

Roi Holzman · Matthew A. Reidenbach
Stephen G. Monismith · Jeffrey R. Koseff
Amatzia Genin

Near-bottom depletion of zooplankton over a coral reef II: relationships with zooplankton swimming ability

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Abstract Intense predation by corals and associated fauna can generate vertical gradients of their zooplankton prey. The goal of this study was to characterize the small-scale distribution of zooplankton above the coral reef of Eilat, Israel. Four vertical arrays, each consisting five underwater pumps attached 0.5–3 m apart on a taut mooring, were deployed for 10 days at two sites over the reef slope. A distinct layer of depleted zooplankton was repeatedly found in the 1.5 m high benthic boundary layer. The gradient was sharpest for strong swimmers (copepods and polychaeta), intermediate for weak swimmers (nauplii, mollusks and appendicularia), and lacking for passive taxa (eggs and foraminifera). Spatio-temporal changes in the abundance of copepods and polychaetes were highly correlated, more so in the water aloft (Pearson $r > 0.9$) than near the bottom ($r > 0.8$). The spatio-temporal correlations between weak swimmers and between passive taxa were much weaker ($r < 0.8$ and $r < 0.4$, respectively). Flow and shear stress did not affect the distribution patterns. The correspondence between the zooplankton distribution and their swimming ability indicates that bottom avoidance contribute to the formation of depleted layer over the reef.

Keywords Behavior · Small-scale distribution · Predation · Boundary layer

Introduction

The patterns of zooplankton distribution above the bottom are most relevant for understanding foraging behavior (Hamner et al. 1988; Kiflawi and Genin 1997), growth (Clarke 1992), and abundance (Hobson and Chess 1978) of zooplanktivorous animals in benthic habitats. Coral reefs are characterized by an occurrence of intense zooplankton predation (e.g. Tranter and George 1969; Hamner et al. 1988; Sebens et al. 1998) and phytoplankton grazing (Yahel et al. 1998; Genin et al. 2002). While near-bottom depletion of phytoplankton are well documented for coral reefs (Yahel et al. 1998; Genin et al. 2002), little is known about the vertical distribution of zooplankton in those habitats (but see Yahel et al. this issue).

Although near-bottom depletion is expected due to benthic predation on zooplankton (Motro et al. this issue), planktivorous fish that forage aloft may outweigh benthic predation rendering nondetectible the depletion below. An occurrence of higher abundance of zooplankton aloft was suggested by Clarke (1992) to explain the enhanced growth and reproductive success of hole-dwelling zooplanktivorous fish (Spinyhead and Rough-head blennies) after being transplanted higher up above bottom. Several studies, however, reported an opposite gradients. Zooplankton density in the GBR, Australia, increased from surface to bottom (see Fig. 4 in Hamner et al. 1988) in spite of an overall decline from the open waters toward the reef. Similarly, at Heron reef, the number of mobile, nocturnal zooplankton caught near the substrate by light traps was 1.2–9 times greater than near the surface (Sale et al. 1976). A difference in species composition suggested that the surface-associated zooplankton might have originated from open sea, while the near-bed zooplankton was resident (Sale et al. 1976).

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R. Holzman · A. Genin (✉)
The Inter-university Institute for Marine Sciences of Eilat
and Department of Evolution, Systematics and Ecology,
The Hebrew University of Jerusalem,
P.O. Box 469, Eilat, 88103, Israel
E-mail: amatzia@vms.huji.ac.il
Tel.: +972-8-6360124
Fax: +972-8-6374329

M. A. Reidenbach · S. G. Monismith · J. R. Koseff
Department of Civil and Environmental Engineering,
Stanford University, Stanford, California,
CA 94305-4020, USA

Present address: M. A. Reidenbach
Department of Civil and Environmental Engineering,
University of California, Berkeley, CA 94720-1710, USA

The abundance of demersal zooplankton over a sand bottom in the Gulf of California decreased as a function of distance from bottom (Alldredge and King 1985).

