Limnol. Oceanogr., 49(5), 2004, 1832–1839

Aeration of corals by sleep-swimming fish

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Abstract

The morphology of branching corals effectively blocks impinging currents. Weak flows in the colony's inner sections can hinder some of the corals' basic physiological functions. At night, high respiration by the coral and the absence of photosynthesis by the symbiotic algae sometimes generate severe hypoxia near coral branches. Nevertheless, branching corals thrive in flow-protected areas. Many of them host resident fish that seek shelter between their branches during the night. In situ observations using an infrared-sensitive video camera revealed that, unlike crevice-dwelling fishes, which sleep motionless, fish (*Dascyllus marginatus, D. aruanus,* and *Chromis viridis*) that spend the night in living hard corals (*Stylophora pistillata, Acropora* spp., *Pocillopora* spp., and *Seriatopora* spp.) exhibit a unique sleep-swimming mode that is characterized by energetic, high-frequency fin motions. In the reef, the presence of fish in the coral *S. pistillata* increased gypsum dissolution and, hence, mass transfer, by ~17% compared with colonies without fish. The extent to which the fish enhanced water replenishment in the inner zone of the coral was assessed in the laboratory using oxygen measurements. In the absence of fish, oxygen levels near the coral tissues (~1 mm) rapidly declined, reaching 10–30% of ambient levels, which was much lower than the nearly steady levels of 60–80% when sleep-swimming fish were present. Individual sleep-swimming fish were spatially separated across the coral, so that most of the coral's inner zone was frequently ventilated. This common, yet so-far overlooked mutualistic relationship is unique by the virtue of its effect, the active modulation of hydrodynamic conditions, and its operation during the sleep of the active animal. The modulation of hydrodynamic conditions by the fish can mitigate flow limitation on the growth and survival of branching corals.

Fundamental functions of corals, including nutrient uptake, gas exchange, and feeding depend on the flow of water over the coral and through its branches (Atkinson and Bilger 1992; Lesser et al. 1994; Sebens 1997; Thomas and Atkinson 1997). Paradoxically, branching corals have evolved with a morphology that effectively blocks the flow and generates a region of weak water exchange between the inner coral branches (Chamberlain and Graus 1975; Lesser et al. 1994; Sebens et al. 1997). Moreover, the development of a boundary layer across the coral-water interface (Shashar et al. 1993, 1996; Vogel 1994) substantially reduces mass fluxes of nutrients and gases to the coral's tissues (Patterson et al. 1991; Shashar et al. 1993; Kühl et al. 1995). In many species, an exposure to strong flow reduces the thickness of the boundary layer and augments photosynthesis, respiration, growth, and survival (Jokiel 1978; Dennison and Barnes 1988; Patterson et al. 1991; Lesser et al. 1994). Nevertheless, many corals grow in reefs where the water is calm and currents are weak (Jokiel 1978; Sebens and Done 1992; Lesser et al. 1994). The hypoxia that develops during the night between branches of corals growing at such sites (Shashar et al. 1993; Kühl et al. 1995), when no oxygen is produced by the coral's symbiotic algae, is severe (~22 μmol O_2 L^{-1}).

In some species, developmental plasticity allows adaptations of the colony morphology and biochemistry to the flow regime, augmenting mass exchange between the coral and ambient waters (Chamberlain and Graus 1975; Helmuth and Sebens 1993; Lesser et al. 1994; Kaandorp 1999). Nevertheless, the inner parts of branching corals usually remain protected from flow, so that any augmentation of mass fluxes in those parts would be highly beneficial.

More than one third of the branching corals in shallow coral reefs in the Gulf of Aqaba, Red Sea, are inhabited by site-attached zooplanktivorous fishes such as *Dascyllus marginatus, D. aruanus,* and *Chromis viridis* (Fishelson et al.

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Acknowledgments

We thank U. Noy-Meir, N. Choresh, D. Porat, R. Kent, R. Motro, S. Eckstein, I. Ayalon, and S. Sabbah for underwater and technical help; Y. Cohen, D. Eisenshtat, G. Yahel, T. Katz, A. Rivlin, T. Rivlin, and M. Dray for help with oxygen measurements and methodology; M. Ohavia for fabricating the video and IR illumination system; and J. Koseff, M. Reidenbach, S. Monismith, N. Shashar, and H. Fricke for helpful comments. We are grateful to the Interuniversity Institute of Eilat for logistical support.

This research was supported by the Israel Science Foundation, funded by the Israel Academy of Science and Humanities. D.W. thanks the Technion VPR fund for Promotion of Research for support. R.G. and R.H. thank the Rieger foundation for their support.

1974; Fricke 1980). The dominant branching corals are *Stylophora pistillata, Acropora* spp., *Pocillopora* spp., and *Seriatopora* spp. Most of the resident fish live in social groups of 2 to >20 fish, with a stable, long-lasting association between the group and their host coral (Sale 1971; Fishelson et al. 1974; Fricke 1980). The association is obligatory for the fish but not for the corals. Nevertheless, corals with fish grow faster and have greater reproductive output than those without fish (Liberman et al. 1995). The resident fish can benefit their host coral through several mechanisms. (1) The coral can utilize nutrients excreted by the fish, enhancing its growth (Meyer and Schultz 1985). (2) The fish can protect the coral from predators such as the crown-of-thorns sea star *Acanthaster planci* (Weber and Woodhead 1970) and butterfly fishes (Liberman et al. 1995). (3) The fish swimming in and out of the coral during the day may resuspend sediment and clear the coral branches of settling particles (Liberman et al. 1995).

