Vol. 482: 181–195, 2013
doi: 10.3354/meps10259

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 22

Benthic processes and overlying fish assemblages drive the composition of benthic detritus on a central Pacific coral reef

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ABSTRACT: While detrital material is recognized as an important food source on coral reefs, its role in reef food webs remains unclear. We quantified standing stock and input rates to the detrital resource pool in exposed forereef and protected backreef habitats of Palmyra Atoll National Wildlife Refuge and measured the trophic structure of the overlying fish assemblage. While detrital standing stock was 1.6 times higher on the backreef than on the forereef, detrital input rates were 1.7 to 2.9 times higher on the forereef. Planktivores were the most abundant guild in the forereef habitat, and stable isotope signatures of detritus reflected a greater input from pelagic sources (i.e. depleted in ^{13}C). In contrast, herbivores and detritivores numerically dominated the backreef habitat and detrital stable isotope signatures appeared to be predominately of benthic origin (i.e. enriched in ^{13}C). Through total organic carbon (TOC) and nitrogen analyses we found that benthic detritus may represent a significant nutritional source. Converting total nitrogen into maximum protein estimates, we found high benthic deposition of protein (104 to 124 mg m^{-2} d^{-1}) and organic carbon (184 to 190 mg m^{-2} d^{-1}), but very low standing stocks of these materials (protein: 5 to 6 mg m^{-2}, organic carbon: 46 to 63 mg m^{-2}). While high water flow rates may explain low standing stocks of detritus in forereef habitats, the lower flow rates in backreef habitats suggest that removal of this material is via consumption by abundant roving detritivorous fishes. Our results provide support for the hypothesis that reef fish detritivory represents a significant consumer-mediated energy pathway, promoting nutrient recycling by linking many elements of a complex food web.

KEY WORDS: Coral reef · Detritus · Food web · Stable isotopes · Carbon · Nitrogen · Detritivore · Fish

INTRODUCTION

A growing body of literature suggests that benthic detritus is an important food source for coral reef fishes (Crossman et al. 2001, 2005, Wilson 2002, Wilson et al. 2003) and that coral reef fishes both contribute to (Chartock 1983, Bellwood 1995, Goatley & Bellwood 2010) and consume material from (Choat 1991, Wilson et al. 2001) this resource pool. Benthic detritus largely consists of degrading micro- and macro-primary producers (Hatcher 1983, Alongi 1998, Wilson et al. 2001) that have passed through the guts of herbivores or been physically detached from the reef (Wernberg et al. 2006). Additional contributions come from microbes, mucus produced by corals or other invertebrates (Alongi 1998), fecal remains of non-herbivores (Meyer et al. 1983, Meyer & Schultz 1985) and other pelagic outfall (Wilson et al. 2003). Based on estimates of detrital nutritional content (Crossman et al. 2001, Wilson et al. 2001, 2003), detritus is likely an important and often overlooked consumer-mediated nutrient and energy flow pathway.

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Detritivory may enhance the transfer efficiency of primary production into higher trophic levels on the reef as it is reprocessed by detritivores and eventually their predators (Cebrian 1999, 2002). While the incorporation of primary production into coral reef food webs has been modeled (Polovina 1984, Atkinson & Grigg 1984), including movement through detrital pathways (Johnson et al. 1995, Arias-González et al. 1997), the magnitude of nutrients and energy flowing from the detrital pool and into reef fish biomass is largely unknown. There is a high biomass of detritivorous and nominally herbivorous fish on many Pacific coral reefs (Wilson et al. 2003, DeMartini et al. 2008), suggesting that detrital production may exert a strong bottom-up control on food web structure.

To date, most of the work on coral reef detritus and its consumption by coral reef fishes has been limited to measurements of the standing stock biomass of detrital material. Strikingly, findings demonstrate that detrital material in the epilithic algal matrix (EAM) is more nutritious than the benthic algae within which it sits and from which it is largely derived (Wilson & Bellwood 1997, Crossman et al. 2001). Standing stock estimations of this material over large spatial areas indicate that detritus taken from the reef crest habitat is the most nutritious, but least abundant due to wave action. Quality decreases and abundance increases as one moves shoreward (Purcell & Bellwood 2001). These findings indicate the potential for spatial variation in the value and abundance of detrital resources to consumers. However, a major outstanding question concerns the production and renewal rates of detrital resources. Without this information it is difficult to compare the importance of detritus as a resource relative to algae, whose production rates are readily quantified. Accurately quantifying production rates (or input rate) is critical to determining the value of the benthic detrital resource to fishes, especially those with high consumption rates.

Detrital material enters and moves within the benthic pool (for consumption by fishes and other consumers) by several pathways. While a significant portion of detrital production is generally thought to be derived from benthic macroalgae (defecated by herbivorous fish or mechanically broken down), it can also be derived from other sources, such as phytoplankton or zooplankton that originate in the water column (Bray et al. 1981, Rothans & Miller 1991). By consuming, processing and defecating these pelagically-produced sources of production onto the reef, planktivorous fish funnel energy from the water column to the benthic detrital pool and thereby link the pelagic and reef ecosystems. Therefore, detrital material may differ in composition across the reef, depending on the processes by which nutrients and energy flow into this pool and then into reef food webs. Fishes both contribute to and consume material from the benthic detrital pool (differentially by species), so fish biomass patterns and spatial differences in assemblage structure could provide insights to explain spatial differences in composition and abundance of detrital resources (Wilson et al. 2003, Choat et al. 2004).

Herbivorous fishes, namely scraping and excavating parrotfish (Scaridae; see Bellwood 1995) and browsing surgeonfish (Acanthuridae; see Chartock 1983, Goatley & Bellwood 2010), contribute the largest inputs to the detrital pool by volume, owing to their high consumption rates and rapid processing abilities of algal material (Polunin et al. 1995). However, in locations where other functional groups are numerically dominant (e.g. exposed forereef environments), groups such as zooplanktivorous fishes may contribute substantially to the benthic detrital pool (Rothans & Miller 1991), providing a rich source of limiting nutrients (Pinnegar & Polunin 2006). Therefore, in various locations across a reef, detrital inputs may originate from different sources, and differences in detrital source composition may have consequences for consumers of these resources. Species of surgeonfish and parrotfish are the primary consumers of detrital material on Pacific coral reefs (Choat et al. 2002, Crossman et al. 2005). The derived ctenochaetid group of surgeonfish (*Ctenochaetus* spp.) possesses comb-like teeth, ideally adapted to capture detrital resources (Purcell & Bellwood 1993) by sweeping particulate matter off the benthos.

To date, no studies have compared input rates to standing stock quantities of detritus in different coral reef habitats nor attempted to assess differences with respect to organic content, nutritional quality and source of material. This invaluable information will improve our understanding of the processes that govern detritus composition and distribution in locations where detritivores feed. Because many coral reef systems have been altered by overfishing and will continue to be negatively affected by global climate change, it is pressing to determine the function of ecosystem processes such as detrital cycling. Palmyra Atoll, a fully protected U.S. national wildlife refuge in the central Pacific, with little history of human impacts, is an ideal location to examine detrital processes and pathways in a healthy reef setting. Given the high biomass of detritivorous fishes on Palmyra's reefs (Sandin et al. 2008), it is likely that

this functional group plays an important role in the ecosystem by keeping reef surfaces clear of algal debris, as well as serving as prey resources for larger predators.