On scales of centimeters to hundreds of meters, patterns in the distribution of zooplankton can be also determined by behavior (reviewed by Metaxas 2001). Most conspicuous is, obviously, the zooplankton diel vertical migration. The waters above coral reefs are swamped at night with demersal zooplankton which emerge from the bottom after sunset and ascend to the water column, thereby actively creating vertical patterns (Alldredge and King 1977; Porter et al. 1977). Acoustic records from a shallow temperate inlet near Orcas Island, NW, USA, showed a rapid ascent of mysids after sunset (Kringel et al. 2003). During the day a dense layer of scatterers, possibly those mysids, was found just above the bottom. A similar trend was reported by Barans et al. (1997) from an estuarine inlet in South Carolina. The intense layer of scatterers found near the bottom during the day consisted mostly of 3–12 mm long zooplankton, separated from the bottom by a layer of suspended fine particles. On scales of <1 m, both *Daphnia* and copepods exhibit oriented swimming toward high phytoplankton densities (e.g. DeMott and Watson 1991; VanGool and Ringelberg 1996). Chemical, mechanical, and visual cues are used by copepods to escape predators (Ohman 1988; Bollens et al. 1994). Hence, in coral reefs, where the near-bottom environment is typically rich with predators and depleted in phytoplankton (Yahel et al. 1998; Genin et al. 2002), zooplankton may actively avoid the bottom. On the other hand, the enhanced turbulence near the bottom (Thomas and Atkinson 1997; Genin et al. 2002), may attract the types of zooplankton that benefit from tur-

bulence (Rothschild and Osborn 1988; Kiorboe and Saiz 1995). Hence, different groups of zooplankton may respond differently to predation and physical conditions.

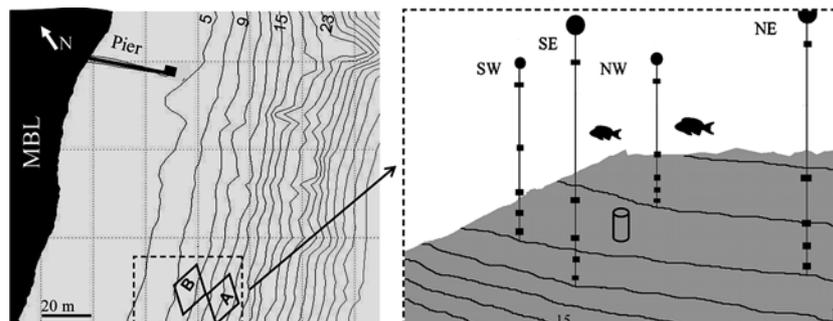
The objectives of this study were to characterize the fine-scale vertical distribution of zooplankton groups over a coral reef during day and night and to evaluate the effects of biological and physical factors on the observed patterns.

Methods

Study site

The study was carried out from 25 August 1999 to 7 September 1999 at the coral reef off the Steinitz Marine Biology Laboratory (MBL), Eilat, Israel ($29^{\circ}30'N$ $34^{\circ}56'E$; Fig. 1). The oceanographic conditions in the region were described by Reiss and Hottinger (1984) and the plankton community by Sommer et al. (2002), and reference therein. The local coral reef community was described by Yahel et al. (1998) and reference therein and the fish community was described by Rilov and Benayahu (2000). Briefly, water in the region is oligotrophic, dominated by small prokaryotic phytoplankton and small zooplankton. The coastal currents are weak, with an average speed of less than 10 cm s^{-1} , with a strong semidiurnal tidal currents during summer. The reef is dominated by hermatypic corals. Hydrozoans, soft corals, mollusks, sponges and tunicates are also abundant. The slope reef at MBL is characterized by approx. 50% cover of rocky substratum, with live coral cover ranging 15–25%. Sand and coral rubbles cover the rest of the bottom, usually in small patches (Israel National Monitoring Program, unpublished report). The average coral density is 30–50 colonies per m^2 (G. Yahel and A. Genin, unpublished data), with a dominance of small, isolated colonies. The guild of diurnal zooplanktivorous fish is dominated by site-attached species including reef *Anthias* (*Pseudanthias squamipinnis*) the damselfishes *Neopomacentrus miryae* and *Dascyllus* spp., and more mobile species such as *Caesio* spp. and *Abudefduf* spp. The most abundant nocturnal zooplanktivorous fishes include Apogonidae (*Apogon cyanosoma*, *A. aureus*, *Cheilodipterus quinquelineatus*), *Myripristis murdjan*, and *Pempheris vanicolensis* (Rilov and Benayahu 2000). Very little is known about the distribution

Fig. 1 *Left*: the bathymetry of the coral reef off Steinitz Marine Biology Laboratory (MBL), Eilat, Israel. The study sites A (deep) and B (shallow) are indicated by the two open diamonds. The pump arrays were deployed at the corners of the diamonds. *Right (inset)*: a perspective illustration of the hardware setup at site B as seen from the east. The pump arrays (vertical lines) are marked according to their position within each site (SW southwest, SE southeast, NW northwest, NE northeast). The five pumps on each array (full squares) were attached to a taut mooring line at 0.25, 0.75, 1.25, 2.25, and 5.25 m above bottom. The full circle at the top of each mooring line indicates a float. The open cylinder at the center indicates the location of ADCP and ADV current meters. Gray background indicates the reef. Contour intervals are 2 m



and abundance of the nocturnal fishes. The zooplankton community is dominated by small (<400 μm) animals, most of them (>60%) copepods (Farstey et al. 2002; Sommer et al. 2002). Zooplankton abundance near the coral reef during the night is approximately two times higher than during the day (1,000–2,000 individuals m^{-3} at night), mostly due to a nocturnal increase in the density of large zooplankters (>200 μm) (Yahel et al. 2002; Yahel et al. this issue).

