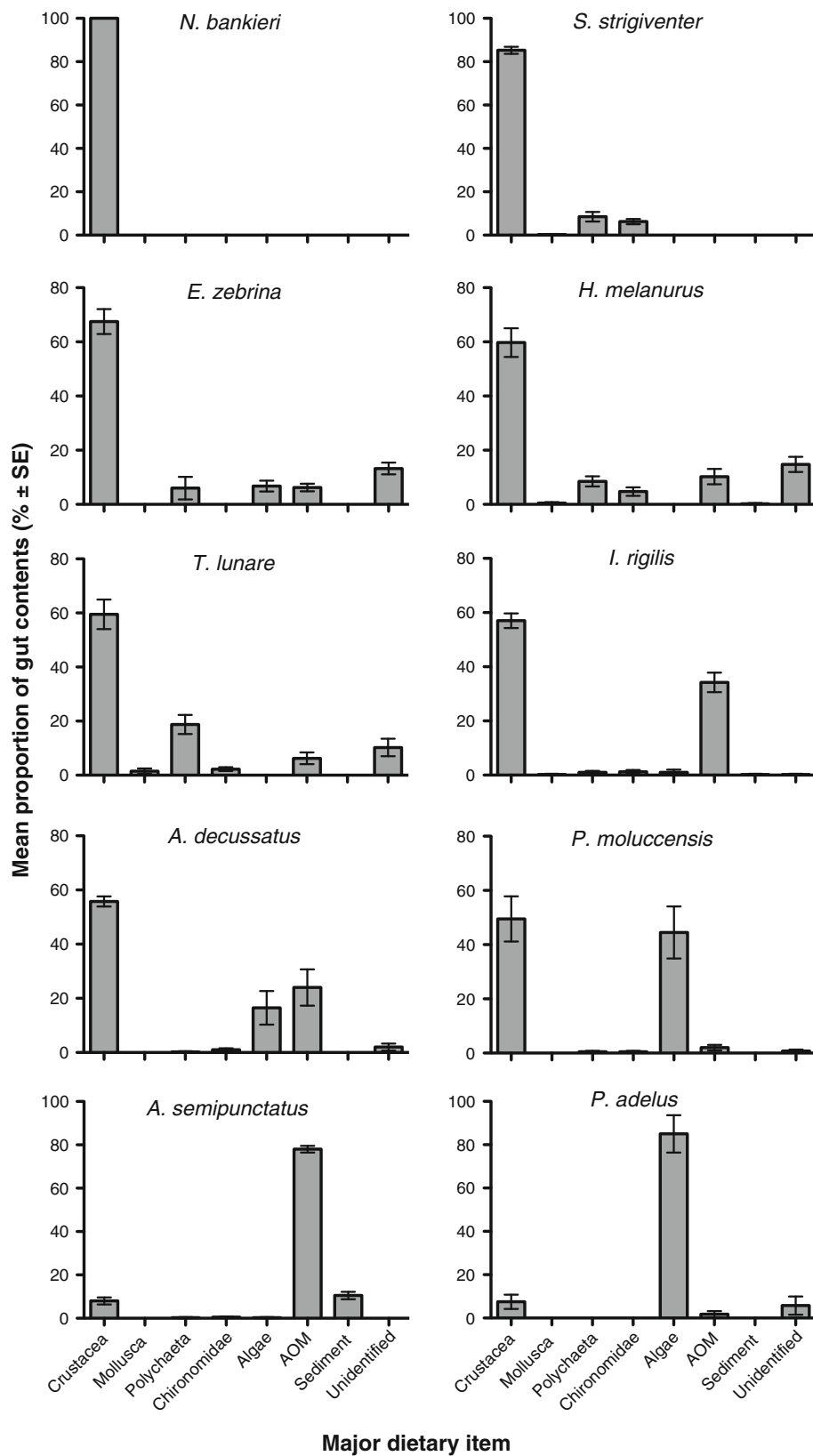
crustacean component of all other species' gut contents,
ranging between 3.8 ± 1.4 % (*A. semipunctatus*) and
49.8 ± 2.0 % (*Amblygobius decussatus*) (ESM Table S2).

