Abundance and distribution of nocturnal fishes over a coral reef during the night

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ABSTRACT: Coral reefs are characterized by high abundance of fishes, which often have marked effects on the recruitment, nutrition, and reproduction of coral reef inhabitants. Despite the fact that fish are active over the coral reef at night, very little is known of their whereabouts or about their contribution to those processes. In the present study, the abundance and distribution of nocturnal fishes were studied over a coral reef near Eilat, Red Sea. Sampling was conducted between the surface and 15 m depth, using a stereoscopic camera system that surveyed 3.5 m^3 of water every 2 min. The density of zooplanktivorous species ranged from 0.7 to 7.4 fish 100 m^{-3}, accounting for >60% of the total nocturnal fishes recorded. Fish abundance decreased with increasing distance from shore and with increasing height above bottom. Larger fish foraged at greater heights above bottom. While the appearance of zooplanktivorous fishes after sunset and their disappearance before sunrise corresponded to that of demersal zooplankton, inter-night variation in fish abundance was unrelated to variation in zooplankton abundance. Furthermore, neither current speed nor moon illumination accounted for inter-night variations in fish abundance, perhaps indicating some degree of site fidelity. The abundance of zooplanktivorous fishes was ~30-fold lower during the night than day. However, since nocturnal fishes feed on larger zooplankters, the biomass of zooplankton preyed upon by nocturnal fishes was similar to that of diurnal species. This study suggests that the paradigm of negligible predation by nocturnal fishes should be reconsidered.

KEY WORDS: Coral reef fishes · Nocturnal zooplanktivory · Nocturnal ascent · Photogrammetry · Fish community

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INTRODUCTION

Several decades of research on the ecology of coral reef fishes yielded much information on the distribution and feeding ecology of diurnal fishes (e.g. Fricke 1980, Hamner et al. 1988, Kingsford & MacDiarmid 1988, Forrester 1991, Hobson 1991, Brokovich 1999, Rilov & Benayahu 2000). However, only a handful of reports on nocturnal fishes are available, and most of this information is either qualitative (Hobson & Chess 1978, Gladfelter 1979) or it is focused on stomach content and dietary partitioning among species (Hobson & Chess 1978, Gladfelter 1979) or on the distribution of these fish during daytime (Brokovich 1999, Rilov & Benayahu 2000, Khalaf & Kochzius 2002). Further-

more, standard methodological approaches, such as the use of flashlights and line transects, limit the relevance of the findings to specific habitats (e.g. lagoons [Marnane & Bellwood 2002] and the benthic boundary layer [Annese & Kingsford 2005]), while data on the temporal patterns of nocturnal fishes during the night are largely restricted to dusk and dawn (Fishelson et al. 1971, Hobson 1972, McFarland et al. 1999, Yahel et al. 2005a). Therefore, a quantitative study of the spatial and temporal distributions of nocturnal fish is necessary in order to understand their role in the ecology of coral reefs.

The distribution and behavior of nocturnal animals can greatly differ from that of related diurnal species. An extreme example is the diel migration of zooplank-

ton, which distinguishes its distribution from that of 'diurnal', non-migrating zooplankton (e.g. Bollens & Frost 1989). In coral reefs, the distribution of diurnal zooplanktivorous fishes is apparently related to their swimming ability, with large, mobile fish found seaward and higher above bottom than small fish (Hobson & Chess 1978, Hamner et al. 1988, Hobson 1991). Since prey availability for those fishes is greater further away from the reef (Hamner et al. 1988, Holzman et al. 2005), the paucity of small fish from preferred, prey-replete zones is believed to be determined by the risk of predation (Fricke 1980, Hixon 1991). However, little is known on the distribution of nocturnal zooplanktivorous fishes across the reef, or the role of predation in structuring that distribution. If predation is lower for nocturnal fish, food may play a major role in determining their distribution. If this is the case, their distribution is expected to follow that of demersal zooplankton (a major component of the diet of coral-reef nocturnal fishes; Hobson & Chess 1978, Gladfelter 1979, Marnane & Bellwood 2002), which emerges from the bottom after sunset and ascends to several meters above bottom (Alldredge & King 1985).

Recent advances in digital photography have made available a wide range of instruments designed to sample fish, micronekton, and zooplankton (Harvey & Shortis 1995, Wiebe & Benfield 2003, Harvey et al. 2004, Benoit-Bird & Au 2006). The use of cameras can help to overcome some of the known biases and artifacts of visual transects (Sale 1997), and uniquely allows the accumulation of time-series data.

The objective of the present study was to quantify the abundance of nocturnal fish along a cross-shore (0 to 90 m from shore) and a depth gradient (0 to 15 m) over a coral reef. Further, the study aims to describe the temporal patterns of fish emergence, abundance, and retreat throughout the night. Lastly, we aimed to examine the possible relationships between fish distribution at a selected depth and potential correlates, including light intensity, flow speed, and zooplankton abundance and distribution.