Zooplankton sampling

Vertical profiles of zooplankton were obtained using four pump arrays (Fig. 1; see Photo 3 in Genin et al. 2002), each consisting of five underwater pumps (AT-2220, Chosen pumps). The five pumps were attached to a taut mooring line at 0.25, 0.75, 1.25, 2.25, and 5.25 m above bottom (MAB). The pumps were powered (220 V) from shore using underwater cables. The experiment was replicated at two sites on the reef slope: first (hereafter site A) with the four arrays deployed at 11–17 m depth, and second (site B) at 7–11 m. At each site, one pump array was deployed at each of the four corners of an imaginary diamond-shape area, approximately 20 m in length, 10 m in width (Fig. 1). The pumping rate was measured and recorded for each pump prior to the deployment (average rate (\pm SD)=1.66 (\pm 0.04) $\text{m}^3 \text{h}^{-1}$, $n=20$ pumps).

Zooplankton was collected from each pump with a small 100 μm mesh sleeve (40 cm long, filtering surface area of \sim 0.12 m^2). Scuba divers attached and removed the nets prior to and at the end of each sampling session (hereafter a “run”), respectively. Each run lasted 60 min and was controlled by turning the power on and off simultaneously for all pumps. The samples were immediately transferred to the shore and preserved in 4% formaldehyde (Omori and Ikeda 1984). An aliquot consisting 15–50% of the original sample was separated with a Stempel pipette (Omori and Ikeda 1984) for microscopic sorting. At least 250 animals were counted in each sample. Counts of replicated aliquots differed by less than 10%. The counted organisms were sorted to the following taxonomic groups: copepoda, copepod nauplii, molluska (bivalves and gastropods), appendicularia (larvacea), polychaeta, eggs and foraminifera (nine runs only). Other taxa, usually comprising <5% of the sample, were pooled into a miscellaneous group. The different taxa were sorted into three groups based on swimming ability: strong swimmers, weak swimmers, and “passive”. Information on the swimming ability of species belonging to each group was reported by Hardy (1956), Mileikovsky (1973), Van Duren and Videler (1995), and Ådlandsvik et al. (2001). The assignment of appendicularia to the weak swimmers group was based on personal communications (G. Gorsky). Note that due to low pumping rates, large zooplankton with good swimming ability was expected to avoid the pumps. Therefore, the conclusions driven from this study should

apply only to small zooplankton (100–1000 μm), which formed the bulk of our samples. Large phytoplankton (mostly *Ceratium* spp.) caught in our nets were not included in our analysis.

A total of 14 runs were made, 7 during the night (2 at site A and 5 at site B respectively) and 7 during the day (3 at site A). For reasons related to a concurrent study using the same pumps, sampling times (Table 1) were determined by the occurrence of stable currents, rather than using fixed sampling intervals. Twenty-four samples were lost during handling and processing, so that the total number of samples analyzed was 256.

Diver safety considerations imposed systematic net collection from bottom to top. Hence near-bottom nets were always collected first. This procedure could have biased our sampling, as more zooplankton could have escaped from the nets aloft. We considered escape unlikely because once the pump was turned off the mesh net bowed, blocking the pump aperture. Nevertheless, we tested the occurrence of escape by comparing the number of zooplankton collected by a pump from which the net was retrieved immediately, to that retrieved 30 min after pumps turnoff. This was a conservative test, since the net collecting in the main experiment took only 15–20 min. The two pumps were deployed side by side (\sim 15 cm apart) at 3.0 m depth (3.0 m above bottom) and simultaneously pumped water for 1 hr. The experiment was replicated four times during the day and three times during the night. The mean difference between the paired samples was 2% (\pm 10.1) for total zooplankton and 3.3% (\pm 9.4) for copepods, not significantly different from zero (Wilcoxon matched pairs test, $P>0.61$, $N=7$).