More specific trophic groupings were assigned to these
fish species based on the knowledge of the origins of
Crustacea in the diet. Planktivores were defined by the

dominance of planktonic calanoid copepods, exemplified in *N. bankieri*. Omnivory appears to be exhibited by *P. moluccensis*, which consumed both benthic algae and calanoid copepods. Benthic carnivores consumed crustaceans of benthic origin, such as harpacticoid copepods, tanaidaceans and amphipods. Benthic carnivory was the most abundant trophic group, including *H. melanurus*, *T. lunare*, *I. rigilis*, *E. zebrina*, *S. strigiventer* and *A. decussatus*.

Rates of predation on harpacticoid copepods

Of those species classified as benthic carnivores, the most abundant, and also the greatest consumer of harpacticoid copepods, was *E. zebrina* (249.6 ± 30.7 harpacticoids m^{-2} day^{-1}, mean $\pm$ SE; Fig. 2a, b). All other species were low by comparison, ranging between 8.9 ± 2.2 harp. m^{-2} day^{-1} (*T. lunare*) and 87.5 ± 15.2 harp. m^{-2} day^{-1} (*A. decussatus*) (Fig. 2b). It is interesting to note that after *E. zebrina*, the two most important consumers of harpacticoid copepods had low abundances of just 0.04 ± 0.003 and 0.02 ± 0.002 ind. m^{-2} for *A. decussatus* and *S. strigiventer*, respectively (Fig. 2a). In this study, the combined consumption of harpacticoid copepods by all 6 species of benthic carnivores was 469.6 ± 39.3 ind. m^{-2} day^{-1}. This equates to 0.21 ± 0.018 % of the available harpacticoid population from the reef crest and reef flat each day.

Based on published data, *C. microrhinos* and *Scarus rivulatus* are estimated to remove a combined total of $12{,}663 \pm 3{,}695$ harpacticoids m^{-2} day^{-1} (Fig. 2b), which corresponds to $5.28 \pm 1.54\%$ of the local harpacticoid copepod population from the reef crest each day (ESM Table S3). This calculation was used for graphical representation as it groups all size classes of *S. rivulatus* in a single group. In comparison, the calculation that incorporated the use of simulated bites, size classes and the abundances of the various size classes of the two parrotfish species estimated that $10{,}795 \pm 507$ harp. m^{-2} day^{-1} were consumed by the two parrotfish species, equating to 4.50 ± 0.24 % of the harpacticoid population being consumed from the reef crest each day (ESM Table S4).

Discussion

The EAM has long been recognised as a substantial contributor to the herbivorous and detritivorous pathways on coral reefs (Wanders 1977; Klumpp and McKinnon 1989; Wilson et al. 2003). Gut content analysis of the ten fish species investigated in this study provided evidence that the EAM is also a significant contributor to other trophic categories, particularly benthic carnivory. Although detritivory, planktivory and herbivory were observed, the majority of species were classified as benthic carnivores
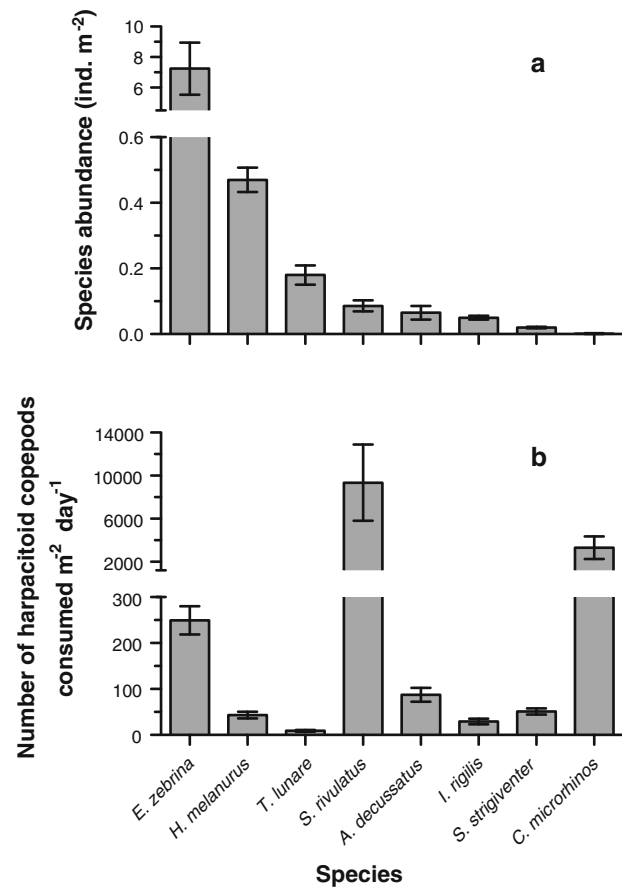