MATERIALS AND METHODS

Study site. The fieldwork was carried out at the coral reef off the H. Steinitz Marine Biology Laboratory in Eilat, Israel (29° 30′ N, 34° 56′ E). The local fish community was described by Brokovich (1999), Rilov & Benayahu (2000), and Khalaf & Kochzius (2002). Briefly, the guild of diurnal zooplanktivorous fish is dominated by site-attached species such as the reef anthias *Pseudanthias squamipinnis*, several damselfishes (including *Neopomacentrus miryae* and *Dascyllus* spp.), and more mobile species such as *Caesio*
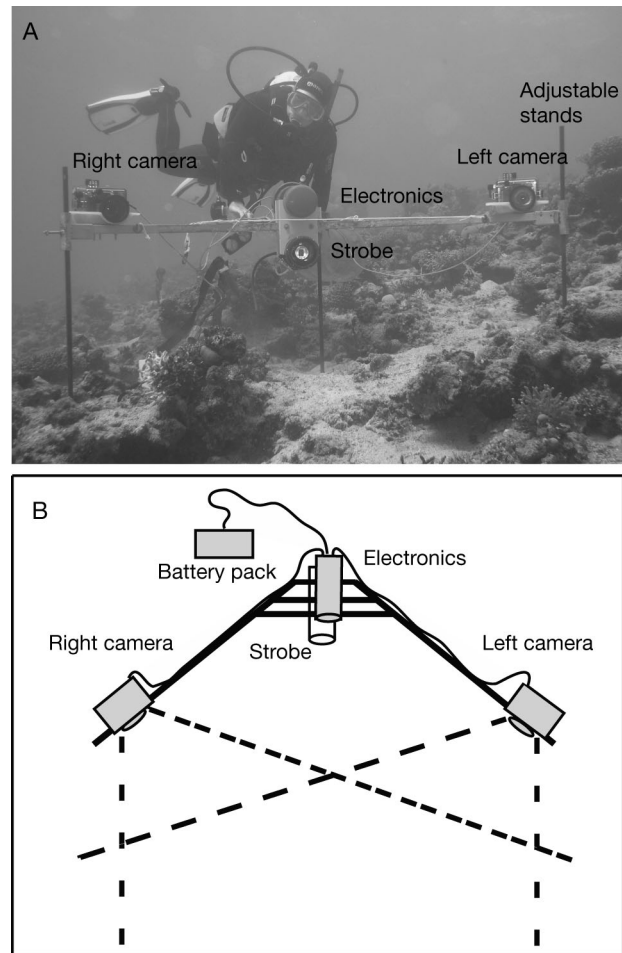

Fig. 1. (A) The fish camera recorder (FCR) deployed in the reef at 5 m depth. The battery pack is obscured by a coral head. (B) Schematic drawing of the FCR. Dashed lines demarcate the field of view of each camera

spp. and *Abudefduf* spp. The most abundant nocturnal zooplanktivorous fishes include several Apogonidae (*Apogon cyanosoma*, *Apogon aureus*, *Apogon annularis*, *Cheilodipterus quinquelineatus*), *Myripristis* spp., and *Pempheris vanicolensis* (Rilov & Benayahu 2000). The benthic community at this low-relief reef (Fig. 1A) was described by Benayahu & Loya (1977). The reef is dominated by hermatypic corals, and hydrozoans, soft corals, mollusks, sponges, and tunicates are also abundant. The coastal currents are weak, with an average speed of ~10 cm s^{-1} and a strong semidiurnal periodicity of current reversal during the warm period (May to September). The zooplankton community in the oligotrophic water around the reef is dominated by small (<0.5 mm) taxa of which copepods comprise >50% (Farstey et al. 2002, Sommer et al. 2002). Zooplankton abundance above the reef nearly doubles at night (1000 to 2000 ind. m^{-3}), relative

to daytime values, mostly due to an increase in large demersal zooplankters (>200 µm) (Yahel et al. 2005b). The distribution of small zooplankton over the reef is characterized by a spatial gradient, its density in the benthic boundary layer (up to ~2 m above bottom [mab]) is about 50% of that in the water above (Holzman et al. 2005, Yahel et al. 2005b).

Photographic system. The abundance of nocturnal fishes over the coral reef was quantified using a stereo photographic system, capable of recording fish within a volume of 3.5 m^3. The system, termed the fish camera recorder (hereafter FCR), consisted of 2 digital cameras (Coolpix 5400, Nikon) in underwater housings (SN 6194, Ikelite) mounted on the arms of a V-shaped steel frame, with a strobe (150 W s^{-1}; PhotoSea 1500sx) located at the frame's base (Fig. 1). The 2 cameras were oriented at 45° to the main axis of the FCR, so that most of their fields of view overlapped (Fig. 1B). The arms of the FCR frame were ~1.5 m in length and perpendicular to one another. The underwater camera housings were attached to the rig using custom-made cradles, molded to fit the bottom of the housings, so that detaching and reattaching the cameras did not change their position and orientation. The 24 V power pack consisted of 2, serially connected 12 V standard motorcycle batteries (sealed, non-spillable lead-acid 6.6 Amp h^{-1}, Yuasa Battery) contained in a custom-made fiberglass housing. The cameras and the strobe were synchronized to simultaneously record a pair of images every 2 min, thereby minimizing artifacts related to attraction or avoidance of fish and zooplankton to the light source (Jaffe et al. 1998, Mueller et al. 2006).

Spatial distribution of fishes over the reef. FCR deployments were made between October 2004 and February 2005 at above-bottom depths of 1, 2, 5, and 15 m, to assess the spatial distribution and abundances of nocturnal fishes along cross-shore (0 to 90 m from shore) and depth (surface to bottom) transects (hereafter 'spatial observations'; see Table 1 and Fig. 2 for information on deployment locations and naming). At the near-bottom stations the FCR was fixed at the designated height using a 3-leg frame made from galvanized steel pipes (Fig. 1A). At the mid-water and near-surface stations, a taut mooring line anchored with a 25 kg weight and suspended with a 18 l subsurface float was used to suspend the FCR at the designated depths. The FCR was deployed >1 h before sunset and retrieved ~1 h after sunrise. Deployments were replicated 6 times per station (total of 42 nights) at different locations on the reef, haphazardly selected along the target bathymetric contours. Since the FCR quantified the abundance of fish at the same position during the entire night, our sampling unit was a whole night and the dependent variable was the average density of fish during each night (see below).

Fishes recorded with the FCR were sorted to the finest taxonomic level possible, usually genus or species. Fishes belonging to Lethrinidae and Lutjanidae could not be resolved one from another and were grouped.

