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Near- bottom depletion of zooplankton over coral reefs: I: diurnal dynamics and size distribution

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Abstract Changes in the near-bottom abundance of zooplankton on scales of centimeters to meters and hours to seasons are of great importance to corals and other benthic zooplanktivores. Our objective was to characterize such spatio-temporal changes over several coral reefs in the Gulf of Aqaba, Red Sea. Using arrays of underwater pumps, we found a substantial depletion of zooplankton near the bottom. Vertical gradients in zooplankton abundance were steeper during the night than day, mostly due to a greater nocturnal increase in zooplankton biomass higher in the water column. On average, the layer < 1 m above bottom (mab) was depleted by $2.6 \pm 2.2 \text{ mg m}^{-3}$ ($46 \pm 35\%$) and $1.4 \pm 1.4 \text{ mg m}^{-3}$ ($37 \pm 43\%$) during night and day, respectively. A long time series of bi-weekly samples at 0.5 mab, lasting 1.5 years, indicated a doubling of the biomass during the night with no apparent seasonality. The diel change was due to an increase in the abundance of only large ($> 200 \mu\text{m}$) zooplankters around dusk and their disappearance in the morning. Diurnal predation by zooplanktivorous fish, sediment resuspension by benthivorous fish and zooplankton behavior appear to control the dynamics of suspended particles over the reef, creating sharp vertical gradients and a remarkable diel cycle in the

ratio between nutritious plankton and inorganic particles.

Keywords Seston quality · Vertical migration · Predation · Boundary layer · Vertical distribution

Introduction

Pelagic zooplankton has a central role as a source for allochthonous nutrients in coral reefs (Tranter and George 1969; Glynn 1973; Hobson and Chess 1978; Gerber and Marshall 1982; Roman et al. 1990; reviewed by Erez 1990; Hatcher 1997; Heidelberg et al. 2004). Consumption of zooplankton and large particulate organic matter is considered a major heterotrophic pathway to many reef inhabitants, including damselfish (Hobson and Chess 1978), sea anemones (Sebens and DeRiemer 1977), crinoids (Rutman and Fishelson 1969), gastropods (Kappner et al. 2000; Ribak and Genin unpublished), and the coral themselves (Porter 1974; Sebens et al. 1998). Most reef planktivores are either sessile (e.g., corals) or site attached (e.g., damselfishes, Hobson and Chess 1978). Thus, plankton concentration in their immediate vicinity is a major factor controlling their feeding rate (Hobson and Chess 1978; Kiflawi and Genin 1997; Sebens et al. 1998).

The zooplankton assembly over coral reefs consists of a complex and highly dynamic mixture of pelagic plankton advected to the reef (Tranter and George 1969; Glynn 1973; Sammarco and Crenshaw 1984; Hamner et al. 1988; Carleton et al. 2001; Heidelberg et al. 2004), eggs and larvae produced by reef inhabitants (Vaissiere and Seguin 1984; Echelman and Fishelson 1990), and demersal plankton (Alldredge and King 1977). The latter group, consisting of plankton which is found near or within the substratum during the day and ascends into the water column at night, is specifically conspicuous over coral reefs (Alldredge and King 1977; Porter and Porter 1977; McWilliam et al.

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1981; Ohlhorst 1982), where visual predation by fish is unusually intense (Helfman 1986; Hamner et al. 1988; Hobson 1991).

Small-scale variations in the distribution of zooplankton were suggested as a key ecological factor in coral reefs. For example, zooplanktivorous fish grew faster 1 mab (m above bottom), where zooplankton was presumably more abundant than closer to the bottom (Clarke 1992). Similarly, corals and numerous other sedentary planktotrophic animals (e.g., sea anemones and crinoids) feed primarily during the night, when zooplankton densities at the anthozoans' height were assumed to be higher in comparison with daytime (Sebens and DeRiemer 1977; Heidelberg et al. 2004; Yahel et al. *in press*).

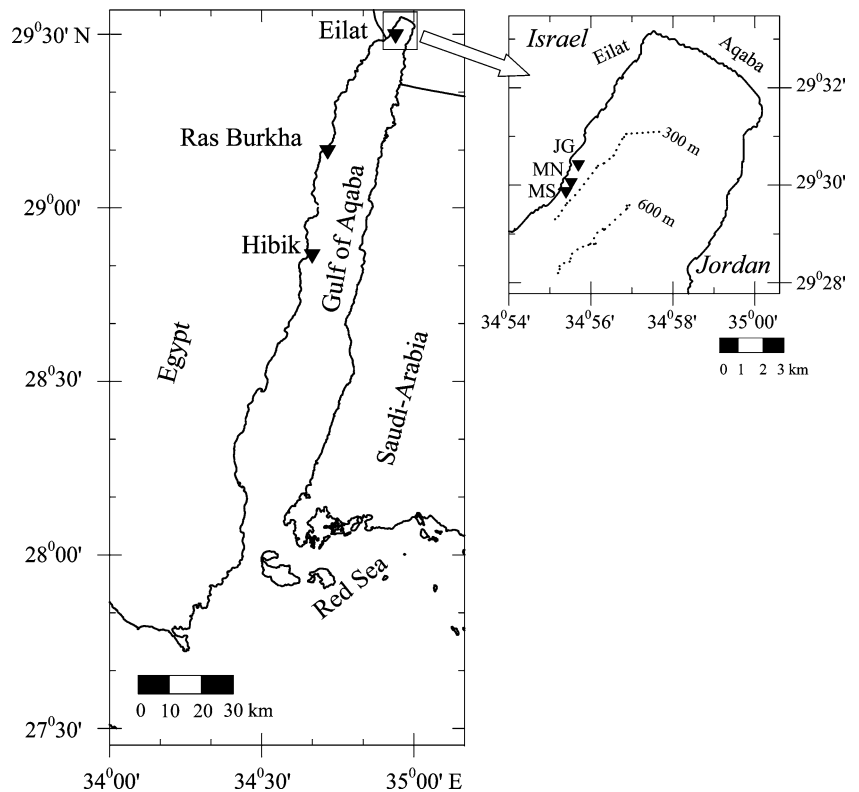
Surprisingly, quantitative data on variations in the abundance, type, and distribution of coral-reef zooplankton on spatial scales of centimeters to meters and temporal scales of one to several hours are lacking. As indicated by Heidelberg et al. (2004), this gap is partly a consequence of the traditional techniques used to sample zooplankton. Net tows (e.g., Tranter and George 1969; Echelman and Fishelson 1990) usually do not sample zooplankton near the typically rough bottom of the coral reef, while light traps are limited to the night sampling and provide highly biased samples (Sale et al. 1978). The objective of this study was to close this gap in our knowledge by sampling near-bottom zooplankton over several coral reefs using appropriate temporal and spatial scales.

