

## Diel pattern with abrupt crepuscular changes of zooplankton over a coral reef

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### Abstract

We studied zooplankton abundance and emergence patterns over coral reefs in the Gulf of Aqaba using high-resolution acoustics (multibeam sonar, FTV, 1.6 MHz, and WH600 ADCP, 614 KHz), emergence traps, and an underwater pump, supplemented with field observations on feeding behavior of zooplanktivorous fish. The zooplanktonic community over coral reefs is a complex and highly dynamic mixture of pelagic plankton advected into the reef, larvae and eggs released by benthic animals, and demersal plankton. At sunset ( $0 \pm 4$  min, mean  $\pm 95\%$  confidence interval) acoustic back-scattering intensity and zooplankton biomass started to increase rapidly. In contrast with this ascent, the predawn decline began much earlier during the dark ( $82 \pm 5$  min before sunrise) and terminated before sunrise. This light-dependent diel behavior was highly consistent throughout the year, regardless of seasonal and environmental changes. Smaller zooplankters ( $500\text{--}700 \mu\text{m}$ ) ascended first and demersal zooplankton accounted for most of the increase in zooplankton soon after sunset. Surprisingly, the emergence of zooplankton occurred while large schools of diurnal zooplanktivorous fish were still foraging in the water column. However, at that time, prey-capture efficiency by the fish is greatly reduced and corals had not yet expanded their tentacles, producing an optimal window of opportunity of low risk for emergence.

Diel vertical migration (DVM) is one of the most conspicuous features of zooplankton behavior, occurring in di-

verse zooplankton phyla, broadly distributed and common in many pelagic marine habitats (Ohman 1988, 1990; Pearre 2003). The dominant DVM pattern is a nocturnal ascent into the photic zone and a predawn return. Avoiding visual predation is considered the ultimate cause of this behavior (Ohman 1988; De Robertis 2002; Pearre 2003). DVM is also a common behavior of the demersal plankton residing in the bottom during part of the day (Mees and Jones 1997).

Coral reefs are situated within the photic zone. Hence, the adaptive value gained by a zooplankter that leaves its shelter and ascends into the reef water column is not well understood. Nevertheless, intense DVM was reported to be a major characteristic of demersal plankton communities at coral reefs (Alldredge and King 1977; Jacoby and Greenwood 1989; reviewed by Heidelberg et al. 2004). Possible benefits associated with the ascent to the water column may include encountering more food higher off the bottom (Yahel et al. 1998, 2002, in press), avoiding reduced oxygen levels in the benthic boundary layer, ease in locating a mate, dispersal, and avoiding nocturnal benthic predators (e.g., corals; Heidelberg et al. 2004 and references therein). As in other marine habitats, the nocturnal ascent in coral reefs is interpreted as a mechanism for avoiding intense daytime predation by the highly abundant visual planktivorous fish (Hamner et al. 1988; Motro et al. in press; Rickel and Genin in press). Yet,

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Table 1. Summary of major characteristics of the sampling instruments used.

Instrument	Temp-oral resolution	Vertical resolution	Sampling unit size	Particle size range	Advantages	Shortcomings
1.6-MHz FTV (multibeam sonar) custom made	<1 s	7.7 mm	<0.3 m <sup>3</sup>	≥1 mm	Track and count individual scatterers, water-column profile (<5 m)	Scatterers' identification unknown; limited sampling volume
614-kHz ADCP (acoustic doppler current profiler) RD Instruments, USA	<1 s	0.5 m		Not well defined (Integrates echo intensities in the insonified volume)	Water column-profile (<40 m); long-term deployments	Scatterers' identification unknown; scatterers' density unknown
High-capacity underwater pump (14 m <sup>3</sup> h <sup>-1</sup> )	1 h	1 m	14 m <sup>3</sup>	>0.1 mm	Actual sampling provides particle composition and identity, size distribution, and concentrations	Coarse temporal resolution, labor-intensive analysis, biased sampling (avoidance)
Emergence traps	1 h	1 m	0.25 m <sup>2</sup>	>0.1 mm		

in contrast with many marine habitats, the near-bottom zone at the reef is characterized by high concentrations of sessile zooplanktivores (such as the stony corals themselves), most of which possess a nocturnal feeding mode (McFarland et al. 1999; Levy et al. 2003). Indeed, near-bottom predation was suggested to be the ultimate factor shaping the spatial and temporal distribution of zooplankton in coral reefs (Yahel et al. in press; Holzman et al. in press). If true, the ascent and return of demersal reef plankton, as well as the release of larvae and eggs by reef dwellers, are expected to be closely related to times of reduced predation pressure (De Robertis 2002).

Studying zooplankton at the vicinity of coral reef bottoms is technically challenging. Traditional sampling methods, such as towing a net from a boat, lack the proper temporal resolution (Table 1) and are often hampered by the rough reef-bottom topography. Moreover, any sampling method carries its inherent shortcomings and biases (Wiebe and Benfield 2003). To overcome these obstacles, the current research used three complementary sampling strategies: (a) innovative, nonintrusive acoustical methods; (b) direct water sampling, using stationary underwater pumps and pump arrays; and (c) zooplankton traps. Our goal was to resolve the exact timing of crepuscular zooplankton increase in the reef's water in relation to plankton emergence from the reef and the activity of planktivorous fish and corals.

## Methods

*Study site*—The study was carried out at the fore reef of the fringing coral reef in front of the Steinitz Marine Laboratory of Eilat, Gulf of Aqaba, Red Sea (Fig. 1, 29°30'N, 34°55'E). General meteorological and oceanographic conditions at the study site were described by Reiss and Hottinger (1984). The reef community was described by Fishelson (1970) and Benayahu and Loya (1977), and the fish community was described by Khalaf and Kochzius (2002). The

neritic and pelagic zooplankton communities in the northern Red Sea were partly described by Vaissiere and Seguin (1984), Echelman and Fishelson (1990), Khalil and El-Rahman (1997), and Farstey et al. (2002). Summarized briefly, the Gulf of Aqaba is a desert-enclosed sea in which the temperature of the water ranges between 20°C in February to 26–28°C in August–September. Sea conditions at the study sites were relatively calm, with <1-m tidal range, <20-cm s<sup>-1</sup> currents, and <0.3-m waves (Yahel et al. 2002). Conditions at the gulf are generally oligotrophic (chlorophyll concentration 0.05–0.8 μg L<sup>-1</sup>) with nanomol L<sup>-1</sup> concentrations of dissolved nitrogen and phosphorous during the stratification period (May–October). The pelagic zooplankton community is dominated by small calanoid copepods (<2 mm; Farstey 2001; Sommer et al. 2002), 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). Stony corals dominate the coral reefs, along with hydrozoan corals (*Millepora* spp.), soft corals, encrusting algae, and other invertebrates. Due to the steep topographic relief of the rift valley, the sun descends behind the nearby mountains >1 h before it sets below the horizon at the study site. Similarly, the sun rises above the eastern mountain rim of the Gulf >1 h after it rises above the horizon. Throughout the text, sunset and rise times refer to the time the sun sets and rises over the horizon, as defined by the Astronomical Applications Department, U.S. Naval Observatory (<http://aa.usno.navy.mil/data/>).

*General methodological aspects*—Acoustic instruments allow noninvasive sampling of the plankton with high temporal and spatial resolution and extremely large numbers of samples. Large plankton that normally avoid traditional sampling methods are better represented by acoustical methods (Wiebe and Benfield 2003). The fundamental measurement used in most acoustic studies is volume backscattering (or

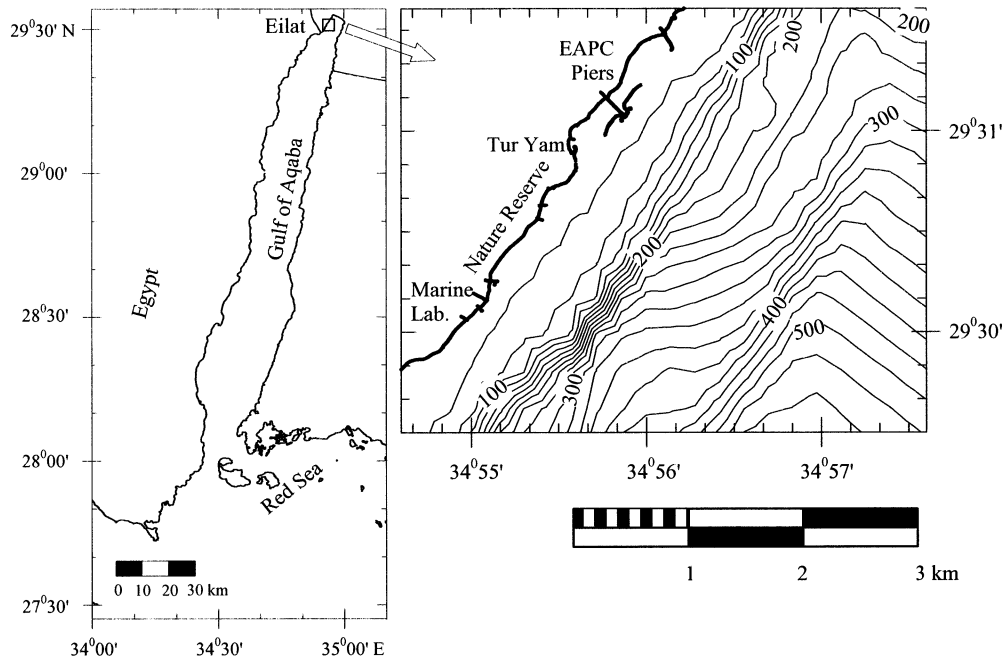


Fig. 1. Map of study site. Gulf shoreline data (right panel)—courtesy of Rich Signell (NOAA-NGDC Coastline Extractor, <http://rimmer.ngdc.noaa.gov/mgg/coast/getcoast.html>). Detailed bathymetry (left panel) was compiled from data collected by the authors with M. Reidenbach and D. Fong ([http://socrates.berkeley.edu/~mattr/Bathymetry\\_Maps.html](http://socrates.berkeley.edu/~mattr/Bathymetry_Maps.html)) and by A. Rivlin and the Steinitz Marine Laboratory staff.