Effects of moonlight, current speed, and zooplankton abundance. The abundance and distribution of fish over the coral reef at our study site were characterized by strong spatio-temporal variations (see 'Results'). To test for possible effects of moon illumination, current speed, and zooplankton density on fish abundance, an extensive, 22 night long set of observations (hereafter 'temporal observations') was recorded during August and September 2005 at Point 12B, located at the bottom depth of 12.5 m (with the FCR positioned 0.8 mab). At that depth, the variation in moonlight between full-moon and moonless nights is expected to have an impact on the feeding rates of nocturnal fish (Holzman & Genin 2003, R. Holzman unpubl. data). Currents were measured simultaneously with FCR records in 20 of these deployments using an upward looking acoustic doppler current profiler (ADCP, 600 kHz Workhorse, RDI Instruments) deployed near (~2 m) the FCR. For logistic reasons, ADCP records were not available on 2 of the nights. The ADCP's echo-intensity records are correlated with the total volume, total cross section, and wet weight of the zooplankton (Flagg & Smith 1989; based on concurrent ADCP records and MOCNESS hauls) and can therefore be used as a surrogate for zooplankton density (Flagg & Smith 1989, Yahel et al. 2005a). Following Flagg & Smith (1989), the backscattering values reported by the ADCP were used as a proxy for zooplankton biomass, with no correction for transmission loss and radial spreading. Therefore, the use of this proxy was limited to comparisons of the same data bins between different nights (at the same location using the same ADCP setup). Note that the above echo-intensity data cannot be used to quantitatively compare zooplankton biomass between different distances from the transducer.

The upward looking ADCP was programmed to record current speed and echo intensity in the range of 0.75 to 6.75 mab (in 0.5 m bins). Thus, the 'noisy' near-transducer and near-surface ranges (10% of the range) were omitted from the measured range according to the manufacturer's instruction manual (RDI Instruments). To improve data visualization and interpretation, the values of acoustic backscatter within the experimental nights were normalized and standardized as: normalized echo intensity = $(E_i - \bar{E})$/SD(E), where E_i is the ith echo intensity value, $\bar{E}$ is the average echo intensity from all the experimental nights, and SD(E) is the respective standard deviation. The FCR was deployed >1 h before sunset and retrieved ~1 h after sunrise. Synchronized half-hourly
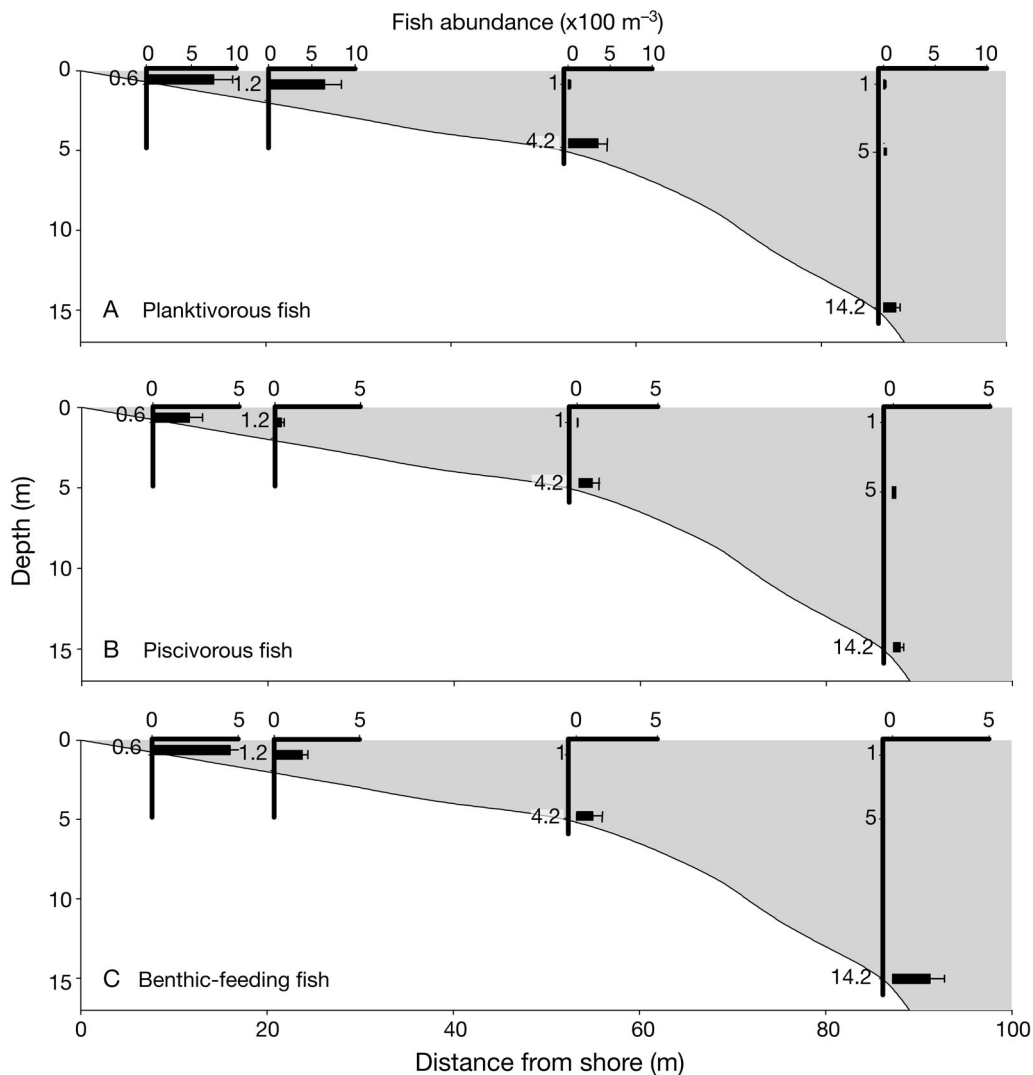
Fig. 2. Spatial patterns: abundance of planktivorous (A), piscivorous (B), and benthic-feeding fishes (C) over the coral reef of Eilat overlaid on bottom topography at the study site. Continuous line demarcates the water column (gray) and bottom (white) areas. Tics in the inner graphs indicate the locations of the camera system and the center of the sampled volume; note the different scales on the *x*-axes for the densities of the different fish guilds (A–C). Error bars = SE, n = 42 nights, 6 nights per sampling point

means of both the FCR (fish densities) and ADCP records were used for the analyses.