This study attempted to quantify the amount of detrital material deposited to, and present on reef substrates in 2 different habitats, the forereef and backreef of Palmyra Atoll, while characterizing the sources and basic nutritional content of detritus in each habitat. Our main goal was to aid in understanding the pathway and flow of detrital material through coral reef food webs. Based on previous studies (Bray et al. 1981, Rothans & Miller 1991), we expected that the fish assemblage present in any one habitat will influence the amount and composition of benthic detrital resources that are produced. We characterized the fish assemblage by trophic level in each habitat and discussed links between fish assemblage and detrital composition. Finally, based on estimates of detrital production rates, as well as fish consumption rates and nutrient requirements, we quantified whether or not the measured benthic detrital pool is sufficient to support the dietary requirements of detritivorous fishes on Palmyra's coral reefs.

MATERIALS AND METHODS

Study site

This study was conducted at Palmyra Atoll National Wildlife Refuge (5.867° N, 162.067° W; Fig. 1). Sites were sampled during August–September 2008 (Trip 1) and again in October–November 2008 (Trip 2). Although altered geomorphologically by the US military, Palmyra contains a largely intact oceanic coral reef system with a trophic structure minimally affected by human disturbances, such as fishing or nutrient pollution. Work was carried out in 2 different reef habitats: the shallow backreef (2 to 4.5 m in depth at low tide) and the forereef slope (10.5 to 16.5 m depth; Fig. 1).

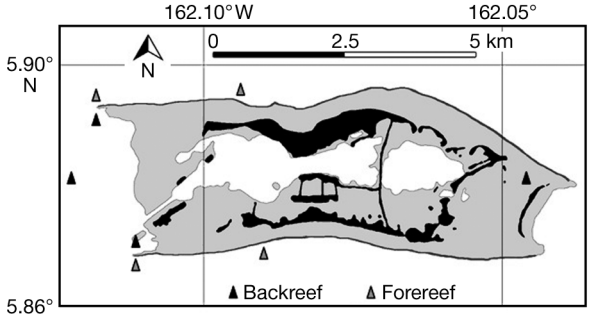

Fig. 1. Sampling sites in backreef and forereef habitats on Palmyra Atoll. Black filled areas are emergent land, gray filled areas are shallow reef flats, and the solid black line is the reef crest. The gray contour line represents the 10 m isobath discerned from a bathymetric map in conjunction with a satellite image

Benthic environments in backreef habitats were generally characterized by high rugosity, continuous reefs consisting of >50% live coral, interspersed with large, dead, standing corals. Dead corals were covered in crustose coralline algae (Maragos et al. 2008), areas of closely cropped turf algae (also referred to as the EAM), patches of *Halimeda* and, to a lesser extent, other fleshy macroalgae. Benthic forereef habitats were dominated by hard coral and crustose coralline algae, together comprising 48% of all surfaces (Sandin et al. 2008). *Halimeda* and turf algae dominated forereef benthic algal assemblages, agreeing with previous studies on Palmyra's forereef (McCauley et al. 2010). The fish assemblages in the backreef (Friedlander et al. 2010 describe nearby Kingman Atoll's backreef) and the forereef (Sandin et al. 2008) contain abundant herbivorous, carnivorous and piscivorous fishes. In addition, Palmyra's reefs, with the exception of some lagoonal habitats, have low abundances of macroinvertebrates, namely echinoderms (Maragos et al. 2008), which, together with cryptic fauna inside the reef, often account for an important consumer group of particulate material (Gili & Coma 1998). Therefore, fishes appear to be the primary detritivores in Palmyra.

Detrital sampling

Two types of detrital samples were taken at each site, along 50 m transects: 'input' samples, collected in sediment traps, and 'standing stock' samples, collected by suctioning material off fixed areas of the benthos. We took these 2 types of samples to compare biomass, quality, and source (i.e. benthic or pelagic origin) of newly settling detritus (sediment traps) with that of existing benthic detritus (suction samples). Comparisons of both detrital measurements can be used to estimate residence time of detrital material (including its nitrogen and organic carbon components) on the benthos. We calculated residence time by dividing the mean standing stock (mg m^{-2}) by the mean deposition rate (mg m^{-2} d^{-1}). We used this metric to describe the physical and biological turnover rate of the resource, reflecting production, consumption and recycling processes. This method was adapted from similar metrics used to measure the balance between production and loss of

organic particles in surface waters (Eppley et al. 1983). We noted that our residence time estimation did not fully account for detritus produced from sources other than materials settling out of the water column.

Sediment trap sampling

In each habitat, tubular sediment traps with aspect ratios of 4:1 and opening diameters of 7.6 cm were secured directly to the benthos, over a reef matrix covered by turf algae, to collect settling detrital material over 48 to 72 h periods (Koop & Larkum 1987, McClanahan & Obura 1997). Traps were constructed of clear co-polyester tubes with vinyl end caps. Sets of 5 traps were repeatedly set out approximately 10 m apart along two 50 m transects parallel to the reef crest at each site. A total of 136 traps were successfully collected. Reviews of sediment traps used in high energy environments found that tubular traps with aspect ratios greater than 3:1 can be efficient collectors when flow rates are no greater than 0.2 m s^{-1} (Gardner 1980, White 1990). Depending on flow and particle size, sediment traps may under- or overestimate absolute particle deposition (Butman 1986, White 1990, Yund et al. 1991). Sediment traps collect newly settling material from the water column, and may also collect resuspended material and material that would otherwise remain in suspension (Bothner et al. 2006, Storlazzi et al. 2011). Such over-collection, particularly of large grained calcium carbonate ($CaCO_3$), may occur in the high flow environments of Palmyra's forereef, but in the more quiescent backreef area, where resuspension is less likely, trap captures reflect true rates of detrital inputs to the benthos more closely. Therefore, we sampled at 10 to 15 m depth on the forereef to minimize the effects of resuspension that occur at shallower forereef depths (3 to 5 m). To check whether or not the traps primarily captured material that would otherwise remain in suspension or resuspended benthic material from the water column, we compared the composition of trap material to standing stock benthic detrital samples and water column particulate organic material (POM) samples.

Standing stock sampling

During the August–September sampling period, standing stock detrital material was suctioned from dead coral surfaces covered in closely cropped turf algae. Samples were taken with 60 cc suction samplers (Manufacturing Design Solutions), which minimize contamination with overlying seawater by collecting samples in pre-filtered seawater (filtered to 0.45 µm). Sampling was standardized using a consistent suction rate and sampling area (35.24 cm^2). We took 24 samples per site. During the October–November sampling period, 12 samples were taken per site with 120 cc syringes fitted with tygon tubing. Samples were taken along the same 50 m transects set out for sediment trap sampling, at the same forereef and backreef sites. As with previous studies examining EAM standing stock, care was taken to avoid pits and erect macroalgae (Purcell & Bellwood 2001).

Resource sampling

Resource samples, including benthic algae, zooplankton, fish feces and water column POM (e.g. phytoplankton and other particulates), were taken at the backreef and forereef sites. These samples were taken to help determine the sources of primary production contributing to the composition of benthic detritus. The most abundant macroalgal species (i.e. those occurring at the greatest % cover) were collected at each site, then picked clean of epiphytes under a dissecting microscope, rinsed with DI water and frozen to −80°C. Zooplankton (daytime holoplankton) samples were collected with a 200 µm mesh hand-held plankton net (30 × 90 cm opening; Aquatic Research Instruments) on timed 5 min swims, 2 m above the benthos using a scuba set. Fish fecal samples were collected by following frequently defecating fishes (namely scarids and some acanthurids) and suctioning their defecations from the water column. Water samples for POM collection were taken 1 m above the benthos at each site. Zooplankton, POM and fecal samples were GF/F filtered onto precombusted pre-weighed (450°C; 4 h) Whatman filters (nominal pore size 0.7 µm) under a vacuum and then rinsed with DI water.