Study sites

The study was carried out at the fore-reef region of four fringing coral reefs and a single sandy site (with no reef) along the northwestern coast of the Gulf of Aqaba, Red Sea (Fig. 1). Three of the reef sites, the Japanese Garden (JG), the Marine lab North (MN) and Marine lab South (MS) were in Eilat, Israel (29°30'N, 34°56'E), while the fourth reef (Hibik, 28°52'N, 34°38'E) and the sandy site (Ras-Burkha, 29°10'N, 34°43'E) were in Sinai, Egypt (Fig. 1).

The Gulf of Aqaba is a desert-enclosed sea. Water temperature ranged between 20 and 21°C in February to 26–28°C in August and September. Sea conditions at our study sites were relatively calm, with <1 m tidal range, <20 cm s⁻¹ currents, and <0.3 m waves (Yahel et al. 2002). Conditions at the gulf are generally oligotrophic (chlorophyll concentration <0.8 µg l⁻¹) with nano mole liter⁻¹ concentrations of dissolved N and P during the stratification period (May–October). The pelagic meso-zooplankton assembly is dominated by small calanoid copepods (<2 mm, Sommer et al. 2002; Farstey 2001); whereas, the neritic zooplankton is a complex mixture of pelagic species, reef originated meroplankton, and demersal forms (Vaissiere and Seguin 1984; Echelman and Fishelson 1990). The benthic reef community is dominated by stony corals. A hydrozoan coral (*Millepora* spp.), soft corals, encrusting algae, and other invertebrates

Fig. 1 The study sites at the Gulf of Aqaba. Sites JG (Japanese Gardens), MN (Marine laboratory North) and MS (Marine laboratory South) were in Eilat (Israel), while Hibik and Ras Burkha were in Sinai (Egypt)



(Fishelson 1970; Benayahu and Loya 1977) are also common.

MS and MN were approx. 200 m apart, in front of the H. Steinitz Marine Biology Station (see Genin et al. 2002 for a bathymetric map). The zooplankton sampling at these sites was carried out at 8.5 m depth, approx. 80 m offshore. The bottom at these fore-reef sites slopes gradually from the shore to ca. 15 m depth with no defined lagoon or reef flat. Exposed beach rock, composed of cemented crystalline pebbles, line the slope to a depth of 7–9 m, providing a substrate for many corals. Deeper than ~7 m, the slope increases and it is covered by a mixture of corals, coral fragments, and carbonate sand punctuated by outcrops of cemented crystalline pebbles. This slope extends down to ~40 m, to a horizontal terrace of carbonate-sand and corals.

Live coral cover at MN and MS was ~15%, with gravel, dead rocks, and sand covering ca. 50, 30, and 5% of the area, respectively (G. Yahel, unpublished data). The most abundant stony corals were *Stylophora* spp., *Cyphastrea* spp., *Favia* spp., *Acropora* spp., *Favites* spp., and *Porites* spp. (8.6, 7.2, 4.3, 4.1, 3.2, and 2.4 colonies m⁻², respectively, mean of 45 1 m² quadrates surveyed, G. Yahel, unpublished data). The soft coral *Xenia* spp. (3.7 colonies m⁻²) and the hydrocoral *Millepora* spp. (4.7 colonies m⁻²) were also very common.

The sampling at JG was carried out at a section of the nature reserve which had been closed to the public, at 5 m depth, approx. 10 m seaward of the reef flat. The sampling at Hibik was carried out at 11 m depth, approx. 100 m seaward of the reef wall, 250 m offshore. The fore reef at Hibik was much richer than those in Eilat. A shallow lagoon (1–3 m deep, 50–100 m wide) and a 10–50 m wide reef flat separated the reef slope from land at JG and Hibik, while at MN and MS the slope started near the shoreline. Large (1–10 m wide) massive corals were much more abundant at JG and Hibik than at MN and MS.

The sampling at Ras-Burkha was carried out at 14 m depth over a wide sand flat densely covered with sea grasses, 50 m seaward of the edge of a steep sandbank, ~400 m from shore. The closest corals to the sampling site were found on a large isolated knoll, some 70 m away.

Methods

Day–night comparison

Zooplankton was sampled every 2 weeks during 1.5 years (February 1996–July 1997) using high-capacity submersible pumps (submersible non-clog pump, 220 V, 14 m³ h⁻¹, Tsurumi Manufacturing, Japan) equipped with a specially designed impeller that insures intact passage of particles up to 15 mm in diameter while maintaining high suction speed at the pump intake (~3 m s⁻¹). The vertical positioning of the pump, with its 40 mm intake facing down, insured minimal

disturbance to the ambient flow field, as verified by our in situ observations of the flow using fluorescein dye. To ensure further separation of the suction volume from the bottom, a horizontal tarp (~0.5 m²) was attached 30 cm below the pump intake. The pumps were deployed 0.5–0.6 mab, except at JG where the pump was deployed 5 m seaward of the reef wall and 1.5 m above the bottom. A long 50 mm diameter PVC pipe, delivered the water to the shore where the water was filtered through a 1-m long, 20-cm diameter, 100 µm mesh sleeve. To avoid excessive pressure on trapped zooplankton, the net was fully submerged in a large tank. Microscopic examination did not reveal any excessive damaged to zooplankton trapped by the pumps in comparison to net tows (diver propelled, simultaneously sampled).