echo integration)—the integration of the energy from all individuals in a given insonified volume (Wiebe and Benfield 2003). This approach was applied here, using a commercial acoustic current meter profiler (600 kHz ADCP, Table 1). This versatile instrument was used to obtain large numbers of diel cycles over the entire water column in several localities along the reef bottom. An alternative approach uses acoustic methods to track and quantify individual particles. The FTV, 1.6-MHz echo sounder for in situ zooplankton studies (Table 1, Jaffe et al. 1995) is a multibeam imaging

system, designed to count and track individual targets (scatterers) in three-dimensional space. Major advantages of the FTV are higher acoustic frequency and high spatial and temporal resolution. The shortcomings are the small sampling volume (Tables 1 and 2) and the logistics involved in its operation.

A major limitation of all acoustic methods is a lack of target (scatterer) identification. To overcome this problem, an underwater pump was operated in the vicinity of the FTV. The time resolution of this method was, however, rather low,

Table 2. Details of the deployment of 1.6-MHz FTV multibeam sonar and the WH-600 ADCP.

A. FTV						
Dates	Bottom depth (m)	Transducer location (mab)	Acquisition delay (ms), distance (m)	Range analyzed (mab)	Volume analyzed (m <sup>3</sup> )	Sampling interval (min)
14–30 Oct 98	9	3.6	12, 0.92	2.7–0.5	0.082	0.5
13–16 Oct 02	16	3.6	12, 0.92	2.7–0.7	0.067	0.5
B. ADCP						
Dates	Bottom depth (m)	Bin width (m)	Ensemble interval (min)	Pings per ensemble	Bins analyzed (bin number (mab))	
16 Feb–04 May 00	17	1	10	1000	1 (2), 6 (7), 13 (14)	
18 Sept–23 October 01	28	1	10	1000	12 (13)	
13–16 Oct 02	16	0.5	2	460	3 (2.4)	

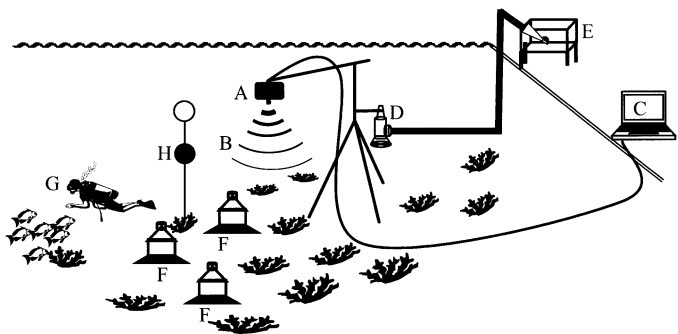


Fig. 2. A schematic description of the plankton and environmental sampling setup at the coral reef (October 1998, not plotted to scale): (A) FTV transducer attached to a tripod and transmitting toward the bottom. (B) The insonified volume. (C) FTV data output onshore. (D) The submersible pump, with its intake apparatus at depth of the center of the insonified volume. (E) Pump outlet and zooplankton filtration point on shore. (F) Emergence traps for demersal plankton. (G) Fish activity recorded by Scuba divers. (H) Electromagnetic current meter (S4).

as long sampling duration was required to obtain a reliable sample size (Table 1). Demersal plankton caught by emergence traps supplied information on the unique behavioral patterns of reef-originated zooplankton. A major difficulty of all direct sampling methods is associated with the unknown bias introduced by selective avoidance (Wiebe and Benfield 2003).

*High-resolution dynamics of acoustics and zooplankton*—To attain high-resolution records of zooplankton diel dynamics over the reef, the FTV sonar was used at high sampling frequency (0.5-min intervals, Table 2) that allowed us to study scatterer concentration in a  $\sim 2$ -m water layer starting  $\sim 0.5$  m above bottom (mab). The acoustic sampling was supplemented by a suit of biological and physical measurements, including zooplankton sampling next to the sonar, timing of the zooplanktivorous fish activity, currents, water temperature, and solar radiation (Fig. 2).

*Acoustic measurements by a multibeam sonar (FTV)*—At 14–30 October 1998, the FTV was deployed  $\sim 80$  m offshore with its transducer facing down, attached to a tripod 3.6 mab over a reef bottom of 9-m depth (Fig. 2A, Table 2). An acquisition delay of 12 ms was employed, so that the insonify volume (Fig. 2B) started 0.9 m away from the transducer, that is, 2.7 m above bottom. Sampling distances exceeding 3.1 m (0.5 mab) from the transducer were excluded from analysis due to the interference of the echo from protruding corals. A portion of 8 cm of the insonifying volume (1.42–1.50 mab) exhibited an excessive electronic noise and was also omitted. As a consequence, the final insonifying volume available for analysis was  $0.082 \text{ m}^3$ . Signal processing was carried out as in Jaffe et al. (1995) using a threshold of  $-95$  dB.

*Plankton composition*—To assess the zooplankton abundance and community composition in the same water volume sampled by the FTV, a high-capacity submersible pump

(Submersible Non-clog Pump, 220 V,  $14 \text{ m}^3 \text{ h}^{-1}$ , Tsurumi Manufacturing) was deployed next to the FTV. The pump was positioned with its intake at 1.5 m above the bottom (Fig. 2D), within the height of the insonifying volume, but outside of the FTV field of view. The pump was powered from shore using underwater cables. A long 50-mm diameter polyvinylchloride pipe delivered the water to the shore (Fig. 2E), where the water was filtered through a 1-m-long, 20-cm-diameter, 100- $\mu\text{m}$  mesh sleeve. To avoid excessive pressure on trapped zooplankton, the net was fully submerged in a large tank. The pumping rate was measured prior to each sampling. Three periods were sampled: day ( $-360$  to  $-210$  min from sunset), dusk ( $-10$  to  $+60$  min from sunset), and evening (60–180 min from sunset).

Each sample was fractionated through a column of three mesh sizes: 1,000, 710, and 500  $\mu\text{m}$  and fixed in 4% buffered-formalin solution in seawater. Zooplankton of each fraction were 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  $>300$  individuals was attained. Typical demersal plankton included primarily cumaceans, tanaids, hyperiid amphipods, and isopods. Meroplankton was composed mostly of fish eggs, zoea, and echinoderms; and other planktonic forms were categorized as copepods, other crustacean, polychaetes, chaetognaths, tunicates, and mollusks.

*Timing the emergence of demersal plankton*—To study the timing of demersal plankton emergence from the reef bottom into the water column, we used flexible pyramid-shape traps (modified after Porter and Porter 1977, Fig. 2F). Traps were made of 100- $\mu\text{m}$  white nylon mesh with a 20-cm-wide skirt made of strong and flexible tarpaulin fabric. A metal chain attached as weights to trap and skirt margins insured good sealing to the bottom and prevented contamination by open-water plankton (Porter and Porter 1977). The interior base (sampling area) was square-shaped, covering a bottom area of  $0.25 \text{ m}^2$ , and trap height was 90 cm. The bottom of the replaceable cod end (collection cup) was equipped with an inverted funnel to prevent the return of trapped organisms. Both net and cod end were attached to small floats, keeping the trap in a taut, upright position.

Three traps were deployed concurrently with the last 4 d of the FTV deployment (26–29 October 1998) several meters south of the FTV tripod, on a 8.5–9-m bottom depth. Each trap was used to continuously sample the same plot during a full diel cycle, divided into four sampling durations: daytime, dusk, evening, and night. Every morning, the three traps were haphazardly relocated. At the end of each sampling duration, scuba divers disconnected and sealed the cod ends, and a new cod end was installed. Daytime samples were terminated a few minutes before sunset, and a 1-h dusk sampling was immediately initiated. The evening samples (2 h) were initiated by the termination of dusk samples and terminated  $\sim 3$  h after sunset, when night sampling began. Samples were transferred to the laboratory and preserved in 4% buffered formalin. Prior to microscopic examination, samples were filtered on a 500- $\mu\text{m}$  net. The  $>500$ - $\mu\text{m}$  content was microscopically enumerated, as described above for the pump samples, but with no further size fractionation.