Throughout the study, the currents were measured and displayed in real time at the shore laboratory using an on-line Acoustic Doppler Current Profiler (ADCP; 600 kHz WorkHorse, RDI, San Diego, USA), deployed on the bottom facing upward, and a vertical array of three Acoustic Doppler Velocimeters (ADV, Sontek, California, USA), deployed 0.08, 0.28, and 1.0 mab. The current meters were deployed near the geometric center

Table 1 Dates and start time of zooplankton sampling at sites A and B. Sunset was around 18:30. Each sampling lasted 1 h

Location	Period	Date	Time started
Site A	Day	30 August 2003	12:00
		31 August 2003	15:20
		01 September 2003	15:30
	Night	31 August 2003	21:30
		01 September 2003	22:10
Site B	Day	03 September 2003	15:45
		05 September 2003	16:10
		06 September 2003	12:00
		07 September 2003	16:20
	Night	02 September 2003	22:17
		05 September 2003	19:30
		06 September 2003	1:50
		06 September 2003	20:40
		07 September 2003	0:17

of the imaginary diamond depicted by the four pump arrays (Fig. 1). Results of the current measurements will be reported elsewhere (Reidenbach et al. submitted manuscript). The main objective of the current measurements was to determine the possible effects of flow and turbulence on the vertical distribution of zooplankton. Friction velocity (U^*) was calculated for each of our zooplankton sampling runs and was used as a proxy for mixing and turbulence. Values of U^* were estimated by assuming a logarithmic velocity profile within the turbulent boundary layer. This profile can be expressed as

$$\frac{U}{U^*} = \frac{1}{\kappa} \times \ln\left(\frac{z}{z_0}\right),$$

where U is the 10-min averaged velocity, U^* the friction velocity, κ the von Karman constant (0.4), z the height above the bottom, and z_0 is the hydraulic roughness—a constant that increases with bottom roughness (Kim et al. 2000). A best fit line was calculated through seven velocity measurements located within the bottom 3.5 m of flow. Six consecutive U^* values were averaged to give a measure of U^* for each hour long zooplankton run. Only profiles with a regression coefficient of $R^2 > 0.8$ were accepted.

Statistical analysis

The degree by which zooplankton density differed between the benthic boundary layer and the water aloft was determined using a vertical density ratio (VDR), calculated by dividing the integrated abundance of zooplankton in the layer 1.75–5.25 mab by that in the 0–1.75 mab layer. The integrated values were calculated using interpolation weighted by inter-pump distances from the bottom to 7.5 mab. The effects of sites (A,B) and time (day, night) on VDR were tested using two-way ANOVA after verifying a homogeneity of variance using C, Cochran's statistics. Cross-taxa correlations were calculated using Pearson correlation between

individual samples. The occurrence of vertical gradients in the densities of zooplankton taxa was 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. Except for the manual calculation of the latter test, all the analyses were made using STATISTICA for Windows (V. 6.0, Statsoft Inc., Tulsa, OK, USA).

Results

Copepods dominated the zooplankton community, with adults and nauplii each comprising some 30% of the total zooplankton (average (\pm SD) $34\% \pm 12$ and $31\% \pm 10$, respectively). Other groups comprised less than 10% each (Table 2). The relative taxonomic composition was similar during the day and night (Table 2), in spite of a dramatic increase ($\times 3$ at the lowest pump, up to $\times 4.5$ higher in the water) in the total density at night (Fig. 2).

A sharp vertical gradient in zooplankton density was observed, with a depleted layer near the bottom and a fairly homogeneous distribution in the layer > 2.25 mab (Fig. 2). The bottom depleted layer had approximately the same thickness across the reef slope. The mean zooplankton density closest to the bottom was about a third that in the layer aloft (Fig. 2). The sharp gradient near the bottom prevailed in most runs in spite of large fluctuations in the total zooplankton density. The average overall VDR value, calculated for total zooplankton density, for all runs was 1.98 (SD = 0.88, $n = 48$) and was significantly different from 1.0 (t -test, $P < 0.001$). This VDR was not significantly affected by site and did not differ between diurnal and nocturnal runs (ANOVA, $F_{1,47} = 0.34$, $P = 0.56$ for site, $F_{1,47} = 0.34$, $P = 0.56$ for time, and $F_{1,47} = 0.009$, $P = 0.92$ for the interaction).