One diurnal and one nocturnal sample were obtained at each of JG, MN, and MS on each sampling day, simultaneously at all three sites. Each sample was taken by pumping water for approximately 4 h (50–60 m³). The pumping rate was measured prior to each sampling. For logistical reasons, the diurnal sampling started 5 h before sunset and nocturnal sampling half an hour after dark. A total of 76 pairs of day–night samples were collected. In the laboratory, the sample was divided into two equal aliquots using a Folsom Splitter (Omori and Ikeda 1984). Half of the sample was fractionated through a column of four mesh sizes: 1350, 500, 200, and 100 µm. To determine the organic content of suspended particles (ash free dry weight, AFDW) and the ash content (inorganic suspended particles), each fraction was collected on a pre-combusted, pre-weighed glass-fiber filter (Whatman, GF/A), dried for 24 h at 60°C (verifying complete desiccation), weighed, combusted for 4 h at 450°C, and weighed again. The weight was measured to the nearest 10 µg by use of Mettler–Toledo analytical balance (AG245, Greifensee). The composition of the suspended particulate matter was analyzed microscopically in a subset of nine day–night pairs of samples (a pair randomly chosen for one of the three sampling sites every 6 weeks). Each sample was size-fractionated as above, and the particulate content of each fraction was sorted and counted by use of a dissecting microscope. Aliquots (2.5 ml) were repeatedly drawn with a Stempel pipette (Omori and Ikeda 1984) and added to the counts until a total of > 300 particles was reached. Living organisms were sorted into seven categories: non-shelled planktonic organisms (primarily copepods, polychaetes, chaetognaths, decapod larvae, and other meroplanktonic forms), gastropods, benthic foraminifers, tintinnids, eggs, crustacean carcasses and molts (as in Genin et al. 1995), and large planktonic algae. Tintinnids were separated from other non-shelled zooplankton due to their strong aggregative appearance in our samples (see Results). Qualitative microscopic assessment indicated that the abundance of detrital particles in our samples was usually low (especially during the night). Therefore, hereafter, the organic matter in our samples is termed “zooplankton biomass”.

To test for an occurrence of a daily pattern in the zooplankton abundance over the reef, the pumps were operated continuously for several days, with separation of the samples into consecutive 4 h intervals. This sampling lasted 3 days at the coral-reef sites MN and MS (18–21 July 1997) and Hibik (14–18 August 1997) and 4 days at the sandy site of Ras-Burkha (18–22 August 1997). At the Sinai sites (Hibik and Ras-Burkha) a single high capacity pump was operated from aboard R/V Sue-Allen using a 5-cm diameter fire hose. In Eilat (MN and MS) the 4 h intervals were set so that the “dawn” sample started ≥ 30 min before sunrise, while at Hibik and Ras-Burkha the sampling intervals included crepuscular times so that the samples that started two hours prior to sunset and those ending two hours after sunrise were defined “dusk” and “dawn” samples, respectively.

Vertical distribution

Vertical profiles of zooplankton biomass were measured at the reef in the vicinity of MN and MS in Eilat. Profiling was carried out using a vertical array of five submerged pumps. To insure high vertical resolution, we used lower capacity pumps ($1.7 \text{ m}^3 \text{ h}^{-1}$, AT-2220, Chosen pumps, China) equipped with a narrow (25 mm) horizontal intake. While this setup resulted in a reduced suction speed at the pump intake ($\sim 1 \text{ m s}^{-1}$), it was yet sufficient to insure minimal sampling bias (Sebens et al. 1996). Zooplankton was trapped using small 100 μm mesh sleeves (40 cm long, filtering surface area of $\sim 0.12 \text{ m}^2$) attached directly to each pump outlet. The five pumps were attached to a taut mooring line (see Photo 3 in Genin et al. 2002) with their intake positioned at 0.2, 0.5, 1.0, 2.3, and 4.3 mab, except during September 1999 when the uppermost pumps were positioned at 7.0 mab. At the end of each session, scuba divers closed the sleeves and transferred the samples to shore. The volume of water filtered was calculated based on the pumping rates of the pumps, measured prior to and after the experiment, and the sampling duration. Each sampling session simultaneously used two arrays deployed 10–50 m apart at approximately the same depth. Altogether 117 profiles were taken at 7 different locations along the 300 m long reef from 4 to 17 m depth. Each sampling session lasted ~ 5 h. At the laboratory, each sample was filtered through 1,350 μm mesh to remove larger particles (extremely rare). The remainder of the sample was collected on a pre-combusted glass fiber filter (GF/A) with no size fractionation and weighted for AFDW and ash as described above.

Statistical analysis

Repeated measures ANOVA was used to test for differences between samples in 1.5 years time series, with

day–night (two levels), fraction (three levels), and site (three levels) being the first, second, and third factors, respectively. Two factor repeated measures ANOVA was used to test for difference between the vertical samples, with day–night (two levels) and height above bottom (five levels) being the first and second factors, respectively. Since the compound symmetry and sphericity assumptions were not fully met in both cases (i.e., differences between levels were correlated across subjects), we used a multivariate criterion (Wilks' λ) to simultaneously test the statistical significance of the repeated measures contrasts. The statistical analyses were carried out using STATISTICA Version 6 (data analysis software system, StatSoft Inc., 2002). The occurrence of vertical gradients in zooplankton biomass was manually tested using the “Page test” for ordered alternatives (Siegel and Castellan 1988). This nonparametric test is a modified version of the Kruskal–Wallis one-way ANOVA of ranked data.

