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Daily cycles of suspended sand at coral reefs: A biological control

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Abstract

Sediment resuspension has a major ecological role in many coastal habitats, lakes, and marine environments. Waves and currents are generally thought to be the major control on sediment resuspension. In this study, the temporal and spatial distributions of suspended sand concentrations (SSAC) were measured at five coral reefs in the northern Gulf of Aqaba, Red Sea, by directly filtering seawater through 100-μm mesh nets. Levels of near-bottom SSAC were twice as high during the day (4.8–9.7 mg m^{-3}) than at night (2.3–5.2 mg m^{-3}). Vertical profiles showed a sharp increase of SSAC (2–6-fold) toward the bottom during the daytime but not at night. The contributions of wind, waves, and currents to variations in SSAC were nonsignificant except during rare southern storms. Temporal and spatial changes in the level of SSAC during the day corresponded with the abundance of benthivorous fish and their activity pattern. Resuspension activities by fish numbered $>$1.5 resuspension events m^{-2} h^{-1} and were confined to daytime. An in situ experiment in which fish were excluded from a large section (250 m^2) of the reef resulted in elimination of the day-night differences and a significant decrease in daytime SSAC over the treated reef section in comparison to the open, control sites. This study is the first report of a daily pattern of suspended sediment at coral reefs with fish activity as its causative agent.

The concentration and characteristics of suspended sediment can greatly affect the biology and ecology of benthic organisms (Snelgrove and Butman 1994) in coral reefs (Dodge et al. 1974; Loya 1976; Larcombe and Woolfe 1999*b*; Larcombe et al. 2001), shallow lakes (Havens 1991; Evans 1994; Bloesch 1995), estuaries (Underwood and Paterson 1993; De Jonge and Van Beusekom 1995), intertidal sandflats (Grant 1983), and the deep sea (Graf 1992). Detrimental effects of high loads of inorganic particles (Rogers 1990) include a reduction in water transparency, which results in lower benthic production (Falkowski et al. 1990; Dodge et al. 1974), clogging of feeding apertures (Wilkinson 1983), necrosis of tissue (Riegl 1995), reduced pumping rates by active suspension feeders (Gerrodette and Flechsing 1979), a reduction of the usable fraction of particulate food for suspension feeders (Bayne 1998), and increased energy expenditures by benthic animals to remove sediments accumulated on them (Stafford-Smith and Ormond 1992; Stafford-Smith 1993). On the other hand, some species, including corals, may benefit from suspended sediments by feeding on bacteria and organic components attached to sediment particles (Mills and Sebens 1997; Rosenfeld et al. 1999; Anthony 1999, 2000).

The concentration of inorganic particles in the water column is controlled both by external forces such as floods, rivers, and aeolian inputs and by internal processes, such as resuspension of sediments by currents and waves (Bloesch 1995). In the marine environment, resuspension is generally thought to be mostly controlled by water motion (Davis 1993; Mei et al. 1997; Larcombe and Woolfe 1999*b*; Prandle et al. 2000 and references therein). In more sheltered environments, including many freshwater lakes, biological mechanisms, primarily the feeding activities of benthic fish, can play a major role in determining the degree of resuspension and the overall water clarity (Meijer et al. 1990). In lakes, the presence of benthivorous fish significantly increases the quantity of resuspended sediments, detritus, and nutrients, leading to an increase in algal biomass and overall decrease in water clarity (Meijer et al. 1990; Havens 1991). In spite of the common presence of a similar guild of fish associated with many coral reefs, their role in determining sediment resuspension is virtually unknown. Clifton and Hunter (1973) reported that the structure of bottom sediments near coral reefs at the Virgin Islands was mostly affected by fish-induced bioturbation and not by waves or currents. Goatfishes (Mullidae) are probably the most conspicuous fishes disturbing and resuspending the sediments at coral reefs (Clifton and Hunter 1973; Bellwood 1995; Montgomery et al. 1989). These fish search for buried prey using a pair of muscular barbells, vigorously stirring up and resuspending sediments (Uiblein 1991). Most members of this guild are diurnal, feeding and reworking the sediment during the day and sleeping in reef crevices during the night (Randall 1983).

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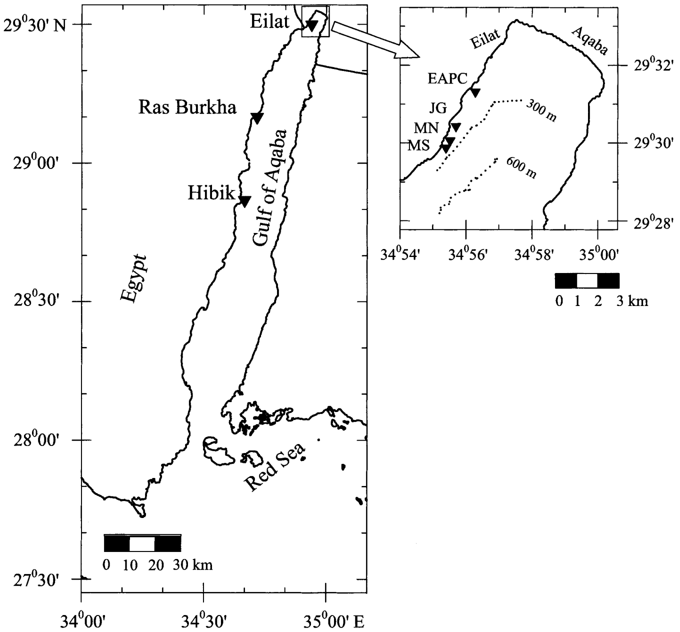

Fig. 1. The study sites at the Gulf of Aqaba. Eilat sites: EAPC, Eilat Ashkelon Pipe Company terminal; JG, Japanese Gardens; MN and MS, Steinitz Marine Biology Laboratory north and south, respectively.

Although the ecological role of suspended sediments has been extensively studied in areas with high rates of natural or anthropogenic sedimentation (e.g., Stafford-Smith and Ormond 1992; Rice and Hunter 1992; Umar et al. 1998), the role of low-level sediment loads, such as those prevailing in numerous coral reefs, is not well known. Suspended inorganic matter in reefs are mostly fine sediments, i.e., silt, clay, and fine sand <100 μm typically constitute $>90\%$ of the suspended sediment. Coarse sediments however, encompass $>70\%$ of the near-bed sediments trapped in sediment traps (Aller and Dodge 1974; Rogers 1983; Riegl et al. 1996).

The goals of this study were (1) to characterize the dynamics of suspended coarse sediments over coral reefs that are located away from external sources of sediments, on spatial and temporal scales that are relevant to the benthic community and (2) to examine the contribution of fish to the observed sand dynamics.

Study sites

This study was carried out at five fringing reefs along the northwestern coast of the desert-enclosed Gulf of Aqaba (Eilat), Red Sea (Table 1, Fig. 1): four sites in Eilat (EAPC, JG, MN, and MS; see Fig. 1 inset) and one in Hibik (HB), Sinai. Sampling sites were located at 8–15 m depth (5 m at JG) at the outer reef slopes, which then descended rapidly to deeper water (>200 m).

Oceanographic and meteorological conditions—The weather and hydrography of the Gulf of Aqaba has been described by Reiss and Hottinger (1984), Genin et al. (1994, 1995), and Genin and Paldor (1998). The tidal range is 0.25–1 m, with a semidiurnal periodicity. Current speeds at the study sites peak at <20 cm s^{-1} and flow primarily along the shore. Semidiurnal reversals of flow direction occurred during May–October, whereas fluctuations of lower frequencies dominate the rest of the year (Genin and Paldor 1998). Currents at EAPC and JG were, on average, weaker than those at MN and MS. Sea conditions at all sites were usually calm with a typical wave period of 2–3 s and wave height <0.3 m. Southerly winter storms ($\sim$1–2 a year), associated with large waves (higher than 2 m), are the only exception. No ripple marks were observed on sand patches at any of the sampling sites except after strong southerly storms.

External inputs of sediments to the gulf are low and include aeolian dust transport and rare ($\ll 1$ yr^{-1}) floods. The water in the Gulf is considered extremely clear (Fishelson 1971; Reiss and Hottinger 1984), but data on sedimentation rates are few. Mohar (1997) measured sedimentation rates of 40–70 mg cm^{-2} d^{-1} at 6–8 m depth at the MN and MS sites during the period of this study. These low sedimenta-

Table 1. Main characteristics of the study sites.

