REPORT

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Composition and sources of near reef zooplankton on a Jamaican forereef along with implications for coral feeding

Abstract Nocturnal near-reef zooplankton from the forereef of Discovery Bay, Jamaica, were sampled during winter and summer 1994 using a diver-operated plankton pump with an intake head positioned within centimeters of benthic zooplanktivores. The pump collected zooplankton not effectively sampled by conventional net tows or demersal traps. We found consistently greater densities of zooplankton than did earlier studies that used other sampling methods in similar locations. There was no significant difference between winter (3491 ± 578 m^{-3}) and summer (2853 ± 293 m^{-3}) zooplankton densities. Both oceanic- and reef-associated forms were found at temporal and spatial scales relevant to benthic suspension feeders. Copepods were always the most abundant group, averaging 89% of the total zooplankton, and most were not of demersal origin. The cyclopoids, *Oithona* spp., were the numerically dominant organisms, with an average density of 1684 ± 260 m^{-3}. Other zooplankton (e.g., shrimp larvae, crab larvae, polychaetes, chaetognaths, amphipods, and isopods) were highly variable and much less abundant. Near-reef zooplankton abundances were high throughout the night sampling period, not just after sunset and before sunrise as previously described. Mean biomass was 4.5 mg C m^{-3}, with values ranging from 1.0 to 15.6 mg C m^{-3}. This work has important implications for evaluating which zooplankton types are available to benthic suspension feeders, including corals.

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Introduction

Coral reef zooplankton are an important trophic link between primary producers and higher trophic levels on reefs, including scleractinian corals and fish (Porter 1974; Hobson and Chess 1978; Gottfried and Roman 1983; Hamner et al. 1988; Sedberry and Cuellar 1993). Zooplankton that are potential prey to benthic organisms come from several sources and include holoplanktonic, meroplanktonic, demersal, and epibenthic species (e.g., Alldredge and King 1977; 1980; Ohlhorst 1982; Porter 1974), although definitions of the different forms and sources vary in the literature (reviewed by Robichaux et al. 1981; Sorokin 1990). As a review, holoplankton and some meroplankton are swept onto reefs by currents and internal waves (e.g., Tranter and George 1972; Roman et al. 1990; Genin et al. 1994; Leichter et al. 1998). However, some species traditionally classified as pelagic holoplankton may alter their behaviors when inhabiting reefs and maintain daytime swarms near reef surfaces (Emery 1968). Meroplankton include species which, at early stages of their ontogenetic development, live and often feed in the water column. As the larvae reach competency, they may hover near reef surfaces.

Demersal zooplankton are larvae or adult invertebrates (mainly crustaceans) that reside on or within the reef during the day and migrate into the water column at night (e.g., Emery 1968; Porter 1974; Alldredge and King 1977; 1980; 1985; Porter and Porter 1977; Sale et al. 1976; Rützler et al. 1980; Robichaux et al. 1981; Ohlhorst 1982). It is often thought that demersal forms maintain a nocturnal position at the substratum-water interface (e.g., Cahoon and Tronzo 1992; Alldredge and King 1985), but some migrate upward sometimes causing ambient zooplankton concentrations to dramatically

increase in surface waters at night (e.g., Roman et al. 1990). Epibenthic forms are those that spend part of their time in close proximity to, or on, reef surfaces (e.g., swarming behaviors; Hamner and Carleton 1979; Ueda et al. 1983), although Alldredge and King (1977) characterized daytime behaviors of demersal zooplankton as epibenthic.

Methods used to measure reef zooplankton abundances include nets, benthic traps, core samplers, bags, video footage, and suction devices. Each method provides information about a specific subset of the zooplankton such as pelagic, demersal, or swarms, but each also has limitations (Alldredge and King 1977; reviewed by Sorokin 1990). Net tows, the most common method for pelagic zooplankton enumerations, may undersample zooplankton due to escape behaviors and cannot provide representative information on the concentration of zooplankton very near the benthos (e.g., < 0.5 m) because of uneven reef topography (Hobson and Chess 1976).

Benthic traps have been the most commonly used method for evaluating near-reef nocturnal zooplankton abundances. However, emergence or settling traps provide information only on the numbers of organisms that leave or enter the substrate per square meter, not the (volumetric) concentration of organisms in the water near benthic zooplanktivore feeding structures. The resulting zooplankton density values reported per unit area of substrate are difficult to extrapolate to potential encounter rates for the three-dimensional feeding environment of benthic zooplanktivores. Other artifacts of traps include contamination from surrounding water and overestimation of nonswimming organisms that crawl up sides and into sampling bottles (Robichaux et al. 1981; reviewed by Sorokin 1990). Finally, shallow core samplers (e.g., Madhupratap et al. 1991) sample organisms residing within the substrate, including taxa that may never migrate vertically or become available to zooplanktivores.

Emery (1968) first documented diurnally migrating zooplankton populations on reefs. Densities over reefs are generally one to two times greater at night than during the day (Table 1). The migration behavior of demersal forms often produces density peaks at various times throughout the night (e.g., Porter 1974; Ohlhorst 1982), sometimes near dusk and dawn. Not surprisingly, the nocturnal zooplankton density increase also coincides with the time of tentacle extension and active feeding by anthozoans (Porter 1974; Lewis and Price

Table 1 Summary of coral reef zooplankton densities (zooplankton m^{-3}) reported from other studies. Data are reported mean values or have been estimated from manuscript graphs or tables. Surface indicates that samples were taken within 1 m of the water surface. *GBR* Great Barrier Reef, *NA* not applicable

Location	No. m^{-3}	Collection depth (m)	Water depth (m)	Mesh size (μm)	Collection time	Source
Pump sampling						
Discovery Bay, Jamaica	3,140	At bottom	11	40	Night	This study
Discovery Bay, Jamaica	6,100	At bottom	11	40	Night	Witting and Sebens in press
Eilat, Israel	850[a]	~7.25 m	8	100	Day	Yahel et al. 2002
Eilat, Israel	1,750[a]	~7.25 m	8	100	Night	Yahel et al. 2002
Net sampling						
Barbados	345	0–5	25	239	Day	Moore and Sander 1976
Lizard Island, GBR	60	Surface	2–3	235	Day	Alldredge and King 1977
Conch Reef, FL	~124[a]	1 m off bottom	22–28	105	Day	Leichter et al.1998
Conch Reef, FL	~1,716[ab]	1 m off bottom	22–28	105	Day	Leichter et al.1998
Davies Reef, GBR	48[a]	Surface	1–5	250	Day	Hamner et al. 1988
Davies Reef, GBR	25[a]	5	6	250	Day	Hamner et al. 1988
Laurel Cay, Puerto Rico	≤ 2,500	Surface	2–6	76	Day	Glynn 1973
Cahuita Reef, Costa Rica	630[a]	Surface	10	280	Day	Morales and Murillo 1996
South Coast Jamaica	1,698	Surface	30–35	203	Day	Moore and Sander 1979
Carrie Bow Cay, Belize	414	Surface	5–8	250	Day/night	Ferraris 1982
Carrie Bow Cay, Belize	374	3	5–8	250	Day/night	Ferraris 1982
Laccadive Archipelago	565	Surface	Shallow	200/330	Night	Tranter and George 1972
San Blas, Panama	1,208	12	13	160	Night	Porter 1974
Laurel Cay, Puerto Rico	≥2,500	Surface	2–6	76	Night	Glynn 1973
Heron Reef Lagoon, GBR	~200	Near bottom	3–4	210	Night	Sale et al. 1976
Heron Reef forereef, GBR	~300	Near bottom	8	210	Night	Sale et al. 1976
Lizard Island, GBR	493	Surface	2–3	235	Night	Alldredge and King 1977
Davies Back Reef, GBR	~37[a]	Vertical tow	20	200	Day	Roman et al. 1990
Davies Back Reef, GBR	~84[a]	Vertical tow	20	200	Night	Roman et al. 1990
San Blas, Panama	4,023	Vertical tow	13	NA	Night	Porter 1974
Copepod Swarms						
Great Barrier Reef	1.5×10^6[c]	Near bottom	NA	235	Day	Hamner and Carleton 1979
Carrie Bow Cay, Belize	2.3×10^7[c]	< 1	< 1	Video	Day	Ambler et al. 1991
Carry Bow Cay, Belize	9.2×10^7[c]	< 1	< 1	Video	Day	Buskey et al. 1996

[a]recalculated from data provided
[b]zooplankton abundance during breaking internal waves
[c]maximum value

1975; Sebens 1997; Sebens and DeRiemer 1977), so the potential for trophic interaction at the substrate-water interface is high. Because of this, there is a need to develop appropriate sampling techniques to quantify zooplankton assemblages that may be available to benthic reef zooplanktivores. None of the methods described above provides information on the concentration of zooplankton at spatial and temporal scales appropriate for estimating contact rates for benthic nocturnally feeding zooplanktivores, including reef corals. The present study is designed to characterize the nocturnal concentration and biomass (individuals per m^{-3}) of zooplankton on the forereef at Discovery Bay, Jamaica, within centimeters of the substrate, which are available to benthic suspension feeders. The abundance, biomass, and types of demersal, meroplankton, and holoplankton per unit volume of water will be quantified, and estimates of the sources of zooplankton to reef communities will be provided. We also will evaluate the appropriateness of predicting biomass from zooplankton densities.