Results

Day–night differences and size distribution

The total biomass (mg ash free dry weight per m^3) of large particulate matter (100–1350 μm) in the water overlying the coral reef was significantly higher during night at all sampling sites (Sign test, $P < 0.05$, Figs. 2, 3 and 4). In Eilat (Figs. 2 and 3, Table 1) nocturnal concentrations ($2.92 \pm 1.28 \text{ mg m}^{-3}$, mean ± 1 SD) were on average 1.8 times higher than the corresponding diurnal values ($1.77 \pm 0.62 \text{ mg m}^{-3}$), with average diurnal biomass (mean of the three sampling sites) exceeding nocturnal means in only 3 of the 30 sampling sessions (Fig. 2). Three factor repeated measures ANOVA (Table 2) indicated that these night-to-day differences were highly significant (Wilks' $\lambda = 0.46$, $F_{2,18} = 21.9$,

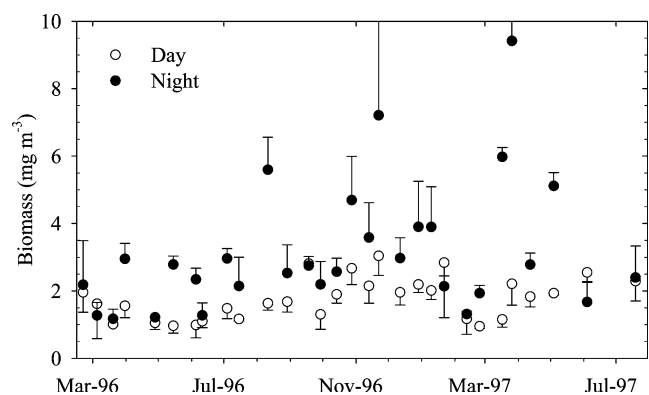


Fig. 2 Average biomass of zooplankton (ash free dry weight, 100–1350 μm) sampled during day (open symbols) and night (filled symbols), 0.5 mab, at Eilat coral reefs between February 1996 and July 1997. Each point indicates an average of three reef sites (MS, MN, and JG sampled simultaneously). Error bars, SE. Biomass values during the night were significantly higher than during the day (Sign test, $P < 0.001$)

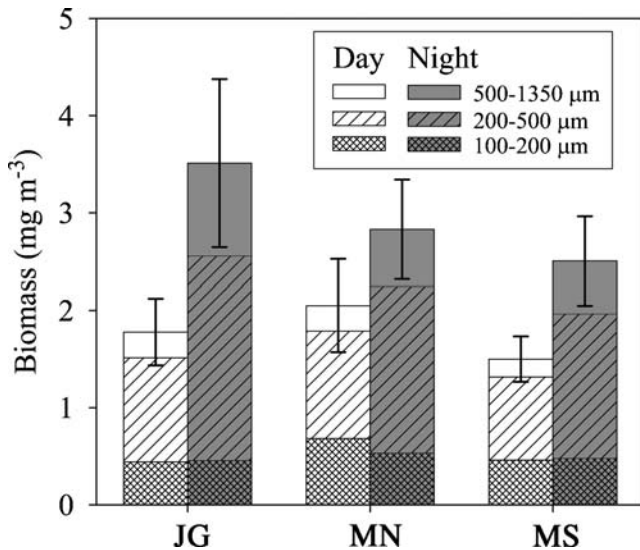


Fig. 3 Average biomass (ash free dry weight) of zooplankton during day and night in three size fractions within the range of 100–1350 μm , at the three reef sites in Eilat (*JG*, *MN*, *MS*) in the 76 biweekly samples (February 1996 – July 1997). The biomass during the night was significantly higher than during the day for the two larger size fractions ($>200 \mu\text{m}$) in each of the sites (Wilcoxon matched pairs test using Scheffe correction for multiple tests, $P < 0.05$) with no significant difference ($P > 0.15$) for the smallest size fraction (100–200 μm). Error bars are 95% confidence interval of the total biomass

$P < 0.001$) with no indication to inter-site difference (Wilks' $\lambda = 0.78$, $F_{2,18} = 2.5$, $P = 0.11$).

The nocturnal increase in the concentration of organic particles was associated with a corresponding increase in the proportion of large zooplankton (Figs. 3 and 4, Table 1), consisting of a threefold increase in the largest fraction (500–1,350 μm), twofold increase in the mid-fraction (200–500 μm) and no increase in the concentration of small zooplankton (100–200 μm) (Tukey HSD post hoc comparison, $P = 0.001$, $P < 0.001$, and $P = 0.99$, respectively). This shift in the size frequency distribution was reflected in the ANOVA (Table 2) as a significant interaction between the sampling period and the size fraction (Wilks' $\lambda = 0.32$, $F_{2,18} = 19.0$, $P < 0.001$). The 200–500 μm fraction dominated the sampled zooplankton during both day and night, contributing

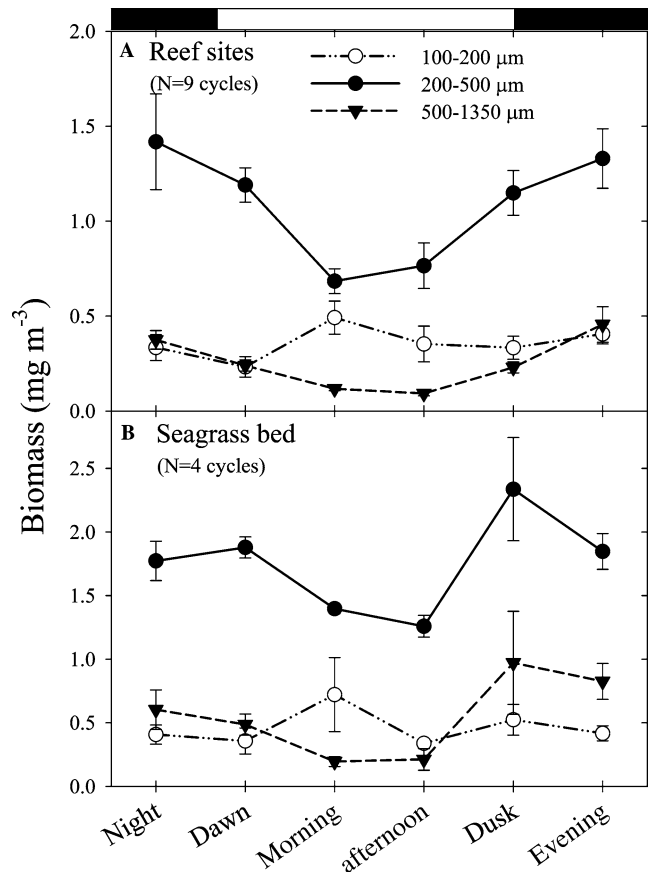


Fig. 4 Daily cycle of zooplankton biomass (ash free dry weight) at (a) three coral reefs (*MN*, *MS*, and Hibik, three daily cycles at each site) and (b) the seagrass at Ras-Burkha (four daily cycles). The horizontal bars at the top indicate day (open) and night (full) hours. Error bars, SE. Note the different vertical scales of the upper and lower panels

$57 \pm 11\%$ (max 91%) and $59 \pm 7\%$ (max. 74%) to the total biomass, respectively. The contribution of the largest size fraction to the total biomass at night ($24 \pm 8\%$, max. 55%) was almost double that during the day ($13 \pm 3\%$, max 24%).