Sampled volume and photogrammetry. The volume sampled by the FCR was measured in a large circular pool, 4 m in diameter and 3 m deep, with the FCR fixed at 1.5 m depth near the pool's wall. The volume of the pool was divided into 10 cm^3 'voxels' (3-dimensional analog of pixels), using a 3-dimensional grid. The center of each voxel was defined by moving a taut mooring line with distinct vertical marks at 10 cm intervals across a 10 × 10 cm grid marked on the pool's floor. A photograph of the mooring was taken at each location by the 2 cameras, and the coordinates of each voxel were recorded using image analysis software

(Imagepro for Windows Ver. 4.5, Media Cybernetics), resulting in a coordinate set of $X_{(left)}, Y_{(left)}, X_{(right)}, Y_{(right)}$ (hereafter 2-dimensional coordinates) for each voxel center. The sampled volume was defined as the cumulative volume of all the voxels appearing in both cameras, up to a distance of 3.5 m from the strobe, forming a 3.5 m^3 polygon, 200 × 140 × 210 cm in maximal height, width, and length, respectively. The length of the sampled volume, defined by the pool diameter, was conservative with regard to visibility as in the field, where fish were frequently observed farther away. We used this shorter range, and made fine adjustment of the FCR position, in order to minimize the obstruction of fish by topographic features.

At the near-surface and -bottom stations, the sampled volume had to be truncated because the water and bottom surfaces, respectively, appeared in the images. The size of the sampled volume at those stations (1.5 to 3.4 m^3) was determined photogrammetrically for each deployment. At Stns 1B and 2B the height of the sampled volume was measured every hour, to account for tidal changes.

Only objects appearing in the 2 cameras were considered valid 'targets'. For each target, we recorded the 2-D coordinates from each of the left and right cameras ($X_{(\text{left})}, Y_{(\text{left})}, X_{(\text{right})}, Y_{(\text{right})}$) using ImagePro (Ver. 4.5). These coordinates were used to resolve the 3-D location of each target relative to the camera (see Fig. 1 in Benoit-Bird & Au 2006). The translation to 3-D was based on a maximum-likelihood algorithm using the target's coordinates and the calibration matrix by finding the voxel for which the RMS distance to the target's 2-D coordinates was minimal. A tank test with haphazardly positioned targets (n = 30) indicated that all position assignments were correct. The precision was ±5 cm in each dimension. For the fish recorded with the FCR (body size in the range of 5 to 35 cm), the spatial resolution had an error that never exceeded the fish's body size, appropriate for measuring the fish's abundance and vertical distribution.

Temporal and statistical analysis. The time of sunrise and sunset, moonrise and moonset, moon phase, and the number of moon minutes in each night were obtained from the Wise Observatory Astronomical Calendar, Tel Aviv University, Israel (http://wise-obs.tau. ac.il/~eran/Wise/wise_calen.html). In order to assess the spatial distribution of nocturnal fishes over the reef, we used 1-way ANOVA with station (7 levels) as the independent factor and the mean density of zooplanktivorous fishes within each sampling night as the dependent variable. We chose to use a 1-way ANOVA rather than a 2-way design with missing cells in the shallow stations (depth × distance from shore) since the FCR surveyed the entire water column in the shallow stations, thereby leaving no gaps in the water column. A similar analysis was made for piscivorous fishes. Since no benthic-feeding fishes were observed at >2 mab (see 'Results'), the effect of station on their density was assessed using only the 4 bottom stations.

In order to assess the effects of environmental parameters on the fish's temporal distribution, we used multiple regression with mean current speed, number of moon minutes, and echo intensity as independent variables and the mean density of nocturnal fishes within each sampling night at the 12 m station as the dependent variable. ANCOVA was used to test the effect of moon illumination (number of moon minutes, continuous predictor) and taxa (categorical predictor) on the foraging height of all fishes observed.

Possible correspondence between temporal variations in the abundance of fish and zooplankton was examined using linear regression, with fish abundance and acoustical backscatter as the dependent and independent variables, respectively. Data for this analysis consisted of half-hourly means of fish densities and backscatter, averaged across sampling nights. In all cases, ANOVA, ANCOVA, and *t*-tests were performed only after verifying homogeneity of variance using Cochran's statistics. *Atherinomorus* spp. was excluded from the analysis of the effect of moon phase on foraging height, since this taxon was observed to be surface bound. Data on the density of predators contained many zeroes; therefore, Spearman rank order was used to test for correlation between the density of planktivorous and piscivorous fish. All the aforementioned statistical tests were performed using STATISTICA Ver. 6.0 for Windows (StatSoft). The differences in species composition and relative abundances across sampling stations were tested using 1-way analysis of similarity (Clarke & Warwick 1994) based on the Bray-Curtis similarity index. To assess the effect of environmental variables on community pattern, we used the BioEnv procedure (PRIMER Ver. 5.0), which selects environmental variables best explaining community pattern by maximizing a rank correlation between their respective similarity matrices (Clarke & Warwick 1994). The latter tests were performed using PRIMER Ver. 5.0 (Plymouth Marine Laboratory).