Site	Acronym	Location	Description	Human activity	Bottom depth (m)	Distance from shore (m)
Eliat Ashkelon Pipe Company terminal	EAPC	Eilat, Israel	Rich reef slope; starts at 7 m depth, no lagoon	Closed to all recreational activities	11	200
Japanese Garden	JG	Eilat, Israel	Rich reef slope starts at 5 m depth; seaward of a reef flat bordering a shallow lagoon	Within the closed section of the nature reserve	5	50
Marine Lab North	MN	Eilat, Israel	Reef slope starts at shoreline, no lagoon	Both researchers and tourists; >10 divers d^{-1}	8	80
Marine Lab South	MS	Eilat, Israel	Reef slope starts at shoreline, no lagoon	Both researchers and tourists; >10 divers d^{-1}	9	75
Hibik	HB	Sinai, Egypt	Rich reef slope; 100 m seaward of an extensive reef flat bordering a shallow lagoon	Extremely scarce; some line fishing activity by Bedouins	11	250

tion rates are comparable to those at the most prolific oceanic reefs (e.g., West and Davies 1981; Rogers 1983, 1990). Fine particles contribute substantially to the suspended particulate pool at the studied coral reefs. For example, the concentrations of particulate carbonates >0.7 μm in diameter in our nocturnal water samples (660 mg m^{-3} [SD 940]; Yahel, Erez, and Genin, unpubl. data) are well within reported values for other undisturbed reef sites (West and Davies 1981; Rogers 1990; Hata et al. 1998) and about two orders of magnitude higher than the suspended sand concentrations (SSAC) measured in the same water samples (3.3 mg m^{-3}, see below).

Reef bottom characteristics—The bathymetry of the Eilat sites is described by Reidenbach et al. (see *http://www.stanford.edu/~mar10/Bathymetry_Maps.html*). The recent sedimentary history of the nature reserve (JG) and the Steinitz Marine Biology Laboratory sites (MN and MS, Fig. 1) has been described by Shaked et al. (in press). In brief, the three dominant sediments groups in these sites are (1) clastic sediments of terrigenous origin (mostly granites, gneisses, and rhyolite from volcanic dykes), (2) clastic marine sediments, and (3) carbonate sediments produced in situ by the reef system. The foundation of the fore-reef slope at MS, MN, JG, and EAPC is a carbonate platform with abundant corals and mobile carbonate sand that ranges in thickness from 1 to 30 cm. Moving seaward down the slope the sedimentary cover is thicker and contains many coral fragments. At the MN and MS sites, broad stretches of exposed beach rock, composed of cemented crystalline pebbles, line the slope to a depth of 7–9 m, which provides a substrate for many corals. Deeper than ~7 m, the slope increases and is covered by a mixture of corals, coral fragments, and carbonate sand punctuated by outcrops of cemented crystalline pebbles. This slope extends down to ~40 m, to a horizontal terrace of carbonate-sand and corals.

The fish and the benthic communities at our study sites have been described by Rilov and Benayahu (2000), Fishelson (1971), and Benayahu and Loya (1977). Stony corals dominate the coral reefs along with the common hydrozoan corals (*Millepora* spp.), soft corals, encrusting algae, anemones, sponges, tunicates, and polychaetes. Branched corals are relatively more dominant at MN-MS and EAPC than at HB and JG. The benthic community at MN and MS has been studied by R. and G. Genin (unpubl. data). Live coral cover at this site is ~15%, and gravel (crystalline pebbles and corals fragments), dead rocks, and sand covered ~50%, 30%, and 5% of the area, respectively.

Materials and Methods

Physical parameters—Wind, as a proxy for surface waves, was measured concurrently with all SSAC measurements. In Eilat, wind measurements were made every 10 min by use of a Met-One gauge (Campbell Scientific) positioned on the roof of the marine biology laboratory. Wind measurements at HB were made aboard ship every hour by use of a manual gauge (Siap-Bologna 17602). An electromagnetic current meter (S4; Inter-Ocean) was used to measure the currents between MS and MN during February–August 1997. The current meter was deployed on a nonmetal rod 1 m above the bottom and set to record the average velocity over 1 min every 2–10 min.

An acoustic Doppler current profiler (ADCP, WH-600 RDI) and two acoustical Doppler velocimeters (ADV; 5 MHz OceanADV and 16 MHz MicroADV; Sontek) were deployed during the fish exclusion experiment (see below). The ADCP was deployed on the bottom facing upward to record the current profile (1-m bins, 10-min averages) next to the MN site from 15 m depth to the surface. The ADV were used to measure currents at the boundary layer 15 cm above the bottom underneath the net and at the control site. The ADV acoustic backscatter strength was recorded as a proxy for fine suspended sediment concentration (Holdaway et al. 1999). The two instruments were used at different frequencies, and the MicroADV had an inherent reduced sensitivity (signal : noise ratio [SNR] < 7) in comparison to the OceanADV (SNR > 12), so the acoustic signal amplitude was normalized within each instrument for further analysis. Both ADV were equipped with tilt, pressure, and temperature sensors and were monitored and controlled in real time from the laboratory. Usually 10-s averages were recorded, but short-term records of higher frequencies (3–25 Hz) were routinely taken to allow wave height and period measurement.

Calculations of the threshold current speed required to resuspend sediment was based on the Shields diagram (van Rijn 1993; Allen 1997) and the hydrodynamic parameters calculated for this site by Reidenbach et al. (unpubl. data), who, in the summer of 1999, carried out an extensive field study of the currents at precisely our fish exclusion site. Using a vertical array of three ADV operated at 25 Hz, they measured average current speeds of 4.7 cm s^{-1} (SD 2.9) and 2.6 cm s^{-1} (SD 1.8) at 1 and 0.1 m above the bottom, respectively. A logarithmic fit was used to calculate the mean drag coefficient for that site ($C_D = 0.01$) and the mean roughness height ($z_o = 16.6$ mm). Thus, the threshold shear velocity for initiation of sand motion (median grain size 150 μm, temperature 23°C, and salinity 40.3‰) was 1.15 cm s^{-1} (corresponding to current velocities of 11.5 and 6.2 cm s^{-1} at 1.0 and 0.15 m above the bottom, respectively). Following the same consideration, the calculated threshold for sand resuspension was 1.24 cm s^{-1}.

Temporal distribution of SSAC—Water samples were taken every 2 weeks simultaneously at JG, MN, and MS for 1.5 years (February 1996–July 1997); two samples were taken at each site on each sampling day, one during the day and the other at night. Each sample was obtained by continuously filtering water for ~4 h (50–60 m^3 seawater per sample). For logistical reasons, the daytime sampling started 5 h before sunset and nocturnal sampling half an hour after dark. On two instances of very calm seas and no wind on the day after our sampling (04 June and 21 July 1997), a second daytime sample was collected at each site. A total of 78 pairs of day-night samples were collected.

A daily pattern in the quantity of resuspended sediments was examined by consecutive 4-h integrated samples taken during 3 d at three coral-reef sites (MN and MS, 18–21 July 1997; HB, 14–18 August 1997). These sequential samples were categorized as ‘‘dawn’’ and ‘‘dusk’’ (beginning 2 h prior and ending 2 h after sunrise and sunset, respectively), midday periods (''morning'' and ''afternoon''), and nocturnal periods (''evening'' and ''night'').

The water samples were taken by use of high-capacity submersible pumps (220 V, 14 $m^3 h^{-1}$, Tsurumi Manufacturing). The pumps were deployed 0.5–0.6 m above the bottom, except at JG, where the pump was deployed 5 m seaward of the wall and 1.5 m above the bottom. At the surface, water was filtered through a 1-m long, 20-cm diameter, 100-μm mesh sleeve. To avoid excessive pressure on trapped particles, the net was fully submerged in a large tank. The pumping rate was measured (±1%) prior to each sampling.

In the laboratory, the sample was divided into two equal aliquots by use of a Folsom splitter (Omori and Ikeda 1984), one for microscopic and isotopic examination of the sample and the second fractionated through a column of four mesh sizes: 1,350, 500, 200, and 100 μm. Each size fraction was collected on a precombusted, preweighed glass-fiber filter (Whatman, GF/A), dried for 24 h at 60°C, weighed, combusted for 4 h at 450°C, and weighed again. In this way, the concentrations (mg m^{-3}) of inorganic particles ($>$100 μm sand, defined as SSAC) and organic particles were obtained for each size fraction. Weighing was done to the nearest 10 μg by use of a Mettler-Toledo analytical balance (AG245, Greifensee).

The composition of the suspended particulate matter was analyzed microscopically in a subset of nine day/night pairs of samples (a pair every 6 weeks). Each sample was size-fractionated as above, and the particulate content of each fraction was sorted and counted by use of a dissecting microscope. Aliquots (2.5 ml) were repeatedly drawn with a Stempel pipette (Omori and Ikeda 1984) and added to the counts until a total of $>$300 particles was reached. Living organisms were sorted into three categories: nonshelled planktonic organisms (primarily copepods, polychaetes, chaetognaths, decapod larvae, and other meroplanktonic forms), shelled organisms (primarily gastropods and benthic foraminifers), and large planktonic algae. Nonliving particles were sorted into organic detritus, crustacean molts, shells, and sand grains. The sand grain category was a mixture of carbonated and quartz grains with a large fraction of small platelet-shaped particles (87% [SD 9%] in the 100–200 μm fraction). The later fraction was composed mostly of mica and feldspars (A. Almogi-Labin, pers. comm.) that originated from the erosion of crystalline rocks.