*Timing the activity of zooplanktivorous fish*—The foraging activity of zooplanktivorous fish was studied in situ concurrently with the last 4 d of the FTV deployment (26–29 October 1998). Observations were made by scuba divers at the vicinity of the FTV tripod (7–11 m in depth), where large schools of zooplanktivorous fish were commonly found. Divers recorded the proportion of actively foraging fish for schools of five of the most conspicuous zooplanktivorous reef fish: *Pseudanthias squamipinnis*, *Dascyllus marginatus*, *Chromis* spp., *Abudefduf saxatilis*, and *Caesio* spp. Each sampling session started 30 min before sunset at full daylight and terminated in the darkness, 30 min after sunset. Fish abundance during the first 15 min of the observation period served as a baseline (100%) for subsequent estimates of the percentage of actively foraging fish, recorded every 2–5 min for each species separately. A similar estimate was also carried out for the schools of emerging nocturnal zooplanktivorous fish with reference to the school size by the end of the observation period. These schools were dominated by cardinalfish (*Apogon* spp.) and sweepers (*Pempheris* spp.). The precision of the estimates was  $\pm 20\%$ .

*Environmental parameters*—Light energy ( $\text{W m}^{-2}$ , global solar radiation, Eppley PSP radiometer) and wind were measured throughout the sampling period by an automated weather station located on the roof of the marine lab,  $\sim 200$  m west of the experimental area at sea. Global solar radiation at the reef was measured concurrently with fish observation and demersal plankton traps (26–29 October 1998). An underwater light sensor (Li-Cor 185A) was fixed at a depth of 9 m in an upright position 100 m north of the FTV tripod. Manual readings of the photon flux ( $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ) were carried out every 2 min, starting 60 min before sunset, until darkness prevailed. Ambient currents and water temperature were measured with an electromagnetic current meter (S4, InterOcean) moored nearby at the FTV's transducers height (5.1 mab) over a 10-m bottom depth (Fig. 2H). Sun and moon data for the study site (time of rise, set, altitude, azimuth, twilight time, and the illuminated fraction of the moon disk) were obtained from the web site of the Astronomical Applications Department, U.S. Naval Observatory (<http://aa.usno.navy.mil/data/>).

*High-resolution diel dynamics over long time periods*—For continuous monitoring of the dynamics of scatterers at the coral reef, we used the acoustic backscatter intensity (ABI) measured by a standard 614-KHz Acoustic Doppler Current Profiler (ADCP, WH-600 RDI). The ADCP was deployed looking upward on the reef bottom at various localities in front of the Steinitz Marine Laboratory for time spans of 4–78 d, from August 1999 to October 2002. To avoid contamination of the acoustic signal with near-surface air bubbles and near-bottom resuspended sediments (Wilson et al. 2002), we chose to focus on ADCP records from mid-water bins.

Due to the high variation of overall ABI in long deployments (see Results), ABI was normalized within each bin as *normalized ABI* =  $(x_{i,d} - X_d)/SD_d$ , where  $x_{i,d}$  is ABI of the  $i$ th ensemble in the  $d$ th date,  $X_d$  is the average ABI of all

ensembles on the respective day, and  $SD_d$  is the respective standard deviation.

ADCP's ABI and FTV's target counts were compared during October 2002 (Table 2). The two instruments operated concurrently for three diel cycles (13–16 October 2002) to sample the same water body. The FTV setup was similar to the one used in October 1998 (Fig. 2) except that the coral effect extended to a higher elevation. Therefore, the range  $>2.92$  m from the transducer (0.7 mab) was excluded from the analysis. As in 1998, a region with excessive electronic noise (1.23–1.38 mab) was excluded from analysis and, thus, the final insonifying volume available for analysis was  $0.067 \text{ m}^3$  (Table 2). For the comparison, we used a single ADCP bin, centered at 2.4 mab within the upper portion of the FTV insonifying volume. The ADCP signal ( $230 \text{ pings min}^{-1}$ ) and FTV frames ( $2 \text{ min}^{-1}$ ) were averaged into corresponding 2-min intervals.

*Environmental parameters*—ADCP readings were supplemented with global solar radiation measurements ( $\text{W m}^{-2}$ , Eppley PSP radiometer) at 10-min intervals. Until the end of 2000, the radiometer was positioned on the roof of the Steinitz Marine Laboratory building, and as of January 2001, the radiometer was transferred to the city of Eilat,  $\sim 10$  km north of the study site. Currents, temperature, and tide (pressure) data were recorded by the ADCP concurrently with each ABI record. Sun and moon data were obtained from the website of the U.S. Naval Observatory, as previously discussed.

*Statistical analysis*—The statistical analyses were carried out using STATISTICA, version 6 (data analysis software system, StatSoft) and MATLAB release 13 (MathWorks). PRIMER version 5.22 (Primer-e) was used for the multivariate analysis of the zooplankton composition.

*Timing the onset and completion of nocturnal migration*—In order to determine the timing and duration of the crepuscular increase and decrease of the acoustic-signal intensity (hereafter ISI and DSI, respectively) and their relation to environmental factors, objective and unambiguous criteria were required. Examination of the signal in several temporal resolutions (0.5, 2, 10 min) indicated that the rate of change was usually  $\geq 10$  min, and therefore, all subsequent analyses of the timing of the ISI and DSI in signal intensity were carried out over integrated 10-min intervals. Our calculation relied on the sign of the first derivative of the 10-min integrated time series. For the determination of the onset of ISI and DSI, single outliers were smoothed using a three-points moving median. The algorithm we used defined the onset of ISI at the middle of the earliest 10-min time interval that was associated with a positive (smoothed) derivative and was followed by at least two subsequent positive derivatives. The time frame for seeking the onset of ISI was limited to  $-30$  to  $+120$  min from sunset. Similarly, the completion of ISI was defined as the middle of the last 10-min interval associated with a series of  $\geq 3$  positive smoothed derivatives in the same series. Onset of DSI and DSI completion were defined by the reversed algorithm (time frame  $-120$  to  $+30$

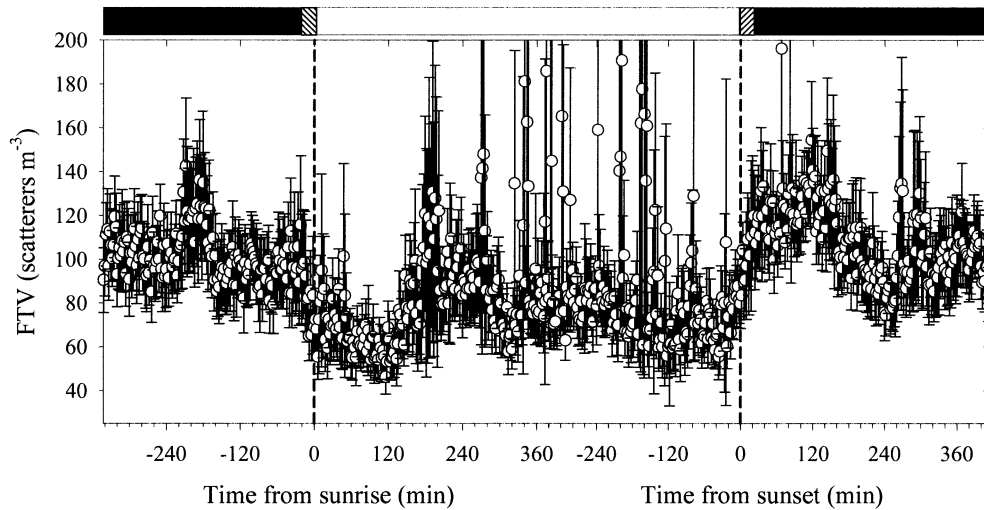


Fig. 3. The concentration of scatterers recorded with a down-looking 1.6-MHz FTV sonar in the water 0.5–2.7 m above bottom in front of the Steinitz Marine Biology Laboratory of Eilat (14–29 October 1998). Each point indicates the average over 2-min intervals ( $\pm 95\%$  confidence interval for the mean). The dashed vertical line indicates times of sunrise and sunset. Darkness, civil twilight, and daytime are denoted in the horizontal bar above the chart as black, hatched, and white shading, respectively.

min from sunrise considering negative smoothed derivatives).