Fig. 2 Mean number $\pm$ standard error of **a** the density of harpacticoid copepod consumers (both benthic carnivores and parrotfishes), and **b** the number of harpacticoid copepods consumed by each species (ind. m^{-2} day^{-1}). Gut content analysis was conducted on all species except for *C. microrhinos* and *S. rivulatus*. The consumption of harpacticoids by these two parrotfishes was estimated by sampling the EAM in the field using an artificial parrotfish maxilla attached to a vacuum sampler

based on the presence of large numbers of EAM crustaceans in their guts. Crustaceans in the EAM were found to be a major source of food for these benthic carnivores.

The observations of benthic carnivory on EAM organisms, especially crustaceans, add to the growing importance of EAM as a trophic resource for fishes on coral reefs (Wilson et al. 2003; Fox and Bellwood 2007; Bonaldo and Bellwood 2011). It is well known that detritivores and detrital-based food webs are important on coral reefs (Arias-Gonzalez et al. 1997; Depczynski and Bellwood 2003; Wilson et al. 2003). Indeed, the presence of detritus (AOM) in the gut of many species investigated in the present study suggests that detritus may be ingested as a supplementary source of nutrition. It is more nutritious than filamentous algae and is easily digested due to the high surface area of detrital particles (Wilson and Bellwood 1997; Wilson et al. 2003). Furthermore, detrital matter is very abundant in the EAM, more so than invertebrates

(Wilson 2000). Nonetheless, the ability of numerous benthic carnivores to extract highly nutritious harpacticoids from other EAM components points to the widespread value of the EAM for herbivores, detritivores and a range of benthic carnivores.

Fish feeding from the EAM have a selection of nutritious resources to choose from, thus supporting a variety of trophic modes in a diverse community of species. Each individual organism is assumed to selectively target a specific resource such as algae, detritus or mobile invertebrates (Choat et al. 2002; Depczynski and Bellwood 2003). Species appear to have adapted morphological and behavioural traits that optimise the cost–benefit ratios associated with utilising each resource, such as soft, bristle-like teeth in detritivorous blennies (Wilson 2000) and the defence of benthic territories by damselfish (Ceccarelli 2007). For small fish, harpacticoid copepods are likely to be an energetically efficient food source, as their movements are slow and inefficient when compared to pelagic calanoid copepods (Hicks 1988; Gee 1989), and therefore easier to capture. Harpacticoid copepods are also highly nutritionally important, providing a variety of valuable nutrients to their predators including essential fatty acids (EFAs) such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Ajiboye et al. 2011). Furthermore, small benthic carnivores such as E. zebrina are often subjected to high predation risk (Depczynski and Bellwood 2006), thus the ability to remain motionless, or rapidly retreat into the complexity of the reef, are essential anti-predation behaviours. As harpacticoid copepods are abundant and ubiquitous EAM inhabitants (Klumpp et al. 1988; Preston and Doherty 1994; Logan et al. 2008; Kramer et al. 2012), the consistent and reliable availability of nutritious harpacticoids to small fishes provides a resource that appears to be both cost-effective and relatively safe. These copepods require minimal energy expenditure to obtain, without having to venture far from shelter.