Post sample processing

Immediately following collection, sediment trap and suction samples were sieved through acid-washed 150 µm sieves; both size fractions were saved. The small size fraction (<150 µm) contains the nutritive fraction of detrital material targeted by detritivores (Wilson 2000, Wilson et al. 2003). Next,

the ≥150 and <150 µm fractions were GF/F filtered onto pre-combusted, pre-weighed (450°C; 4 h) Whatman filters (nominal pore size 0.7 µm) under a vacuum and then rinsed with DI water. Each standing stock sample was pooled from 4 individual 60 cc syringe samples, covering 141.37 cm^2 of reef surface per pooled sample. Filters were frozen at –80°C upon filtration and then oven dried at 60°C before chemical analyses. Subsamples of the fractioned trap and standing stock samples were weighed (once dry) to determine settlement rates and standing stock amounts for both size fractions (trap samples: $n_{backreef}$ = 20, $n_{forereef}$ = 15; suction samples: $n_{backreef\ (pooled)}$ = 12, $n_{forereef\ (pooled)}$ = 9). Resource samples collected in water were GF/F filtered and dried as above, while the remainder (including algal resource specimens) were dried whole, then ground prior to subsampling. For algal specimens, sections of several individuals of a given species from a given site were pooled to form each sample used for chemical analyses.

Laboratory analyses

We used stable isotope analysis to examine differences in the composition and source of detritus between the forereef and backreef habitats. The ratio of organic ^{13}C to ^{12}C (expressed as $\delta^{13}C$ ‰) varies, based on the source of primary production: benthic macroalgae are often enriched in ^{13}C relative to pelagic phytoplankton (France 1995). The ratio of ^{15}N to ^{14}N (expressed as $\delta^{15}N$ ‰) is indicative of the trophic level of that material: ^{15}N is enriched at higher trophic levels (Peterson & Fry 1987). Comparing isotopic signatures of detritus samples to that of potential source materials (resource samples described above), collected from the same sites, provides insight into the source of the detrital samples. We used $\delta^{13}C$ to discern the influence of pelagic versus benthic inputs by sample type (sediment trap versus standing stock) and by habitat. If pelagic inputs to the forereef benthos were higher than on the backreef, we expected forereef samples of a given detritus type to be depleted in $\delta^{13}C$ relative to backreef samples. For a given location we expected sediment trap material to be depleted in $\delta^{13}C$ relative to suction samples, as sediment traps are more likely to capture settling pelagic materials, whereas suction samples represent an amalgam of settling materials and benthic-generated materials.

Simultaneously with stable isotopes, we measured organic carbon and nitrogen content to estimate the nutritional quality of detrital samples. TOC measurements provide an upper limit for the amount of high quality carbon compounds in a sample. We use total nitrogen as an upper limit proxy for total protein and amino acid nitrogen. Since protein and amino acids can potentially limit fish biomass production on reefs, and many nominally herbivorous and detritivorous fish can be considered 'protein scavengers' (Crossman et al. 2005), assessing the availability of protein and amino acid nitrogen in reef detritus is likely a better estimate of quality than organic carbon. We used TOC, total nitrogen, and the ratio between them (organic C:N) to express quality.

Prior to analyses for stable isotopes, TOC and N, detrital and resource samples were acidified dropwise with 1N HCl, until bubbling ceased. This procedure was carried out to remove carbonates and isolate the organic fraction from the detrital and resource samples. Detrital samples on GF/Fs and resource samples from each site (these included algae, >200 µm zooplankton, and fish feces) were analyzed simultaneously for carbon and nitrogen stable isotopes and TOC and nitrogen using an elemental analyzer (Costech EAS Elemental Analyzer) and continuous flow isotope ratio mass spectrometry (Thermo-Finnigan Delta+ Advantage Mass Spectrometer) (trap samples Trip 1: $n_{backreef}$ = 20, $n_{forereef}$ = 15, Trip 2: $n_{backreef}$ = 38, $n_{forereef}$ = 26; suction samples Trip 1: $n_{backreef\ (pooled)}$ = 9, $n_{forereef\ (pooled)}$ = 12, Trip 2: $n_{backreef\ (pooled)}$ = 24, $n_{forereef\ (pooled)}$ = 19) at the Marine Science Institute of the University of California Santa Barbara (UCSB). Isotopic results are expressed as δ values, $\delta^{13}C$ or $\delta^{15}N = 1000[(R_{sample} / R_{standard}) - 1]$, where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the samples and standards respectively, in parts per thousand (‰) or parts per million (ppm). The standards are Vienna-Pee Dee Belemnite (V-PDB) for carbon and atmospheric N_2 for nitrogen. The within-run standard deviation of acetanilide and alanine standards was ≤0.25 ‰ for $\delta^{13}C$ and $\delta^{15}N$. In addition, several large size fraction samples (≥150 µm, n = 21 pooled suction samples, n = 27 sediment traps), whose <150 µm fraction was analyzed as stated above, were analyzed on a Carlo Erba/Fisions NA1500 Series 2 CHN analyzer to measure TOC and nitrogen content, without simultaneous stable isotope measurements.

Fish surveys

Fish surveys were carried out in order to assess the potential relationship between fish abundance and benthic detrital resources. Surveys were carried out

at 4 forereef and 4 backreef sites, with forereef surveys carried out with scuba sets and backreef surveys with snorkel and scuba sets. Fish surveys were carried out at the same scale as detrital sampling at each site. At each site at least two 50 m transects (each divided into 2 contiguous 25 m transects) were laid out and left alone for at least 10 min. Two divers then swam at a fixed pace, counting and estimating the size of each fish encountered to the nearest 5 cm (forereef transects: n = 16, backreef transects: n = 25). The first swimmer counted large, roving and easily frightened species (e.g. sharks, jacks, parrotfish, surgeonfish, etc.), while the second swimmer counted small site-attached species (e.g. damselfish, small seabasses, wrasses, etc.). All fish ≥15 cm total length were counted within a 5 m wide belt, while species <15 cm in length were counted within a 2 m wide belt. Fish density and biomass were determined per 100 m^2 or per ha of each habitat surveyed. To calculate biomass we used published species- or genus-specific length-weight parameters (Kulbicki et al. 2005, www.fishbase.org) to convert length into weight for each fish counted.

Data analyses

To analyze the measurements made on input and standing stock of detrital material, samples were nested by site into forereef and backreef habitats. To examine differences between habitats for each measured detrital parameter (deposition or input rate, standing stock, stable isotopes, TOC, total nitrogen and C:N ratio), we used mixed-model ANOVAs with each individual site as a random factor and reef habitat and collection period as fixed factors.

To compare fish assemblages among back and forereef sites and determine the relationship between this structure and the characteristics of detritus in each habitat, fishes were classified into broad functional categories based on their dominant food source: piscivores (fish), carnivores (fish and invertebrates), omnivores (wide range of foods), zooplanktivores (zooplankton), herbivores (benthic micro- and macroalgae) and detritivores (benthic detritus). The distinction between herbivores and detritivores was made based on a conservative interpretation of Choat et al. (2002), who used short-chain fatty acid analyses of gut content material to distinguish dietary strategies, as well as on other published classifications (Robertson & Gaines 1986, Bellwood & Choat 1990, Choat 1991, Wilson 2000) and on the authors' observations of fish feeding behaviors on Palmyra. Fish species were only classified as detritivore over herbivore if the distinction was explicit in the literature and observed in the field. All parrotfish species were classified as herbivores due to field observations, although Choat et al. (2002) classified *Chlorurus sordidus, C. microrhinos* and *Scarus schlegeli* as detritivores. Fish biomass and density were compared between sites and between habitats by these functional groups. To determine the source of variation and calculate habitat means, we performed a 2-way ANOVA with site as a random factor nested within habitat type.