Methods

Site description

Discovery Bay, on the north coast of Jamaica (77°20′W, 18°28.8′N), is popular for coral reef research because of its close proximity to the Discovery Bay Marine Laboratory. Our study site was located on the forereef 0.5 km west of the Discovery Bay shipping channel at 11 m depth. Reef topography is a spur-and-groove formation, and benthic community assemblages are primarily composed of hard and soft corals, sponges, and algae. Biotic communities at this site and the surrounding area are well characterized elsewhere (e.g., Liddell and Ohlhorst 1987; Helmuth and Sebens 1993; Hughes 1994; Andres and Witman 1995; Webber and Roff 1995b; Sebens et al. 1998).
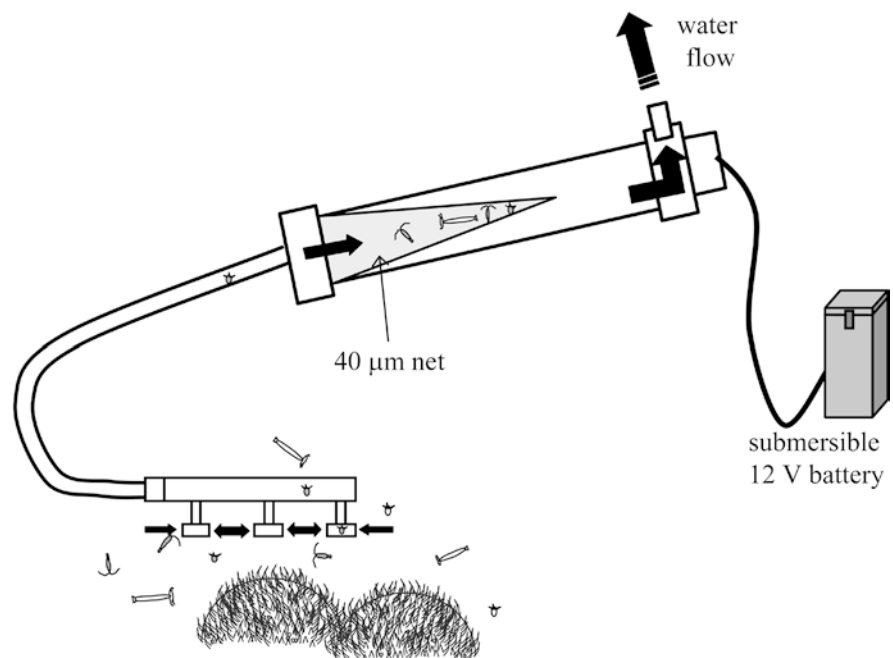
Sample collection

SCUBA divers collected multiple nightly near-reef zooplankton samples between 80 and 373 min after sunset during January and June/July 1994. Sample times and dates were contingent upon weather conditions and were set to coincide with a concurrent in situ coral feeding study. All samples were collected without the use of dive lights to avoid attracting zooplankton to the area. A diver-deployed plankton pump (Sebens et al. 1992; Fig. 1) was used to collect plankton within centimeters of the substrate. The pumping rate was determined from replicate measures of the time required to fill a container of known volume, and was generally about 1 L s^{-1} (=600 L in 10 min). The pump intake wand was placed in a stand that held the intake heads oriented horizontally over the bottom 10–20 cm above flat substratum, equal to the height of surrounding coral colonies and branches. This design had several advantages including (1) flow into the intake heads was omni-directional and lateral (intake was irrespective of ambient flow direction). (2) flow at the intake is more rapid than the swimming speeds of most zooplankters (> 30 cm s^{-1}), and (3) intake heads could be positioned within a few centimeters of a benthic suspension feeder surface without impacting the organism or the flow around it. Plankton were collected in a 40 μm Nitex mesh conical net inside a PVC-pipe housing upstream of the pump rotor, so that organism damage was minimal. Immediately after the pump was turned off, the net was closed at depth, transported to the surface, and preserved in a 5% solution of Formalin in seawater. Field calibration tests of pump selectivity at this site showed only minor differences in types and relative amounts of zooplankton sampled, compared to all zooplankton entrained within a large enclosure (Sebens et al. 1996).

Sample analysis

Plankton samples were analyzed using a dissecting microscope and CUE2 image analysis system (ver. 4.5 Galai Instruments). First, all large rare organisms from each sample were measured, counted, and removed. Then, entire samples or subsamples of known volume (depending on zooplankton density) were enumerated and measured in a zooplankton counting wheel. Individuals were measured and identified to taxonomic group (i.e., calanoids, cyclopoids, harpacticoids, amphipods, mysids). Copepods were

Fig. 1 Submersible plankton pump used for sampling near-reef zooplankton. Design based on Sebens et al. 1992. Flow into the intake heads (> 30 cm s^{-1}) was omnidirectional and lateral to allow for positioning close to substratum. Power was supplied by a battery in an underwater housing or by a cable to a battery in a boat above the site

further identified to genus whenever possible (Owre and Foyo 1967; A. Gauzens pers. comm.). Last, zooplankton were characterized by origin (reef associated or pelagic) and by type (holoplankton, demersal, or meroplankton). Foraminiferan abundances were omitted from counts due to the difficulty in determining live vs. dead organisms.

Ambient zooplankton concentrations (C_{zp}, zooplankters m^{-3}) were calculated from the number of plankters of type i in a subsample (P_{ss}), the subsample volume (V_{ss}, m^{-3}), the preserved sample volume (V_{sam}, m^{-3}), and the total amount of water pumped to obtain the sample (V_{tot}, m^{-3}), using the equation:

$$C_{zp} = (P_{ss}V_{sam})/(V_{ss}V_{tot}) \tag{a}$$

Literature values were used to generate regressions for zooplankton carbon content in µg C by taxon and size (Glynn 1973; Roman et al. 1990). Copepod carbon content was approximated using the regression equation, LN Copepod Biomass = 1.82*LN(S) + 1.28, where LN is Natural Log and S is body length in mm ($r^2 = 0.893$; df = 16; F = 125; sig. = 1.12×10^{-8}). Other zooplankton taxa were estimated using the equation, LN Other Biomass = 1.46*LN(S) + 1.03 ($r^2 = 0.733$; df = 16; F = 80.7; sig. = 3.47×10^{-7}). After values were converted to carbon biomass using regression equations, log-transformed biomass carbon values were then backtransformed, and the mean value for each zooplankton category was multiplied by sample density. Individual zooplankton biomass values were summed for each sample and multiple nightly samples were averaged to yield mean carbon biomass m^{-3} $night^{-1}$. Variations due to shrinkage with preservation may make biomass estimates subject to some underestimation error. However, estimating carbon content for each individual zooplankter based on its size is useful for comparisons of biomass distributions at least within this study.

Statistical analyses

Sigma Stat software (ver. 2.03, 1998) was used for data analysis. Data were tested for normality and homogeneity of variance prior to mean comparison procedures. For data that failed assumption tests, a ($log_{10} + 1$) transformation or Mann-Whitney Rank Sum Tests was used. Student-Neuman-Keuls pairwise multiple-comparison procedures were used to compare among groups within significant ANOVAs (Sokal and Rohlf 1995). All values are presented as mean ± SE m^{-3}, unless otherwise noted.

Results

Density of near-reef zooplankton

Overall zooplankton community assemblages were similar among seasons (winter = 46 groups; summer = 50 groups; Tables 2, 3). Near-substratum, nocturnal zooplankton density ranged from 1,252 to 5,698 m^{-3}. Densities were not significantly different between winter and summer (3,491 ± 578 and 2,853 ± 293 SE m^{-3}, respectively; $t = 1.04$, df = 18, p = 0.31; Table 2). Densities were variable among nights, but differences were not significant (mean 3,140 ± 306; Kruskal-Wallis One-Way ANOVA on ranked data H = 18.68, df = 19, p = 0.48; Fig. 2).

Nocturnal, near-reef zooplankton were dominated by copepods, approximately 89% of the samples averaged over both seasons (Fig. 2; Table 2). Of the postnaupliar stages, cyclopoid copepods were always more abundant than either harpacticoids or calanoids, and the cyclopoids, *Oithona* spp., dominated all samples, accounting for 55% in winter and 47% in summer (2,087 ± 542 and 1,354 ± 206 ind. m^{-3}; Fig. 3; Table 3). Of the *Oithona* spp., >90% were identified as *O. colcarva*, a reef-associated holoplankter as seen by Ohlhorst (1982). Other *Oithona* spp. included the offshore *O. plumifera*, also found by Webber and Roff (1995b) offshore of Discovery Bay, and two unidentified species. Harpacticoid copepods were the second most abundant type of copepod (8.5%) and members of the Family Laophontidae were the most common harpacticoid (approximately 50%). Calanoid copepods were less than 5% by number of the copepod zooplankton collected during the study (Table 3).

Copepod nauplii accounted for 23% (702 ± 105 ind. m^{-3}) of individuals (Table 3), and were the second-most abundant group in the study. All other zooplankton types accounted for an average of only 10.6% (Fig. 2; Table 2). Of these, the five next most abundant groups of organisms, reported as mean density ± SE m^{-3}, averaged over both seasons, were polychaetes (49 ± 12), barnacle nauplii (42 ± 1), fish eggs (42 ± 16), ostracods (35 ± 17), and larvaceans (appendicularians; 33 ± 1; Table 2). There were seasonal differences among only a few of the zooplankton taxa (Table 2). Amphipods, barnacle cyprids, ostracods, and echinoderm larvae all were significantly more abundant in the winter samples, while barnacle nauplii and isopods were significantly more abundant in summer samples. Among the copepods, only copepodites varied by season, with higher densities in the summer samples (Student's t-test, p = 0.002; Table 3).