## Results

*Diel pattern of the acoustic signal*—A consistent daily cycle in the scatterers' concentration above the reef of Eilat was evident in the 2 weeks of high-resolution FTV measurements carried out in October 1998 (Fig. 3). This daily cycle was clearly light dependent. The density of scatterers increased rapidly at sunset, reaching a maximal level  $\sim 30$  min after sunset. A second peak of scatterers' abundance was evident in the second half of the night. The scatterers' abundance began to gradually decrease about 3 h before sunrise with a sharper, but not consistent, decrease during the predawn hour. The lowermost level of scatterers' concentration was attained 2 h after sunrise. Daytime concentration was generally lower ( $82 \pm 105$  individuals  $m^{-3}$ , mean  $\pm 1$  SD) in comparison with nighttime concentration ( $105 \pm 77$  individuals  $m^{-3}$ ) and much more variable (daytime and nighttime coefficients of variance were 128% and 73%, respectively), with considerable spikes of up to 160 scatterers in the insonifying volume ( $\sim 2,000$  scatterers  $m^{-3}$ ). In a comparison of the FTV scatterer counts to the ABI measured by an ADCP, the same diel pattern was reconstructed (Fig. 4), and the two (normalized) signals were significantly correlated (Spearman  $r = 0.65$ ,  $p < 0.001$ ).

A light-dependent daily pattern with an abrupt increase at sunset and a predawn decrease was also evident in each day of the long-term acoustic backscatter intensity records made with the ADCP (Fig. 5A,B). The diel cycle was highly consistent throughout the year regardless of seasonal and environmental changes. For example, the daily average ABI increased consistently during spring 2000 ADCP deployment

(Spearman  $r = 0.84$ ,  $p < 0.001$ ) and decreased during the first half of the fall of 2001 (Spearman  $r = -0.74$ ,  $p < 0.001$ ). Despite a considerable variability in overall ABI, as well as in the fine details of the daily pattern (e.g., Fig. 5E), the major features of the diel cycle were remarkably consistent, as indicated by the low variability associated with the normalized 10-min means (Fig. 5A,B). The diel pattern shown in the two examples presented in for the spring of 2000 and the fall of 2001 was almost indistinguishable from those recorded in several other ADCP deployments located at various depths along Eilat's reefs (e.g., September 1999, December 2000–January 2001, November–December 2001, and February–April 2002, data not shown).

*Timing of ISI and DSI*—On average, the nocturnal ISI started exactly at the time of the regional sunset ( $0 \pm 19$  min, 95% confidence interval for the mean = 4 min), when ambient illumination at the reef bottom was relatively high ( $\sim 1.5 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ). The ISI lasted about 60 min (Table 3). In contrast, the morning DSI occurred much earlier during predawn hours, starting  $82 \pm 35$  min before sunrise and terminating at darkness,  $-31 \pm 44$  min before sunrise. Despite the high consistency of the diel behavior, a considerable day-to-day variability was evident in the exact timing of the onset of ISI and DSI, their duration, and time of completion (Table 3, Fig. 6; see also Figs. 3 and 5). During the measurement period, there was no evidence for a seasonal trend in the timing of ISI and DSI; nor have we found any evidence for an association between any of these parameters and moon phase (data not shown). Cloudy days occurred only five times (during the February–May observation period); in four of them, the onset of the nocturnal ISI was relatively late (after sunset).

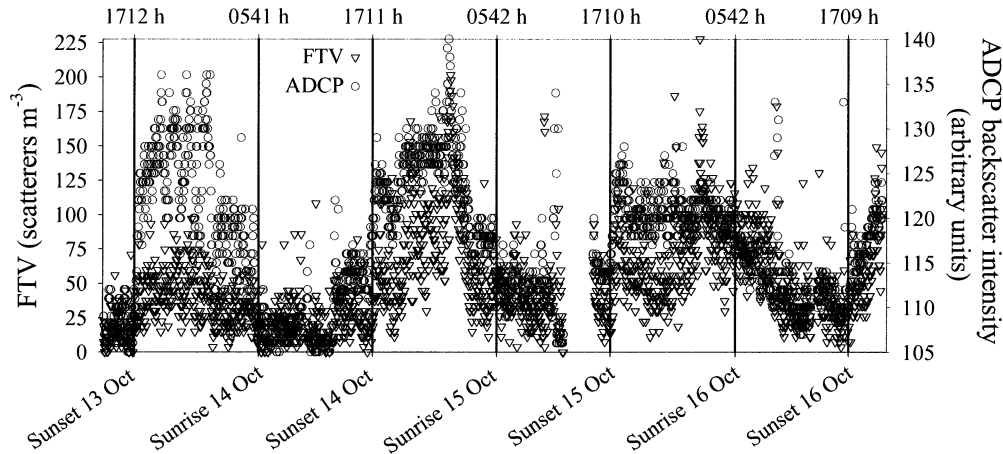


Fig. 4. Comparison between the 1.6-MHz FTV counts and the WH600 ADCP backscatter intensity (raw data) during three daily cycles (13–16 October 2002). The two instruments were deployed in front of the Steinitz Marine Biology Laboratory of Eilat ( $\sim 8$  m apart) to probe approximately the same water body ( $\sim 2$  mab,  $\sim 13$  m depth). Sunset and sunrise times are denoted on the upper axis.

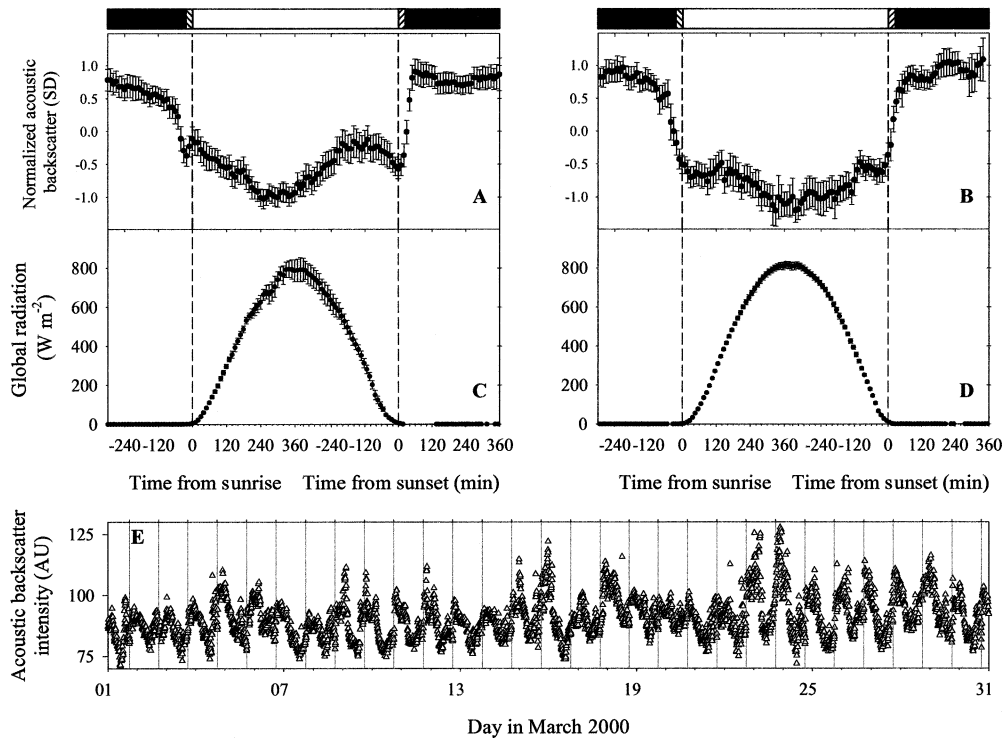


Fig. 5. Acoustic backscatter intensity and light measurements at the coral reef of Eilat. (A) Averages of normalized ABI measured by a WH600 ADCP ( $\pm 95\%$  confidence interval) over 78 daily cycles during the spring bloom (16 February–04 May 2000). Presented data are from a single bin (7 m above bottom, 10 m below surface). (B) As in A, but for 35 diel cycles during the end of summer stratification (18 September–23 October 2001) at a deeper site (13 m above bottom, 15 m below surface). (C) Averaged surface global radiation of 16 February–04 May 2000 ( $\pm 95\%$  confidence interval). (D) As in C, but for 18 September–23 October 2001. (E) A 1-month (01–31 March 2000) example of the raw ADCP data (summarized in A) showing day-to-day variability. Dashed vertical lines denote sunset and sunrise in A–D and sunset only in E. Darkness, civil twilight, and light-time are denoted in the horizontal bar above the chart as black, gray, and white shading, respectively.

Table 3. Statistics for the timing of onset, completion, and duration of the nocturnal increase (ISI) and morning decrease (DSI) of the acoustic backscatter intensity recorded in the long-term ADCP deployments during spring 2000 and fall 2001 (see Methods for definitions). Data presented are mean  $\pm$  SD and (median).  $p$  values are for Mann–Whitney  $U$ -test of the differences between the medians of the spring and the fall ( $H_0$ : no difference). NS, not significant.