RESULTS

Spatial patterns

A total of 2277 fish were observed with the FCR during 64 nights (Tables 1 & 2). The density of zooplanktivorous fishes, which accounted for ~60% of the fishes observed, varied significantly with sampling station (ANOVA, $F_{6,35} = 6.31$, p < 0.001; Fig. 2A, Table 1). The highest density of zooplanktivorous fish was observed near the bottom at the shallowest stations (Stns 1B and 2B; average ± SE: 0.074 ± 0.028 and 0.066 ± 0.019 fish m^{-3}, respectively). The abundance values of nocturnal fishes at Stns 5S (0.0019 ± 0.0009), 15S (0.0016 ± 0.0005), and 15M (0.0007 ± 0.0004 fish m^{-3}) were 1 to 2 orders of magnitude lower than those at Stns 1B and 2B (Tukey honestly significant difference, p < 0.05 for all cases).

The abundances of piscivorous fishes were also significantly different between different sampling locations (ANOVA, $F_{6,35} = 5.14$, p < 0.001). The density of piscivorous fishes was positively correlated to that of zooplanktivores (Spearman rank order, r = 0.65, n = 42, p < 0.01; Fig. 2B). Nocturnal benthic-feeding fish ap-

peared only near the bottom (Fig. 2C), with a non-significant effect of sampling location (ANOVA, $F_{3,20}$ = 2.56, p = 0.083, 'bottom' locations only).

The taxonomic composition of the fish community differed significantly between sampling locations (ANOSIM, R = 0.5, p < 0.05). At the shallow stations (1 and 2 m), small zooplanktivores accounted for > 64 % of the planktivores (41 % of total fish), compared with < 30 % of planktivores (19 % of total fish) at the deeper stations (5 and 15 m). Together, *Myripristis* spp. and *Pempheris vanicolensis* accounted for 51 and 24 % of the total fish density in deep and shallow stations, respectively.

A calculation of the integrated fish abundance throughout the water column (Table 1) indicates that the abundances of planktivorous, benthic-feeding, and piscivorous fishes were 2.5 to 3 times greater at the shallow stations (1, 2, and 5 m) than at 15 m depth.

Temporal patterns

Planktivorous fish were first to emerge after sunset (22 ± 10 min after sunset, n = 22 nights; Fig. 3). The time of disappearance in the pre-dawn hours varied greatly between different deployments, with a mean (±SE) of 1.43 ± 1.26 h before sunrise (Fig. 3). Benthic-feeding and piscivorous fishes retreated to their daytime shelters 1.16 ± 1.066 h before sunrise (n = 22).

During the night at the 12 m station, the density of nocturnal fish was correlated with normalized echo-intensities (linear regression, R^2 = 0.44, $F_{1,22}$ = 18.8, p < 0.01; Fig. 3). At that depth, there was no significant effect of current speed, number of moon minutes, or echo intensity on the density of the zooplanktivores (multiple regression, adj. R^2 < 0.1, $F_{3,16}$ = 1.68, p > 0.2; Fig. 4A) or on the density of benthic-feeding and piscivorous fishes (multiple regression, adj. R^2 < 0.1, p > 0.1 for both; Fig. 4B,C). Similarly, independent variations in average backscatter intensity, the number of moon minutes, or current speed could not explain the variations observed in average fish density between sampling nights (Spearman correlation, r = 0.01, –0.04, and –0.21, respectively, df = 19, p > 0.05 for all 3 variables; Fig. 4D). Within sampling nights, the density of planktivorous fish was not signifi-

Table 1. Spatial patterns: sampling locations and variation in the integrated abundance of nocturnal fishes at our study site. Camera position indicates the height at which the camera was positioned above the bottom or below the surface. Abundance values were integrated from the bottom to the surface using the mean density at each site at each depth (n = 6) for all the deployments made at 1, 2, 5, and 15 m depths (mean ± SE; total of 42 nights). Data are presented in abundance per area to facilitate comparison with other studies. Zoo: zooplanktivorous fish; Pisc: piscivorous fish; Bent: benthic-feeding fish

Sampling depth (m)	Stn	Camera position	Integrated abundance (fish 100 m^{-2})		
			Zoo	Pisc	Bent
1	1B	0.4 m above bottom	5.2 (1.2)	1.1 (0.27)	3.11 (0.9)
2	2B	0.8 m above bottom	4.7 (1.4)	0.33 (0.1)	1.3 (0.3)
5	5B	0.8 m above bottom	4.6 (0.3)	0.6 (0.13)	2.3 (0.55)
	5S	1 m below surface			
15	15B	0.8 m above bottom	1.9 (0.05)	0.35 (0.1)	1.1 (0.5)
	15M	5 m below surface			
	15S	1 m below surface			

Table 2. Spatial patterns: summary data for the abundance of the common fish species observed at the coral reef of Eilat, Israel. Data are averages for all sampling stations for all sampling nights of 'spatial pattern' deployments (1, 2, 5, 15 m depths; B, M, S stations; total of 42 nights). 'Number of nights' in which a fish from a given species was observed at least once is given. 'In stations' indicates sampling locations in which fishes of a given species were found; underlining indicates the stations at which the average density of the species was highest. About 1 % of the fish observed with the fish camera recorder could not be identified