Vertical distribution of SSAC—Vertical profiles of SSAC were measured by use of two vertical pump arrays, each of which consisted of five small, submerged pumps (220 V, 1.7 $m^3 h^{-1}$, AT-2220, Chosen Pumps). The five pumps were attached to a taut mooring line with their apertures at 0.2, 0.6, 1.1, 2.1, and 7.1 m above the bottom (hereafter ''mab''), suspended by a subsurface buoy. The two arrays were moored 25 m apart, at 15 and 13 m depth, 80 and 90 m offshore, respectively, at the reef slope between MN and MS. The samples were filtered by use of small 100-μm mesh sleeves (50 cm long and 20 cm diameter) attached to each pump outlet. At the end of each sampling session (lasting ~5 h), scuba divers closed the sleeves and transferred the samples to the laboratory. Very large particles were removed from the samples by filtering the water through a 1,350-μm mesh. The remainder was collected on a precombusted glass-fiber filter (Whatman, GF/A). The organic and inorganic mass of all particles was determined as above with no size fractionation. Four daytime (0800–1300) and four nocturnal (2300–0400) sampling sessions carried out during 13–18 September 1999.

Sediment resuspension by fish—Sediment disturbance rates per reef area by different reef fish and other reef organisms were directly measured at the MS site over four adjacent reef plots (3.5 × 10 m each). Two stationary scuba divers at 4–8 mab measured the duration of all fish resuspension events occurring within the plot for 1 h. These sampling sessions ($N = 30$) were replicated throughout the day for 6 consecutive days (19–24 August 1998).

The direct measurements at MS (see ''Results'' section), as well as additional observations and fish surveys in the other sites, led to the three most conspicuous sediment-disturbing fishes being selected as our target species for monitoring biological resuspension activity: Forsskal's goatfish (*Parupeneus forsskali*, Fourmanoir and Gueze 1976) searches for food by rapidly burrowing and pushing its mouth into sand or coral gravel patches or by ejecting water jets from its mouth to vigorously blow off sediments (Gosline 1983); the longbarbel goatfish (*Parupeneus macronema*, Lacepede 1801) rarely burrows into the sediment but instead uses its hyoid barbels to probe the substratum (Gosline 1983); the bluethroat triggerfish (*Sufflamen albicaudatus*, Ruppell 1829) probes or burrows for benthic invertebrates in the sediment by ejecting strong water jets.

The activity of individual fish belonging to the above-selected benthivorous fish was recorded concurrently with the daily periodicity of SSAC sampling at the Hibik and Eilat sites. Observers tracked three–eight different individual fish during a typical 60-min dive, each for a maximum time of 5 min. The abundance of the three taxa was estimated at the end of each dive by counting all individuals along a prefixed belt transect 10 m width and 150 m length. Fish abundance was also estimated at EAPC, where only daytime SSAC levels were measured. The resuspension activity of the fish was estimated in terms of activity time per area (s $m^{-2} h^{-1}$), calculated as the product of fish density and the average amount of the time a fish resuspended sediment.

Fish exclusion experiment—To experimentally test the role of benthivorous fish in determining sediment resuspension over the coral reef, a fish exclusion experiment was carried out in front of the marine biology laboratory, between the MN and MS sites, at the site where the above-mentioned vertical gradients were measured. A slightly buoyant plastic net (1.5 × 1.5 cm hole size) was used to exclude fish from a large (25 × 10 m) section of the reef (10–14 m depth). The long axis of the area was parallel to the prevailing along-shore current. A 20-cm wide strip of chicken net (1 × 1 cm hole size) was attached along the margins of the plastic net with a 6-mm cable, which served as a weight for the net margins and allowed a tight fitting of the cage to the complex reef bottom, preventing fish from penetrating from the side. Extra pieces of chicken net were used where needed to seal the many crevices, tunnels, and gaps between corals. None of the target species (*P. forsskali, P. macronema,* and *S. albicaudatus*) were observed to enter the exclusion area.

Vertical profiles of SSAC were measured, as described above, during both day and nighttime, at the center of the caged area. A second pump array was used as a control over adjacent open reef sites (see below). The same sampling design that was used to study the vertical distribution of SSAC was used throughout the cage treatment (21–27 December 2000) and after cage removal (4–8 January 2001) over both the caged reef section and the nearby control sites.

Logistical limitations and restrictions imposed by the Nature Reserve Authority allowed only a single deployment of the exclusion cage. We thus used (1) an intrasite comparison (“within”) of the treatment period with pre- and posttreatment effects; and (2) an intersite comparison (“between”) the treated site and several control sites. During the preliminary experiment (no cage), the two arrays were moored within the reef section that was afterward caged. After caging, one vertical pump array was positioned in the center of the caged section (12 m depth), and the other was used as a control (with no net cover). The control array was located at the vicinity of the MS site and was relocated every 2 d within the 10–14 m depth contours and a distance of 80–120 m south of the enclosure, to sample a variety of microhabitats. An underwater video camera was used to monitor online the fish activity next to the vertical pump arrays throughout the experiment.

Statistical analysis—Statistical analysis was done by use of STATISTICA software (version 2000; StatSoft). The occurrence of a vertical gradient in SSAC was tested by use of the Page test for ordered alternatives (Siegel and Castellan 1988). This nonparametric test is a modified version of the Kruskal-Wallis one-way ANOVA of ranked data. ADV and ADCP data were processed by use of MatLab 6.0 (R12; MathWork).

Results

Physical parameters—The average current speed at MN and MS between February and August 1997 was 4.6 cm s^{-1} (SD 1.9), similar to that reported by Genin and Paldor (1998) and Reidenbach et al. (unpubl. data), with currents slightly stronger at night than during the day (4.9 cm s^{-1} [SD 2.1] and 4.4 cm s^{-1} [SD 1.5], respectively). The maximum current speed recorded at Eilat during the sampling sessions was 9.6 cm s^{-1}. Current speed exceeded the threshold for initiation of sediment motion only <4% of the time, and this threshold was more often exceeded at nighttime.

Moderate northerly winds prevailed during our 1.5-yr time series. Only 2 of the 32 sampling days occurred during southerly storms, which produced waves >2 m at the coastline. These storms redistributed bottom sediments and greatly increased turbidity. All instruments had to be shut down or retrieved because of rough sea conditions during storms, so no measurements were made during those events. Therefore, our analysis was limited to the prevailing conditions of northerly winds and small waves.

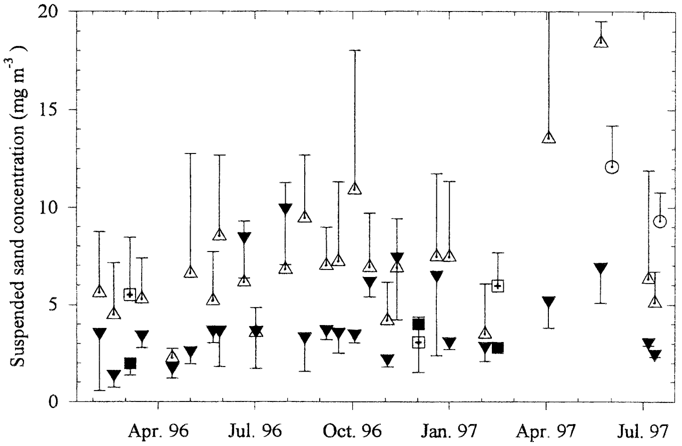

Fig. 2. Average day- and nighttime SSAC (100–1,350 μm) at Eilat coral reefs from February 1996 to July 1997. Open symbols (+SE) represent daytime; filled symbols (−SE) represent nocturnal samples. Each point indicates an average of three reef sites (MS, MN, and JG). Sampling dates with weak wind (<3 m s^{-1}) during the day and stronger wind during the night are marked with squares. Open circles (4 June and 21 July 1997) indicate a day during which the sea was very calm (no wind or waves). SSAC values during the day were significantly higher than during the night (sign test, $P <$ 0.001).

The average wind speed in Eilat during our time series was 4.4 m s^{-1} (SD 1.4), with an average daytime speed of 4.9 m s^{-1} (SD 1.7) and a nocturnal speed 4.0 m s^{-1} (SD 0.9). Wind speed >7 m s^{-1} was recorded in only two sampling sessions (13 November 1996 and 19 July 1997). Similarly, the wind in Hibik was stronger during the day than night (6.3 m s^{-1} [SD 1.5] and 5.3 m s^{-1} [SD 1.1], respectively).