Date	$n$	Increase of signal intensity (ISI)			Decrease of signal intensity (DSI)		
		Onset (min of sunset)	Duration (min)	Completion (min of sunset)	Onset (min of sunrise)	Duration (min)	Completion (min of sunrise)
Feb–May 00	78	3 $\pm$ 20 (7)	60 $\pm$ 31 (60)	63 $\pm$ 29 (61)	–81 $\pm$ 39 (–94)	52 $\pm$ 33 (40)	–29 $\pm$ 46 (–27)
Sep–Oct 01	35	–7 $\pm$ 17 (–5)	51 $\pm$ 30 (51)	58 $\pm$ 31 (50)	–85 $\pm$ 27 (–92)	51 $\pm$ 35 (40)	–34 $\pm$ 41 (–34)
$p$ -Values		<0.01	NS	<0.05	NS	NS	NS
Grand average	113	0 $\pm$ 19 (1)	60 $\pm$ 31 (50)	59 $\pm$ 30 (59)	–82 $\pm$ 35 (–94)	52 $\pm$ 34 (40)	–31 $\pm$ 44 (–39)

*The nocturnal increase in scatterers' density*—The most conspicuous feature of the diel cycle recorded by both the FTV (Figs. 3 and 4) and the ADCP (Fig. 5A,B,E) was the abrupt increase at dusk (Fig. 5A,B). The decrease in signal intensity toward dawn exhibited higher day-to-day variations in comparison with the increase at sunset (Fig. 7 insert, and see following). A comparison of the average first derivative of the ADCP's records at several elevations above the bottom (Fig. 7) indicated a directional propagation (or ascent) of the scattering intensity (or scatterers' concentration) from the bottommost layers (2 mab) toward the uppermost layers (14 mab, 2 m below surface), at an approximate rate of 1.1 cm s<sup>–1</sup> (Fig. 7A). The rate of signal increase accelerated in

the first 30 min after sunset and then slowed down in the following 30 min (Fig. 7). Unlike reports from other localities (Kringel et al. 2003), we did not observe a defined scattering layer ascending from the reef bottom. Instead, we observed a gradual increase in the acoustic backscattering intensity spreading throughout the water column (Fig. 7B).

*Zooplankton abundance and composition in the water column*—The abundance of zooplankton (>500  $\mu$ m) in samples obtained concurrently with the FTV deployments in October 1998 demonstrated low daytime abundance (average 9  $\pm$ 9 individuals m<sup>–3</sup>) of all the examined fractions (Fig. 8B). In contrast, a sharp increase (greater than fourfold) was observed at dusk, with most of the concentration increase observed for the 500–710- $\mu$ m fraction (from 7  $\pm$ 6 individuals m<sup>–3</sup> at daytime to 30  $\pm$ 31 individuals m<sup>–3</sup> at dusk, Fig. 8B). The abundance of larger zooplankters (>710  $\mu$ m) increased only >60 min after sunset when complete darkness prevailed. At that time, the abundance of all size fractions (total 59  $\pm$ 42 individuals m<sup>–3</sup>) was greater than sixfold that of the daytime concentration (Fig. 8B).

The composition of reef zooplankton underwent considerable shifts during the transition from daylight to twilight to darkness (one-way analysis of similarity  $R = 0.546$ ,  $p < 0.001$ , Tables 4 and 5). Relatively high abundance of 500–710- $\mu$ m copepods (37%) and low abundance of 500–710- $\mu$ m fish eggs characterized the reef zooplankton during the daytime. Small pelagic tunicates were also relatively abundant (18%). Organisms >710  $\mu$ m were nearly absent from daytime samples (Table 5). At dusk, demersal forms made their first appearance along with an order-of-magnitude increase in the abundance of fish eggs, chaetognaths, polychaetes, veligers, and planktonic mollusks (Tables 4 and 5). Interestingly, the abundance of copepods of all size fractions was reduced in the dusk samples in comparison with both day and night samples, but a reliable test of this trend was precluded by the small sample size. The transition to nighttime conditions was characterized by a fivefold increase in the 500–710- $\mu$ m copepods and a further (greater than fourfold) increase in the abundance of 500–710- $\mu$ m zoae and other demersal crustacean. However, the most remarkable shift was evident for the larger zooplankters (>710  $\mu$ m), many of which increased their abundance by more than an order of magnitude (e.g., copepods, zoea, tunicates, and polychaetes; see Table 5, part C).

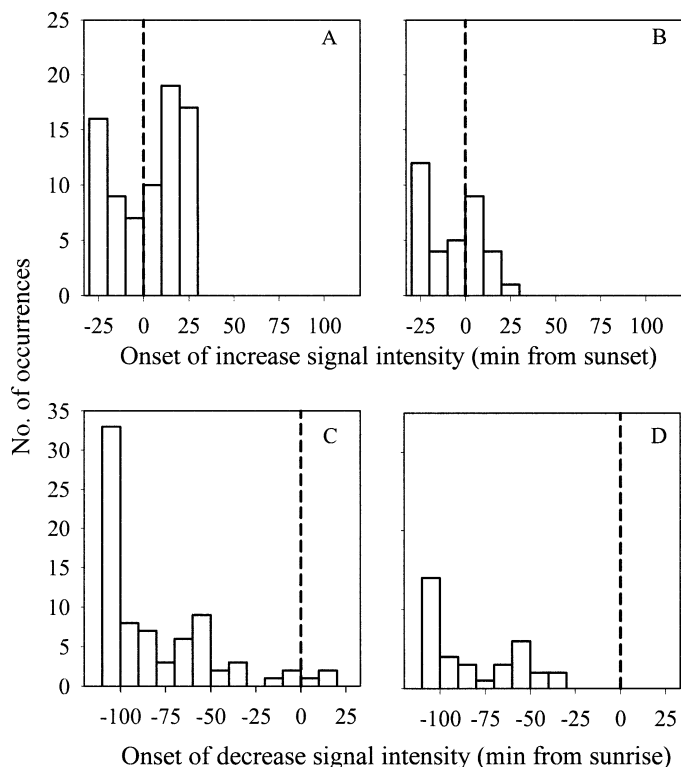


Fig. 6. Frequency distribution of the onset of increase (ISI) and decrease (DSI) of acoustic-signal intensity (see Methods) during ADCP deployment in the spring of 2000 (A, C,  $n = 78$ ) and the fall of 2001 (B, D,  $n = 35$ ).



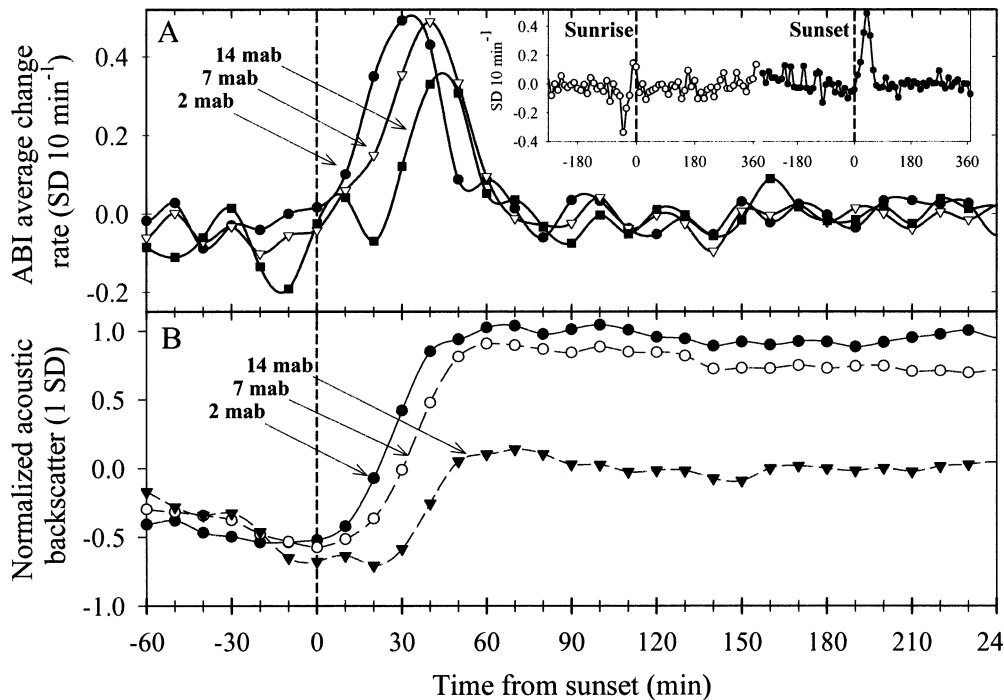


Fig. 7. (A) Average rate of change of the acoustic backscatter intensity (ABI) at three heights above the reef bottom during the 78 d presented in Fig. 5A for the 6th ADCP bin (7 m above the bottom, mab). The first derivative of the ADCP normalized data was calculated for bins 1, 6, and 13 (corresponding to 2, 7, and 14 mab, respectively), and thus the rate units are in 1 standard deviation (SD) per 10 min (the sampling interval). The insert presents the entire average diel cycle. The error bars were omitted for clarity (the average 95% confidence interval was 0.10 SD for bins 1 and 6 and 0.12 SD for bin 13). (B) Normalized acoustic backscatter intensity (ABI) of the same bins as in A.