Simple mass balance calculation

Protein and organic carbon represent important energy sources for fish (Weber & Haman 1996). It has been argued that herbivorous and detritivorous fish growth is limited by protein supply (Horn 1989). A simple mass balance was calculated in order to determine if the material collected in sediment traps contained a sufficient amount of protein and organic carbon to support the biomass of detritivorous fish in each habitat. We focused our mass balance energy requirement calculations on the genus *Ctenochaetus*, because the literature indicates that these species are obligate detritivores (Purcell & Bellwood 1993) and because they represent approximately 80% of the detritivorous fish biomass on Palmyra.

First, to obtain the total protein input to the benthos per unit of habitat, the total nitrogen input per m^2 was multiplied by a conservative nitrogen-to-protein conversion factor of 4.58, developed for micro-algae (Lourenço et al. 2002). This protein amount is an upper-bound estimate, because not all of the nitrogen is incorporated into proteins or amino acids and some nitrogen is likely to be non-assimilable (Crossman et al. 2000). Second, to estimate the protein-nitrogen requirements of *Ctenochaetus* per m^2, an upper- and lower-bound protein requirement per g of fish flesh was used as a multiplier. The lower-bound requirement used was an estimate of the amount of nitrogen ingested by *Stegastes nigricans* (1.3 mg N g^{-1} d^{-1}; de Loma & Harmelin-Vivien 2002), allometrically scaled to the metabolic requirements of a fish the size of the average *C. striatus* using the ¾ power law for metabolic rates (0.7 mg N g^{-1} d^{-1}, which converts to 3.1 mg protein g^{-1} d^{-1}; West et al. 1997). The upper-bound requirement used was the protein turnover rate for rainbow trout *Oncorhynchus mykiss* (8.0 mg g^{-1} d^{-1}; Kaushik & Seilez 2010). Generally, fish fall within a similar range of protein needs and turnover rates (Kaushik & Seilez 2010),

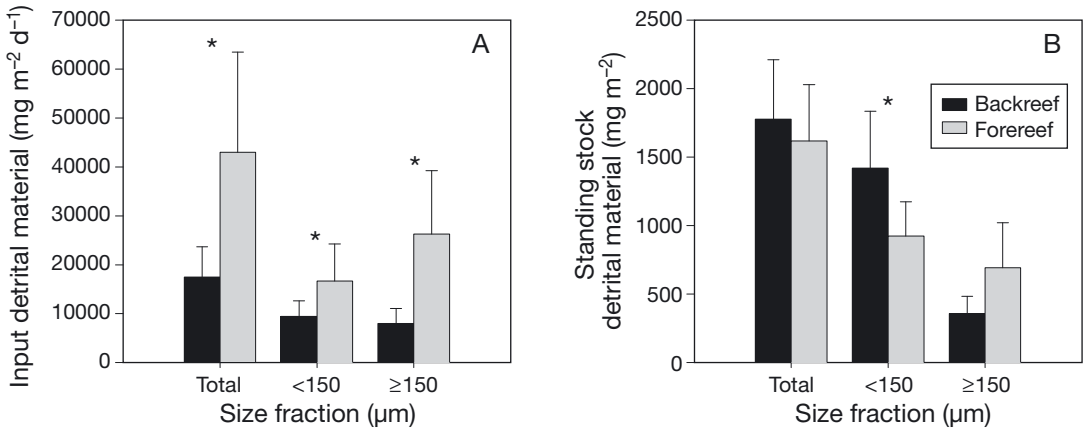

Fig. 2. (A) Input rates of detrital material into sediment traps deployed on backreef (black bars) and forereef (gray bars) habitats on Palmyra Atoll. Shown is the total deposition rate and those of the 2 size fractions, averaged over both sampling periods (August–September and October–November 2008). Error bars = 1 SE. Mean deposition rates were higher in forereef relative to backreef areas for total material (ANOVA: $F_{9,81}$ = 29.43, p < 0.0001) and for all size fractions for all collections (ANOVA: ≥150 µm $F_{9,81}$ = 26.33, p < 0.0001; <150 µm $F_{9,82}$ = 24.48, p < 0.0001), with overall higher flux rates recorded for the October–November samples (ANOVA: $F_{9,81}$ = 10.44, p = 0.002; see Fig. S1 in the supplement at www.int-res.com/articles/suppl/m482p181_supp.pdf for input rates for each collection period). (B) Standing stock benthic detrital material, collected by suction sampling from backreef (black bars) and forereef (gray bars) habitats. Shown is the total average mass collected from standardized suction samples and the masses of the 2 size fractions. Mean total standing stocks were calculated using individual suction sample totals, rather than summing the size fraction means. Error bars = 1 SE. An asterisk above a backreef/forereef pair denotes significant differences detected by ANOVA. Backreef and forereef habitats had similar standing stocks of total benthic detrital material (ANOVA: $F_{4,16}$ = 2.22, p = 0.11). The backreef had higher standing stock of the small size fraction (ANOVA: $F_{4,16}$ = 4.52, p = 0.01)

providing a justification for this approach. This represents an upper-bound requirement, because protein synthesis and deposition in fish are dependent on both dietary supply and reutilization of amino acids (Fauconneau 1985). For organic carbon requirements, we scaled the ingestion rate for *S. nigricans* (12.2 mg C g^{-1} d^{-1}; de Loma & Harmelin-Vivien 2002) to that of *C. striatus* (6.5 mg C g^{-1} d^{-1}).

As an additional estimate, we calculated the dietary needs of detritivorous fish in forereef and backreef habitats, based on the density of *Ctenochaetus* sp. and measurements of *C. striatus* consumption from the Great Barrier Reef (8.8 ± 2.4 to 66.1 ± 14.4 g d^{-1}; see Goatley & Bellwood 2010). These values were compared to the residence time of detrital material to ascertain whether or not fish consumption rates scale with the turnover time of benthic detrital resources.

RESULTS

Volume of detrital resources by habitat

The total input rate of detrital material to the benthos differed significantly between reef habitats (Fig. 2A). The forereef experienced higher and more variable deposition rates of detrital material into sediment traps for both size fractions than the backreef, with this pattern holding for both the August–September and October–November collection periods (Fig. 2A, Fig. S1 in the supplement at www.int-res.com/articles/suppl/m482p181_supp.pdf). There was no significant interaction between habitat and collection period for either size fraction or the total of the 2 size fractions. For all size fractions, there was a general trend for higher deposition occurring during October–November than August to September (Fig. S1). In both sampling periods, backreef material contained more small, relative to large, size fraction particles than the forereef material (Fig. 2A, Fig. S1).