Of the carnivores in the present study, the greatest consumer of harpacticoid copepods per unit area is also the smallest of all the fishes examined. This species (E. zebrina) has previously been recognised as an important contributor to carnivorous trophic pathways (as food for larger fishes) due to its high densities, early onset of reproductive maturity, high mortality rates (7–8 %) and relatively short life span (<100 days), suggesting a life history characterised by high predation rates (Reznick and Endler 1982; Depczynski and Bellwood 2006). This study indicates that E. zebrina plays an important trophic role in transferring energy from small crustaceans to higher trophic levels, thus the knowledge of this trophic link is extended. Previous investigations into the trophic nature of the cryptobenthic fish community on a coral reef suggest that a variety of trophic modes exist and that detritivorous taxa are abundant (Depczynski and Bellwood

2003). However, E. zebrina is an overwhelmingly abundant cryptobenthic species (Depczynski and Bellwood 2003), and as such, the trophic contribution of this fish as a small benthic carnivore is likely to be an important component of reef trophodynamics.

The dietary preference and high densities that E. zebrina exhibits on the coral reef in the present study indicate that this small goby may be an important contributor in the flux of energy derived from crustaceans in the EAM. Although the gut throughput rate calculated by Marnane and Bellwood (1997) is an accurate experimental study, it is conducted on a species (Pomacentrus amboinensis) with a longer relative gut length when compared to E. zebrina (Marnane and Bellwood 1997; Depczynski and Bellwood 2003). It is likely that the gut throughput rate of the smaller E. zebrina may be more rapid than that indicated by Marnane and Bellwood (1997), and thus, the magnitude of consumption of harpacticoid copepods presented in the present study is likely to be conservative. The contribution of small benthic carnivores such as E. zebrina to the transfer of energy may be greater than previously estimated.

The limiting factor to the role of harpacticoid copepods as dietary items, particularly those in the EAM, is their small size (Bowen et al. 1995; Choat and Clements 1998). Fishes that feed on mobile benthic invertebrates display a diverse array of morphological and behavioural adaptations to optimise the available energy derived from this food source (Wainwright et al. 2004). To effectively utilise the crustaceans within the EAM, individual fishes must either be relatively small (e.g., Bellwood 1988; Depczynski and Bellwood 2003) or have particularly efficient feeding mechanisms to selectively ingest organisms from amongst the algae and particulate matter of the EAM (Wainwright and Bellwood 2002; Wainwright et al. 2004). These two separate attributes, small size and high selectivity, were particularly apparent in two species in this study: E. zebrina and Stethojulis strigiventer, respectively. The small size of E. zebrina is an indication that this species is able to visually locate, and accurately manipulate and consume small prey items in the EAM. In contrast, S. strigiventer is a much larger and highly mobile species that was observed to take apparently indiscriminate bites from the EAM (Bellwood and Wainwright 2001). The high abundance of crustaceans in the gut of S. strigiventer indicates that it is very efficient at removing food items from amongst sediment and detritus using its oral jaws and buccal apparatus (Wainwright and Bellwood 2002; Wainwright et al. 2004).

The importance of small crustaceans to juvenile fish in early stages of their life history has been documented in a variety of species from both tropical and temperate habitats (Coull 1990; Edgar and Shaw 1995; Toepfer and Fleeger

1995). Seagrasses, for example, are known to harbour many small crustaceans that are consumed by a wide variety of fishes (Hall and Bell 1993; Edgar and Shaw 1995; de Troch et al. 1998; Nakamura et al. 2003). On coral reefs, harpacticoid copepods are major components of the diet of juvenile parrotfishes (Bellwood 1988) and wrasses (Berkström et al. 2012). The nutritional quality and widespread availability of harpacticoid copepods in a coral reef environment suggests that these small crustaceans may be important for not only small fish species, but also for the growth and survival of newly settled fishes. In the early stages of the life of a fish, the rate of growth is rapid, thus producing a linear relationship between size and age, which later asymptotes to a maximum length as the fish reaches sexual maturity (e.g., Choat and Axe 1996; Choat et al. 1996; Depczynski and Bellwood 2006). For small fishes on coral reefs, the ability to cost-effectively utilise an abundant and ubiquitous resources that support the nutritional and energetic requirements for rapid growth is vitally important (Depczynski and Bellwood 2006). Harpacticoid copepods in the EAM fill this role.