The average taxon-specific VDR values were significantly greater than 1.0 for all taxa except foraminifera and eggs (Table 2). VDR values of the latter species were not significantly different than 1.0, indicating a nearly homogeneous distribution. Eggs, foraminifera,

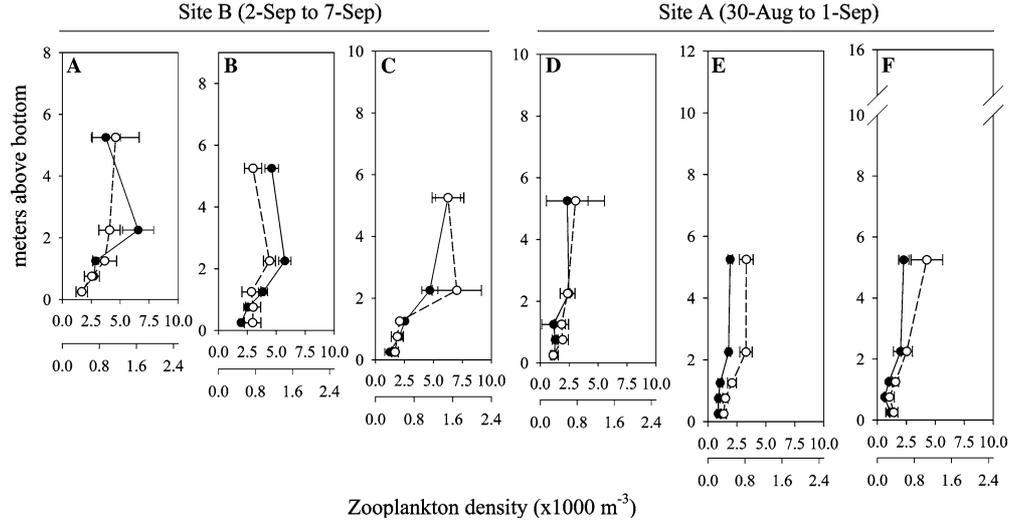
Table 2 Mean (\pm sd) density and VDR values of the taxonomic groups during the day and night. Densities were integrated for the 7.5 m column above bottom using interpolation weighted by inter-pump distances. $N = 27$ and 25 for the diurnal and nocturnal samples, respectively (19 and 13 for foraminifera)

Taxonomic group	Integrated density ($\# \text{ m}^{-2}$)		VDR		P (VDR \neq 1)		P gradient	
	Day	Night	Day	Night	Day	Night	Day	Night
Nauplii	2511 (1821)	7938 (4402)	2.28 (1.46)	2.2 (0.87)	***	***	***	***
Copepods	1761 (992)	7658 (5035)	2.08 (1.28)	2.46 (0.98)	***	***	***	***
Appendicularia	883 (656)	2075 (1183)	1.85 (1.10)	1.78 (0.68)	***	***	***	***
Mollusks	477 (309)	1847 (1018)	1.44 (0.51)	2.04 (0.90)	***	***	**	***
Eggs	172 (204)	1314 (806)	1.29 (0.97)	1.12 (0.74)	NS	NS	NS	NS
Polychaeta	121 (101)	1391 (1243)	1.76 (1.42)	3.38 (2.06)	*	***	NS	***
Foraminifera	165 (122)	195 (125)	0.89 (0.53)	1.60 (1.23)	NS	NS	NS	NS

Significance values are for t -test comparing the VDR values against a uniform distribution (VDR = 1.0) and for Page test for gradient
NS not significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fig. 2 Mean density (\pm SE) of zooplankton above the coral reef of Eilat during the day (open circle, lower scale) and night (filled circle, upper scale). Panels A–C and D–E are for samples taken at sites B and A, respectively, each representing a different bottom depth over which zooplankton was sampled. Panels bottom and top correspond to the reef bottom and sea surface, respectively



and polychaetes exhibited the largest variation in VDR (CV values of 0.69–0.8). Vertical gradients in the densities of Copepods, appendicularia, copepod nauplii, and mollusks were observed during the day (as indicated by Page test; Table 2; Fig. 3). At night, all taxa except eggs and foraminifera exhibited this distribution pattern.

The densities of copepods, nauplii, mollusks, appendicularia, and polychaeta, despite their very high variance ($CV > 0.99$), were highly and significantly correlated with one another (Table 3). Foraminifera were not correlated with any of the other taxa, while eggs exhibited an intermediate level of correlation with the other taxa ($r < 0.59$; Table 3). The inter-taxon cor-

relations also varied with distance above bottom (Fig. 4). While the correlation between strong swimmers (polychaeta and copepods) was high ($r > 0.8-0.9$) throughout the water column, the correlation between weak swimmers increased from $r = 0.4$ near the bottom to $r > 0.7$ at 1–2 mab (Kruskal–Wallis ANOVA, $H_{(4, n=15)} = 10.93$, $P < 0.05$). The correlations between passive taxa (eggs and foraminifera) were low and insignificant (Fig. 4), except for the significant correlation at 2.25 mab (Spearman rank order, $r = 0.39$, $P > 0.05$).