**Demersal zooplankton emergence**—Emergence traps placed on the reef bottom during the hours of light and up until sunset were almost empty of zooplankton (Fig. 8C). In sharp contrast, traps deployed during dusk contained 10s of zooplankters as well as eggs and larvae. Polychaetes (27%), zoea (22%), and copepods (10%) dominated the dusk catch, but typical demersal forms, such as cumaceans, mysids, tanaids, ostracod, isopods, and hyperiid amphipod, as well as fish egg, chaetognaths, and gastropods were all present. The average emergence rate during the evening deployment (1–3 h after sunset, Fig. 8C) was higher than the average dusk rate, but this difference was not significant (median emergence rates were in fact 36 and 51 individuals  $m^{-2} h^{-1}$  for evening and dusk, respectively). Closer examination indicated that the high mean of the evening rate was attributed solely to a fish-spawning event that occurred in the evening of 27 October 1998 when egg release (535 eggs  $m^{-2} h^{-1}$ ) accounted for >90% of the total emerging plankton. Disregarding fish eggs, the average evening emergence rate was in fact lower than those observed at dusk ( $36 \pm 18$  vs.  $58 \pm 50$  individuals  $m^{-2} h^{-1}$  for evening and dusk, respectively) but this difference was also not significant (Tukey post hoc pairwise comparison,  $p = 0.31$ ). Post hoc pairwise multiple comparisons of the medians using Dunn's method for unequal sample size indicated a significant difference ( $p < 0.05$ ) for day versus evening and day versus dusk but not

for dusk versus evening emergence rates. Moreover, the taxonomic composition of the evening and dusk catches were similar (ANOSIM, post hoc pairwise test,  $p > 0.33$ ), although zoea (29%) and copepods (25%) were somewhat more prevalent at the evening. The evening-sample composition was different from both the day and the late night catches (ANOSIM, post hoc pairwise test,  $p < 0.01$ ). The late night was characterized by lower emergence rate (median 10 individuals  $m^{-2} h^{-1}$ ) and a different taxonomic composition (Table 6) with dominance of copepods (27%) and higher abundance of stomatopods (alima, 18%), zoea (18%), and cumacea (10%).

**Zooplanktivorous fish behavior**—Monitoring the foraging activity of several conspicuous zooplanktivorous fish in the study site indicated that most of these fish continued to forage for some time after sunset (Fig. 8D). At sunset, schools of damselfish (Pomacentridae, e.g., *Dascyllus marginatus*, *Chromis* spp.) and other site-attached fish (*Pseudanthias squamipinnis*) showed a substantial reduction in their activity. The smallest fish in the schools spent prolonged durations within shelters, while the larger fish that were still active reduced their foraging range and hovered closer to their night shelters. At the same time, schools of larger fish that normally forage further off the reef during daylight (e.g., *Abudefduf saxatilis* and *Caesio* spp.) came closer to the bot-

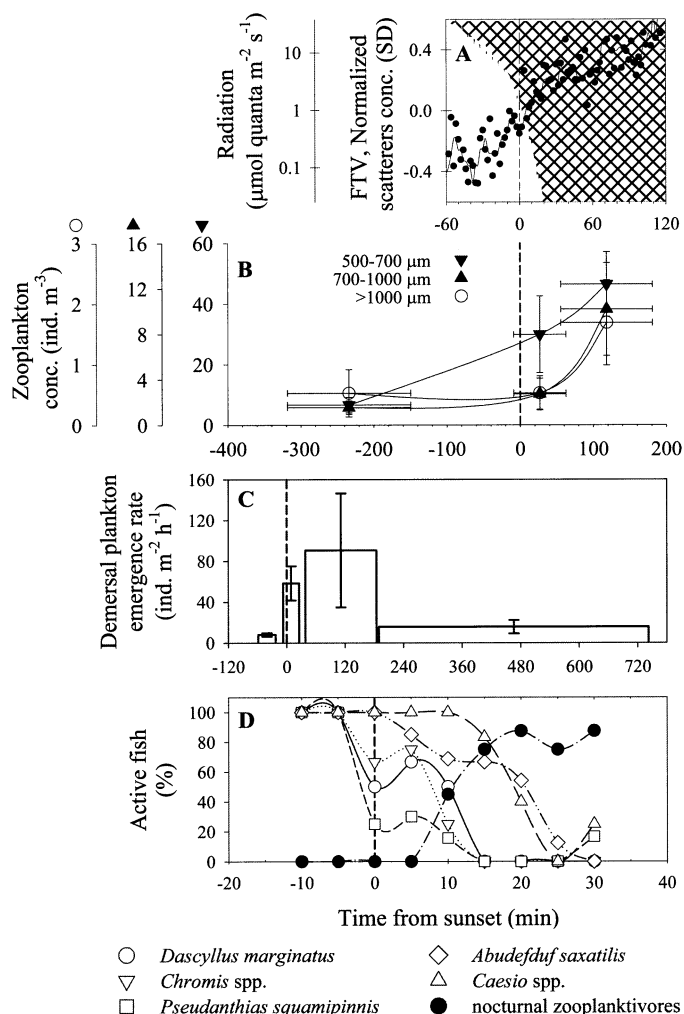


Fig. 8. Simultaneous records of zooplankton concentrations, using high-resolution FTV sonar and a high-capacity pump, accompanied by light measurements, demersal plankton traps, and visual observation of zooplanktivorous fish activity (see Fig. 2 for a scheme of the sampling setup). (A) Normalized scatterers' concentration (SD units) measured by the FTV during the October 1998 deployments focusing on the nocturnal ISI period (see Fig. 3 for details). The solid line is a five-point (10-min) moving median. Error bars were omitted for clarity. The unshaded area represents the global radiation at the reef bottom. (B) Average zooplankton abundance (total counts) in pump samples obtained simultaneously with the acoustic measurements. Vertical error bars, standard error (SE). Horizontal bars indicate sampling duration. (C) Average demersal plankton (total counts) emergence rate obtained with traps simultaneously positioned at the same site of the pumps and acoustic sampling. Error bars, SE. Bar widths span the average sampling duration. (D) Average percentage of actively foraging zooplanktivorous fish observed next to the sampling site at 9-m depth during 1-h scuba diving observations. Darkness settled  $\sim 30$  min after sunset. The observed diurnal fish were *Dascyllus marginatus*, *Chromis* spp., *Pseudanthias squamipinnis*, *Abudefduf saxatilis*, *Caesio* spp. Nocturnal zooplanktivores are denoted by filled circles. Error bars were omitted for clarity of presentation. FTV and pump sampling were carried out during 14–30 October 1998. Fish observations, light measurements, and demersal trap sampling were carried out during the last 4 d of that period (26–29 October).

tom. While most of the damselfish ceased their foraging activity 15 min after sunset (with the exception of the *Amblyglyphidodon flavilatus*), intense feeding activity of *A. saxatilis* and *Caesio* spp. was evident for at least 25 min after sunset (Fig. 8D). The nocturnal cardinalfish (*Apogon* spp.) and sweepers (*Pempheris* spp.) began their emergence from day shelters only 10 min after sunset and their numbers were continually rising throughout the observation period.

*Cross-shore entrainment of pelagic zooplankton*—To assess the potential contribution of cross-shore currents in advecting pelagic zooplankton onto the reef, the accumulative cross-shore component was calculated from the ADCP current measurements. The accumulative onshore advection throughout the dusk and evening was relatively small (few 10s of meters) throughout the water column during both the spring of 2000 and the fall of 2001. Even when the maximal on-shore advection was considered (Fig. 9), it never exceeded 200 m during 2 h, starting 1 h before sunset. However, over longer time scales ( $>4$  h), cross-shore advection may be significant ( $>350$  m).

## Discussion

This study shows a clear daily cycle of zooplankton over a coral reef in the northern Gulf of Aqaba, Red Sea. Similar to previous reports (Glynn 1973; Alldredge and King 1977; Yahel et al. in press), nighttime zooplankton ( $>500$   $\mu\text{m}$ ) densities were  $>10$ -fold higher than during the day. The abrupt increase in the abundance of small zooplankton ( $<710$   $\mu\text{m}$ ) observed at sunset is attributed primarily to the emergence of reef-originated demersal plankton and to the release of eggs and larvae of reef dwellers. Zooplankton emergence (as well as the release of eggs and larvae) occurred at a time when the schools of daytime zooplanktivorous fish were still actively foraging in the water column, although in reduced quantities (see also Rickel and Genin in press). In comparison with the timing of zooplankton emergence, the predawn zooplankton descent (DSI) took place during darkness, long before sunrise.