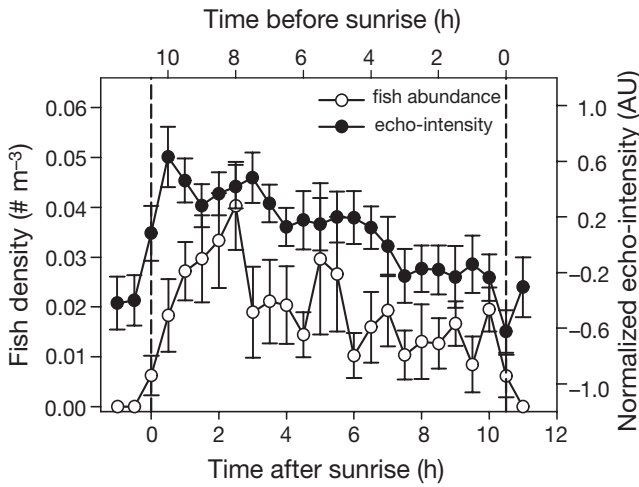| Guild	Species	Abundance (fish 100 m^{-3})	Total fish (%)	No. of nights	In Stns
Zooplanktivorous fish	*Myripristis* spp.	0.84	19.0	19	1, 2, 5B, 5S, 15B
	Atherinomorus spp.	0.606	13.6	9	1, 2, 5S, 15S
	Apogon cyanosoma	0.58	13.1	8	1, 2, 5B
	Pempheris vanicolensis	0.357	8.0	25	All (1)
	Other Apogonidae	0.19	4.3	13	1, 2, 5B, 15B
	Apogon annularis	0.12	2.6	6	2, 5B, 15B
Benthic-feeding fish	*Sargocentron* spp.	0.63	14.2	20	1, 2, 5B, 15B
	Lethrinidae and Lutjanidae	0.49	11.1	20	1, 2, 5B, 15B
	Scolopsis ghanam	0.187	4.2	6	1, 5
Piscivorous fish	*Epinephelus summana*	0.07	1.6	9	1, 2, 5B, 15B
	Other piscivores	0.29	6.7	22	All (1)

Fig. 3. Temporal patterns: within-night variations in the abundance of zooplanktivorous fish and echo intensity (zooplankton relative abundance) above the coral reef measured at 0.75 to 2.25 m above bottom at 12 m depth (n = 20 nights). Sunrise was 10.5 h after sunset. Error bars = SE

cantly different before or after moonrise (paired *t*-test, df = 19, $t = -1.55$, p > 0.13). Variation in environmental variables (number of moon minutes, current speed, and echo-intensity) could not explain the observed variations in the community pattern of planktivorous fishes (BioEnv R > 0.2 for all combinations).

Foraging heights

The vertical height above bottom of different taxa differed significantly (ANOVA, $F_{11,779} = 98.3$, p < 0.001; Fig. 5). Within the guild of planktivores, larger species were found higher above the bottom (Spearman correlation between standard length and the average foraging height of each species, r = 0.76, n = 7, p < 0.05; maximal length taken from Randall 1983). *Myripristis* spp. and *Pempheris vanicolensis*, the largest planktivorous fishes observed, were found highest above the bottom, at 77 ± 6 and 125 ± 23 cm above bottom, respectively. *Apogon cyanosoma*, the
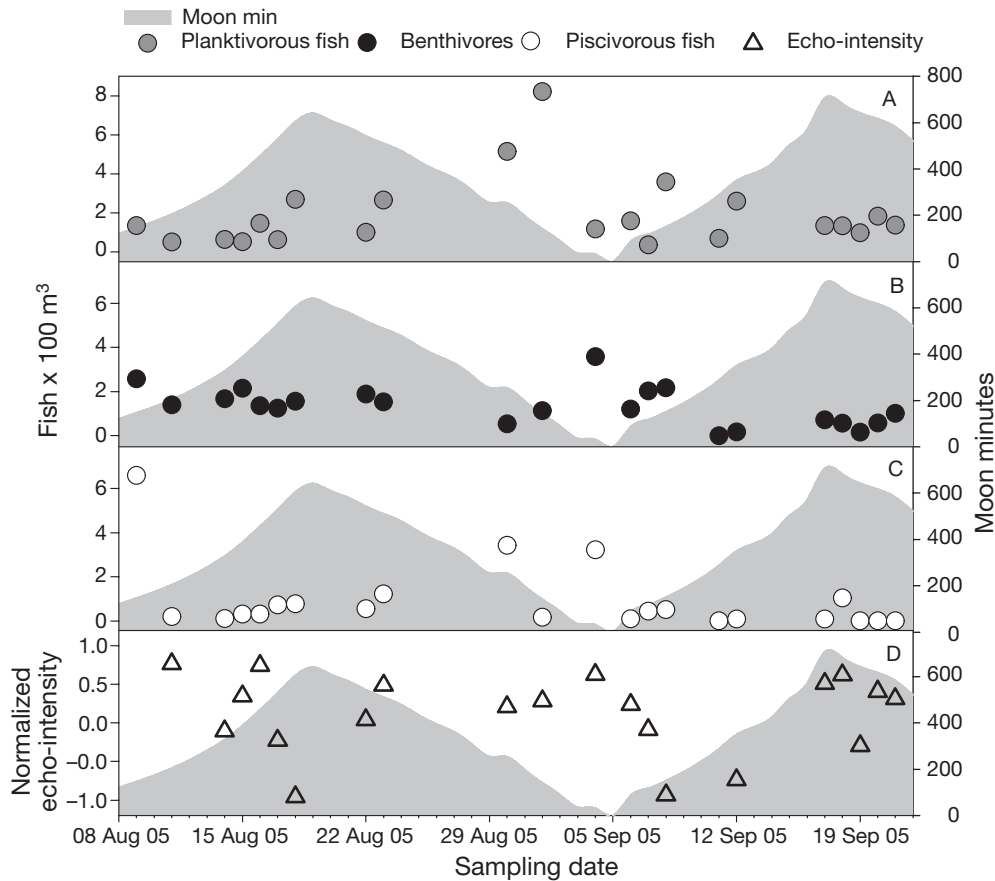