No significant correlation ($P > 0.1$) was found between VDR (both for total zooplankton and for individual taxa) and any of the following physical

Fig. 3 Mean (\pm SE) density of eight taxonomic groups above the coral reef of Eilat during the day (open circles, panels A–C) and night (filled circles, panels D–E). Panels A and D describe the distribution of strong swimmers (polychaeta and copepods, lower and upper scales, respectively), B, E of weak swimmers (nauplii and appendicularia, upper scales, mollusks, lower scales), and C, F of passive taxa (eggs and foraminifera)

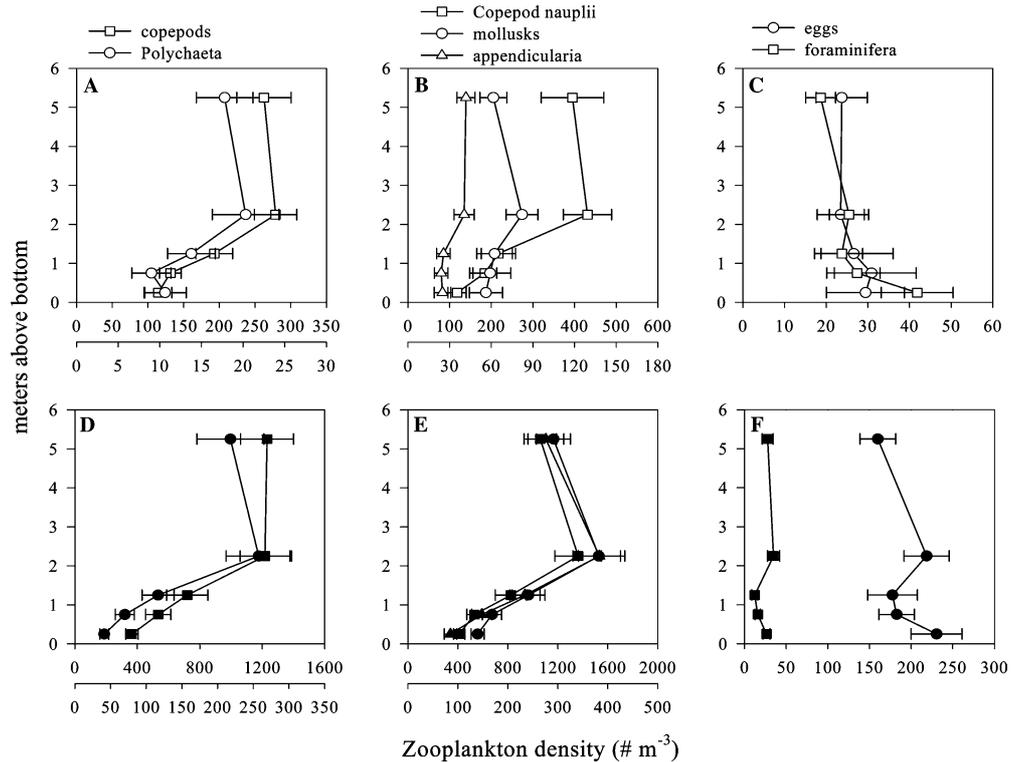


Table 3 Pearson cross-correlations between the densities of the different taxa in all our samples ($N=256$)

	<i>Foram</i>	<i>Eggs</i>	<u><i>Poly</i></u>	<i>Append</i>	<i>Mollusks</i>	<i>Nauplii</i>
<u>Copepods</u>	0.09 NS	<i>0.55</i> ***	<i>0.91</i> ***	<i>0.75</i> ***	<i>0.38</i> ***	<i>0.86</i> ***
Nauplii	0.10 NS	<i>0.48</i> ***	<i>0.78</i> ***	<i>0.75</i> ***	<i>0.78</i> ***	
Mollusks	0.21 **	<i>0.5</i> ***	<i>0.79</i> ***	<i>0.67</i> ***		
Append	0.07 NS	<i>0.59</i> ***	<i>0.66</i> ***			
<u><i>Poly</i></u>	0.12 NS	<i>0.39</i> ***				
<i>Eggs</i>	0.08 NS					

Numbers in italics indicates Pearson $r > 0.5$. Taxonomic groups are abbreviated as follows: foram-foraminifera, poly-polychaeta, append-appendicularia, nauplii-copepod nauplii. NS not significant. Different fonts indicating swimming ability (see Fig. 5): strong swimmers (underlined), weak swimmers (bold), passive (Italics) ** $P < 0.01$, *** $P < 0.001$

parameters: current velocity in the long-shore, cross-shore and vertical directions at different heights above bottom and U^* at 1 mab. Nor were there any apparent relationships between VDR and vertical shear in the flow.