The ratio between the weights of organic and inorganic particles (a proxy of seston quality) in the samples next to the corals was doubled at nights in all size

Table 1 Average concentration (\pm SD) of large particulate organic matter measured in biweekly samples over the *MN*, *MS* and *JG* coral reefs in Eilat between February 1996 and July 1997

Size fraction (μm)	Biomass (mg m^{-3})			Night/day (ratio)	Seston quality (Zoo/SSAC)	
	Day	Night	<i>P</i>		Day	Night
100–200	0.52 ± 0.18	0.49 ± 0.24	0.31	1.0 ± 0.5	0.17 ± 0.09	0.37 ± 0.23
200–500	1.02 ± 0.45	1.75 ± 0.86	< 0.001	1.9 ± 1.1	0.46 ± 0.26	0.97 ± 0.52
500–1350	0.23 ± 0.10	0.68 ± 0.31	< 0.001	3.2 ± 1.6	0.66 ± 0.86	1.22 ± 0.70
Total	1.77 ± 0.62	2.92 ± 1.28	< 0.001	1.8 ± 0.9	0.30 ± 0.20	0.73 ± 0.40

P values pertain to the biomass differences between night and day in each sampling session and are based on a Wilcoxon Matched Pairs Test. Zoo – zooplankton; SSAC – suspended sand concentration (Yahel et al. 2002). The seston quality as Zooplankton/Sand ratios were calculated separately for each sampling session

Table 2 Three factor repeated measures ANOVA testing the effects of sampling period (day, night), size fraction (100–200, 200–500, 500–1,350 μm) and sampling site (MN, MS, and JG reefs) and their interactions on zooplankton biomass during the biweekly sampling in Eilat

Effect	Wilks' λ	F	Df		P
			Effect	Error	
Period (day or night)	0.46	21.9	1	19	0.000
Fraction (size fraction)	0.14	55.7	2	18	0.000
Site (sampling site)	0.78	2.5	2	18	0.108
Period \times Fraction	0.32	19.0	2	18	0.000
Period \times Site	0.85	1.6	2	18	0.234
fraction \times Site	0.65	2.1	4	16	0.123
Period \times Fraction \times Site	0.80	1.0	4	16	0.447

fractions (Table 1). This shift was consistent for all sites sampled (data not shown).

Microscopic counts

Microscopic examination of pump samples allowed the separation of organic particles into nonliving (detrital) particles, resuspended benthic organisms, and “true” zooplankton. The latter group consisted mostly of holoplanktonic taxa (copepods, other crustacean, polychaetes, chaetognaths, and tunicates) and a few meroplanktonic groups. In terms of zooplankton density, the nocturnal increase in the abundance of organic particles included a 2.5 fold increase in “true” zooplankton (Table 3, Wilcoxon Matched Paired test, $P=0.01$; $2,132 \pm 2,094$, and 793 ± 484 organisms m^{-3} , during night and day, respectively). In contrast, no significant day–night difference was found in the density of zooplankton molts and phytoplankton (Table 3). Resuspended forms (benthic foraminifers and mollusks) exhibited an opposite trend, with elevated concentrations during the day (Table 3, see also Yahel et al. 2002). Methodological limitation prohibited detritus quantification. Nevertheless, qualitative observation indicated a common occurrence of detrital particles during the day and their almost complete absence during the night (see also Yahel et al. 2002). Numerically, the smallest sized zooplankton (100–200 μm) dominated the reef water during the day ($61 \pm 18\%$, max = 88%) but not during the night ($46 \pm 15\%$, max = 63%) even though its density did not differ significantly between day and night (570 ± 394 and 657 ± 582 organisms m^{-3} , respectively, Table 3, Wilcoxon matched paired test, $P=0.37$). The concentrations of medium-sized (200–500 μm) zooplankton were almost threefold higher during the night ($1,004 \pm 1,047$ organisms m^{-3}), when they numerically dominated the reef zooplankton ($52 \pm 14\%$, max = 81%). The most significant diel change was found for the largest (500–1350 μm) zooplankton, with an increase from 7 (± 11) animals m^{-3} during the day to 66 (± 77) organisms m^{-3} at night. Nevertheless, the numerical contribution of the larger zooplankton to the total concentration never exceeded 3%.

Table 3 (A) Average (\pm SD) concentration of different taxonomic groups in a subset of the biweekly samples (see text for details). Night/day ratios of the concentrations and the P values for the difference between day and night concentrations for each taxonomic group