There was no significant trend of zooplankton density with time after sunset when data from both seasons was combined (regression analysis, $R^2 = 0.048$, p = 0.162; Fig. 4). The phase of the moon (Fig. 2) appears to influence zooplankton density, although we did not design the study with sufficient replication across moon phases to analyze these patterns statistically. The highest densities, however, occurred during first-quarter moon nights.

Zooplankton biomass

Mean nightly near-reef biomass (mg C) averaged over both seasons was 4.5 ± 0.7 SE mg C m^{-3}. Biomass ranged from 1.0 to 15.6 mg C m^{-3} in the winter samples (mean 5.9 ± 1.3) and 1.9 to 4.5 mg C m^{-3} in the summer (mean 3.4 ± 0.3; Fig. 5). Although there was no significant difference between the two seasons (Student's t-test, df = 19, p = 0.06), winter samples tended to have a higher nightly biomass due to slightly higher abundances of the larger demersal forms (Fig. 5). The average nightly non-naupliar copepod biomass was 67.7% of the total. While copepod nauplii contributed 23.0% of the zooplankton abundance, they accounted for only 2.8% of the biomass. All other zooplankton taxa accounted for

Table 2 Mean number m^{-3} ($\pm$SE), range, and percent composition of zooplankton taxa for near-substratum nocturnal zooplankton on the forereef of Discovery Bay, Jamaica, in 1994. Zooplankton type are indicated by the following based on literature definitions: *M* meroplankton, *D* demersal, *H* holoplankton, where superscripts indicate sources of the definitions or provides additional information (see table notes). Origin designations indicate whether the zooplankton are pelagic (*P*), reef-associated (*R*), or both (*PR*), depending on species. NP indicates not present. Ranges are mean nightly minimum and maximum values. Student's *t*-test comparisons of seasonal differences performed on nightly means of $\log_{10}+1$ transformed values (indicated by $^{\pm}$). Significance at the $p < 0.05$ level indicated by * after p value (df = 18)

Zooplankton taxa	Type	Origin	Winter (9 nights)			Summer (11 nights)			p value
			No. m^{-3}	Range	%	No. m^{-3}	Range	%	
Total			3,491 (577.8)	1,252–5,698	100	2,853 (293.2)	1,465–5,059	100	0.31
Annelida, Polychaeta	H^{c}M^{b,g}D^d	PR	49 (18.2)	0–139	1.2	49 (17.6)	5–196	1.9	0.95
Arthropoda									
Amphipoda, Gammaridea	D^d	R	5 (2.0)	0–10	0.1	2 (1.0)	0–7	< 0.1	0.03*
Amphipoda, Hyperiidea	H	P	3 (2.2)	0–6	0.1	1 (1.0)	0–2	< 0.1	0.32
Cladocera	H	P	NP			1 (0.4)	0–3	< 0.1	
Copepoda	D^{d}H^{b,f}	PR	3,187 (577.3)	1,197–5,146	91.1	2,558 (323.7)	1,303–4,865	88.3	0.31
Cirripedia, cyprid	M^e	P	13 (5.5)	0–27	0.3	2 (1.1)	0–10	0.1	0.02$^{\pm}$*
Cirripedia, nauplii	M^e	P	25 (14.0)	0–128	0.7	57 (13.5)	11–120	2.1	0.03$^{\pm}$*
Cumacea	D^{c,d}	R	6 (3.0)	0–26	0.2	6 (2.0)	0–19	0.2	0.99
Decapoda									
Crab megalopa	M^c	R	NP			0.4 (0.5)	0–5	< 0.1	
Crab zoea	M^c	PR	1 (0.7)	0–6	< 0.1	1 (0.8)	0–8	< 0.1	0.88$^{\pm}$
Other larvae^a	DM^c	PR	22 (13.3)	0–113	0.7	8 (1.3)	2–14	0.3	0.48$^{\pm}$
Euphausida			3 (1.3)	0–9	0.1	NP			
Insect larvae			NP			0.4 (0.2)	0–3	< 0.1	
Isopoda	D^d	R	13 (2.4)	5–24	0.4	25 (4.3)	6–50	1.0	0.03*
Arachnida (mites)	D	R	1 (0.9)	0–7		1 (0.8)	0–8	< 0.1	0.90$^{\pm}$
Mysidacea	D^d	R	6 (2.7)	0–24	0.1	6 (2.0)	0–21	0.2	0.95
Ostracoda	D^d	R	64 (37.6)	7–336	1.8	11 (3.6)	1–5	0.5	0.01$^{\pm}$*
Pycnogonida	D	R	NP		0.1	0.2 (0.2)	0–3	0.1	
Stomatopoda, larvae	M^e	R	1 (0.6)	0–5	< 0.1	0.1 (0.1)	0–1	< 0.1	0.79$^{\pm}$
Tanaidacea	D^d	R	1 (0.9)	0–8	< 0.1	1 (0.5)	0–2	< 0.1	0.82$^{\pm}$
Chaetognatha	H^{f}D^d	P	9 (4.7)	0–42	0.2	9 (2.0)	0–19	0.3	0.73$^{\pm}$
Chordata									
Larvaceans	H^{b,c,d,g}	P	30 (10.5)	0–77	1.0	35 (9.2)	0–80	1.4	0.70
Fish eggs	M^g	P	23 (9.9)	0–83	0.8	57 (29.9)	0–317	2.4	0.32
Fish larvae	M^g	P	0.3 (0.3)	0–3	< 0.1	0.2 (0.2)	0–2	< 0.1	0.94$^{\pm}$
Cnidaria, Hydromedusae	H^g	P	0.2 (0.2)	0–2	< 0.1	NP			
Echinodermata, larvae	M^g	P	17 (5.7)	0–40	0.5	4 (1.7)	0–14	0.2	0.04$^{\pm}$*
Mollusca									
Cephalopoda, larvae	H	P	NP			0.2 (0.2)	0–3	< 0.1	
Gastropoda	H^3	P	NP			10 (4.5)	0–40	0.4	
Pteropoda	H	P	NP			1 (0.5)	0–5	< 0.1	
Veligers	M^1	P	12 (5.3)	0–28	0.4	6 (3.4)		0.3	
Nematoda	D	PR	NP			3 (0.8)		0.1	

^{a}Includes Anomura, Caridea, and Penaeidea larvae
^{b}Glynn 1973
^{c}Sale et al. 1976
^{d}Ohlhorst 1982
^{e}Sorokin 1990
^{f}Webber and Roff 1995b
^{g}Morales and Murillo 1996

29.4% of the total biomass (Fig. 5). There is a significant relationship between density and biomass (Fig. 6; R^2 = 0.73), although caution should be used to predict biomass from density alone because the estimate from the best-fit line has high associated variance. For example, although there were three samples that had densities just over 5,000 organisms m^{-3}, biomass for these samples ranged from 3.8 to 13.6 mg C m^{-3} (Fig. 6). Nightly abundance variations of the larger epibenthic organisms (e.g., amphipods, mysids, and shrimp) or smaller, abundant taxa (e.g., copepod nauplii) greatly affected the overall estimates of biomass.

Origin of reef-associated zooplankton

Zooplankton behaviors occur along a continuum, and the sources and characterizations of the reef-related zooplankton described above cannot always be easily distinguished. Our pump sampled all available zooplankton that occurred near extended coral feeding tentacles and included plankton of demersal, holoplanktonic, and meroplanktonic types. We used literature characterizations of demersal zooplankton sampled in benthic traps at Discovery Bay (Ohlhorst 1982) and other sites (Glynn 1973; Sale et al. 1976; Morales and Murillo 1996), and a study of offshore, pelagic copepod

Table 3 Mean number m^{-3} ($\pm$SE), range, and percent composition (%) of copepod taxa for near-substratum nocturnal zooplankton on the forereef of Discovery Bay, Jamaica, in 1994. Zooplankton types are indicated by the following, based on literature definitions: *M* meroplankton, *D* demersal, *H* holoplankton, where superscripts indicate sources of the definitions or provides additional information (see table notes). Origin designations indicate whether the zooplankton are pelagic (*P*), reef-associated (*R*), or both (*PR*), depending on species. *NP* indicates not present. Ranges are mean nightly minimum and maximum values. *T*-test comparisons of seasonal differences performed on nightly means or log$_{10}$ + 1 transformed values. Comparisons with transformed data ($^{\pm}$). Significance at the $p < 0.05$ level indicated by * after p value (df = 18)