Backreef and forereef habitats had similar standing stocks of total benthic detrital material, but the back reef had higher standing stock of the small size fraction (Fig. 2B), confirming the expectation that smaller particles would not remain on the benthos in more wave-exposed environments. A comparison of standing stocks with input rates suggests that the residence time of total particulate matter on the benthos was short in both backreef (4.9 ± 1.5 h) and forereef habitats (2.8 ± 1.6 h) and particularly so on the forereef. When broken down by size fraction, <150 µm material had a higher residence time than ≥150 µm material, in both backreef (<150 µm: 6.8 ± 1.9 h, ≥150 µm: 2.3 ± 1.4 h) and forereef environments (<150 µm: 3.7 ± 1.7 h, ≥150 µm: 2.1 ± 1.6 h).

Organic carbon and nitrogen

Forereef habitats had lower C:N ratios for input and standing stock material in the large size fraction than backreef habitats (Table 1), indicating that the forereef contained more nitrogen-rich detritus relative to the backreef. In both habitats, sediment trap samples were more nitrogen-rich than corresponding standing stock samples for both the ≥150 µm and <150 µm size fractions (Table 1). Water column POM C:N ratio values (backreef = 15.7 ± 0.2, forereef = 17.8 ± 0.7) were considerably higher than backreef or forereef detrital values, regardless of sampling method, indicating that resuspension did not create a large reserve of high quality detrital material in the water column above the benthos. We used rates of deposition and standing stock detritus values along with TOC and total nitrogen measurements to estimate nutrient availability and content. The amounts of nitrogen and organic carbon entering the benthic detrital pool were similar for backreef and forereef environments, with higher nitrogen deposition in the second sampling period (Fig. 3). Available nitrogen was significantly higher on backreef than forereef habitats (Fig. 4). For both elements, the relatively high rates of deposition, compared to standing stock, suggest that organic carbon and nitrogen did not accumulate on the benthos; if they had accumulated, greater quantities of these nutrients would be present in standing stock detritus samples than sediment trap samples.

Using nitrogen as a proxy for protein, we also developed crude protein estimates to compare to gross

Table 1. C:N ratios (means, SD in parentheses) for Trip 1 (August–September 2008) and Trip 2 (October–November 2008) for <150 and ≥150 µm material, collected from sediment traps (input) and from suction samplers (standing stock). The ≥150 µm standing stock was not sampled (na) for Trip 2. In both habitats, sediment trap samples had lower C:N ratios than corresponding standing stock samples for both size fractions (ANOVA: ≥150 μm_{Trip1}, $F_{1,21} = 10.98$, $p = 0.0033$; <150 $\mu m_{Trip1\&2}$, $F_{3,78} = 17.97$, $p < 0.0001$)

	<150 µm input	≥150 µm input	<150 µm standing	≥150 µm standing
Trip 1				
Backreef	8.66 (0.05)	9.62 (2.85)	10.68 (1.24)	15.38 (2.13)
Forereef	7.42 (0.19)	7.03 (0.53)	8.48 (0.05)	13.98 (2.01)
Trip 2				
Backreef	7.87 (0.53)	8.90 (0.59)	9.24 (0.96)	na
Forereef	7.03 (0.53)	6.79 (0.41)	6.53 (0.23)	na

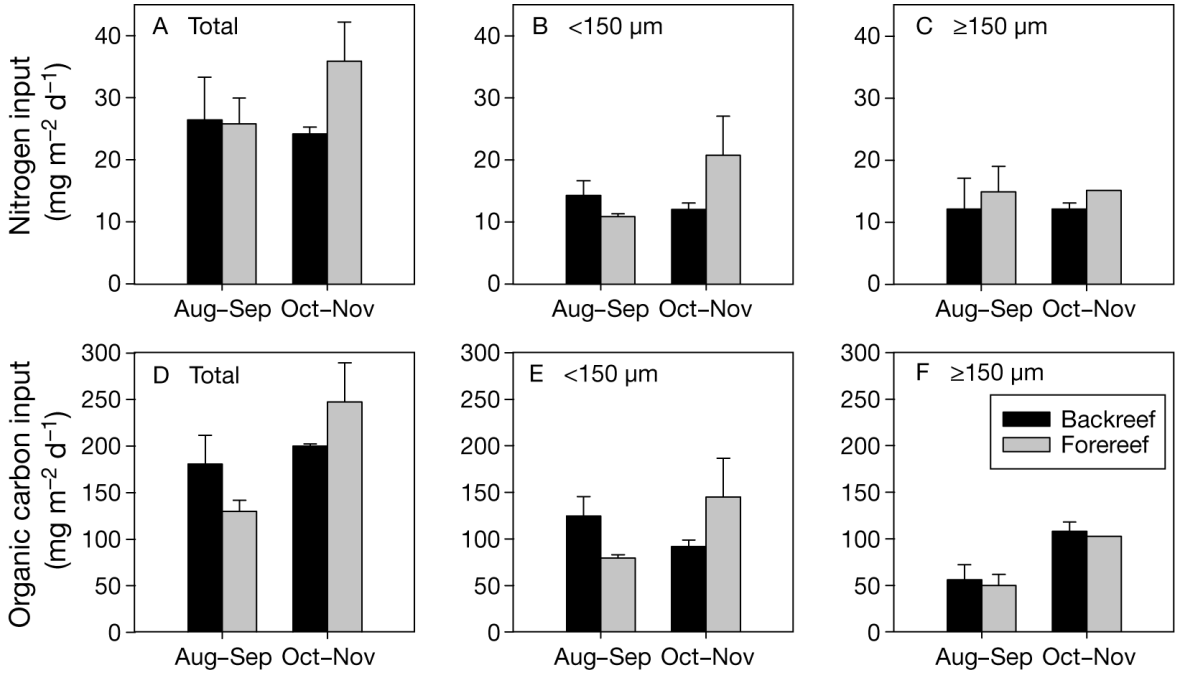

Fig. 3. (A–C) Nitrogen and (D–F) organic carbon content (mean + 1 SE) in detrital material input collected with benthic sediment traps on 2 different deployments to backreef (black bars) and forereef (gray bars) habitats on Palmyra Atoll. Input samples are broken down by size fraction: (A, D) total, (B, E) <150 µm and (C, F) ≥150 µm. Mean total nitrogen and organic carbon were calculated using individual sediment trap totals, rather than summing the size fraction means

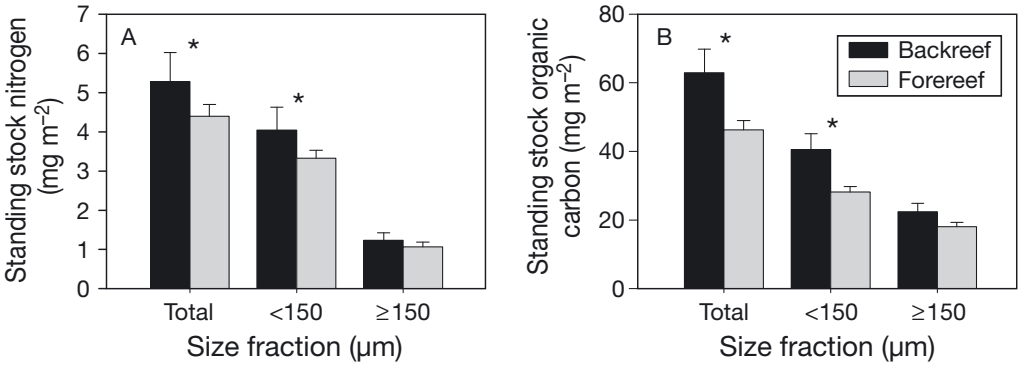

Fig. 4. (A) Nitrogen and (B) organic carbon content (mean + 1 SE) in standing stock detrital material, collected by suction sampling from backreef (black bars) and forereef (gray bars) habitats on Palmyra Atoll. Mean total standing stocks were calculated using individual suction sample totals, rather than summing the size fraction means. An asterisk above a backreef/forereef pair denotes significant differences detected by ANOVA. Available nitrogen was significantly higher on backreef than forereef habitats (ANOVA: $F_{4,16} = 5.21$, p = 0.007)

nutritional needs of detritivorous fishes. Using input measurements for the October–November sampling period, we found protein deposition to be approximately 123.9 ± 19.1 mg m^{-2} d^{-1} on the forereef, while ~4.9 ± 0.6 mg protein m^{-2} existed as standing stock. Protein deposition on the backreef was ~104.1 ± 5.1 mg m^{-2} d^{-1}, while ~5.6 ± 0.9 mg protein m^{-2} existed as standing stock.