Taxon	A						B						P values								
	Day ($\# \text{m}^{-3}$)			Night ($\# \text{m}^{-3}$)			night/day concentration ratios			Total			100–200 μm			200–500 μm			500–1,350 μm		
	100–200 μm	200–500 μm	Total	100–200 μm	200–500 μm	Total	100–200 μm	200–500 μm	Total	100–200 μm	200–500 μm	Total	100–200 μm	200–500 μm	Total	100–200 μm	200–500 μm	Total			
Zooplankton	570 \pm 394	361 \pm 255	7 \pm 11	657 \pm 582	1,004 \pm 1,479	1,940 \pm 2,043	1.15	2.78	9.79	1.15	0.89	1.13	NS	NS	NS	NS	NS	NS			
Eggs	88 \pm 66	21 \pm 22	1 \pm 2	171 \pm 110	36 \pm 32	4 \pm 3	1.94	1.77	5.47	1.94	1.30	0.98	NS	NS	NS	NS	NS	NS			
Zooplankton + eggs	632 \pm 415	376 \pm 265	7 \pm 12	805 \pm 621	1,032 \pm 1,482	2,132 \pm 2,094	1.27	2.75	9.49	1.27	1.20	0.56	NS	NS	NS	NS	NS	NS			
Molts	105 \pm 75	94 \pm 71	1 \pm 2	120 \pm 130	83 \pm 67	2 \pm 2	1.15	0.89	1.39	1.15	0.30	1.13	NS	NS	NS	NS	NS	NS			
Phytoplankton	187 \pm 84	44 \pm 39	3 \pm 4	223 \pm 132	57 \pm 55	1 \pm 1	1.19	1.30	0.30	1.19	1.20	0.98	NS	NS	NS	NS	NS	NS			
Tintinids	978 \pm 597	4 \pm 11	0 \pm 1	434 \pm 633	5 \pm 8	0 \pm 1	0.44	1.20	0.44	0.44	1.11	0.56	*	NS	NS	NS	NS	NS			
Benthic foraminifers	143 \pm 71	21 \pm 17	8 \pm 8	94 \pm 88	23 \pm 35	3 \pm 8	0.66	1.11	0.44	0.66	1.11	0.56	*	NS	NS	NS	NS	NS			
Benthic	256 \pm 458	17 \pm 31	0 \pm 0	101 \pm 111	57 \pm 83	4 \pm 7	0.40	3.38	0.73	0.40	3.38	0.73	NS	*	NS	NS	NS	NS			
Gastropods																					

(Wilcoxon matched pairs test, NS no significant differences; * $P < 0.05$; ** $P < 0.01$). Ratios were not calculated in cases where the day sample was nearly zero. No statistics were calculated for tintinids as their appearance was extremely patchy

Daily cycle

A clear daily cycle of elevated zooplankton biomass during the night and reduced concentrations during the day was observed during the three days of continuous sampling at each of the three reef sites (Fig. 4a). Zooplankton average biomass was lowest throughout the day and twofold higher during the night. The nocturnal biomass increase from the day level was on average 188 ± 32 , 204 ± 79 , 139 ± 43 , and $193 \pm 152\%$ at MN, MS, Hibik, and Ras-Burkha, respectively. The increase in plankton concentration occurred at dusk whereas the decrease occurred at dawn (Fig. 4). On several occasions, a peak in zooplankton biomass occurred at dusk, rather than later at night. Over the sandy seagrass meadow at Ras-Burkha, zooplankton concentration was much higher during both day and night and the daily cycle showed a similar but less pronounced pattern (Fig. 4b). The nocturnal increase of zooplankton biomass of the largest size fraction (500–1350 μm) was significant (Kruskal–Wallis ANOVA, $P < 0.05$); whereas, the smallest size fraction (100–200 μm) showed no significant diel variation in all four sites (Kruskal–Wallis ANOVA, $P > 0.2$). The intermediate fraction (200–500 μm) was significantly elevated at MN and Hibik but not at Ras-Burkha and MS. At the MN site, where reef biota was more sparse, zooplankton biomass was somewhat higher than at MS (Wilcoxon Matched Pairs Test, $P = 0.016$). Nevertheless, the simultaneously collected samples at both sites were highly correlated (MN = $1.03 \times \text{MS} - 0.3$, $R^2 = 0.86$, $P < 0.001$).

Fig. 5 Vertical distribution of zooplankton biomass along a cross shore transect over the coral reef of Eilat during day (*open symbols*) and night (*full symbols*). Two adjacent pump arrays were used simultaneously at each sampling session (*South, triangles* and *North, circles*). The panels are positioned on this plot so that the lower horizontal axis of each panel crosses the bottom line at a point indicating the depth of the pump array. The significance of the gradient (Page test) in each profile is indicated above the corresponding panel (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Error bars (SE) were omitted in panels B and E due to the small N

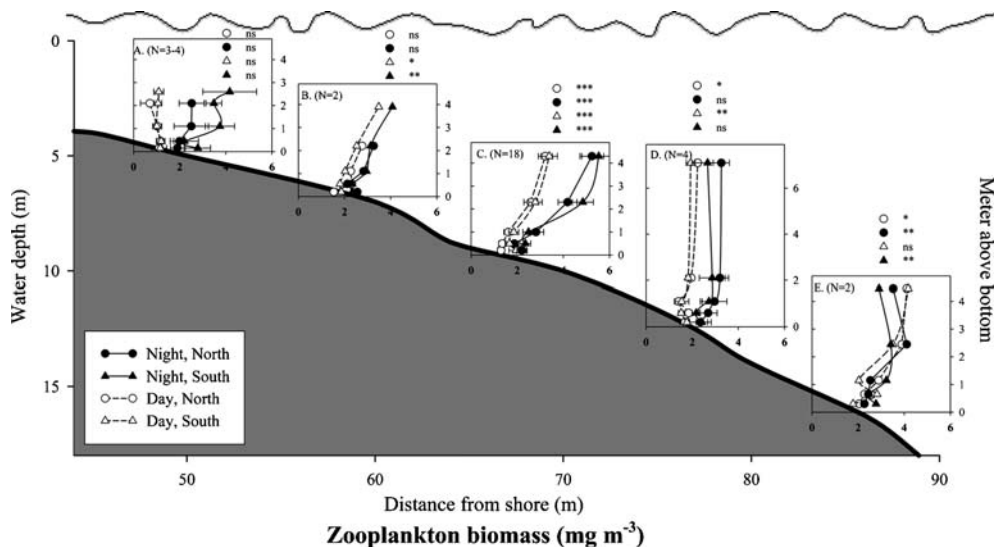


Table 4 Two factor repeated measures ANOVA testing the effects of day-night (DN) and the distance from the bottom (MAB) and their interactions on zooplankton biomass sampled using the vertical pump arrays at Eilat

Effect	Wilks' λ	F	Df	P	
				Effect	Error
DN (day/night)	0.46	23.7	1	20	< 0.001
MAB (pump height)	0.29	10.5	4	17	< 0.001
DN \times MAB	0.44	5.5	4	17	< 0.001