Copepod genera	Type	Origin	Winter (9 nights)			Summer (11 nights)			P value
			No. m^{-3}	Range	%	No. m^{-3}	Range	%	
Calanoida					2.9			4.5	
Acartia	H[c,f]	P	31 (13.5)	0–125	1.2	34 (7.2)	0–65	1.5	0.55$^{\pm}$
Calanopia	H[c,f]	P	33 (11.6)	0–95	0.9	28 (11.2)	0–96	1.1	0.55$^{\pm}$
Calocalanus	H[f]	P	6 (3.0)	0–26	0.2	27 (11.6)	0–126	1.1	0.11
Eucalanus	H[f]	P	2 (2.3)	0–19	<0.1	1 (0.8)	0–8	<0.1	0.88$^{\pm}$
Labidocera			1 (0.4)	0–3	<0.1	0.4 (0.3)	0–3	<0.1	0.54$^{\pm}$
Mecynocera	H[f]	P	0.4 (0.4)	0–4	<0.1	NP			
Microcalanus	H	P	6 (5.6)	0–48	0.1	9 (5.8)	0–57	0.5	0.40$^{\pm}$
Paracalanus	H[f]	P	8 (4.5)	0–38	0.2	5 (2.1)	0–19	0.2	0.57$^{\pm}$
Temora	H[c,f]	P	2 (2.0)	0–17	<0.1	4 (2.0)	0–18	0.2	0.146$^{\pm}$
Unidentified[a]	H?	P?	3 (1.6)	0–12	0.1	1 (0.9)	0–8	<0.1	
Cyclopoida					56.1			47.9	
Corycaeus	D[d]	R	13 (6.0)	0–52	0.5	33 (12.0)	7–112	1.2	0.09$^{\pm}$
Oithona	D[d]H[b,f]	PR	2,087 (541.5)	552–4,682	54.8	1,354 (206.2)	593–2,425	46.5	0.17
Oncaea	H[f]	P	1 (0.5)	0–4	0.1	2 (0.9)	0–8	0.1	0.760$^{\pm}$
Unidentified[a]			26 (12.4)	0–111	0.7	7 (2.2)	0–18	0.3	
Harpacticoida					7.7			9.4	
Copilia	H[f]	P	17 (9.8)	0–88	0.5	17 (4.4)	5–42	0.7	0.96
Family Laophontidae [a]	D[d]	R	158 (62.1)	37–555	5.0	161 (27.9)	52–378	5.8	0.96
Macrosetella	H[f]	P	4 (3.8)	0–33	0.2	6 (2.9)	0–25	0.3	0.27$^{\pm}$
Microsetella	D[d]	R	7 (2.9)	0–25	0.3	12 (2.5)	4–25	0.4	0.14
Tigriopus	H	P	NP			6 (2.7)	0–25	0.1	
Tisbe	D	R	17 (8.0)	0–72	0.5	9 (3.4)	0–28	0.4	0.38
Compressed[a]	D	R	33 (14.1)	1–132	0.9	32 (4.8)	11–57	1.2	0.48$^{\pm}$
Unidentified[a]	D?	R?	14 (6.3)	0–48	0.4	16 (5.3)	0–51	0.6	
Monstrilloida[a]	D[e]H[f]	PR	1 (0.5)	0–3	<0.1	0.1 (0.1)	0–1	<0.1	0.32$^{\pm}$
Copepod nauplii[a]	D[d]H[f]	PR	689 (127.5)	205–1,383	23.5	713 (177.4)	272–2100	23.2	0.92
Copepodites[a]	D[d]H[f]	PR	28 (11.6)	0–111	0.8	83 (16.7)	25–218	3.2	0.002$^{\pm}$*

[a]Not identified to genus
[b]Glynn 1973
[c]Sale et al. 1976
[d]Ohlhorst 1982
[e]Sorokin 1990
[f]Webber and Roff 1995b

samples near the study site (Webber and Roff 1995b) to characterize zooplankton by origin (pelagic or reef associated) and by type (holoplankton, meroplankton, or demersal) (Tables 2 and 3). An unknown origin category included unidentified copepods, (mostly copepod nauplii and copepodites) and organisms (e.g., polychaetes and nematodes) that had conflicting definitions in the literature (Table 2). By abundance, this category accounted for approximately 27% of the samples. Using our classifications, at least 56% of the zooplankton available to benthic suspension feeders was reef-associated in origin, while the remaining 18% originated offshore (Fig. 7). Admittedly, these numbers could vary with characterization of the "unknown" organisms, although the biggest proportion of these is the copepod nauplii. Given that *Oithona* spp. (90% *O. colcarva*) comprises the majority of the adult copepod assemblage (Table 2), probably many of the nauplii and copepodites were of this genus. If true, this would shift a large portion of the "unknown" category into the reef-associated proportion (Fig. 7). In terms of biomass, 26% came from offshore, 61% was reef-associated, and 13% was of the "unknown category" (Fig. 7). Interestingly, 48.2% (winter) and 43% (summer) of the reef-associated zooplankton biomass consisted of organisms traditionally categorized in other studies as holoplanktonic.

Discussion

This study addresses a major gap in our understanding of zooplankton availability for nocturnally feeding benthic organisms, including the reef-building corals.

Fig. 2 (A) Night-time density (mean ± range) of reef-associated nocturnal zooplankton on the forereef at Discovery Bay, Jamaica, winter and summer 1994. Moon phase is shown *above* each nightly mean. Numbers *below* moon phase indicate the number of samples taken each night.
(B) Percent composition of zooplankton. Copepods (*hashed bars*); Copepod nauplii (*white*); all other zooplankton taxa (*black*)
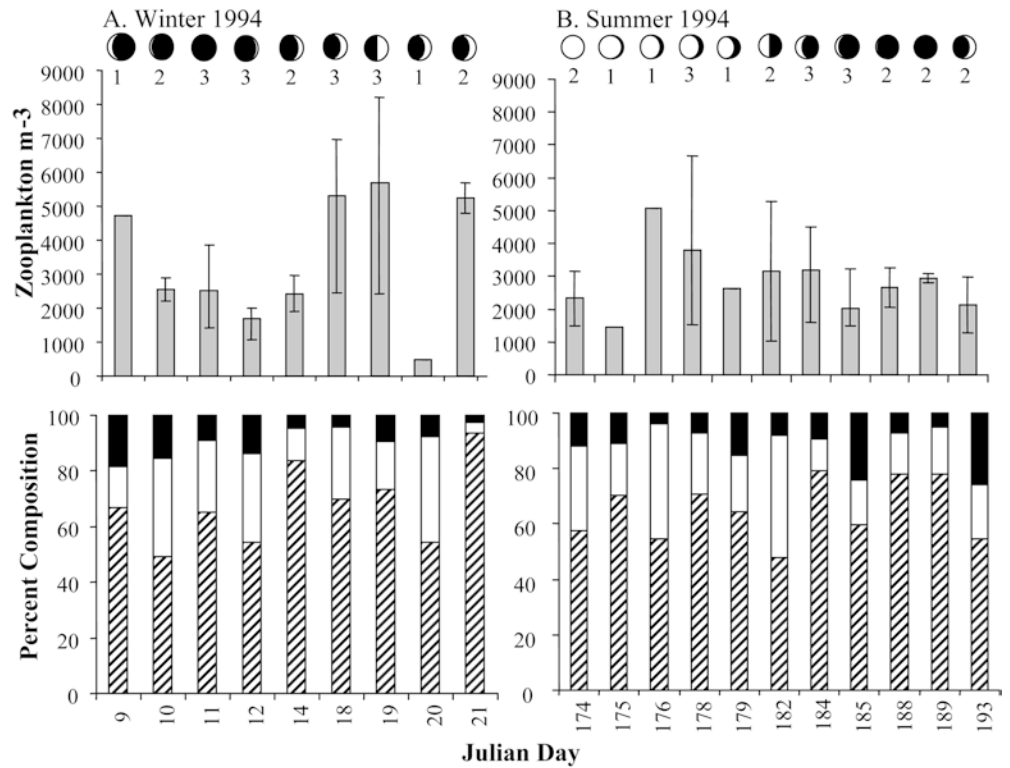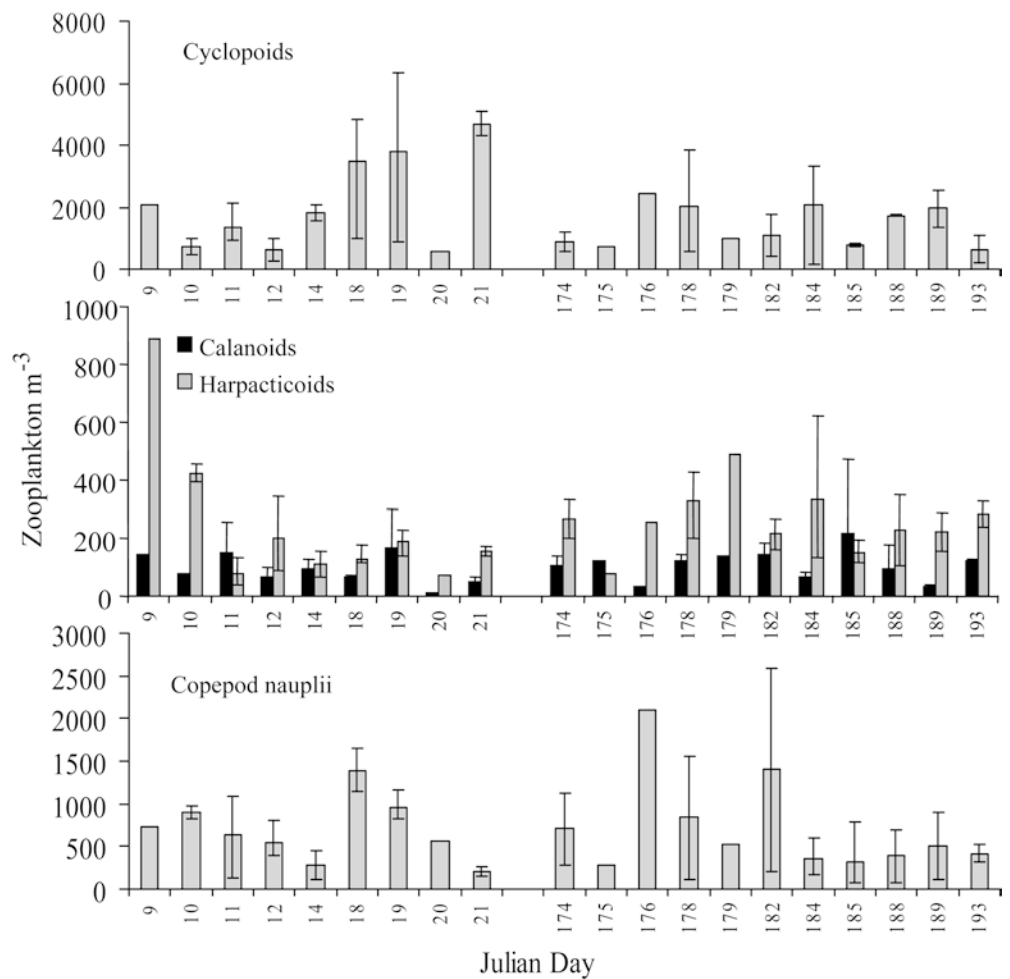