Discussion

A well-defined layer, approximately 2 m thick, of depleted zooplankton was observed over the coral reef during both day and night (Fig. 2). Similar depletion was exhibited by taxa belonging to different phyla. Consequently, densities of different taxa were highly correlated. Such magnitudes of the inter-taxonomic correlations, with correlation coefficient values exceeding 0.75 (Table 3), are rarely found in the literature (e.g. Star and Mullin 1981; Greenblatt 1982; Wiebe et al. 1992). The near-bottom depletion, reported here based on microscopic counts, was corroborated by Yahel et al.

(this issue) based on total zooplankton biomass. Hence, the forces structuring the zooplankton community on the small spatial scale of our sampling (order of < 1 m) are general, rather than taxon-specific, but appear stronger for the mobile taxa. While the ultimate cause for the observed gradients is, most probably, bottom bound predation (Motro et al. this issue), two proximal mechanisms are possible—selective predation and zooplankton behavior.

That the VDR values were highest for the mobile taxa suggested that behavior (i.e. predator avoidance or bottom avoidance) was a likely explanation for the general near-bottom depletion of the better swimming zooplankton. Swimming ability was shown to affect small-scale patchiness in zooplankton (Gallager et al. 1996; Maar et al. 2003). To further explore the relationships between the zooplankton's swimming capability and depletion, we examined possible correspondence between VDR and swimming speeds reported for species belonging to the taxa we analyzed. The observed trend (Fig. 5) indicates a positive correlation between the two parameters. That is, stronger near-bottom depletion was found for taxa with faster "typical" swimming speeds. Stronger avoidance is expected for zooplankton that can swim better. Bottom avoidance at the coral reef is beneficial as it drives the animals away from a predator-rich environment (see Motro et al. this issue) and into a layer which is relatively enriched with phytoplankton (Yahel et al. 1998; Genin et al. 2002). Most of the zooplanktivorous predators in coral reefs are either benthic (e.g. corals, hydrozoans, crinoids) or forage near the bottom (e.g. damselfishes). Zooplankton behavior was similarly proposed to determine the horizontal distribution of various zooplankters across fjords (Kaartvedt 1993) and lakes (Wicklum 1999).

An additional cause for the observed zooplankton depletion near the bottom could have been actual predation by benthic predators. Zooplanktivory could have

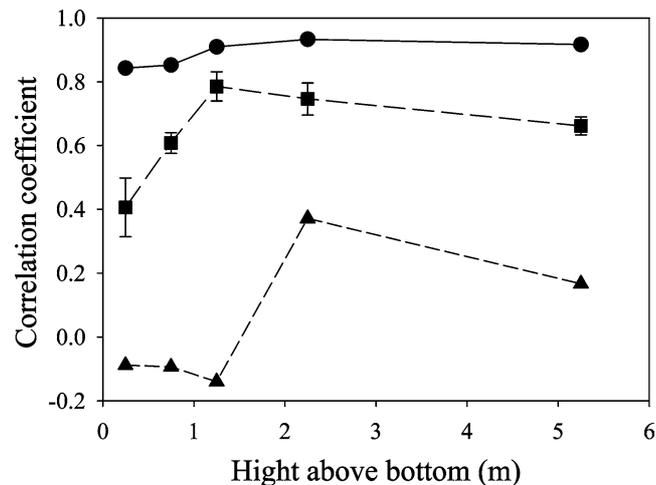


Fig. 4 Values of pair-wise inter-taxon correlation coefficient (Pearson r) at different heights above bottom for strong swimmers (copepods and polychaetes; full circles; $N=1$ Pairs per height), weak swimmers (copepod nauplii, appendicularia and mollusks; full squares; $N=3$ pairs) and passive plankton (foraminifera and eggs; full triangles $N=1$ pair)

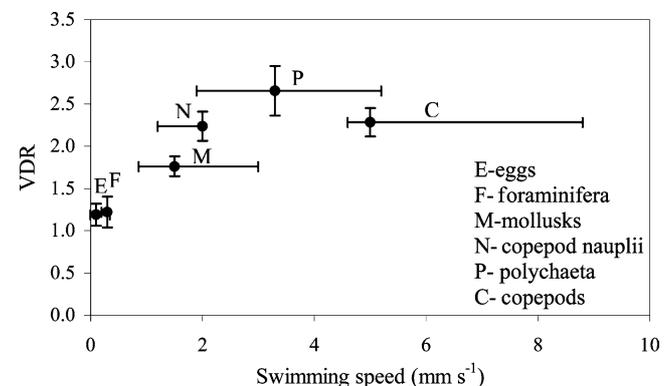


Fig. 5 The average (\pm SE) vertical distribution ratio (VDR) plotted against the taxon's published "typical" range (horizontal lines) of swimming speeds. The vertical lines (mean VDR \pm SE) cross the horizontal ones at the point indicating the median value of swimming speeds we found in the literature (see Methods)