Stable isotopes

The $\delta^{13}C$ values of detritus were significantly higher for backreef samples than for forereef samples, both for sediment trap input samples and standing stock suction samples (Table 2, Fig. 5). Standing stock detritus was consistently and significantly enriched in ^{13}C relative to the material collected in sediment traps (Fig. 5). The $\delta^{15}N$ values did not differ significantly between backreef and forereef sites, between sediment trap and standing stock material, nor between input and standing stock material (Fig. 5).

Due to a general lack of differences between backreef and forereef stable isotope signatures within resource sample type (fish feces, POM, zooplankton and algae), values from both habitats were pooled by type for comparison with detrital signatures. In examining the carbon stable isotope signatures of potential end members (sources of detrital material), benthic material was significantly enriched in ^{13}C relative to POM and zooplankton (Fig. 5). While we sampled only the dominant species of macroalgae, several studies report a similar range of macroalgal $\delta^{13}C$ values for several species common to Palmyra (Table S1 in the supplement).

Fish surveys

Fish surveys indicated that significant differences existed between backreef and forereef environments in terms of total biomass (backreef: 1293.4 ± 232.4 kg ha^{-1}, forereef: 2250.2 ± 396.5 kg ha^{-1}), total density (backreef: 113.9 ± 15.1 ind. 100 m^{-2}; forereef: 686.7 ± 187.0 ind. 100 m^{-2}) and overall composition (Fig. 6, Table S2 in the supplement). For both biomass and density, significant differences between backreef and forereef habitats were found for some trophic groups (Fig. 6). The biomass of piscivores, carnivores, and zooplanktivores was significantly higher

Table 2. Stable isotope measurements (‰) for standing stock (suction) and input (sediment trap) samples by habitat and period of measurement (t_1 = August–September 2008, t_2 = October–November 2008). Values are means (SD in parentheses). The $\delta^{13}C$ values were significantly higher for backreef than for forereef samples, both for input samples (ANOVA: $F_{9,80} = 6.12$, p < 0.0001) and standing stock samples (ANOVA: $F_{8,55} = 6.85$, p < 0.0001)

Sample type	$\delta^{13}C$	$\delta^{15}N$
Standing stock, <150 µm		
Backreef t_1	−16.83 (3.68)	8.82 (0.21)
Backreef t_2	−14.74 (1.84)	7.60 (1.05)
Forereef t_1	−19.84 (0.29)	8.33 (0.05)
Forereef t_2	−17.67 (0.49)	8.50 (0.43)
Input, <150 µm		
Backreef t_1	−17.18 (2.68)	9.87 (0.08)
Backreef t_2	−17.58 (1.38)	8.63 (1.08)
Forereef t_1	−20.01 (0.20)	9.21 (0.56)
Forereef t_2	−20.26 (0.71)	8.32 (0.82)
Input, ≥150 µm		
Backreef t_2	−15.75 (1.15)	8.55 (0.62)
Forereef t_2	−19.90 (0.51)	7.24 (2.63)

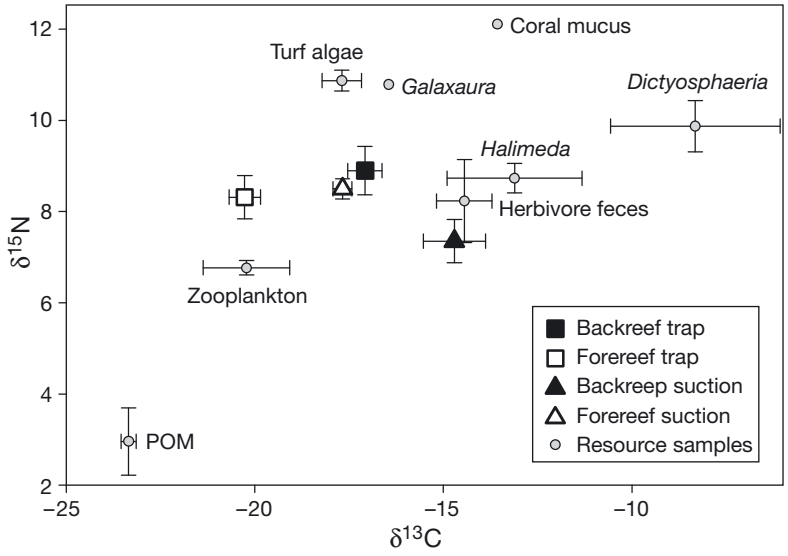

Fig. 5. Stable isotope biplot showing signatures of $\delta^{13}C$ and $\delta^{15}N$ ratios for detrital material collected by suction sampling (squares) and by sediment traps (triangles) from backreef (black symbols) and forereef (white symbols) habitats on Palmyra Atoll. Delta (δ) values indicate the difference between the sample measurement and standard. Standing stock detritus was significantly enriched in ^{13}C relative to the material collected in sediment traps (ANOVA: forereef, $F_{1,63}$ = 79.28, p < 0.0001; backreef, $F_{1,74}$ = 29.36, p < 0.0001). There was no significant difference in $\delta^{15}N$ between sampling types or habitat (ANOVA: forereef, $F_{1,63}$ = 0.15, p = 0.70; backreef, $F_{1,75}$ = 1.22, p = 0.27). Also shown are stable isotope signatures of potential end member materials (gray circles) collected at the same sampling locations, including POM (phytoplankton), zooplankton, herbivore feces, coral mucus, macroalgae (*Halimeda* sp., *Dictyosphaeria* sp., *Galaxura* sp.) and turf algae. Error bars = ±1 SE. Turf signatures provided by McCauley et al. (2012)

on the forereef, while the biomass of detritivores and herbivores was significantly higher on the backreef (Fig. 6). Fish density followed similar patterns to biomass, except that, while zooplanktivores were numerically dominant on the forereef, this group did not dominate the biomass patterns due to their small size (Fig. 6). In addition, carnivores had significantly higher densities on the forereef than on the backreef (Fig. 6). Herbivores were numerically the most common trophic group in backreef habitats, while carnivores had the highest density in forereef habitats (Fig. 6, Table S2). Of the detritivorous fish biomass, *Ctenochaetus striatus* dominated the composition of backreef detritivores and comprised 25.3 ± 0.3% of all backreef fish biomass, while *C. marginatus* and *C. cyanocheilus* were most common in the forereef habitat (Table S2).