Fig. 4. Temporal patterns: between-night variations in the abundance of zooplanktivorous (A), benthic-feeding (B), and piscivorous fishes (C), and in echo-intensity (D) at 12 m depth in the coral reef of Eilat, overlaid on the number of moon minutes in each deployment night (gray background). Note, however, that shorter moon illumination corresponds to partial moon and, hence lower light intensity during those nights. n = 22 nights (20 for D)
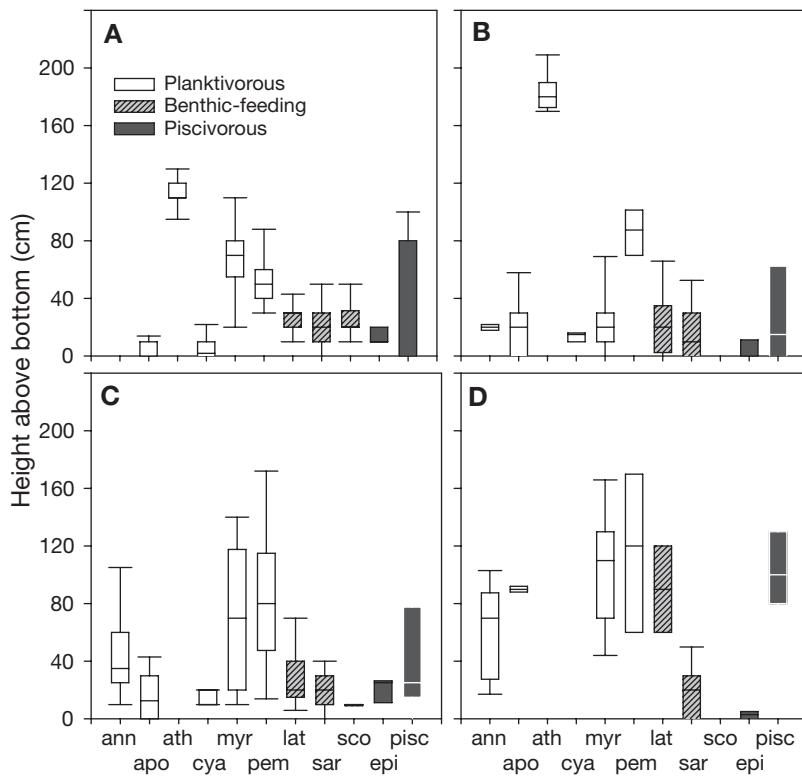
Fig. 5. Spatial patterns: foraging height for 11 fish taxa observed at bottom stations 1B (A), 2B (B), 5B (C), and 15B (D). Upper and lower portions of each box indicate the 75th and 25th percentiles of foraging heights, vertical line within each box indicates the median, and error bars denote the 10th and 90th percentiles. ann: *Apogon annularis*; apo: other Apogonidae; ath: *Atherinomorus* spp.; cya: *Apogon cyanosoma*; myr: *Myripristis* spp.; pem: *Pempheris vanicolensis*; lat: Lethrinidae and Lutjanidae; sar: *Sargocentron* spp.; sco: *Scolopsis ghanam*; epi: *Epinephelus summana*; pisc: piscivorous fish

smallest planktivorous fish, was found at an average height of 9 ± 1 cm above bottom. *Atherinomorus* spp. were observed only near the water surface above all bottom depths, at an average depth of 15 ± 10 cm below the surface.

Some of the fish taxa were foraging higher above the bottom during full moon nights, as indicated by the significant interaction term between taxa and number of moon minutes (ANCOVA, $F_{8,809}$ = 4.08, p < 0.001). The height above bottom observed for *Myripristis* spp., *Pempheris vanicolensis*, *Epinephelus summana*, and 'other piscivores' was positively correlated with the number of moon minutes (Spearman correlation, p < 0.005; Bonferroni correction applied), indicating that these fish foraged higher during better-illuminated nights. For example, *Myripristis* spp. and *P. vanicolensis* were foraging 0.5 and 0.25 m higher above bottom, respectively, during full moon nights than during no-moon. No significant effect of moon phase on foraging height was observed for other planktivorous or benthic-feeding species (Spearman correlation, p > 0.005

for all cases; Bonferroni correction applied). Similarly, no moon effect on echo intensities in the bottom layer (0.75 to 2.25 mab) was observed (*t*-test, df = 38, *t* = 0.88, p > 0.38) or on the vertical gradient of echo intensity, calculated as the ratio between echo intensity at 0.75 to 1.25 and at 1.75 to 2.25 mab for all available records (38 nights; *t*-test, df = 37, *t* = 1.82, p > 0.05).

DISCUSSION

Quantitative estimates of the abundance of nocturnal fishes are usually made using belt transects or sampling quadrates (Marnane & Bellwood 2002, Annese & Kingsford 2005) that require the use of continuous artificial light. In addition to possible artifacts due to attraction and avoidance of nocturnal fish (and their food) by light, belt transects may be biased due to a narrow field of view that is delimited by the artificial light source and the consequent increased probability of fish passing undetected through the transect area (Sale 1997). The key advantages of the FCR were the provision of accurate time series of high-resolution images. The sampled volume's proximal edge was ~1.5 m away from the FCR, minimizing the effect of its presence on the fish. The powerful strobe we used could have temporarily 'blinded' the fish, but we used a short (4 ms) pulse and a long interval between successive records (2 min) to minimize this effect.

The density of nocturnal planktivores recorded in our study was about 30 times lower than that of diurnal planktivores at the same site (diurnal fish quantified using 50 × 2 m belt transects; E. Brokovich unpubl. data, R. Holzman unpubl. data). These densities are similar to those reported by Annese & Kingsford (2005) for nocturnal Pempheridae in temperate reefs in Australia (~10 fish 100 m^{-2}). However, zooplanktivorous fish at their study site were more abundant in the depth range from 10 to 14 m, while in Eilat their density was higher in shallow (1 to 2 m) waters. The densities reported for both reef habitats are higher than those reported for 2 pempherid fishes collected by otter trawling in a non-reef habitat in the coastal waters of southwestern Australia (~0.01 to 1 fish 100 m^{-2}; Platell & Potter 1999).