been stronger on the more mobile taxa, as their motion should augment their visibility (O'Brien 1987 and reference therein) for fish and their encounter rate with sessile predators such as corals (e.g. Ohman 1988; Rothschild and Osborn 1988). During daytime, the probability of survival for *Artemia* tethered in the upper water layer was >1.5-fold higher than for *Artemia* tethered at the bottom layer (Motro et al. this issue).

Obviously, avoidance and actual predation could have both contributed to the observed near-bottom depletion. Our results cannot resolve between the two mechanisms. The close similarity between the diurnal and nocturnal gradients (Figs. 2, 3) can be considered surprising if predation was the major cause for the gradients. During daytime, most of the zooplankton predation is attributable to planktivorous fish that typically forage above the bottom, with some fish reaching the upper water column (Motro et al. this issue). During the night, zooplankton predation probably occurs mostly at the bottom, by corals and other sessile taxa. Although nocturnal fish forage in the water column aloft, their diet consists of much larger zooplankton than those sampled with our small pumps (Hobson and Chess 1978; Holzman and Genin 2003). Further support for the role of behavior is the lack of near-bottom depletion in eggs, which are readily consumed by diurnal fish (Hobson and Chess 1978; Hamner et al. 1988) but do not swim. However eggs cannot be considered a passive tracer, as their buoyancy may not be neutral (Ådlandsvik et al. 2001 and reference therein).

The vertical changes of the inter-taxon correlations (Fig. 4) could be attributed to differential affects of predation and avoidance. If bottom avoidance is a shared trait, it should increase the inter-taxon correlation of the swimmers. On the other hand, actual predation, which substantially varies in space and time, is expected to lower inter-taxon correlations. Accordingly, strong swimmers, the distribution of which is determined mostly by behavior, were highly correlated at all heights while weak swimmers were highly correlated only aloft, where predation is less intense. Passive taxa, the vertical distribution of which is unrelated to behavior, were weakly correlated throughout.

Over sandy bottoms, small (<2 mm) demersal zooplankton tends to remain within 1 m from the bottom at night (Alldredge and King 1985), forming an opposite gradient to that reported in this study. In some nonreef habitats, layers of high zooplankton densities are found just above the bottom also during the day (Barans et al. 1997; Kringel et al. 2003). A most likely explanation for the difference of the vertical patterns between reef and non-reef habitats is the relative scarcity of site attached zooplanktivorous fish and benthic invertebrates at the latter habitats (e.g. Fishelson 1971; Khalaf and Kochzius 2002). The near-bottom aggregations of zooplankton at sandy sites may be due to the protection from transient predators that forage aloft (Barans et al. 1997).

Our counts did not separate demersal from pelagic zooplankton. Demersal zooplankton are likely capable

of effective vertical migration. As reef residents, they are also likely to be well adapted to escape the strong bottom bound predation (Motro et al. this issue).

Despite of the different methods used, the general taxonomic composition found in this study was in agreement with other reports on resident reef zooplankton. Over coral reefs in the Indo-Pacific region copepod species were the dominant group (<40% in Sale et al. 1976; Porter et al. 1977), followed by larvaceans (~10% in Porter et al. 1977) or cumaceans and decapod larvae (~20 and 10%, respectively, in Sale et al. 1976). The small pumps we used probably excluded large zooplankton which could easily avoid the pump's inflow, rendering underestimated the densities of large zooplankton, which is commonly reported in studies where different sampling techniques are used (e.g., emergence traps in Alldredge and King 1977; light traps in Sale et al. 1976).

The lack of correspondence between the vertical zooplankton distribution and turbulence is noteworthy. One would expect mixing to homogenize the distribution of plankton, including zooplankton of the size we sampled (e.g. Farstey et al. 2002; Marr et al. 2003). The occurrence of high VDR values under intense mixing, with U^* values as high as 0.86 cm s^{-1} , indicates that the mechanisms creating and maintaining the benthic depletion layer, either behavior, actual predation, or both, are strong.

Benthic zooplanktivores appear to reside within a suboptimal habitat with respect to the density of their zooplankton prey. The correspondence between the zooplankton distribution and their swimming ability indicates that bottom avoidance contributes to the formation of depleted layer over the reef. Thereby, zooplankton behavior determines prey availability for benthic predators.

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