Temporal distribution of SSAC—Throughout our time series at MN, MS, and JG, daytime values of SSAC averaged 7.1 mg m^{-3} (SD 3.6), nearly two times higher than the nocturnal levels (4.4 mg m^{-3} [SD 2.3]; repeated-measures ANOVA, $F_{1,18} = 24.90$; $P < 0.0001$) (Fig. 2). Microscopic counts of sand grains in the size range of 100–1,350 μm indicated that this daily difference in weight mostly reflected a threefold increase in the number of total sand grains (3,990 grains m^{-3} [SD 2,617] during the day and 1,379 grains m^{-3} [SD 727] during the night; paired *t*-test, $P < 0.01$). Numerically, sand grains formed 67% of the suspended particulate matter (organic + inorganic) during the day but only 32% at night (Fig. 3).

The intersite variability in SSAC was significantly higher during the day than the night (coefficient of variance 48% and 37%, respectively, paired *t*-test, $P < 0.001$). No significant correlation was found between the sites for daytime SSAC, compared with a significant correlation (Spearman $r > 0.49$, $P < 0.05$ for each) during the night. Daytime SSAC were significantly higher at MN than at the other two sites (Tukey HSD, $P < 0.05$), but nocturnal values were not (Table 2). Daytime and nocturnal SSAC correlated only within the MS site (Spearman $r = 0.49$, $P = 0.03$). The fraction of the smallest particle size (100–200 μm) contributed 54% (SD 19%) to the total SSAC during the day (Table 2) but

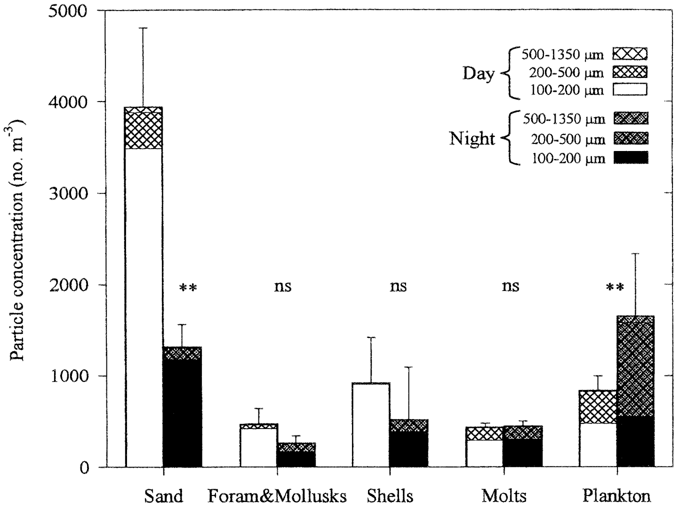

Fig. 3. Daytime (left bars) and nighttime (right bars) particulate composition of the coral reef water collected on nine different dates in Eilat. Sand, sand grains (100–1,350 μm); Foram&Mollusks, living organisms with a carbonated shell, primarily benthic foraminifers and gastropods; shells, identifiable carbonated shells of dead mollusks; molts, empty, noncarbonated husks, mostly of copepods and other crustaceans; and plankton, nonshelled plankton. Error bars are SE of the total counts (100–1,350 μm). The significance of the difference between day and night concentrations was tested by use of the Wilcoxon matched-pairs test: ns, no significant difference; $^{**}P < 0.01$.

declined to 41% (SD 15%) at night, concurrent with the general decrease in SSAC. The numeric contribution of these fine sand grains to the total grain density similarly decreased from 97% during the day to 88% at night (Fig. 3).

The organic particles in our samples were mostly zooplankton, which exhibited a mirror-image distribution compared with that of SSAC, with nocturnal densities being about twice those of daytime (Fig. 3). At night, but much less so during the day, zooplankton and inorganic masses were correlated ($r = 0.57$ and 0.27, respectively), which indicates some contribution of armored zooplankton shells to the inorganic particulate pool.

A clear daily cycle of elevated SSAC during the day and lower concentrations at night was observed during the 3 d of continuous sampling at the three sites (Fig. 4; two-way ANOVA, $F_{5,23} = 4.26$, $P = 0.007$). The daytime increase of SSAC from the nocturnal levels was, on average, 260% (SD 104) at Eilat (Fig. 4A) and 211% (SD 99) at Hibik (Fig. 4B). On some occasions, a peak in SSAC occurred at dusk rather than noon. A similar daily pattern was evident in the acoustic record during the fish exclusion experiment at both the control site (normalized backscatter of 0.4 [SD 1.2] at day and −0.4 [SD 0.5] at night) and the experiment site after net removal (normalized backscatter of 0.4 [SD 1.2] at day and −0.4 [SD 1.6] at night, Table 3). These differences were highly significant at both sites (t-test, $P < 0.001$). The SSAC level at the MN-MS site was significantly higher than at Hibik (planed comparison, $F_{1,23} = 5.0$, $P = 0.35$; Table 2, Fig. 4).

Vertical distribution of SSAC—During the day, the concentrations of suspended sediments sharply increased near the bottom (Page test, $P < 0.01$,), with SSAC levels near the bottom being about twice those at ~1 m above the bottom. Above that height, the SSAC was fairly uniform throughout the water column and did not change much with time. The SSAC during the night was nearly homogenous throughout the water column, with no significant gradient near the bottom (Page test, $P > 0.5$). The daytime concentrations aloft were similar to those found throughout the water column at night (Fig. 5). The organic particles (zooplankton) exhibited a reverse gradient, with a nocturnal decrease in concentration near the bed (R. Yahel and Genin, unpubl. data). This decrease was much less pronounced during the day. The concentrations of organic particles and SSAC were correlated ($r = 0.57$, $P < 0.001$) during the night but not ($r = 0.23$, $P = 0.15$) during the day.

Sediment resuspension by fish—The three monitored benthivorous fish species resuspended sediment only during the daytime. *P. forsskali*, the most abundant of the three, was also the most active. The fish usually emerged from its nocturnal shelters ~40 min after sunrise and started to explore the area from aloft (>1 mab) but rarely approached the bottom. The proportion of time devoted to probing and digging into the bottom gradually increased, reaching typical daytime values ~1.5 h after sunrise, when the fish spent 28%–44% of the time resuspending sediments (Fig. 6A). Of this time, ~30% was spent probing the sediment and 50% digging. Occasionally, the fish dug a trench 10–15 cm deep, a few decimeters in length, in a single burrowing event. The resuspension was enhanced when the fish ejected sediment from its mouth or through the operculum while swimming

Table 2. Day and night SSAC at four coral reef sites (see Table 1 for site description). The average (SD) contribution of each size fraction is presented as % of total sample for fine (100–200 μm), medium (200–500 μm), and coarse (500–1350 μm) sand grains. Day : night ratios were not significantly different between the four sites (Kruskal-Wallis test: $H_{(4,\ N\ =\ 80)} = 3.84$, $P = 0.40$). N = number of sampling dates; P values are for paired t-test of the total day and night SSAC; nd = not determined because of insufficient N.

	Day					Night					Day : night ratio	
Site	N	SSAC (mg m^{-3})	Fine (%)	Medium (%)	Coarse (%)	N	SSAC (mg m^{-3})	Fine (%)	Medium (%)	Coarse (%)	Average	P
JG	25	5.85 (3.41)	52 (19)	39 (17)	9 (5)	25	3.84 (2.67)	34 (17)	52 (15)	14 (5)	1.92 (1.16)	0.01
MN	25	9.74 (5.18)	54 (20)	37 (19)	9 (1.3)	29	5.24 (3.38)	44 (14)	41 (13)	15 (10)	2.32 (1.47)	0.001
MS	30	7.08 (5.75)	53 (19)	39 (19)	8 (5)	29	4.38 (2.71)	41 (16)	45 (15)	14 (7)	1.64 (1.06)	0.026
Hibik	3	4.82 (0.38)	60 (19)	37 (20)	3 (0.3)	4	2.31 (0.29)	57 (9)	33 (8)	9 (3)	2.14 (0.19)	nd