Fig. 3 Nighttime densities (mean ± range) of near-substratum copepods and copepod nauplii in winter and summer 1994 on the forereef of Discovery Bay, Jamaica. Number of samples as in Fig. 2
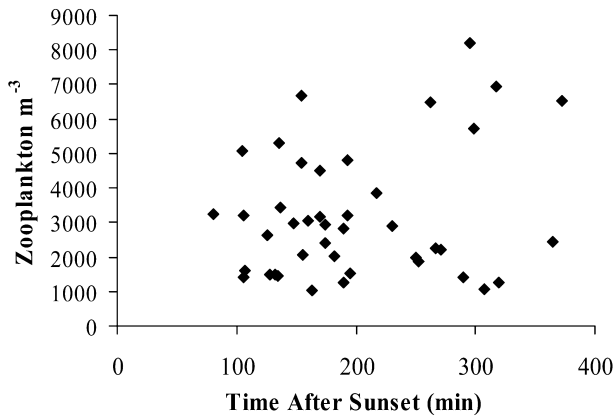
Fig. 4 Near-substratum zooplankton density vs. time after sunset for each sample on the forereef of Discovery Bay, Jamaica. There was no significant relationship (regression analysis; $R^2 = 0.048$, $p = 0.162$)
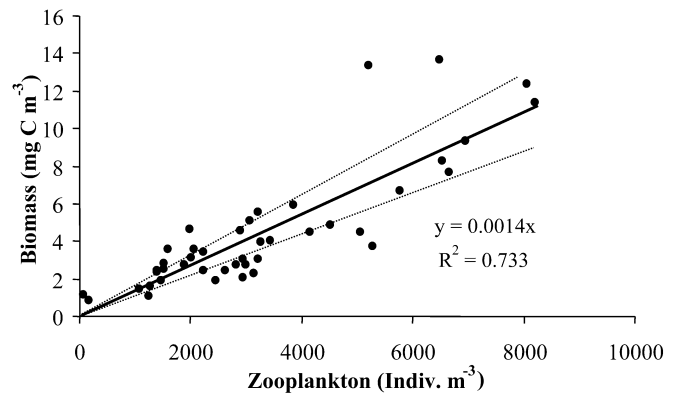

Fig. 6 Relationship between biomass (mg C m^{-3}) and zooplankton density (ind. m^{-3}) ($y = 0.0014$ x; $R^2 = 0.73$; $p = 2.54 \times 10^{-13}$). *Dotted lines* represent 95% confidence intervals. Biomass was estimated for nightly zooplankton samples as described in methods

Our nocturnal zooplankton densities were generally much higher than those calculated from net tows at other reefs, except for enumerations of zooplankton swarms (Hamner and Carleton 1979; Ueda et al. 1983; Ambler et al. 1991, Buskey et al. 1996; Table 1). Nocturnal, near-substratum (1 m off bottom) abundances determined using net tows, ranged from 200 to 1264 zooplankters m^{-3}. Obviously, net mesh size and taxa chosen for enumeration affect the final outcome, but the patterns suggest that our pump sampled a larger population of potential prey available to organisms feeding at the benthic interface. Like any methodology, pumps have sampling artifacts (reviewed by Powlik et al. 1991). Many zooplankton can detect flow differences created by wakes or shears at very small scales, which can elicit escape responses away from pump intake heads. To

minimize this, our intake heads were designed to sample in a lateral, ominidirectional way with high flow speed at the inlet (Fig. 1). Also, we designed the intake wand to be distant from the pump motor to minimize potential acoustical avoidance by zooplankton.

Only a few other studies have used in situ pumps to quantify near-reef zooplankton assemblages (Table 1). Witting and Sebens (in press) sampled at the same study site using the same pump design as in this study. Their zooplankton abundances were higher, with the main difference being that they included foraminiferans in total counts, whereas, we did not. Omitting this category, their densities are very comparable to ours. O'Neill et al. (unpubl. data) used a similar pump design to sample at four consecutive heights (substrate, 0.5, 2.0 m, and surface) on a coral reef in the Florida

Fig. 5 (**A**) Nightly biomass (mean ± range) of reef-associated nocturnal zooplankton on the forereef at Discovery Bay, Jamaica, in winter and summer 1994. Moon phase and sample numbers as in Fig. 3. (**B**) Percent composition of biomass by group: Copepods (*hashed bars*); Copepod nauplii (*white*); all other zooplankton taxa (*black*)
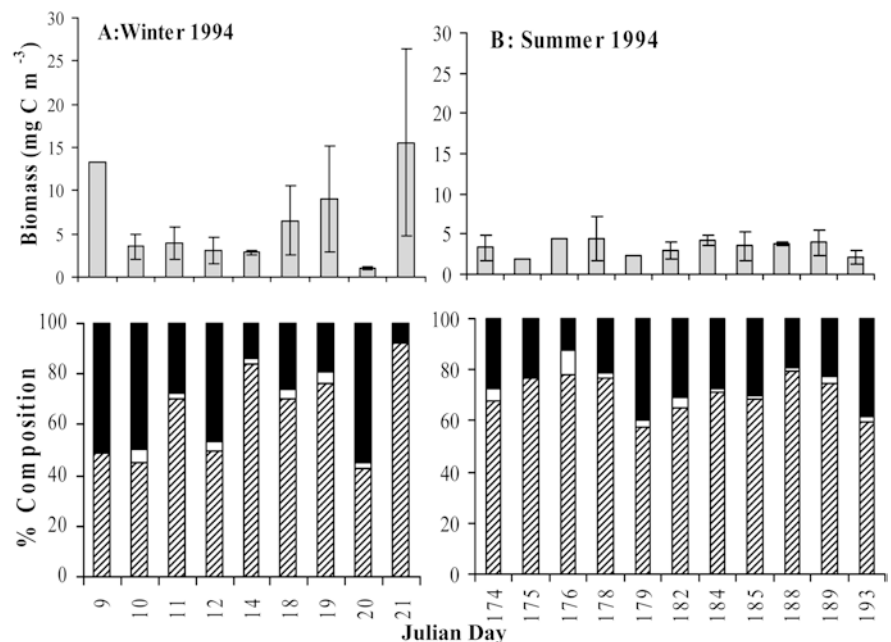
Fig. 7 Density and biomass of near-substratum zooplankton characterized by origin and type. Numbers *above* bars represent the percent composition of the category. The unknown origin category includes unidentified copepods (mostly copepod nauplii and copepodites) and organisms (e.g., polychaetes and nematodes), which had conflicting definitions in the literature (designated in Tables 2, 3). If we assumed that most of the unknown nauplii and early stage copepodites were of the dominant *Oithona* sp. (*O. colcarva*), a large percentage of the unknown category would be shifted to the reef-associated taxa, as explained in the text
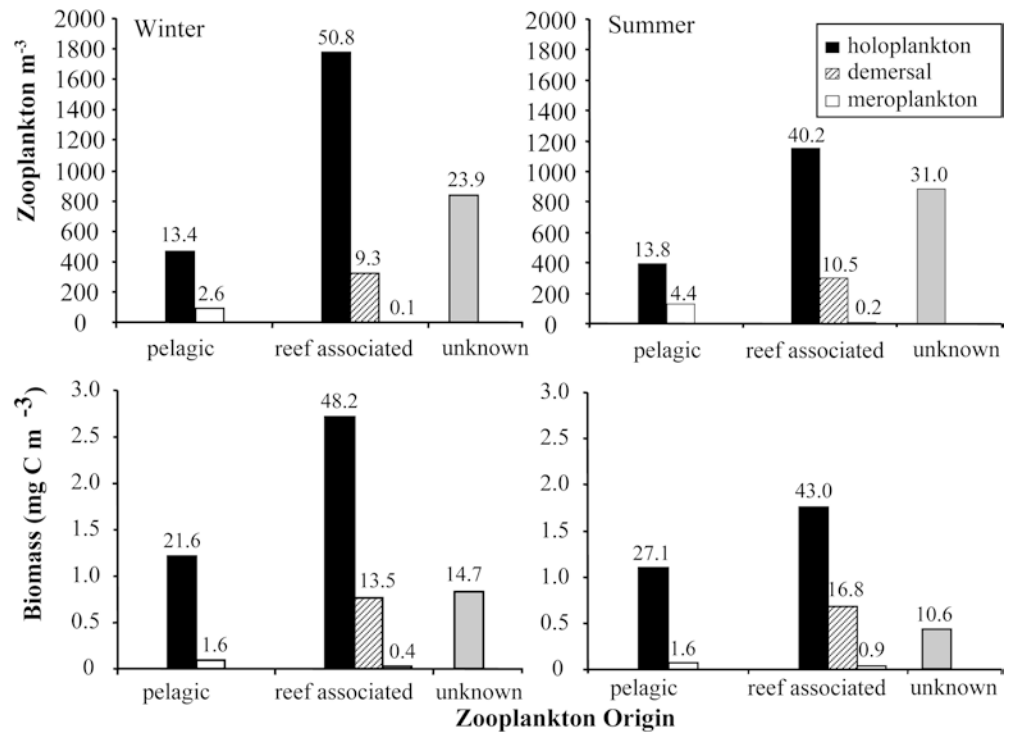
Keys. They found similarly high concentrations of prey close to the substrate. Only Glynn (1973) reported comparably high numbers of nocturnal zooplankton using nets; however, his samples were collected from the side of a boat at night in very shallow water with no mention of controlling for the effects of artificial lights, which attract zooplankton (Sale et al. 1978).