At the site level, there were significant associations between fish biomass and standing stock detrital stable isotope values; detritivore biomass was positively associated with $\delta^{13}C$ (Pearson's r = 0.85, p = 0.03) and negatively associated with $\delta^{15}N$ (r = −0.93, p = 0.01), while zooplanktivore biomass was negatively associated

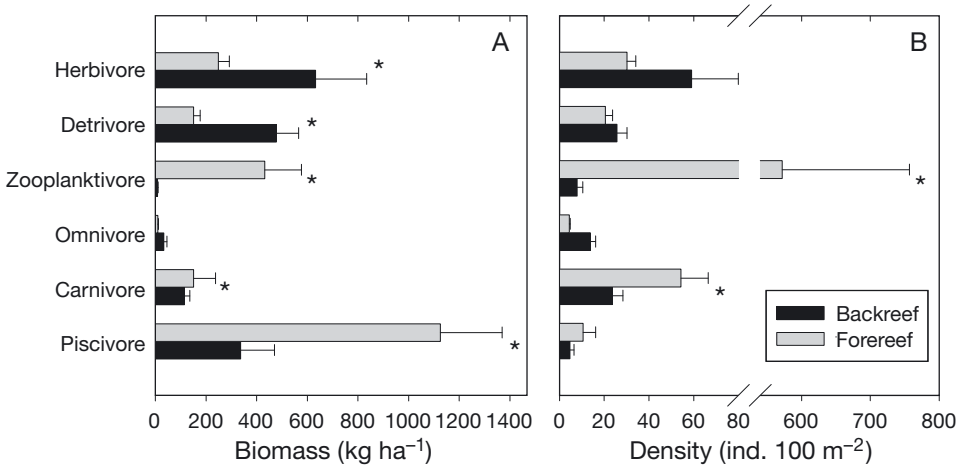

Fig. 6. (A) Biomass (kg reef fish per ha of water column above the benthos) and (B) density (number of reef fish per 100 m^2 of water column above the benthos), recorded on belt transect surveys on Palmyra's forereef and backreef habitats and summarized by trophic group. Shown are mean values + 1 SE. Trophic groups include piscivores, omnivores, herbivores, detritivores and zooplanktivores. An asterisk next to a backreef/forereef pair denotes significant differences detected by ANOVA (α = 0.05). Overall biomass (ANOVA: $F_{8,40}$ = 3.04, p = 0.01) and density (ANOVA: $F_{8,40}$ = 13.44, p < 0.0001) were significantly higher on the forereef. Detritivore (ANOVA: $F_{8,40}$ = 7.09, p < 0.0001) and herbivore (ANOVA: $F_{8,40}$ = 2.91, p = 0.01) biomass were significantly higher on the backreef, while piscivore (ANOVA: $F_{8,40}$ = 2.76, p = 0.02), carnivore (ANOVA: $F_{8,40}$ = 2.52, p = 0.03) and zooplanktivore (ANOVA: $F_{8,40}$ = 15.98, p < 0.0001) biomass were significantly higher on the forereef. Zooplanktivores (ANOVA: $F_{8,40}$ = 17.89, p < 0.0001) and carnivores (ANOVA: $F_{8,40}$ = 5.54, p < 0.0001) had significantly higher densities on the forereef

with $\delta^{13}C$ ($r = -0.82$, $p = 0.04$). In the backreef, where herbivores dominated, detritus was enriched in ^{13}C and resembled end members such as benthic macroalgae (Fig. 5), the primary food source of the herbivores in that habitat. However, on the forereef, detritus was depleted in $\delta^{13}C$ and reflected end members such as phytoplankton (POM) and zooplankton (Fig. 5), the major food source of the numerically dominant planktivores.

Simple mass balance estimates of detritivore dietary requirements

Based on our calculations, the maximum protein (123.9 mg m^{-2} d^{-1}) and organic carbon (184.0 mg m^{-2} d^{-1}) input rates of detrital material are generally sufficient to sustain the dietary energy requirements of *Ctenochaetus* spp. on Palmyra's forereef (protein: 61.3 to 157.4 mg m^{-2} d^{-1}, organic carbon: 128.6 mg m^{-2} d^{-1}). However, the same calculations suggest that the backreef input contained both less protein (104.1 to 157.4 mg m^{-2} d^{-1}) and less carbon (190.5 mg m^{-2} d^{-1}) than the measured backreef biomass of *Ctenochaetus* spp. is likely to require (protein: 181.3 to 465.1 mg m^{-2} d^{-1}, organic carbon: 380.0 mg m^{-2} d^{-1}). The protein requirement of these detritivores exceeds production by 1.7 to 4.5 times on the backreef.

In contrast to our calculations above, an analysis of *Ctenochaetus* spp. dietary needs based on the mass of material consumed (using estimates developed on the Great Barrier Reef) indicated that there was an adequate amount of material in total input detritus (forereef: 74 909.4 ± 25 058.8 mg m^{-2} d^{-1}, backreef: 26 223.7 ± 1902.1 mg m^{-2} d^{-1}) to sustain their ingestion needs (forereef: 794.1 to 5964.9 mg $m^{-2}d^{-1}$, backreef: 2237.5 to 16 806.9 mg m^{-2} d^{-1}). The mass of <150 µm input material (forereef: 27 335.9 ± 5324.9 mg m^{-2} d^{-1}, backreef: 13 943.0 ± 1106.1 mg m^{-2} d^{-1}) approximates *Ctenochaetus* consumption needs more closely, particularly on the backreef.

DISCUSSION

Processes influencing patterns of detrital composition and abundance

Our results suggest that benthic and pelagic processes influence the composition of benthic detrital resources differently on Palmyra's forereef habitats than on its backreef habitats. On the forereef, where residence times of detrital material appeared to be lower, it is possible that physical processes exert a greater influence over detrital composition and abundance than in shallow backreef habitats. Backreef habitats, which experience lower flow rates and less turbulence than more exposed forereef environments, appeared to entrain benthic materials on the benthos. This is suggested by their higher standing stocks and by the enriched $\delta^{13}C$ signatures of standing stock detrital particles relative to those captured in sediment traps (indicative of benthic sources of primary production). Thus, backreef environments may be more reliant on internal energy and nutrient cycling compared to more exposed forereef environments that may rely more heavily on oceanic subsidies to supply energy and nutrients to the benthic detrital food web.

The activity of benthic foraging fishes on the backreef may be an important contributor to the content and abundance of detrital material in this study. Large, roving, benthic-foraging fishes, namely herbivorous and detritivorous scarids and acanthurids, reprocess benthic algae and were found in high densities in the backreef study area over hard reef surfaces. While a subset of these species (such as *Ctenochaetus striatus*) moves away from feeding areas to defecate, others (such as *Chlorurus sordidus*) frequently defecate onto these surfaces (Bellwood 1995, Goatley & Bellwood 2010). Given the high consumption and defecation rates of these fishes, it is likely that they are an important recycler of benthic algae, returning material to the benthos in their defecations. These fish may not only generate detrital material through defecation, but also redistribute fine particles by physically disturbing the benthos while foraging, as found in other coral reef (Yahel et al. 2002) and aquatic (Meijer et al. 1990, Havens 1991) systems.

High detrital inputs and a low standing stock on Palmyra's reefs suggest that detrital particles have short residence times. Therefore, biotic processes (e.g. consumption by reef biota, microbial breakdown) and/or abiotic processes (e.g. flow, physical disturbance) are sufficiently intense to prevent detrital build-up on the reef. Measurements of detrital standing stock alone would not reveal the significance of these key processes. Although we did not measure flow directly, currents and surge are more intense on the exposed forereef compared to the well-protected backreef in Palmyra, similar to other reefs (Storlazzi et al. 2004, 2011). Therefore, the physical processes of increased delivery through flow-mediated transport and resuspension due to wave action may explain the counterintuitive pattern

of elevated input of large grained (≥150 µm) particles to sediment traps, compared with the relatively low standing stock of detritus in forereef habitats.