At sunset, an abrupt increase of both the acoustic backscattering intensity (ADCP, Figs. 4 and 5) and scatterers' concentration (FTV, Figs. 3 and 4) was evident throughout the acoustical records. This pattern was highly consistent and persisted in each and every deployment at all seasons and locations throughout the reef's depth range (8–30 m, R. Yahel and T. Berman, unpubl. data). Direct water sampling at the study site indicated that zooplankton concentration increased at nighttime and decreased during daytime (Yahel et al. in press). Moreover, suspended sediments that are likely to affect the acoustic backscatter intensity followed a reverse pattern, with a daytime increase at near-bed elevations ( $<1$  mab) and a relatively invariant distribution higher in the water column ( $>2$  m; Yahel et al. 2002). These data, together with the direct zooplankton sampling presented here (Fig. 8B,C), clearly indicate that it is the change in zooplankton concentration that accounts for the sudden nocturnal increase in the acoustic signal over the reef as well as for the subsequent elevation of the acoustic signal throughout the night.

In accordance with previous reports from other reef en-

Table 4. The abundance and contribution to similarity of the major groups characterizing the zooplanktonic composition of each sampling period (listed are only groups accounting for >50% of the within-sampling period similarity). The calculations were made using Bray Curtis similarity index and the post hoc Simper procedure (Clark 1993). Twenty-two zooplankton samples were collected concurrently with the FTV sampling (14–29 Oct 1998), using a submerged pump located 1.5 mab at a 7.4-m depth. The three sampling periods were day, ~5–2 h before sunset; dusk, a few minutes before sunset to 1 h after sunset; and evening, ~1–4 h after sunset. The average similarity within each sampling period is given in the leader row. % Cont. is the relative contribution of the planktonic group to the within-period similarity. Abundance is the average concentration of the respective planktonic group. The totals row sums the abundance of the listed groups. The contribution of the cumulative abundance of the listed groups to the entire zooplankton abundance in the respective sampling period is given (as %) in parentheses. The Other crustacean and Misc. are miscellaneous categories.

Day (similarity within samples=56%)			Dusk (similarity within samples=69%)			Evening (similarity within samples=72%)		
Group and size ( $\mu\text{m}$ )	Abundance		Group and size ( $\mu\text{m}$ )	Abundance		Group and size ( $\mu\text{m}$ )	Abundance	
	% cont.	(individuals $\text{m}^{-3}$ )		% cont.	(individuals $\text{m}^{-3}$ )		% cont.	(individuals $\text{m}^{-3}$ )
Copepods (500–710)*	17	3.6	Fish eggs (500–710)*	13	7.3	Copepods (500–710)*	9	15.02
Fish eggs (500–710)*	13	0.8	Copepods (500–710)*	11	3.1	Zoea (500–710)†	9	11.62
Tunicates (500–710)†	11	1.8	Zoea (500–710)†	10	1.7	Fish eggs (500–710)*	9	8.95
Copepods (710–1,000)†	10	1.0	Chaetognaths (500–710)	8	0.8	Tunicates (500–710)†	6	4.9
			Misc. (500–710)†	7	0.5	Other crustac. (500–710)	6	1.5
						Zoea (710–1,000)	5	4.1
						Misc. (500–710)†	5	1.1
						Copepods (710–1,000)†	5	2.6
Total		7.1 (82%)			13.5 (41%)			41.9 (72%)

\* Groups common to all three sampling periods.

† Groups common to two of the three sampling periods.

vironments (Emery 1968; Alldredge and King 1980; Ohlhorst 1982), demersal plankton, as well as fish eggs and larvae of reef dwellers, appeared in high numbers in the emergence traps and in the water samples obtained by the pump just after sunset (Fig. 8). Pumps and emergence traps

lack the temporal resolution required to resolve the rapid changes observed in the acoustic signal. Nevertheless, the lack of emergence until a few minutes before sunset, the intense emergence at dusk (~0–60 min after sunset), and the appearance of typical demersal forms in the water col-

Table 5. Dissimilarity analysis of zooplankton composition in different periods of the day, sampled by the underwater pump. For each pair of sampling periods, we list the planktonic groups accounting for >50% of the between-sampling periods dissimilarity. The calculations were made using the Bray Curtis similarity index and the post hoc Simper procedure (Clark 1993). The average dissimilarity between periods and the  $p$ -values for a post hoc pairwise analysis of similarity (ANOSIM, Clark 1993) is given in the leader row of each subtable. See Table 4 for sampling details. Table abbreviations: Eve, evening; Dem, demersal plankton; Chae, Chaetognaths; F egg, fish eggs; Crus, other crustaceans; Cop, copepods; poly, Polychaetes; Misc, miscellaneous; Moll, molluscs; Tunic, tunicates.

A. Evening versus day, dissimilarity between sampling periods=47%, $p=0.001$				B. Day versus dusk, dissimilarity between sampling periods=44%, $p=0.005$				C. Evening versus dusk, dissimilarity between sampling periods=34%, $p=0.01$			
Group and size ( $\mu\text{m}$ )	% cont.	Abundance (individuals $\text{m}^{-3}$ )		Group and size ( $\mu\text{m}$ )	% cont.	Abundance (individuals $\text{m}^{-3}$ )		Group and size ( $\mu\text{m}$ )	% cont.	Abundance (individuals $\text{m}^{-3}$ )	
		Eve	Day			Day	Dusk			Eve	Dusk
Zoea (500–710)	7.6	11.6	0.1	F egg (500–710)	5.9	0.8	7.3	Zoea (710–1,000)	5.5	4.1	0.3
Zoea (710–1,000)	5.7	4.1	0.0	Chae (500–710)	5.8	0.0	0.8	Zoea (500–710)	5.0	11.6	1.7
Dem. (500–710)	5.3	0.6	0.0	Zoea (500–710)	5.7	0.1	1.7	Cop (500–710)	4.9	15.0	3.1
Chae. (500–710)	4.5	1.3	0.0	Dem (500–710)	4.5	0.0	0.1	Cop (710–1,000)	4.7	2.6	0.2
F egg (500–710)	4.5	9.0	0.8	Moll (500–710)	4.4	0.0	0.3	F egg (>1,000)	4.6	0.2	0.0
Crus (500–710)	4.3	1.5	0.0	Cop (>1,000)	4.4	0.4	0.0	Tunic (500–710)	4.2	4.9	1.0
Crus (710–1,000)	3.7	0.4	0.0	Cop (710–1,000)	4.3	1.0	0.2	Tunic (710–1,000)	4.2	1.2	0.1
Cop (500–710)	3.7	15.0	3.6	Poly (500–710)	4.1	0.0	0.3	Chae (>1,000)	3.9	0.4	0.1
F egg (>1,000)	3.6	0.2	0.0	Zoea (710–1,000)	4.0	0.0	0.3	F egg (500–710)	3.6	9.0	7.3
Poly (500–710)	3.4	0.4	0.0	Crus (710–1,000)	3.8	0.0	0.1	Poly (500–710)	3.3	0.4	0.3
Misc (710–1,000)	3.4	0.4	0.0	Chae (710–1,000)	3.4	0.1	0.4	Cop (>1,000)	3.3	0.3	0.0
Moll (500–710)	3.2	0.4	0.0					Poly (710–1,000)	3.2	0.2	0.0
Total	52.9	44.9	4.7		50.4	2.5	11.6		50.1	50.1	14.2

Table 6. The abundance and contribution to dissimilarity of the major taxa discriminating between the evening and the night catches in the emergence traps in October 1998 (taxa accounting for >90% of the average dissimilarity between the two groups). Average dissimilarity between sampling periods=77%,  $p=0.008$ . See Table 4 for times of sampling periods.

Taxonomic group >500 $\mu\text{m}$	% cont.	Abundance (individuals $\text{m}^{-2} \text{h}^{-1}$ )	
		Evening	Night
Decapods	25.1	10.5	1.8
Copepods	19.8	8.9	2.6
Polychaete	18.8	6.2	0.3
Tanaids	6.0	2.0	0.7
Chaetognaths	4.8	1.3	0.1
Zoea	4.8	1.4	0.7
Other crustaceans	4.7	1.4	0.0
Cumacea	3.8	1.0	0.8
Mysids	2.7	0.9	0.3
Total	90.5	33.5	7.3

umn all strongly suggest that demersal plankton together with larvae and eggs released by reef dwellers are major contributors to the increase in the acoustic signal at sunset (Fig. 8).

Scatterers' concentration increased from the reef bottom, gradually spreading throughout the entire water column (Fig. 7B). Our estimates of the average propagation speed of this increase suggest an ascending rate of  $1.1 \text{ cm s}^{-1}$ . This estimate is in accordance with published rate for pelagic zooplankton (e.g., Rippeth and Simpson 1998; Thomson and Allen 2000; De Robertis et al. 2003) and for rate of plankton ascending from the bottom of a boreal inlet (Kringel et al. 2003). However, unlike the latter two reports, no defined thin scattering layer could be discerned with the FTV or the ADCP in the reef waters studied here.