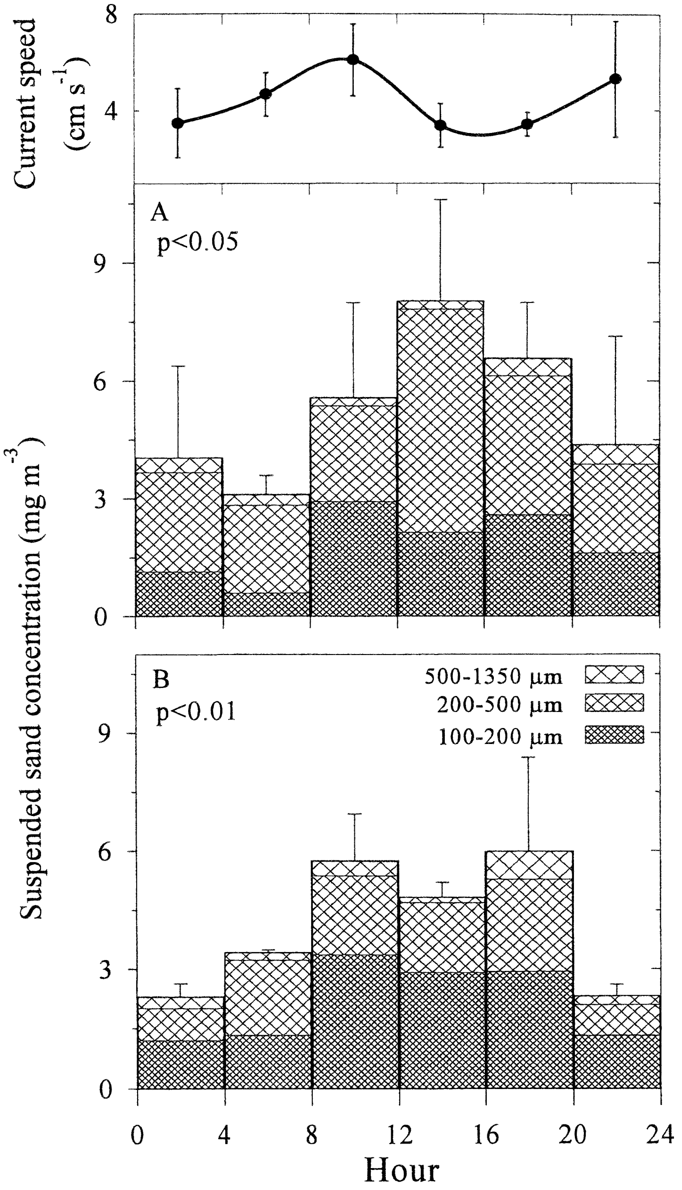

Fig. 4. Daily cycle of SSAC during 3 consecutive days at the coral reefs of (A) Eilat (MN and MS pooled) and (B) Hibik. Error bars are SD of total SSAC. The corresponding average current speeds (±SD) for Eilat are also plotted. Significant differences between sampling periods refer to Kruskal-Wallis ANOVA. The two sites at Eilat (MN and MS) were not significantly different (two-way ANOVA, $F_{1,23} = 0.66$, $P = 0.80$) and are therefore pooled for presentation.

aloft (0.5–2 mab). The fish commonly created visual sediment plumes of up to 2 m^2 in cross section. It took >1 min for the plume to disperse and become invisible. Feeding activity declined ~1 h before sunset, when the fish spent larger fractions of its time aloft. Before darkness, some of the fish schooled and swam away to deeper waters, whereas others descended to sleeping sites at the reef.

The daytime densities of the three fish species (combined) at MN-MS, Hibik, and EAPC were 21 (SD 6), 11 (SD 5), and 11 (SD 4) 1,000 m^{-2}, respectively. The abundance of

Table 3. Summary of ADVs measurements during the fish exclusion experiment and the corresponding SSAC. Day and night averages (SD) of current speeds and acoustical backscatter amplitude (a proxy for fine suspended sediment concentrations) were measured 15 cm above bottom. Acoustic backscatter was normalized within each instrument to allow comparison and is presented in 1 SD units. Near-bottom SSAC (<70 cm above bottom) were averaged over the lower two pumps. An ADV was deployed at the control site only during the treatment period.

	Enclosed site during net cover	Enclosed site after net removal	Control site during net cover
Instrument	Ocean ADV	Ocean ADV	Micro ADV
Dates	21–27 Dec 2000	4–8 Jan 2001	21–27 Dec 2000
Current speed (cm s^{-1})			
Day	3.0 (1.6)	4.1 (2.2)	4.4 (1.7)
Night	3.2 (1.5)	4.6 (2.1)	4.9 (1.9)
Difference	−0.2	−0.5	−0.5
% of time current exceed threshold for sand motion (6.2 cm s^{-1})			
Day	8.5	17.1	12.8
Night	5.3	20.0	22.7
Difference	3.2	−2.9	−9.9
Near bottom SSAC (mg m^{-3})			
Day	5.6 (2.4)	7.6 (6.6)	30.3 (43.0)
Nigh	4.4 (1.9)	3.3 (1.3)	4.7 (2.5)
Difference	1.3 (3.1)	4.3 (5.3)	25.6 (41.9)
Normalized acoustical backscatter			
Day	0.1 (1.0)	0.4 (1.2)	0.4 (1.2)
Night	−0.3 (0.7)	−0.4 (1.6)	−0.4 (0.5)
Difference	0.3	0.8	0.7

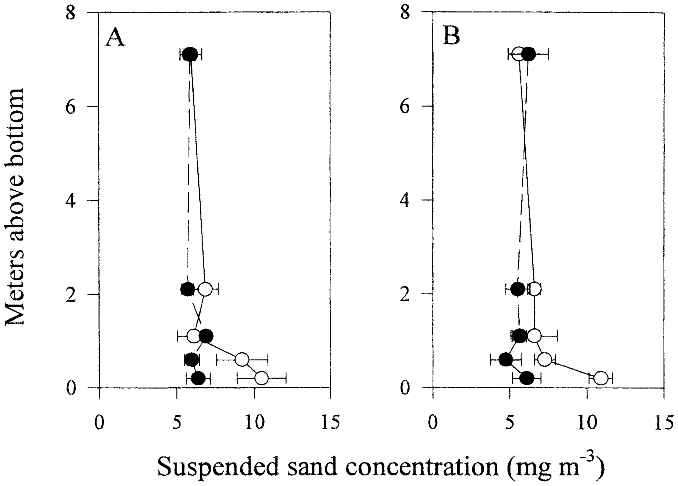

Fig. 5. Vertical distributions of suspended sand above the coral reef of Eilat (13–18 September 1999) during the day (open symbols) and night (filed symbols) at two adjacent vertical pump arrays (A) and (B). The vertical gradient in SSAC was significant at daytime (Page test for ordered alternatives, $P < 0.01$) but not at night. Error bars, SE.

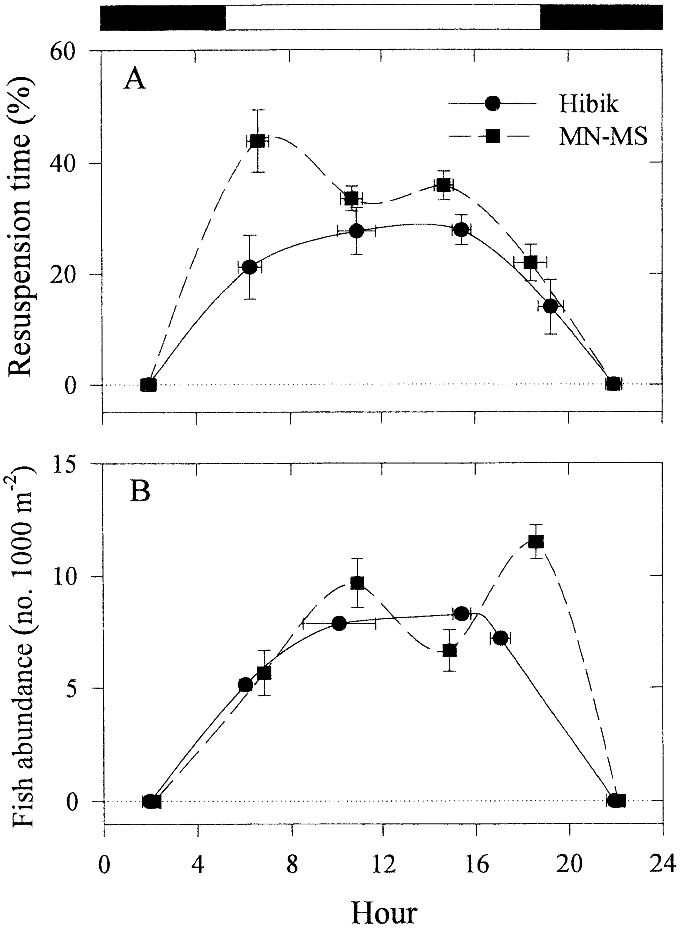

Fig. 6. (A) Daily sediment disturbance time and (B) abundance of the goatfish *P. forsskali* at the coral reefs of Hibik and Eilat (between MN and MS). Resuspension time is presented as the average percentage of the time the fish spent resuspending sediment (see "Materials and Methods" section). Vertical error bars, SE; Horizontal bars, time span of fish surveys.