Vertical distribution

Zooplankton biomass was depleted over the reef during both day and night (Page test, $P < 0.001$, Fig. 5, Table 4). A depleted layer was evident in $> 90\%$ of the 117 vertical pump arrays sampled; an inverse pattern with zooplankton increase toward the bottom occurred in ten cases (8.5%). The only exception was the shallowest site where no depletion was evident during day (Fig. 5a). At this site the pump arrays were located over a large sand patch with sparse coral cover. The thickness of the depleted layer and the shape of the concentration gradient differed between day and night (Figs. 5 and 6a, b) as indicated by a significant interaction term between the sampling period (DN) and the vertical location along the transect (mab) in the ANOVA analysis (Table 4) and the post-hoc analysis (Table 5). During the night, the depleted layer was thinner (~ 0.5 m) and zooplankton biomass > 0.5 mab consistently increased in comparison to the lower most sampling point at 0.2 mab (28 ± 27 , 78 ± 57 , and $116 \pm 94\%$ at 1, 2.3, and 4.3 mab, respectively). The two lowermost sampling points (0.2 and 0.5 mab) were similarly depleted with no significant concentration difference (Table 5, Fig. 6b). During the day the zooplankton depleted layer was thicker (> 1 m) and an increase in concentration was evident only at 2.3 mab ($52 \pm 63\%$, Table 5).

The nocturnal increase in biomass found by the vertical pump arrays (Night/Day ratio, 1.8 ± 1.0) was highly

Table 5 *P* values for post hoc pair-wise comparisons using Tukey HSD testing for differences in the biomass between five different heights above bottom (mab) sampled in Eilat with the vertical pump arrays during the day (upper-right section of the matrix) and night (lower-left section with italics and bold italics values). *P* values < 0.05 are in bold. Within *MS* = 0.44, *df* = 80

mab	0.2	0.5	1	2.3	4.3
0.2		1.000	1.000	0.008	0.000
0.5	<i>1.000</i>		1.000	0.011	0.000
1	<i>0.024</i>	<i>0.006</i>		0.013	0.000
2.3	0.000	0.000	0.000		0.041
4.3	0.000	0.000	0.000	0.231	

significant (Table 4) and identical to that measured with the stronger pumps at the biweekly sampling (1.8 ± 0.9 , Table 1). This rise was evident throughout the water column (Figs. 5 and 6a), but was more considerable at the upper layers > 0.5 mab (85–109%) in comparison to the bottom depleted layer (< 0.5 mab, 45–64%, Figs. 6a, b). The nutritious quality of the suspended particles, defined as the weight ratio between organic and inorganic particles, has shown a pronounced daily shift (Fig. 6c), with significantly higher quality during the night in all but the highest (> 4 mab) elevation. The maximum diel difference was found at 1 mab.

Discussion

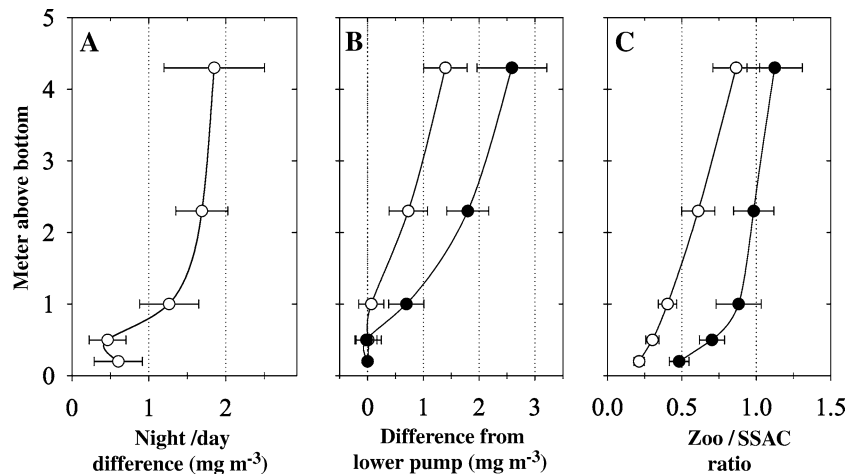
This study shows substantial near bottom depletion of zooplankton and suspended organic particles (Figs. 5

and 6; see Figs. 2 and 3 in Holzman et al. this issue) and diel changes in their key characteristics (Figs. 2, 3 and 4) over coral reefs. During the night, the quantity of organic particles, mostly zooplankton, nearly doubled, much due to an increase in the abundance of large (> 200 μm) animals (Figs. 3 and 4, Table 1). Consequently, the ratio between the concentration of organic and inorganic particles increased from approximately 3:10 during the day to 7:10 at night (Table 1). The depletion of organic particles in the benthic boundary layer was more pronounced during the night than day (Fig. 6b). This pattern was corroborated for zooplankton counts at the same study site by Holzman et al. (this issue). The nocturnal increase in zooplankton abundance was more pronounced a few meters above bottom than near it (≤ 1 m), with a thicker benthic depleted layer during the day (Fig. 6a).

We propose that intense near-bottom predation, characterizing coral reefs (Glynn 1973; Hamner et al. 1988; Motro et al. this issue), is the *ultimate* factor determining vertical distribution of zooplankton and its diel behavior at the reef. Intense daytime zooplanktivory by fish typified coral reefs (Hamner et al. 1988). Nocturnal zooplanktivory by reef fishes is considered low although no direct measurements of the vertical distribution of this predation are yet available (Helfman 1986; Hobson 1991; Holzman and Genin 2003). Depletion of smaller particulate organic matter (phytoplankton) towards the bottom at the same reef sites was ascribed by Yahel et al. (1998) to intense benthic grazing. However they did not find evidence for a daily pattern in phytoplankton distribution over the reef. Unlike phytoplankton, most reef zooplankters are capable of controlling their vertical location in the water column (Holzman et al. this issue). Nocturnal emergence, active bottom avoidance, and direct predation are thus suggested as complimentary and most significant mechanism controlling small scale distribution of zooplankton at coral reefs.