The gradual propagation of the acoustic signal from the bottom toward the surface (Fig. 7) further supports the assertion that the rapid addition of zooplankton to the reef water just after sunset results from the emergence of local plankton from the reef bottom (compare with De Robertis et al. 2000; De Robertis 2002; Kringel et al. 2003). The gradual decrease of predation intensity by the diurnal fish (McFarland et al. 1999; Rickel and Genin in press) should also contribute to the observed increase of zooplankton density and acoustic signal. However, planktivorous fish predation diminished first at higher elevation above the bottom resulting in a quiet period at the water a few meters above the bottom (see also McFarland et al. 1999), whereas the increase of the acoustic signal began next to the bottom (Fig. 7), where fish predation is most intense (Motro et al. in press), especially at dusk (see Results). It is thus unlikely that the cessation of diurnal fish predation alone could account for the increase in zooplankton concentration.

Entrainment of pelagic zooplankton into the reef is a major contributor to reef zooplankton assemblages (Glynn 1973; Porter 1974; Hamner et al. 1988; Echelman and Fishelson 1990; Heidelberg et al. 2004). Nocturnal migrators en-

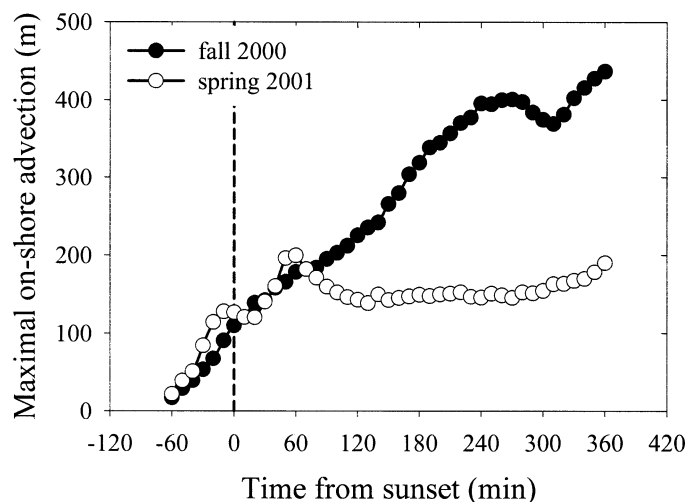


Fig. 9. Predicted maximal on-shore accumulative advection encountered during two ADCP deployments, starting 60 min before sunset. Spring 2000: 7 m above bottom, 10 m below surface. Fall 2001: 13 m above bottom, 15 m below surface.

trained onto the reef by cross-shore advection from the nearby open sea could possibly contribute to the observed zooplankton increase at dusk. However, analysis of the ADCP current measurements indicated that the cross-shore currents were insufficient to account for the early increase in zooplankton at the reef (Fig. 9; see also Fig. 4 in Genin et al. 2002). In fact, the maximal advection observed within an hour from sunset was less than 100 m, whereas the pelagic zooplankton at the nearby open waters ( $\sim 2 \text{ km}$  of shore) ascended to the upper 20 m only 40 min after the onset of ISI at the reef (R. Yahel, unpubl. acoustic data). Thus, cross-shore advection could potentially become an important source for zooplankton assemblage at the reef only later at night, as the 300-m isobath is  $\sim 1 \text{ km}$  off the reef (Fig. 1).

In contrast with temperate and boreal habitats, where the nocturnal migration is sometimes mono- or oligo-specific (e.g., Mackas and Tsuda 1999; De Robertis et al. 2000; Kringel et al. 2003), at the coral reef, the migrating community was highly diverse and many different taxa ascended to the water column in a highly synchronized manner. The diverse nature of the nocturnal zooplankton assemblage at the reef was highlighted by the similarity analysis we conducted, despite using a rather crude taxonomic resolution. Eight different planktonic groups were typical of the nocturnal samples, as opposed to only four in the daylight samples (Table 4). The 11–12 planktonic groups we analyzed had nearly equal contribution to the dissimilarity between the three sampling periods (Table 5).

The scatterer counts made by the FTV (82 and 105 individuals  $\text{m}^{-3}$  for daytime and nighttime, respectively) were considerably higher than those obtained by the pump (9 and 58 individuals  $\text{m}^{-3}$ , for daytime and nighttime, respectively). However, only zooplankton specimens were counted in the pump samples, whereas the FTV recorded the entire range of scattering particles. Sediment grains resuspended by ben-

thivorous fish are much more abundant at daytime (Yahel et al. 2002), contributing to higher FTV counts at that time (see the higher deviation within the FTV daytime counts compared with nighttime counts in Fig. 3). Avoidance of good swimmers from the pump could also contribute to lower catches at nighttime.

Size fractionation of the underwater pump samples suggests that the abrupt increase in the scatterers' concentration at sunset (Fig. 8B) was attributed chiefly to an increase in zooplankton of <710- $\mu\text{m}$  size fraction, whereas larger zooplankters emerged into the water column only at dark (>1 h after sunset). A dusk-time increase in the concentration of even smaller zooplankton (200–500  $\mu\text{m}$ ) was previously observed at the study site to coincide with an increase in the concentration of the >500- $\mu\text{m}$  zooplankton (Yahel et al. in press). Unfortunately, the crude resolution (4 h) used in that research renders impossible discrimination between the timing of increase of the two size fractions. An earlier ascent of smaller euphausiids was reported by De Robertis et al. (2000) at Saanich Inlet, British Columbia, Canada. As prey detection by visual predators is typically size dependent (reviewed by De Robertis et al. 2000; Holzman and Genin 2003), the risk in early ascent is relatively lower for smaller zooplankton (De Robertis 2002).

The early onset of demersal plankton emergence and eggs and larvae release immediately at sunset (Table 3) was unexpected. At that time, light intensity was still relatively high (1.5  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  at the reef bottom, 9-m depth) and many zooplanktivorous fish were still foraging (Fig. 8D; Rickel and Genin in press). While traditional methods lack the time resolution provided by the acoustic instruments we used, previous reports provide support for the finding of early ascent at the reef. For instance, using direct sampling of the sediment, Madhupratap et al. (1991) showed an abrupt disappearance of demersal zooplankton from the substrate of a coral-reef lagoon immediately after sunset. This early ascent is in sharp contrast with findings reported from other shallow habitats (e.g., Kringel et al. 2003; Teasdale et al. 2004) and from pelagic populations (e.g., Thomson and Allen 2000), where nocturnal migrators ascend to the surface water only at darkness. In fact, boat-mounted ADCP records made concurrently with measurements at the reef suggest that in the nearby open sea (~2 km offshore), the nocturnal migrators ascended close to the surface (<20 m) only at darkness (>30 min after sunset; R. Yahel unpubl. data). Moreover, both the onset and the termination of the morning DSI at the reef occurred at the predawn hours in complete darkness (Table 3, Fig. 5).

While an abrupt nocturnal ISI was evident in almost all of the acoustic records (>250 d), the exact timing of the onset and completion of the ISI showed a significant day-to-day variability. The onset of ISI ranged from 30 min before sunset to 30 min after sunset (Table 2). This variability could be an artifact of our definition of onset and completion of ISI and DSI. Nevertheless, manual timing of the ISI and DSI throughout the time series (see, e.g., Fig. 5E), as well as runs of the algorithm with different parameter sets, confirmed the ISI and DSI timing presented above. Correlation analysis indicated no significant association or trend between any of the ISI and DSI parameters (time of onset, duration,

and time of termination). Nor did we find any correlation or trend indicating relationships of these parameters to moon phase or moon illumination (four lunar cycles) or to the seasonal trend of the ABI. Late ISI (postsunset) was evident in 4 of the 5 cloudy days that occurred during the study period. We cannot, at this stage, put forward any compelling explanation for the observed variation. However, one can speculate that, if the demersal plankton and the benthic brooders can sense or assess the presence of zooplanktivorous fish in their vicinity (e.g., Neill 1990; Lauridsen and Lodge 1996), they should respond accordingly by postponing their ascent.

Visual planktivorous fish have a crucial role in the ecology of reef-associated plankton (Hobson and Chess 1978; Ohlhorst 1982; Hamner et al. 1988; Motro et al. in press), and fish schools at the fore-reef were reported to decimate most of the zooplankton drifted onto the reef during daytime (Hamner et al. 1988). Surprisingly, zooplankton begins its ascent into the reef waters at a time when many of the planktivorous fish are still foraging (Fig. 8D; Rickel and Genin in press), although in considerably reduced feeding efficiency (~50%; Rickel and Genin in press). On the other hand, the role of corals and other nocturnal, sessile zooplanktivores is less understood. Most reef corals expand their tentacles only at night (Porter 1974; Lewis and Price 1975). In our study site, the massive corals *Favites* sp., *Favia fava*, and *Platygyra* spp. began to expand their tentacles only 15–45 min after sunset and reached their fully expanded mode only >60 min after sunset (O. Levy unpubl.).

We suggest that the early emergence of reef zooplankton and the release of eggs and larvae rely on a windows of opportunity when nocturnal predation risk posed by sessile zooplanktivores (e.g., corals; Levy et al. 2003, O. Levy unpubl.) is still low and the efficiency of visual predators is already reduced (Rickel and Genin in press). The intense predation of various diurnal fish is thus assumed to be the driving force that directly and indirectly shapes the temporal distribution and taxonomic composition of reef zooplankton as well as the timing of larvae and eggs release.

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