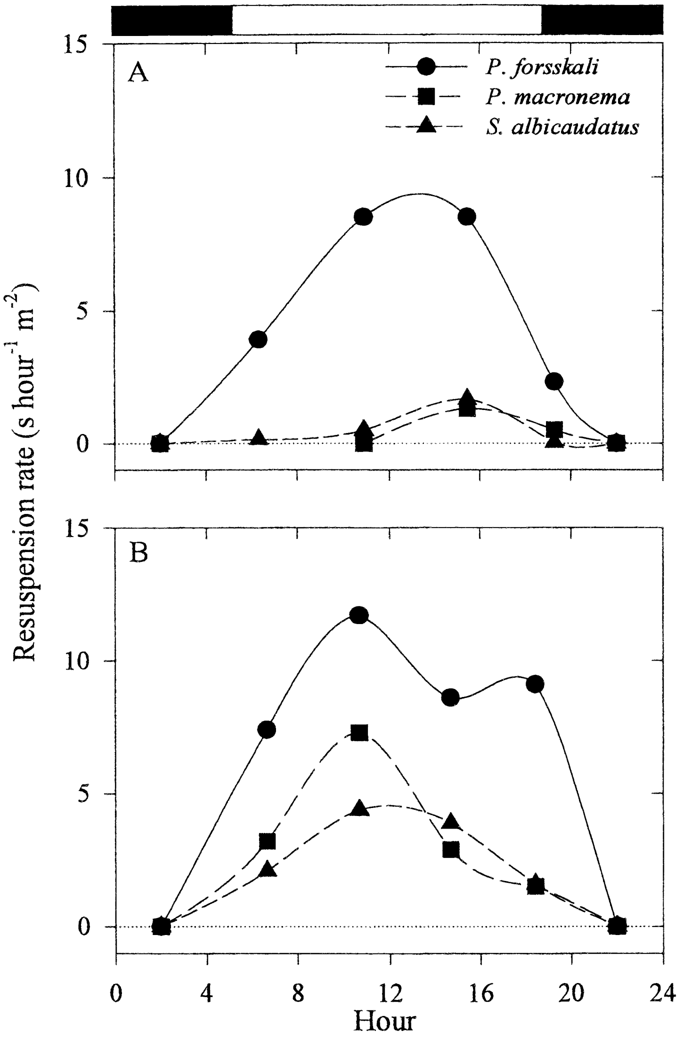

Fig. 7. Daily resuspension rate of the three monitored benthivorous fish at Hibik (A) and Eilat (between MN and MS, B). The areal resuspension rate was estimated as the product of proportion of time fish spent resuspending sediment and their corresponding abundance. Typical resuspension events lasted 4.5 s (SD 3.4) for *P. forsskali* and were usually much longer than those for the other two species. Error bars were omitted for clarity of presentation.

these fish was significantly higher at MN-MS than that at Hibik and EAPC (Tukey HSD test, $P < 0.001$), whereas the latter two sites did not differ one from another. *P. forsskali* and *S. albicaudatus* were two–three times more abundant than *P. macronema.* Variations in the abundance of fish during the day corresponded with the observed pattern in their diurnal activity (Fig. 6). No activity was observed in our nocturnal dives except from two observations of a single stingray (*Taeniura lymma,* Forsskal 1775) digging into the sediment. The relatively high abundance of *P. forsskali* at dusk at MN-MS (Fig. 6B) was due to the encounter of schools that gathered together prior to their nocturnal descent to deeper waters.

The rate of sediment disturbance by the three fish peaked at midday (Fig. 7). For *P. forsskali,* for example, the average abundance at midday at Hibik was 8.5 fish 1,000 m^{-2} (Fig. 6B) resuspending sediments 27.8% of the time (Fig. 6A), providing an average of 8.6 s of sediment resuspension m^{-2} per h (Fig. 7). Because each resuspension action in this species lasted, on average, 4.5 s (SD 3.4, $N = 1,043$), each square meter at the reef was exposed to about two midday digging events per hour by this fish alone. The total midday resuspension activity of the three species together was 11.5 and 23.4 s m^{-2} h^{-1} at Eilat and Hibik, respectively. The rates of resuspension during dawn and dusk were 25%–50% of the midday values. Our direct observations at the defined plots indicated similar values, with 4.4 s m^{-2} h^{-1} (SD 3.7) for *P. forsskali* and 7.0 s m^{-2} h^{-1} (SD 5.4) for all the fishes observed. Similarly, the observed average frequency of a single resuspension event was 0.8 m^{-2} h^{-1} (SD 0.4) for *P. forsskali* and 1.5 m^{-2} h^{-1} (SD 0.5) for the other species.

Fish exclusion experiment—The exclusion of fish produced a considerable reduction (26%–86%) of the daytime, near-bottom SSAC (Fig. 8, Table 3). This reduction was ev-

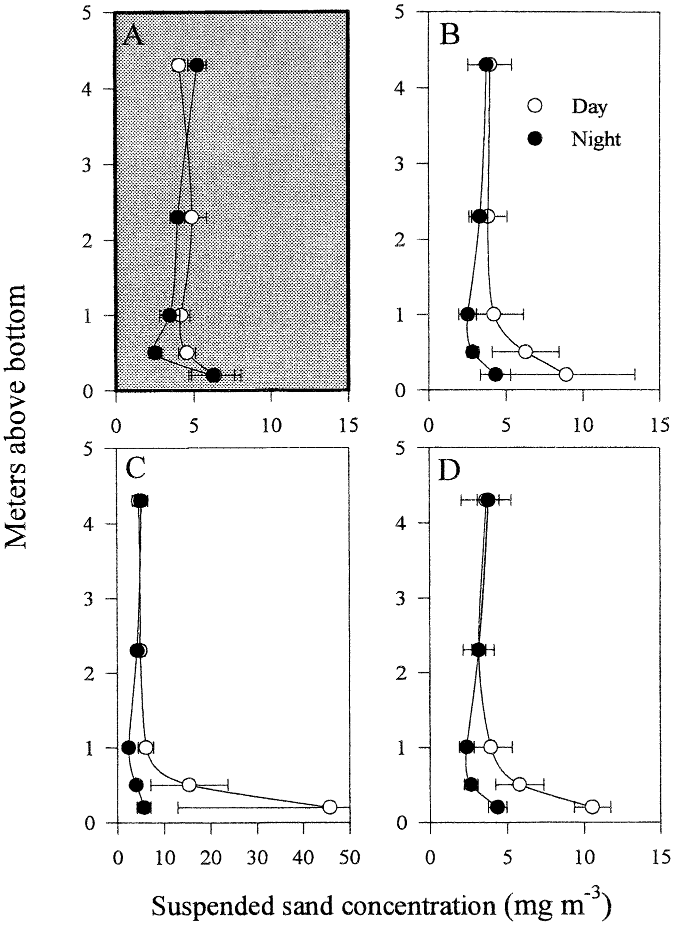

Fig. 8. Vertical distributions of suspended sand during the fish exclusion experiment for both day (open symbols) and night (filled symbols) at the treated (net cover) and control (no net) sites. Upper panels: the site of the net enclosure during (A) net cover and (B) after net removal. Lower panels: control sites during the same periods as above but without a net cover (C, during net cover of treated site and D, after net removal). Error bars, SE.

ident both in comparison with the control sites (Fig. 8C,D, see below) and with the same site before and after the experiment (Figs. 5 and 8B, respectively). Above the cage, the vertical distribution of SSAC was similar during the day and the night; however, a marginally significant daytime gradient was still evident (Page test $P = 0.05$). On average, daytime near-bottom SSAC over the cage increased by only 28% (1.2 mg m^{-3} [SD 1.3]) in comparison with the upper water column. This vertical difference was about three times smaller than the one observed at the enclosed site after net removal (94%) or at the open site before and after net removal (609% and 140%, respectively). Similarly, the near-bed increase in SSAC between night and day was much smaller over the cage (29%) than in the open control locations (>133%).

In contrast to the caged site, spatial and temporal distribution patterns of SSAC at each of the control treatments (Fig. 8B–D) resembled our previous observations of vertical SSAC gradients as described above (Fig. 5). During daytime, near-bottom SSAC were considerably elevated (more than twofold) above the nocturnal levels, both at the control (open) sites and at the enclosed site after net removal (Fig. 8, Table 3). No nocturnal SSAC gradient occurred throughout the experiment in any of the treatments, whereas daytime SSAC vertical distribution at the open treatments exhibited a significant gradient toward the bottom (Page test, $P < 0.01$), with an average increase of near-bottom SSAC of 3.7–25.6 mg m^{-3} (difference between the two upper- and two lowermost sampling points in each treatment).