Using the FCR, we tested the effects of 3 possible factors on the spatial distribution of nocturnal planktivorous fishes above the coral reef at night: the density of piscivorous fishes, light intensity (moon phase), and prey density. The positive correlation in the abundances of piscivorous and planktivorous fishes might indicate that predation risk affected the tendency of smaller fish to remain near the bottom. Reduced feeding rates at lower light intensities in deeper waters (Holzman & Genin 2003) might explain the lower abundance of fish at greater depths. For *Apogon annularis*, under equal prey density, the potential feeding rate under the light intensity at 2 m is 95% of that at 1 m, but only ~80 and 35% at 5 and 15 m depths, respectively (Holzman & Genin 2003). However, the relative rarity of zooplanktivorous fishes near the surface indicates that attraction to stronger light was not a major factor determining their foraging location (Fig. 2). Apparently, fish avoided foraging away from the bottom (mid-water and near-surface water) due to the lack of either topographic shelters or navigational markers, or another unknown reason. The weak correlations between environmental factors and the abundance of nocturnal fishes ('temporal patterns') might indicate some degree of site fidelity (Marnane 2000) through niche separation, territoriality, or another mechanism.

An abrupt increase in the density of zooplankton was observed exactly at sunset (0 ± 8 min after sunset), peaking 30 min after sunset (Yahel et al. 2005a; Fig. 3 in the present study). In accordance, the nocturnal fish emerged, on average, 22 min after sunset (Fig. 3). Similarly, the fish disappeared from the water column 86 ± 76 min before sunrise (Fig. 3), in accordance with the timing of the descent of nocturnal zooplankton (82 ± 10 min before sunrise at our study site; see Yahel et al. 2005a). This temporal overlap persisted through the night, as indicated by the correlation between the half-hourly means of nocturnal zooplanktivorous fish and backscatter intensity at 12 m depth.

The ADCP backscatter was used as a proxy for the density of zooplankton. However, the fish themselves could have contributed to the backscatter values, rendering trivial the correlation between the fish and ADCP backscatter intensity (Fig. 3). To indirectly test this possibility, we compared the ADCP backscatter values at 0.75 mab (where fish are abundant) to those at 5.25 mab (where the density of fish was very low). In a previous study (Holzman et al. 2005), we showed that the densities of zooplankton at 0.25 to 1.25 mab and at 5 mab were strongly correlated. Thus, if the backscatter intensity is determined mostly by fish, no correlation of that intensity between 0.75 and 5.25 mab should be expected. The fact that the correlation in zooplankton densities was high (Spearman correlation, r = 0.88,

p < 0.001) and similar to that (r = 0.82) observed for zooplankton counts (Holzman et al. 2005) suggests that the backscattering value was mostly determined by zooplankton density.

The pattern observed in the backscattering values could have been affected by suspended sediments. However, the quantity of suspended sediments at our site exhibits a diel cycle only in the 1 mab, with a sharp decrease during the night, but no detectable changes higher (>1 m) in the water column (Yahel et al. 2002, 2005b). This cycle is due to reduced resuspension by burrowing fish, which are active only during the day (Yahel et al. 2005b). Therefore, it is highly unlikely that the increase in echo intensity at nightfall (Figs. 3 & 5; Yahel et al. 2002, 2005a) is due to suspended sediments.

Our findings can be used to estimate the overall zooplanktivory rate by the entire guild of nocturnal zooplanktivorous fish at our study site. To do so, we use the *in situ* feeding rates found for the nocturnal fish *Apogon annularis* by Holzman & Genin (2003) as the representative feeding rate for all planktivorous species. Since this species is smaller than most of the zooplanktivorous fishes observed in this study, our estimate is likely to be conservative, as feeding rate increases with body size (Jobling 1993). Multiplying the average feeding rate of 25 µg C min^{-1} fish^{-1} (observed in the field, under natural zooplankton densities; Holzman & Genin 2003) with the interpolated density of zooplanktivorous fish between the shoreline and 15 m depth (3.7 fish m^{-1}; Table 1), the total zooplankton predation is approximately 6.5 mg C m^{-2} d^{-1} (considering 11 h of feeding each night, on average) or 2.4 g C m^{-2} yr^{-1}. The integrated abundance of zooplanktivorous fish on the reef was calculated based on lengths of 15, 20, 35, and 20 m for 1, 2, 5, and 15 m depths, respectively (Fig. 2, Table 1). These estimates are similar to those calculated by Hamner et al. (1988) for diurnal zooplanktivores at Davis Reef, Great Barrier Reef (2.8 g C m^{-2} yr^{-1}). This high predation rate can substantially contribute to import of carbon and nutrients from the open water to the reef community (Erez 1990). However, unlike diurnal fish, which feed primarily on neritic and pelagic holoplankton, a large portion (40 to 70%; Marnane & Bellwood 2002, Holzman & Genin 2003) of the zooplankton consumed by nocturnal fish is of reef origin (mero- and demersal plankton). This high predation by nocturnal zooplanktivores can be the reason for the gradual decline in zooplankton abundance during the night (Fig. 3). However, behavioral causes, such as a gradual descent of satiated zooplankton to the bottom late at night (Pearre 2003), cannot be ruled out.

It is generally accepted that zooplankton detection by visual predators is much reduced at night (e.g. Gli-

wicz 1986, O'Brien 1987, Bollens & Frost 1989, Giske et al. 1994) and that the weak predation pressure in darkness is the most likely explanation for other major trends in benthic ecosystems, including the nocturnal release of gametes and larvae (Harrison & Wallace 1990, Morgan & Christy 1995, Hovel & Morgan 1997), the occurrence of larval recruitment during the night (e.g. Acosta et al. 1997, Acosta & Butler 1999), and the nocturnal ascent of many demersal (bottom-associated) zooplankton species into the water column (Yahel et al. 2005a). However, the claim that zooplankton is protected from visual predation at night is hard to reconcile with the high abundance of nocturnal, visual zooplanktivorous fishes over the coral reef, as reported in this study. The role of nocturnal fishes in the trophic dynamics of shallow benthic communities can be far more important than has so far been assumed.

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