Reef zooplankton assemblages are highly variable in space and time (e.g., Lewis and Boers 1991), and both abundance and community composition vary with physical and biological factors. Physical factors include tides (Roman et al. 1990; Genin et al. 1994; Morales and Murillo 1996; Saigusa et al. 2000), breaking internal waves (Leichter et al. 1998), season (Glynn 1973; Sammarco and Crenshaw 1984), and rainfall (Glynn 1973; Sammarco and Crenshaw 1984; Ohlhorst 1985). Demersal populations also vary by time of day (Glynn 1973; Alldredge and King 1980; Ohlhorst 1982), lunar cycle (Glynn 1973; Alldredge and King 1980), depth (Ohlhorst 1985), and substrate type (Glynn 1973; Alldredge and King 1977; Sale et al. 1978). Biological parameters affecting the composition of the zooplankton community could include reproductive cycles (Moore and Sander 1976), phytoplankton concentrations (Yoshioka et al. 1985; Lewis and Boers 1991), zooplankton swarming behaviors (Emery 1968; Hamner and Carleton 1979; Ueda et al. 1983), and heavy predation by fish (Hamner et al. 1988; Genin et al. 1995). We saw little evidence of seasonal variation in nocturnal zooplankton density (Tables 2 and 3). Admittedly, our sampling was not of long enough duration to evaluate the full temporal variability (see Lewis and Boers 1991), but our lack of seasonal differences matches patterns observed for the same reef by Ohlhorst (1982) and for other Carribean reefs (e.g. Moore and Sandler 1976; Morales and Murillo 1996). However seasonal variations in zooplankton community structure do occur in certain other tropical locations (Glynn 1973; McWilliams et al. 1981; Sammarco and Crenshaw 1984; McKinnon and Thorrold 1993).

Lunar effects on zooplankton density were beyond the scope of this study, since all four lunar phases were not represented in each sampling season. Ohlhorst (1982) did not detect significant demersal migration patterns with moon phase at Discovery Bay. However, we observed that mean copepod density appeared to be greater during the first-quarter moon phase (Fig. 2, Julian days 18 and 19). It is interesting to note that lunar effects on zooplankton abundances were observed by Alldredge and King (1980), who found that most zooplankton did not migrate vertically during full-moon nights. Our amphipods densities were lowest during the full-moon nights (Julian Days 174, 175; Fig. 2), which may indicate a lack of vertical migration from the substrate, possibly as a means of avoiding predation by visual predators such as fish. An interesting hypothesis for a future study is that, during the first-quarter moon phase, corals would receive the greatest energetic contribution from zooplankton. If true, feeding during this period may be important for coral gamete formation, since most corals spawn within one week of the full moon (e.g., Caribbean: Gittings et al. 1994; Pacific: Hayashibara et al. 1993).

Porter (1974) suggested that near-reef nocturnal zooplankton densities are highest during a 2-h period near sunset and sunrise when demersal forms were migrating off the bottom into the water column and back down to the reef. Ohlhorst (1982), using demersal traps near our study site, reported a peak in demersal zooplankton 2 h after sunset, later than Porter's dusk observations. However, Ohlhorst only evaluated demersal forms using benthic traps, which would have excluded nondemersal forms. We did not observe a clear peak in zooplankton density (Fig. 4). Our pump samples did not start until 1 h after sunset partly because we found that there were insufficient zooplankton at dusk for our concurrent coral feeding experiments, and also because many corals did not extend tentacles earlier. Given this observation, it is doubtful that the peak zooplankton density occurred at dusk on this reef. Instead, we found high densities close to the substrate, and feeding corals, throughout the sampling period (Fig. 4), suggesting that abundant zooplankton could be available to corals during large portions of the night, not just during the demersal migration periods described by Porter (1974) and Ohlhorst (1982).

Origin of reef-associated zooplankton

The relative importance of the various zooplankton sources to coral energetics and reef communities has been a subject of many studies (e.g., Odum and Odum 1955; Johannes et al. 1970; Porter 1974; Robichaux et al. 1981; Walter et al. 1981; Ohlhorst 1985). Porter (1974) suggested that the majority of zooplankton available to benthic predators is of demersal origin. Others suggested that offshore (pelagic, nonreef) holoplankton could play an important role in reef energetics. In this study, we characterized our zooplankton as ''reef associated'' or ''pelagic'' (Tables 2, 3; Fig. 7). The reef-associated zooplankton include zooplankters routinely found in close proximity to the reef, whether they were holoplankton, meroplankton, swarmers, demersal, or benthic (resuspended) forms, at various times throughout the diel cycle and that could thus contribute energy to the trophic structure of the reef via consumption by the benthos. Nocturnally, this group includes organisms such as pelagic and demersal copepods, ostracods, cumaceans, amphipods, decapod larvae, some polychaetes, and even some open-ocean meroplankton (Robichaux et al. 1981; Vaissière and Seguin 1984; Alldredge and King 1985; this study). Organisms in this study categorized as pelagic in origin, based on literature classifications, are identified in Tables 1 and 2 and primarily include organisms such as chaetognaths, larvaceans, some copepods, hyperiid amphipods, and most of the mollusks. However many holoplanktonic species behave like typical reef zooplankton when they inhabit a coral reef environment, forming daytime swarms near reef structures for protection, as first described by Emery (1968). For example, some species traditionally charac-

terized as pelagic (e.g., *Oithona colcarva*) may change behaviors when residing on reefs to prevent being swept off the reef by surface currents (Alldredge and King 1977) or to avoid heavy predation by abundant visual predators such as fish. In such environments, we propose that these organisms be considered reef-associated. It is also possible that pelagic species, which have a diel migration offshore, retain that migration behavior when advected into shallow water, but cannot reach their normal maximum depth. Avoidance behavior of any surface would result in such species aggregating just above reef substrates.

We found approximately 60% of the individuals in our nocturnal samples to be holoplankton, including the copepods, *Oithona* spp., *Calanopia americana*, and *Acartia spp.*, and other taxa such as chaetognaths and appendicularians (Tables 2, 3; see also Sale et al. 1978; Ohlhorst 1982; 1985; Webber and Roff 1995b; Sebens et al. 1996, 1998). *Oithona* spp., in particular, are not demersal (Madhupratap et al. 1991). In other areas, these cyclopoids were observed to disperse at night from daytime swarms (e.g., *Oithona oculata*, Hamner and Carleton 1979; *Dioithona oculata*, Buskey et al. 1996; Table 1) and maintain a position close to the substrate (Emery 1968; Alldredge and King 1985; Ohlhorst 1985). Interestingly, the holoplankton (especially copepods) tend to be the organisms that have the best escape behaviors and are the forms rarely caught by most corals (Sebens et al. 1996; Heidelberg 1999; Heidelberg et al. 1987).

Copepod nauplii were second in density to *Oithona spp.* adults. Although numerous when compared with all other taxa, the density of copepod nauplii was unexpectedly low relative to copepodite and adult abundances (Table 3). Naupliar stages averaged only 26% (winter) and 27% (summer) of all copepod individuals. Ecologically, there should be higher abundaces of naupliar stages than adult stages. Webber and Roff (1995b) found much higher percentages of nauplii compared with adults and copepodites just offshore of our study site. Other researchers have shown that there is a locational separation between adult and juvenile copepod stages (Ueda et al. 1983; Ambler et al. 1991; Fornshell 1994), possibly due to differential migration at night to prevent cannibalism from adult copepods (e.g., Ueda 1987; Ueda et al. 1983)

Noncopepod taxa accounted for numerically only about 10% of the organisms in our samples (Fig. 2; Table 2). Of these, 9.9% were demersal organisms including many of the larger zooplankton such as decapod larvae, amphipods, and polychaetes. Although only 9.9% by number (325 ind. m^{-3} in winter and 300 ind. m^{-3} in summer), these larger organisms accounted for an average of 15.1% of the biomass (Fig. 7). It is still unclear where the noncopepod zooplankton reside after leaving the substrate. Our data suggest that they are not residing in close proximity to reef surfaces, as the percentage that we saw was relatively small. The height that reef associated zooplankton migrate above the reef is

still not well understood. Either these organisms are not residing near reef surfaces, or some organisms were able to avoid pump intake heads. In a temperate zone, subtidal sandflat habitat, Alldredge and King (1985) placed settling traps at different heights off the substrate. They concluded that the larger demersal forms were residing somewhere above 30 cm, but below surface waters. In a zooplankton study conducted to specifically sample zooplankton abundances simultaneously at four heights off the substrate at multiple times throughout the 24-h cycle on a coral reef in the Florida Keys, O'Neill et al. (unpubl. data) found that many of the larger zooplankters such as the decapods, were residing at 0.5–2 m above the substrate throughout the night.