The removal of settling detritus may also be caused by the foraging activities of detritivorous fishes. *Ctenochaetus* spp. have one of the highest consumption rates of any coral reef fish (Polunin et al. 1995) and their density is twice as high and their biomass about 3 times higher on backreef compared to forereef habitats. In particular, *C. striatus*, a species documented on the Great Barrier Reef as moving large volumes of sediment from reef surfaces (Goatley & Bellwood 2010), occurs at >6 times higher density and nearly 14 times higher biomass on the backreef relative to the forereef. Palmyra's biomass of this fish is approximately double that of other documented occurrences throughout the Indo-Pacific (Galzin 1987, Sabater & Tofaeono 2006). This high biomass and the species' estimated consumption requirements (by mass of material ingested) suggest that these fish may contribute to the high turnover rates of benthic detritus in backreef habitats.

The C:N ratio values (a proxy for nutrient content) in input versus standing stock samples reveal a pattern that points to the role of consumption in the process of detrital removal. Whereas <150 µm input C:N ratio values are similar across both habitats, backreef standing stock samples are more depleted in nitrogen per unit carbon than forereef samples. Thus, freshly settled (i.e. new) detritus is of similar nutritional value in each habitat, whereas standing stock detritus (i.e. a mix of new and old or reprocessed detritus) is of a lower nutritional content only in backreef habitats. This pattern, along with nitrogen's low residence time on reef surfaces (compared to that of carbon), may be explained by the fact that detritivorous fishes, such as *Ctenochaetus striatus*, are protein scavengers (Crossman et al. 2005; H. Choat pers. comm.). The high population density of these fish on the backreef could selectively deplete nitrogen from the detrital pool, as this material is reprocessed many times by the detritivore community. The backreef is protected from wave action and experiences weaker currents than the forereef and therefore detritus is less likely to be removed by physical processes and replaced by fresh inputs. In contrast, physical processes are more likely to influence detrital dynamics on the forereef.

The trends we observed in the stable isotope composition and nutrient availability (i.e. nitrogen content) of detritus collected on the forereef and backreef of Palmyra Atoll revealed intriguing patterns when interpreted in light of the differences in fish assemblage structure observed in these 2 habitats. The high abundance of zooplanktivores on the forereef and the large amount of fecal input they may be contributing to the forereef benthos, may be important factors influencing the more pelagic-like (i.e. depleted in $\delta^{13}C$) signature of forereef deposited material. Zooplanktivores exhibit higher biomass and abundance in forereef habitats and this reef zone on Palmyra typically experiences strong currents, likely carrying abundant planktonic food sources (Hamner et al. 1988). In contrast, herbivores achieve a higher biomass in backreef areas, potentially due to reduced predator abundance (Madin et al. 2010) and elevated algal growth rates in these shallower, protected waters (Carpenter 1985, Polunin & Klumpp 1992). These major differences in fish assemblage structure between forereef and backreef habitats may have influenced the shift in detrital composition we measured on the reef. Friedlander et al. (2010) described similar differences in fish assemblage structure between forereef and backreef habitats at nearby Kingman Reef. Consistent with the depleted $\delta^{13}C$ values we measured for detrital material from forereef relative to backreef habitats, McCauley et al. (2012) found a depletion gradient in primary producer and consumer $\delta^{13}C$ values between Palmyra's lagoon and forereef.

Microbial activity may play a role in regulating the composition and abundance of Palmyra's detrital resources, but it is not likely a limiting factor on availability. Of Palmyra's reef microbes, 84% are autotrophs (Dinsdale et al. 2008). As a result, it is likely that microbes contribute to the primary producer component of detrital material and that heterotrophic activity, breaking down reef detritus, is relatively low. The low residence time of detrital material on Palmyra's reef surface may not provide adequate time for heterotrophic microbial colonization, whereas there may be more heterotrophic microbial activity within the reef matrix (Scheffers et al. 2005), where detrital residence times are likely higher.

Detrital inputs and fish dietary requirements

The nitrogen and C:N ratio data indicate that detritus may be a nutritious food resource. However, it is possible that Palmyra's detrital resources do not occur in sufficient quantities to fully support the nutritional requirements of the detritivorous fish assemblage and other detritivorous organisms (particularly on the backreef, where inputs are lower). Previous studies documented low C:N ratios (Wilson

& Bellwood 1997, Purcell & Bellwood 2001), high protein (Wilson 2000) and high amino acid (Crossman et al. 2001) concentrations in detritus. Other studies quantified the amount of standing stock detritus on reef surfaces (Crossman et al. 2001, Purcell & Bellwood 2001), but none have quantified the production rates that would indicate the capacity of detrital resources to fuel secondary production. Given the large biomass of detritivorous fishes on Palmyra's reefs, particularly in backreef habitats, the measured input rates of detrital material and the estimated nutritional consumption needs of the dominant detritivore (*Ctenochaetus* spp.), it is possible that they may be supplementing their nutritional requirements from other sources. *Ctenochaetus* spp. may receive part of their nutritional needs by ingesting fragments of algae and infaunal or epiphytic invertebrates, while scraping turf, macroalgae or other reef surfaces with their comb-like teeth. For example, a recent experimental study showed significant removal of turf algae from the EAM by the foraging activities of *C. striatus* (Marshell & Mumby 2012). Given the estimated inadequacy of nutritional input to the detrital pool (rather than the total mass input to this pool) and the likelihood that sediment traps do not fully capture the products of benthic detrital generating processes, there may be additional factors contributing to the generation of new detrital material. Benthic processes such as microbial enrichment (Bowen 1987, Wilson et al. 2001, 2003) as well as enrichment by algal exudates (Haas et al. 2010) and coral mucus (Wild et al. 2004) will tend to add nutritional value to standing stock detrital material. The interaction between benthic enrichment and pelagic input to benthic detrital resources warrants further study.

CONCLUSIONS

We found significant differences in the composition and amount of detritus produced and standing on reef surfaces between forereef and backreef environments. The $\delta^{13}C$ measurements of input and standing stock detrital materials were consistent with a more pelagic origin in forereef habitats, compared to a more benthic origin in backreef habitats. We also found significant differences in fish biomass between habitats, with Palmyra's backreefs supporting a high mass of detritivorous fish. While standing stock levels of detritus were low in both back- and forereef environments, input rates indicate that there is sufficient production of this material in forereef environments to support detritivorous fishes. However, in backreef environments, where detritivore biomass and density were highest, there are likely additional sources of limiting nutrients and energy to feed these fish. There is much research to be done on the functional role of detritus and fish detritivores in coral reef systems that can help illuminate how energy and nutrients are cycled through coral reef food webs.

Acknowledgements. We thank S. Finsted, S. Horii, M. Lynch and Y. Papastamatiou for help with field collections, J. DiPrima and S. Kettwich for help with laboratory analyses, D. McCauley for providing stable isotope data for algal turfs from Palmyra, and G. Bergsma for creating a base map of Palmyra. This manuscript was greatly improved, based on constructive commentary by 3 anonymous reviewers, and by J. Fodrie and L. Dee. K. Clements, H. Choat and J. Caselle provided helpful discussion. L.M. was supported by a US National Science Foundation Graduate Research Fellowship, a National Wildlife Refuge Centennial Scholarship from the National Fish and Wildlife Foundation, and by the Marisla Foundation while conducting this research.

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Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany

Submitted: December 7, 2012; Accepted: January 14, 2013
Proofs received from author(s): April 22, 2013