Scuba dives and continuous real-time video monitoring of the caged reef indicated a complete exclusion of the benthivorous fish. Smaller planktivorous fish such as *Pseudanthias squamipinnis* and *Chromis* spp. could easily pass through the net, and their behavior seemed unaffected by the net. A few benthic-dwelling ambushing fish (e.g., scorpion fish *Scorpaenopsis barbatus* and lizard fish *Synodus variegatus*) remained confined under the net and exhibited normal behavior with no evidence of stress. Flat, calm seas (maximal wave height <0.1 m) and relatively strong current speeds (average 7.7 cm s^{-1} [SD 4.1], maximum 17.7 cm s^{-1} at 2.5 m above bottom) with semidiurnal reversal of flow direction prevailed throughout the experiment. The average flow speed at 15 cm above the bottom was 4.6 cm s^{-1} (SD 1.8), with an ~10% increase during the night (Table 3). Near-bottom currents at the control site exceeded the threshold for initiation of sand motion (Allen 1997) for 18% of the time, with two-thirds of these cases occurring at night (Table 3, Fig. 9). The net cover was found to reduce the near-bottom current by ~1 cm s^{-1}. The percentage of time the currents exceeded the threshold for sand motion underneath the net was only ~7% (Table 3), with a somewhat larger percentage during the day. After net removal, current speeds were elevated again, and the percentage of time the currents exceeded the threshold was two times higher at night (Table 3, Fig. 9).

Daily changes in the acoustic backscatter strength at the open sites cooccurred with changes in SSAC, displaying a midday elevation and a nocturnal reduction of signal amplitude (Fig. 10, *t*-test, $P < 0.001$). Spikes of high backscatter intensities (>3 SD) in the acoustic record were obvious during the day but much less so at night (Fig. 10). In some cases, a spike in the acoustic record cooccurred with nearby resuspension activity by fish observed on our video monitor. Neither the SSAC nor the acoustic backscatter intensity exhibited any correspondence with the tide or current speed, either below or above the calculated thresholds for initiation of sand grain motion (Figs. 9, 10). Average day-night differences in the acoustical backscatter signal as well as the frequency of backscatter spikes underneath the net were significantly reduced in comparison to both the control sites during the enclosure period and the caged area after net removal (Table 3, Fig. 10D).

Discussion

Although numerous studies have measured suspended sediment concentration and sedimentation rates over coral reefs (Loya 1976; Rogers 1990; Larcombe et al. 1995; Larcombe and Woolfe 1999*a*), this is the first report of a daily pattern of suspended sediment concentrations at coral reefs with fish activity as its causative agent.

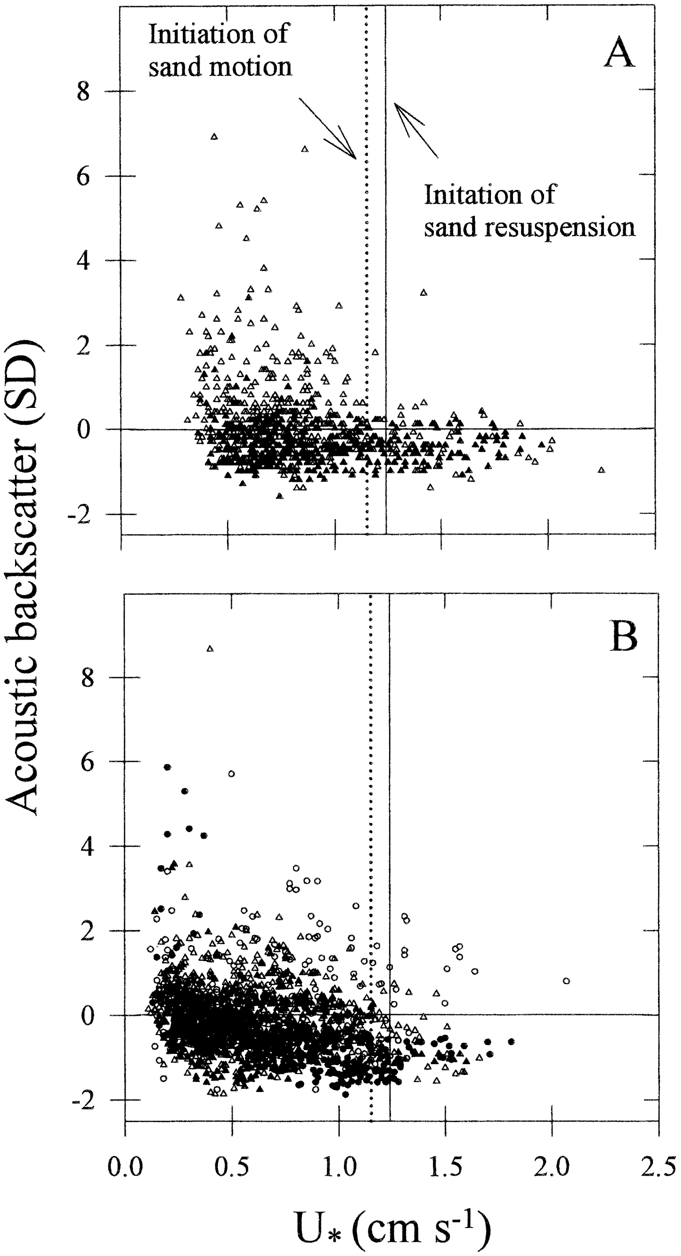

Fig. 9. Normalized acoustic backscatter measurement 15 cm above the bottom of the fish-exclusion experiment site plotted as a function of shear velocity (U_*). (A) At the control site during fish exclusion experiment (net cover). (B) At the enclosed site during net cover (triangles) and after net removal (circles). Night- and daytime measurements are marked by filled and open symbols, respectively. The dashed and solid vertical lines correspond to the critical shear velocities for initiation of sand motion (median grain diameter, 150 μm, Shields criteria; Allen 1997) and sand resuspension (van Rijn 1993) at the experimental conditions, respectively. Each datum is a 10-min average of ADV records.

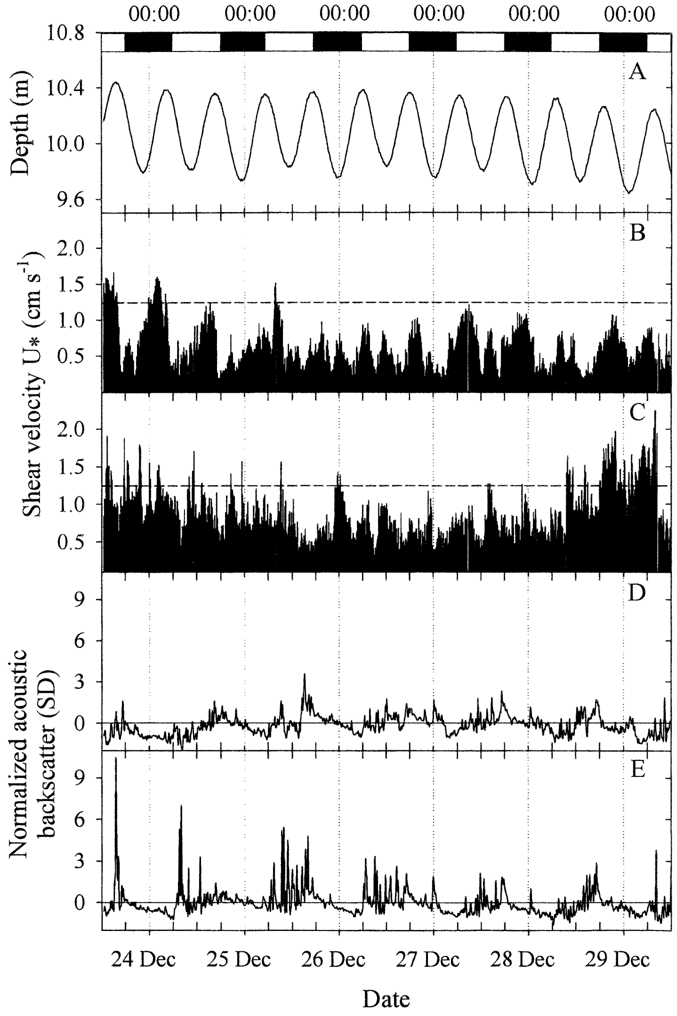

Fig. 10. Time series of ADV records (10-min averages, 15 cm above the bottom) during the fish exclusion experiment: (A) tidal cycle, (B and C) shear stress underneath the net and at the control site, respectively, and (D and E) normalized acoustic backscatter underneath the net and at the control site, respectively. The high acoustic backscatter spikes (>3 SD) at the control site were most likely induced by fish reworking the sediment next to the ADV, as confirmed by real-time video observations.