Sample biomass

Our estimates of average nightly biomass, 4.5 mg C m^{-3}, were higher than in other comparable studies. For example, nightly biomass calculated by Roman et al. (1990) from nocturnal net samples collected at the surface over a reef located with the Great Barrier Reef system were about a third of our estimates per m^{-3}. Sample biomass estimates offshore from our site were also much lower. Copepod biomass offshore from Discovery Bay ranged from 1.14 to 2.89 mg AFDW for the top 60 m of water and 0.12 to 1.99 mg AFDW below 60 m (Webber and Roff 1995a).

There is a significant relationship between zooplankton density and biomass (Fig. 6; $R^2 = 0.73$), but the estimate from the best-fit line has high variance. Nightly abundance variations of the larger epibenthic organisms (e.g., amphipods, mysids, and shrimp) or smaller, abundant taxa (e.g., copepod nauplii) greatly affected the overall estimates of biomass. The less abundant, large, reef-associated demersal zooplankton such as amphipods, some decapod larvae, and cumaceans, are potentially important prey for benthic zooplanktivores because of their larger individual biomass and higher nutrient content compared with holoplanktonic forms (5–21% more; Glynn 1973; Alldredge and King 1977). However, this study clearly shows that holoplanktonic organisms account for at least 45% (48%, winter; 43%, summer, not including unknown organisms) of the reef-associated zooplankton biomass available to benthic zooplanktivores (Fig. 7).

The potential importance of zooplankton for coral nutrition

Zooplankton and other particulates provide both energy and nutrients (e.g., nitrogen and phosphorus) for scleractinian corals, although the importance of zooplankton capture in coral budgets has been debated for the better part of this century (e.g., Yonge and Nicholls 1931; Johannes et al. 1970; Goreau et al. 1971; Sorokin 1973; Porter 1974; Davies 1977; Sebens et al. 1996; 1998;

Titlyanov et al. 2000; Witting and Sebens in press). However, researchers previously have had difficulty estimating the potential contribution of zooplankton to coral nutrient budgets (e.g., Bythell 1988), partly because accurate estimates of available zooplankton densities and capture rates are difficult to quantify at a scale relevant to benthic zooplanktivores (Johannnes et al. 1970; Porter 1974; Alldredge and King 1977; 1980; Ohlhorst 1982; Edmunds and Davies 1986; Sorokin 1993). An initial estimate of the importance of zooplankton to coral metabolism was estimated by calculating the potential contribution of zooplankton based on densities calculated from stationary net samples (e.g., Johannes et al. 1970), which probably greatly underestimated zooplankton available to corals. Low zooplankton densities in these samples led early investigators to conclude that zooplankton prey could not be nutritionally important to corals. Subsequent studies on available zooplankton showed that corals and other benthic zooplanktivores had a second, possibly more abundant, source of zooplankton, that of demersal origin. The discovery of this source of zooplankton led scientists to believe that demersal forms were probably the most important type of zooplankton for corals. Many of the demersal taxa are routinely found in guts of nocturnally feeding benthic zooplanktivores such as fish (Sedberry and Cuellar 1993) and corals (Porter 1974; Sebens et al. 1996; 1998). Recent studies have shown compelling evidence that coral growth rates may be controlled, in part, by the amount of zooplankton that they capture. Witting and Sebens (in press) showed that artificially increasing zooplankton abundance in situ resulted in significantly enhanced growth for five species of Caribbean corals.

Past researchers have also proposed that a 2-h window at dusk and dawn was probably the most important time for nocturnally feeding cnidarians (Porter 1974; Sebens 1977). Our data, however, suggests that there are high abundances of zooplankton throughout the night near reef surfaces, not just around dawn and dusk, when the demersal forms migrate. The existence of high average densities throughout the night has important implications for calculations of potential zooplankton contribution to coral energy and nutrient budgets, since corals and other nocturnal benthic zooplanktivores could capture prey for a much longer feeding period than just the 2-h windows at dusk and dawn.

Results of this study show that import of pelagic holoplankton is probably a very important source of zooplankton for reef energetics. The high frequency of nondemersal organisms in our samples found in close proximity to the reef throughout the night suggests that the pump provided a more inclusive assemblage of zooplankton available to reef zooplanktivores than results obtained from the use of traps or nets alone. While many demersal forms have larger individual biomass, our data showed that, in terms of biomass, holoplanktonic forms may provide as much, or more, potential

energy to the reef (Fig. 7; see also Leichter et al. 1998). In fact, several studies have shown that holoplanktonic organisms can make up a significant portion of coral gut contents (Porter 1974; Lewis 1992; Johnson and Sebens 1993; Coma et al. 1994), even though many have effective avoidance or escape behaviors from benthic suspension feeders (Sebens et al. 1996; 1998; Heidelberg 1999; Heidelberg et al.1997). For example, Lewis (1992) found that copepods contributed 63% of the diet of the hydrocoral, *Millepora complanata*. This is probably attributed to the high nocturnal abundance of copepods near the reef surfaces.

Prior to our study, reef-associated zooplankton had not been adequately quantified on a scale relevant to in situ nocturnally feeding benthos, namely sampling centimeters above the substratum and taking samples at multiple times throughout the feeding period to provide adequate information on available prey types. Zooplankton sampling must be designed to quantify all available taxa and pair values with estimates of capture probabilities to estimate a potential contribution of zooplankton to reef energetics and nutrient cycles. This study provides important new information on densities of near-substratum nocturnal reef zooplankton.

References

Alldredge AL, King JM (1977) Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar Biol 41:317–333

Alldredge AL, King JM (1980) Effects of moonlight on the vertical migration patterns of demersal zooplankton. J Exp Mar Biol Ecol 44:133–156

Alldredge AL, King JM (1985) The distance demersal zooplankton migrate above the benthos: implications for predation. Mar Biol 84:253–260

Ambler JW, Ferrari FD, Fornshell JA (1991) Population structure and swarm formation of the cyclopoid copepod *Dioithona oculata* near mangrove cays. J Plank Res 13:1257–1272

Andres NG, Witman JD (1995) Trends in community structure on a Jamaican reef. Mar Ecol Prog Ser 118:305–310

Buskey EJ, Peterson JO, Ambler JW (1996) The swarming behavior of the copepod *Dioithona oculata*: in situ and laboratory studies. Limnol Oceanogr 41:513–521

Bythell JC (1988) A total nitrogen and carbon budget for the Elkhorn coral *Acropora palmata*. In: Choat JH (ed) Proc 6th Int Coral Reef Symp, Townsville, Australia, August 1998, pp 535–540

Cahoon LB, Tronzo CR (1992) Quantitative estimates of demersal zooplankton abundance in Onslow Bay, North Carolina, USA. Mar Ecol Prog Ser 87:197–200

Coma R, Gili J-M, Zabala M, Riera T (1994) Feeding and prey capture cycles in the aposymbionic gorgonian *Paramuricea clavata*. Mar Ecol Prog Ser 115:257–270

Davies PS (1977) Carbon budgets and vertical zonation of Atlantic reef corals. In: Proc 3rd Int Coral Reef Symp, Miami, Florida, May 1977, pp 391–396

Edmunds PJ, Davies PS (1986) An energy budget for *Porites porites* (Scleractinia). Mar Biol 92:339–347

Emery AR (1968) Preliminary observations on coral reef plankton. Limnol Oceanogr 13:293–303

Ferraris JD (1982) Surface zooplankton at Carrie Bow Cay Belize, In: Rützler K, MacIntyre IG (eds) The Atlantic Barrier Reef ecosystem at Carrie Bow Cay Belize I. Structure and communities. Smithsonian Institution, Washington, DC, pp 143–151

Fornshell JA (1994) Copepod nauplii from the barrier reef of Belize. Hydrobiologia 292–293:295–301

Genin A, Gal G, Haury L (1995) Copepod carcasses in the ocean. II. Near coral reefs. Mar Ecol Prog Ser 123:65–71

Genin A, Greene C, Haury L, Wiebe P, Gal G, Kaartvedt S, Meir E, Fey C, Dawson J (1994) Zooplankton patch dynamics: daily gap formation over abrupt topography. Deep-Sea Res 41:941–951

Gittings SR, Inglehart WA, Rinn GS, Dokken QR (1994) Coral mass spawning on the Flower Garden Banks, NW Gulf of Mexico. Symp on Florida Keys Regional Ecosystem, Nov. 1992, Bull Mar Sci 54:1076

Glynn PW (1973) Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope: plankton community with evidence for depletion, part II. Mar Biol 22:1–21

Goreau TF, Goreau NI, Young CM (1971) Reef Corals: autotrophs or heterotrophs? Biol Bull 141:247–260

Gottfried M, Roman MR (1983) Ingestion and incorporation of coral-mucus detritus by reef zooplankton. Mar Biol 72:211–218

Hamner WM, Carleton JH (1979) Copepod swarms: attributes and role in coral reef ecosystems. Limnol Oceanogr 24:1–14

Hamner WM, Jones MS, Carleton JH, Hauri IR, Williams DM (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bull Mar Sci 42:459–479

Hayashibara T, Shimoike K, Kimura T, Hosaka S, Heyward A, Harrison P, Kudo K, Omori M (1993) Patterns of coral spawning at Akajima Island, Okinawa, Japan. Mar Ecol Prog Ser 101:253–262