More importantly, however, detritivorous parrotfishes were found to incidentally consume an estimated mean of 5.28 % of the available benthic harpacticoid copepods each day. The removal of harpacticoid copepods from the EAM by grazing and excavating parrotfish in Pioneer Bay was particularly striking. In this study, parrotfishes consumed approximately 27 times more harpacticoids than all of the observed benthic carnivores combined. Although the number of harpacticoids removed by parrotfish is much higher than the consumption of copepods by small benthic carnivores, harpacticoids make up only a small proportion of the material that the parrotfish remove from the EAM. Detrital material accounts for 5.44 g m^{-2} of organic carbon on the reef crest (Purcell and Bellwood 2001), whereas harpacticoid copepods comprise 0.29 g m^{-2} of carbon (Williams and Robins 1982; Kramer et al. 2012). Likewise, available nitrogen in the form of copepods is much less than for detritus, at 0.048 and 0.68 g m^{-2}, respectively (Williams and Robins 1982; Purcell and Bellwood 2001; Kramer et al. 2012). These values indicate that the nutritional yield from harpacticoid copepods is only 5.3 % of the carbon and 7.1 % of the nitrogen from the same unit area of detritus. Although information on detailed nutritional information of detritus is lacking, it is very likely that harpacticoid copepods produce comparatively greater nutritional value, by weight, than detrital matter (Wilson et al. 2003; Ajiboye et al. 2011). Nonetheless, parrotfishes unintentionally remove a comparatively large component of the harpacticoid population from the EAM when compared to benthic carnivores in the present and previous studies, which all report daily consumptions of less than 0.2 % of the standing copepod population (Alheit and Scheibel 1982; Hicks 1985; Gee 1987; Coull 1999). Thus, parrotfishes are likely to stimulate rapid life history traits and high productivity in harpacticoids as seen in algae (Russ 2003) and in small cryptobenthic fishes (Depczynski and Bellwood 2006). However, the population control of harpacticoid copepods is unlikely to be solely due to consumption by parrotfishes or benthic carnivores (Coull 1999). Other factors, such as habitat complexity (Zeller 1988; Kramer et al. 2012) and food availability (Montagna et al. 1995), are also likely to be important drivers of harpacticoid population dynamics.

The present study has revealed that benthic carnivores are an abundant trophic category, with direct links as important predators on EAM crustaceans. Additionally, many are prey themselves for higher piscivores. Thus, small benthic carnivores fill the role of an important trophic link between a highly nutritious food source (harpacticoid copepods in the EAM) and higher trophic levels. The EAM provides the basis for the three most important trophic pathways for fishes on coral reefs: algal (Choat et al. 2002; Bonaldo and Bellwood 2011), detrital (Wilson 2000; Wilson et al. 2003), and as found in the present study, carnivorous pathways. All of these sources are derived directly from the EAM and are transferred rapidly up through the trophic levels via small fishes (Depczynski and Bellwood 2003). However, these small fishes are not the most influential consumers of harpacticoid copepods from the EAM. Instead, the nominally herbivorous, or detritivorous, parrotfishes remove a greater proportion of the harpacticoid population, despite gaining little nutrition in comparison with detritus. By understanding the part in which the EAM plays in directly supporting a wide range of trophic modes (i.e., herbivory, detritivory and carnivory), one can begin to appreciate the role that this microhabitat, and its associated organisms, plays in the functioning of a coral reef ecosystem.

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