Agents of sediment resuspension—The exclusion of all the large benthivorous fish by the cage significantly reduced the resuspension of sediment during the day. Consequently, the daytime SSAC over the enclosed area was similar to the nocturnal levels. The two- to sixfold increase of SSAC in the benthic boundary layer, which was observed in the open reef areas during the days, did not occur in the fish-exclusion area (Fig. 8). During the night, when the benthivorous fish were asleep, the SSAC level was lower and its vertical distribution more homogenous over both the open and the enclosed sites. The daily cycle was corroborated by the acoustic record, which indicates the occurrence of strong resuspension spikes, some of which cooccurred with observed resuspension activities of fish within the field of view of our video camera and were overall much weaker both during the night and over the fish exclusion area (Table 3).

Throughout the experiment, wave height was extremely low (<10 cm) and could not contribute to sediment resuspension at the sampling points (>8 m deep, >80 m offshore). The currents exceeded the van Rijn resuspension threshold for ~15% of the time (Figs. 9, 10) and mostly

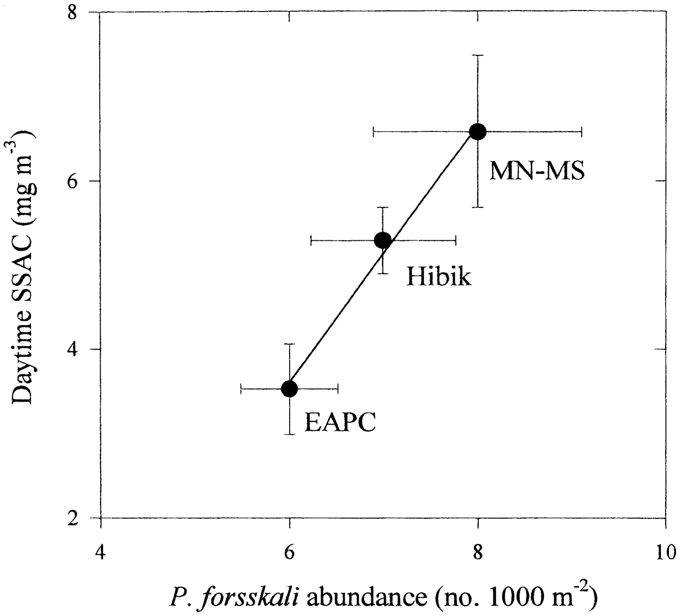

Fig. 11. Average daytime SSAC versus the corresponding abundance of *P. forsskali* at three sites along the northwestern coasts of Gulf of Aqaba. Error bars, SE.

during the night, except under the cage. Therefore, the current regime was opposite to the daily SSAC pattern. Currents above the threshold could, however, explain the slight nocturnal increase in near bottom SSAC observed during the experiment but not during the preliminary measurements (Figs. 8, 5, respectively).

A similar daily cycle with a midday peak was also observed by Heap et al. (1999) in the optical backscatter signal recorded 0.5 mab at protected reef sites at the Great Barrier Reef, Australia (their figs. 3 and 7). As in our case, Heap et al. did not find any correspondence between the backscatter levels and a set of physical factors, even though the waves, currents, and wind at their site were much stronger than in Eilat. The diurnal activity of the benthivorous fish in our study sites (Figs. 6, 7), however, closely corresponded to the observed daily shifts of SSAC in our 1.5-yr time series (Fig. 2) and to the consecutive daily cycles (Fig. 4), as well as to the disappearance of the vertical gradient during the night (Fig. 5). The overall SSAC levels at the different sites were positively correlated with the density of the most abundant and most actively resuspending fish, *P. forsskali* (Fig. 11). The sporadic nature of resuspension events is reflected both by the higher variance in SSAC observed during the daytime (Fig. 2) and our acoustical record (Fig. 10).

The two goatfishes (*P. forsskali* and *P. macronema*) and the trigger fish (*S. albicaudatus*) included in our observations of fish activity (Fig. 7) exhibited a diurnal pattern similar to that reported for numerous other benthic-feeding fishes at coral reefs (Randall 1983; Montgomery et al. 1989). Another guild of common diurnal species, the parrotfish (Bellwood 1995 and references therein) scrape off the rocky substrate, releasing particles both directly through their feeding activity and through their excretions, which are typically released in the water column aloft (Bellwood 1995). Torovezky (1997) measured bioerosion by parrotfish at our study sites in Eilat and estimated that the amount of carbonates excreted by parrotfish alone may reach as much as 12 mg cm^{-2} d^{-1}. Excretion patterns in parrotfish, both at our study sites (five species, Torovezky 1997) and at the Great Barrier Reef (two species, Bellwood 1995), show a bimodal curve, with peaks around midday and dusk but inactivity at night.

Many reef dwellers resuspend sediment by their movement near the bed, but the most conspicuous resuspension occurs when fish blow, probe, and rework the sediment (Clifton and Hunter 1973; Randall 1983; Uiblein 1991; Bellwood 1995). The relatively high abundance of *P. forsskali,* together with its assiduous feeding manner, probably make this species the most effective in sediment resuspension. Each square meter of reef in Eilat was subjected, on average, to 10 s h^{-1} of resuspension activity by this species alone. *S. albicaudatus* and *P. macronema* dig less frequently than *P. forsskali* and spend relatively more time feeding over hard substrate. *S. albicaudatus,* as is common to other triggerfish, creates large clouds of resuspended sediments when it blows water to overturn sea urchins or to expose buried invertebrates (Clifton and Hunter 1973). The combined effect of the three species resulted in 2–20 resuspension events m^{-2} h^{-1}. Sediment plumes resuspended by a fish reached 1 m above bottom and were clearly visible for 1–2 min afterward.

The local wind could have potentially caused the observed daily pattern, but the role of this was ruled out. The daily cycle of SSAC was obvious both under conditions of normal winds and in absolutely calm days (wind <3 m s^{-1}; wave height <10 cm; Fig. 2). The fact that the daytime SSAC increased near the bottom, rather than aloft (Figs. 5, 8), clearly indicated a resuspension of bed load sediments, excluding lateral aeolian transport. Wind-generated waves were not responsible for the observed daily pattern in SSAC, because, under normal conditions, the amplitude of surface waves at our study sites was <0.5 m and the wave period was <3 s. Such waves are not expected to induce any sand resuspension at water depths >6 m (Prandle et al. 2000 and references therein). The typically weak currents at our study sites are also not likely to control sediment resuspension, because they rarely exceeded the threshold required to initiate sediment motion. Moreover, currents exhibited a semidiurnal periodicity, with no correspondence to the diurnal SSAC periodicity.

Human activity, primarily recreational diving, could have also produced a daily cycle in SSAC. However, its effect was probably negligible at our sites, because no dives were allowed in JG and Hibik, and the divers' abundance and diver-induced resuspension event frequency at MN and MS were very low (<0.7 divers 1,000 m^{-2} and <0.01 resuspension events m^{-2} h^{-1}, respectively, Zakai and Chadwick-Furman 2002).

Ecological implications—During the daytime, inorganic particles dominate the pool of suspended particles (>100 μm) over coral reefs in the Gulf of Aqaba (Figs. 2, 3). Most (77%) of these inorganic suspended particles were sand grains, and these were mainly (97%) in the smallest size range (100–200 μm, Fig. 3). Although suspended sand is only one component of the total sediment suspended at a coral reef, it can constitute a major fraction of the material trapped in near bottom sediment traps (Aller and Dodge 1974; Rogers 1983). Our direct measurements of the daily pattern in resuspended sand are likely to reflect a similar pattern in smaller grain sizes, as is evident from our acoustical records, as well as from the nephlometer used by Heap et al. (1999) in Australia.

Similar to coral reefs, benthivorous fish are abundant in ponds and lakes, where their sediment resuspension activity controls water turbidity, nutrient cycling, and the trophic status of the habitat (Meijer et al. 1990; Havens 1991; Bloesch 1995; Meijer et al. 1999). Benthic fish activity at coral reefs is expected to produce similar effects. The relative control fish activity exerts over these parameters at coral reefs is expected to vary as a function of water transport magnitude between the reef and the surrounding open sea.

The daily cycle of sediment resuspension by fish may have several important ecological effects at our study sites. The quality of the seston available for benthic suspension feeders was reduced during the day (Fig. 3), with $<30\%$ of the particles encounters by a coral, for example, being organic, compared with $>55\%$ at night (Fig. 3). Moreover, zooplankton composed most (70%) of the organic particles at night, whereas suspended detrital particles dominated the organic matter at day. The daytime elevation in SSAC has the potential to increase the rates of tissue damage and clogging of filtration organs among reef animals (Gerrodette and Flechsing 1979; Wilkinson 1983; Rogers 1990). Indeed, many suspension feeders (e.g., corals, crinoids, and polychaetes) extend their feeding tentacles only at night. Although this nocturnal activity had been attributed to predation avoidance, we suggest that it may also be an adaptation to avoiding the potential for the above-mentioned damage. The relevance of these findings to other aquatic systems has yet to be studied.

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