Heidelberg KB (1999) The effects of water flow and zooplankton prey behavior on scleractinian coral heterotrophy. PhD Thesis, University of Maryland, College Park, 210 p

Heidelberg KB, Sebens KP, Purcell JE (1997) Effects of prey escape behavior and water flow on prey capture by the scleractinian coral, *Meandrina meandrites*. In: Proc 8th Int Coral Reef Symp, Panama City, June 1996, pp 1081–1086

Helmuth B, Sebens K (1993) The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus). J Exp Mar Biol Ecol 165:251–278

Hobson ES, Chess JR (1976) Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish Bull 74:567–598

Hobson ES, Chess JR (1978) Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. Fish Bull 76:133–153

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Johannes RE, Coles SL, Kuenzel NT (1970) The role of zooplankton in the nutrition of some scleractinian corals. Limnol Oceanogr 15:579–586

Johnson AS, Sebens KP (1993) Consequences of a flattened morphology: effects of flow on feeding rates of the scleractin-

ian coral *Meandrina meandrites*. Mar Ecol Prog Ser 99:99–114

Leichter JL, Shellenbarger G, Genovese SJ, Wing SR (1998) Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? Mar Ecol Prog Ser 166:83–97

Lewis JB (1992) Heterotrophy in corals: zooplankton predation by the hydrocoral *Millepora complanata*. Mar Ecol Prog Ser 90:251–256

Lewis JB, Boers JJ (1991) Patchiness and composition of coral reef demersal zooplankton. J Plank Res 13:1273–1289

Lewis JB, Price WS (1975) Feeding mechanisms and feeding strategies of Atlantic reef corals. J Zool Lond 176:527–544

Liddell WD, Ohlhorst SL (1987) Patterns of reef community structure, North Jamaica. Bull Mar Sci 40:311–329

McKinnon AD, Thorrold SE (1993) Zooplankton community structure and copepod egg production in coastal waters of the central Great Barrier Reef Lagoon. J Plankton Res 15:1387–1411

McWilliam PS, Sale PF, Anderson DT (1981) Seasonal changes in resident zooplankton sampled by emergence traps in One Tree Lagoon, Great Barrier Reef. J Exp Mar Biol Ecol 52:185–203

Madhupratap M, Achuthankutty CT, Sreekumaran Nair SR (1991) Estimates of high absolute densities and emergence rates of demersal zooplankton from the Agatti Atoll, Laccadives. Limnol Oceanogr 36:585–588

Moore E, Sander F (1976) Quantitative and qualitative aspects of the zooplankton and breeding patterns of copepods at two Caribbean coral reef stations. Est Coast Mar Sci 4:589–607

Moore E, Sander F (1979) A comparative study of zooplankton from oceanic, shelf, and harbor waters of Jamaica. Biotropica 11:196–206

Morales R, Murillo MM (1996) Distribution, abundance and composition of coral reef zooplankton, Cahuita National Park, Limon, Costa Rica. Rev Biol Trop 44:619–630

Odum HT, Odum EP (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol Monogr 25:295–320

Ohlhorst SL (1982) Diel migration patterns of demersal reef zooplankton. J Exp Mar Biol Ecol 60:1–15

Ohlhorst SL (1985) Reef zooplankton collected along a depth gradient at Discovery Bay, Jamaica. In: The ecology of coral reefs, vol 3. Symp Ser for Undersea Res US Dept Commerce, NOAA Undersea Res Prog, Silver Springs, Maryland, pp 101–116

Owre HB, Foyo M (1967) Copepods of the Florida Current with illustrated keys to genera and species. Inst Mar Sci Univ Miami, Miami, Florida

Porter J (1974) Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavernosa*. In: Proc 2nd Int Symp on Coral Reefs, Great Barrier Reef Committee on board the M.V. Marco Polo cruising in the waters of the Great Barrier Reef Province, Australia, June 1973, pp 111–125

Porter JW, Porter KG (1977) Quantitative sampling of demersal plankton migrating from different coral reef substrates. Limnol Oceanogr 22:553–555

Powlik JJ, St. John MA, Blake RW (1991) A review of zooplankton pump systems, with notes on the comparative efficiency of towed nets. J Plank Res 13:901–912

Robichaux DM, Cohen AC, Reaka ML, Allen D (1981) Experiments with zooplankton on coral reefs, or, will the real demersal zooplankton please come up? Mar Ecol 2:77–94

Roman MR, Furnas MJ, Mullin MM (1990) Zooplankton abundance and grazing at Davies Reef, Great Barrier Reef, Australia. Mar Biol 105:73–82

Rützler K, Ferraris JD, Larson RJ (1980) A new plankton sampler for coral reefs. P.S.Z.N. I: Mar Ecol 1:65–71

Saigusa M, Oishi K, Ikumoto A, Iwasaki H, Terajima M (2000) Emergence patterns of small subtital arthropods in relation to day/night, tidal and surface/bottom factors: investigations in the boreal sea, Japan (Akkeshi, Hokkaido). J Oceanogr 56:295–310

Sale PF, McWilliam PS, Anderson DT (1976) Composition of the near-reef zooplankton at Heron Reef, Great Barrier Reef. Mar Biol 34:59–66

Sale PF, McWilliam PS, Anderson DT (1978) Faunal relationships among the near-reef zooplankton at three locations on Heron Reef, Great Barrier Reef, and seasonal changes in this fauna. Mar Biol 49:133–145

Sammarco PW, Crenshaw H (1984) Plankton community dynamics of the central Great Barrier Reef Lagoon: analysis of data from Ikeda et al. Mar Biol 82:167–180

Sebens KP (1997) Adaptive responses to water flow: morphology, energetics, and distribution of reef corals. In: Proc 8th Int Coral Reef Symp, Pananma City, June 1996, pp 1053–1058

Sebens KP, DeRiemer K (1977) Diel cycles of expansion and contraction in coral reef anthozoans. Mar Biol 43:247–256

Sebens KP, Maney EJ Jr, Witting J (1992) A portable dive operated plankton sampler for near-substratum use. In: Cahoon L (ed) American Academy Underwater Sciences. Am Acad Underwater Sciences, Costa Mesa, California. pp 167–172

Sebens KP, Vandersall KS, Savina LA, Graham KR (1996) Zooplankton capture by two scleractinian corals, *Madracis mirabilis* and *Montastrea cavernosa*, in a field enclosure. Mar Biol 127:303–317

Sebens KP, Grace SP, Helmuth B, Maney EJ Jr, Miles JS (1998) Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa* and *Porites porites*, in a field enclosure. Mar Biol 131:347–360

Sedberry GR, Cuellar N (1993) Planktonic and benthic feeding by the reef-associated vermilion snapper, *Rhomboplites aurorubens* (Teleostei, Lutjanidae). Fish Bull 91:699–709

Sokal RR, Rohlf FJ (1995) Biometry: The principles and practice of statistics in biological research, 3rd edn. Freeman, New York

Sorokin YI (1973) On the feeding of some scleractinian corals with bacteria and dissolved organic matter. Limnol Oceanogr 18:380–385

Sorokin YI (1990) Plankton in the reef ecosystems, Chap. 11. In: Dubinsky Z (ed) Ecosystems of the world, 25: coral reefs. pp 291–327

Sorokin YI (1993) Coral reef ecology. Springer, Berlin Heidelberg New York

Titlyanov EA, Leletkin VA, Dubinsky Z (2000) Autotrophy and predation in the hermatypic coral *Stylophora pistillata* in different light habitats. Symbiosis 29:263–281

Tranter DJ, George J (1972) Coral reefs as biotopes: invertebrates: zooplankton abundance at Kavaratti and Kalpeni atolls in the Laccadives. In: Mukundan C, Gopinadha Pillai CS (eds) Proc 1st Int Symp on Corals and Coral Reefs. Mandapam, India, June 1969, Marine Biological Association of India, Cochin, pp 239–256

Ueda H (1987) Small-scale ontogenetic and diel vertical distributions of neritic copepods in Maizuru Bay, Japan. Mar Ecol Prog Ser 35:65–73

Ueda H, Kuwahara A, Tanaka M, Azeta M (1983) Underwater observations on copepod swarms in temperate and subtropical waters. Mar Ecol Prog Ser 11:165–171

Vaissière R, Seguin G (1984) Initial observations of the zooplankton microdistribution on the fringing coral reef at Aqaba (Jordan). Mar Biol 83:1–11

Walter C, Pasamonte JN, Talaue L (1981) A preliminary quantitative study on emergence of reef associated zooplankton from a Philippine coral reef. In: Proc 4th Int Coral Reef Symp, Manila, 1981, pp 443–451

Webber MK, Roff JC (1995a) Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. Mar Biol 123:481–495

Webber MK, Roff JC (1995b) Annual structure of the copepod community and its associated pelagic environment off Discovery Bay, Jamaica. Mar Biol 123:467–479

Witting JH, Sebens KP (2004). The role of capture in six Carribean Seleractinian corals: in situ evidence that heterotrophy enhances calcification and tissue growth rates. Mar Biol (in press)

Yahel R, Yahel G, Genin A (2002) Daily cycles of suspended sand at coral reefs: a biological control. Limnol Oceanogr 47:1071–1083

Yoshioka PM, Owen GP, Pesante D (1985) Spatial and temporal variations in Caribbean zooplankton near Puerto Rico. J Plank Res 7:733–751

Yonge CM, Nicholls AG (1931) Studies on the physiology of corals. V. The effects of starvation in light and darkness on the relationship between corals and zooxanthellae. Sci Rep Great Barrier Reef Exped 1:177–211