The nocturnal increase of zooplankton biomass at the fore reefs can be attributed to three factors: (1) the emergence of demersal plankton, (2) the advection of

Fig. 6 Vertical profiles of suspended particles above the coral reefs at *MN* and *MS*. (a) Average day-night difference in AFDW calculated for consecutive 24 h intervals ($N=40-49$ for different heights). (b) Average deviation of the biomass from that measured at the lowest elevation (0.2 mab) in each profile during day (*open symbols*, $N=60$) and night (*full symbols*, $N=57$). Average biomass at the lower-most elevation was 1.6 ± 0.9 and 2.3 ± 0.8 mg m^{-3} , during day and night, respectively. (c) The average ratio between the weights of organic (AFDW- mostly zooplankton) and inorganic particles at night (*full symbols*, $N=45$ profiles) and day (*open symbols*, $N=43$ profiles). Error bars, 95% confidence intervals



migrating zooplankters from the nearby open sea, and (3) the cessation of visual predation by the fish. In a related study (Yahel et al. *in press*), we have found that the proportion of demersal zooplankton and meroplankton released by benthic reef inhabitants in samples obtained at dusk could explain most of the corresponding increase in total zooplankton biomass. However, later during the night, other, non-demersal zooplankton increased in abundance. A similar trend was reported by Echelman and Fishelson (1990) who observed high proportions of pelagic zooplankton in samples obtained during the night over the fore-reef in Eilat. A dominance of pelagic copepods (>85%) was reported by Heidelberg et al. (2004) for nocturnal samples obtained near the reef bottom at Discovery Bay, Jamaica. In agreement with our finding, the density of reef zooplankton in Jamaica remains high throughout the night (Heidelberg et al. 2004). A nocturnal increase in the abundance of pelagic zooplankton over the reef is expected if migrating zooplankton is advected horizontally from the open waters onto the reef. Indeed, our study sites were close (<1 km) to deep (>200 m) waters (Fig. 1). Such an onshore advection was suggested by Yahel et al. (1998) and Genin et al. (2002) to explain the phytoplankton dynamics over the reef. The cessation of the intense diurnal zooplanktivory by visual fish (Motro et al. this issue) undoubtedly contributes to the increase of zooplankton density over the reef, regardless of the emergence of demersal animals or advection of migrating zooplankton from the open water. On the other hand, zooplanktivory by nocturnal fish that start foraging at dusk may partly offset that effect. The relative contribution of each of the three processes is yet to be quantified.

The biomass of zooplankton retained on our >100 μm mesh over the coral reef ranged from 0.6 to 6 mg m^{-3} , corresponding to densities of 300–7,000 ind. m^{-3} . These values are similar to those reported for other coral reefs in the Indo-pacific (Khalil and El-Rahman 1977; Gulf of Aqaba; Alldredge and King 1977; Roman et al. 1990; Great Barrier Reef; Gerber and Marshal 1982; Marshal Islands), but are lower than in the Caribbean (Glynn 1973; Heidelberg et al. 2004 and references therein). At the sandy bottom site of Ras-Burkha, where zooplanktivorous fish were rare, zooplankton densities were higher and the diel change was less pronounced (Fig. 4). The nocturnal increase of zooplankton abundance was more pronounced in terms of numerical density than biomass (compare Tables 1 and 3). This difference may be partly explained by a daytime elevation of resuspended detrital particles (Yahel et al. 2002).

As discussed by Heidelberg et al. (2004) underwater pumps are the preferred method for sampling near bottom zooplankton at scales relevant for the benthic consumers. A comparison between our high capacity pumps (14 $\text{m}^3 \text{h}^{-1}$, used for the biweekly and daily cycle sampling) and samples taken simultaneously with nets towed by a pair of scuba divers at the same depth yielded similar biomass quantities (7.3 ± 5.3 and $7.5 \pm 2.2 \text{ mg m}^{-3}$,

$N=6$, respectively). A comparison between our samples and those obtained near MN with a 300 μm stationary Bongo net (Holzman and Genin 2003) may suggest some avoidance of large zooplankters (>1,000 μm) from our pumps. However, these animals were always rare (average 0.63 ind. m^{-3} , Holzman and Genin 2003). Hence, the samples obtained with our pumps can be considered as adequately representing the bulk zooplankton up to at least 1000 μm in size. It should be noted that no evidence for selective (biased) sampling was found by Sebens and his co-workers using a less powerful pump (Sebens et al. 1996 and references therein).

Similar to other coral reefs (reviewed by Heidelberg et al. 2004), zooplankton biomass started to increase at dusk. This increase was by and large due to the addition of relatively large (>200 μm) animals (Figs. 3 and 4), with a two to threefold increase of the 200–500 μm and 500–1,350 μm sizes (Table 1). A nocturnal increase of similar magnitude was reported from Lizard Island by Alldredge and King (1977). Numerically, the increase was due to the nocturnal addition of animals belonging to the group we termed “true” zooplankton, with an order of magnitude increase in the density of animals in the size range 500–1,350 μm size range (Table 3). No diel differences were found for small (100–200 μm) animals, neither in biomass nor in density.

In terms of food availability, elevated topographies (>1 m in height) and nocturnal feeding mode should be beneficial for corals and other suspension feeders, particularly for animals which can be damaged by inorganic particles. The vertical difference in habitat quality is further accentuated for species for which feeding is flow dependent due to the gradual weakening of the flow toward the bottom (Genin et al. 2002). Protruding structures such as isolated knolls should be favorable for corals and zooplanktivorous fishes.

The data presented here, together with the reports of Yahel et al. (1998), Yahel et al. (2002) and references therein, indicates that the boundary layer overlying coral reefs is depleted of nutritious particles and enriched in inorganic, possibly deleterious particles (Riegl 1995; Stafford-Smith 1993), with both parameters exhibiting sharp vertical gradients and substantial diel changes. The synergistic activity of two diurnal guilds of reef fish appears to control the vertical and temporal distribution as well as the nutritious quality of suspended particles over coral reefs.

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