During the day, the fishes forage for zooplankton near the coral, using the coral as a shelter from occasional predators or other dangers (e.g., storms). After sunset, the fishes retreat to the coral and spend the entire night among its branches (Fishelson et al. 1974). Holbrook and Schmitt (2002) reported that *Dascyllus* spp. in Moorea (French Polynesia) actively interact with each other throughout the night, exhibiting an apparent intragroup territorial behavior for space among the coral branches. Our observations in the Red Sea partially corroborated these observations—we saw that the fishes indeed swim throughout the night but that their nocturnal motions are not limited to territorial behavior. Furthermore, we noted that fishes continuously move their fins, even when they are holding a fixed position. This nocturnal behavior, which we call ''sleep swimming,'' sharply contrasts the stationary sleep of other diurnal coral reef fishes that spend the night in nonliving shelters such as caves and crevices (Fishelson et al. 1974; Dubin and Baker 1982). In the present study, we put forward and test the hypothesis that sleep swimming in coral-inhabiting fishes increases water motion, mass transfer, and aeration in the inner parts of coral colonies.

Materials and methods

Study site—The study was carried out at 5–10 m depth at the upper slope of the coral reef in front of the H. Steinitz Marine Biology Laboratory (29°30′N, 34°56′E), Eilat, Red Sea. The local community structure has been described by Fishelson (1971), Loya and Slobodkin (1971), and Benayahu and Loya (1977). In brief, the community is dominated by hard corals living on a steep (10–30°) slope between shallow subtidal depths and >50 m. Branching corals hosting symbiotic fish dominate the upper 20–30 m of the reef (Loya and Slobodkin 1971). Pomacentrid fishes associated with living corals account for ~20% of the total fish found in the reef (Khalaf and Kochzius 2002). Flow speed at 0.15 and 0.27 m above bottom (8.5 m bottom depth), representing the exposure to flow of most corals at this site, was measured during 8 d (1–8 September 1999) using a pair of acoustic Doppler velocitometers (5 MHz; Sontek). The currents at those coral heights were weak. Flow speed <3.0 cm s^{-1} prevailed for 43–50% of the time, whereas flows >5.0 cm s^{-1} was found <16% of the time (Fig. 1).

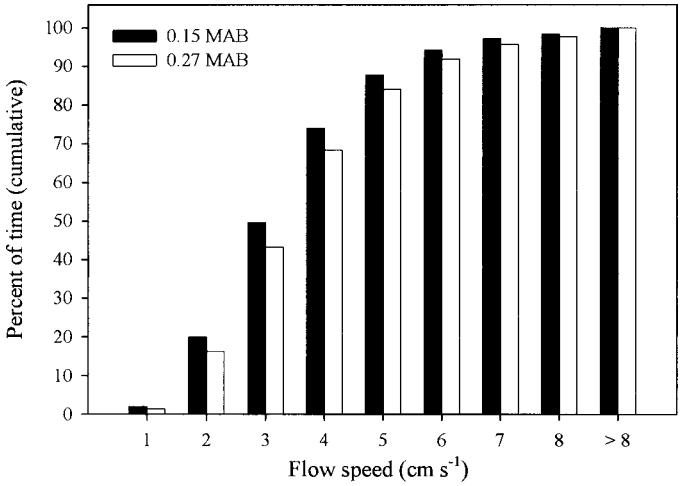

Fig. 1. Cumulative frequency distribution of flow speed at 0.15 and 0.27 m above bottom (MAB) at 8.5 m depth at the coral reef of Eilat, 1–8 September 1999. The frequency distribution was constructed on the basis of a total of 11,220 data points, an average 1-min interval each.

For the laboratory experiments, *D. marginatus* were collected at the reef by injecting the anesthetic Benzocaine (5 g dissolved in 30 ml ethanol diluted with seawater to a total volume of 150 ml) between the branches of fish-hosting colonies. The fish were transferred to an 8-liter holding tank with running seawater and fed with nauplii of brine shrimp (*Artemia salina*). A bare skeleton of branching coral was placed in the tank and used as a shelter. Corals used for the laboratory experiments were collected from the reef, glued to 10 × 10 cm ceramic tiles (using Kop-Coat epoxy glue; Kop Coat), and maintained in the reef until the experiment.

Behavioral observations—The in situ swimming motions of *D. marginatus* and *D. aruanus* (inhabiting colonies of *S. pistillata*) and *C. viridis* (inhabiting *Acropora humilis*) were video recorded using natural and infrared (IR) illumination during the day and night, respectively. An online black-and-white, IR-sensitive video camera was deployed at the reef, positioned on a tripod, looking downward at the coral from ~30 cm above. Six custom-made packages, which consisted of 30 molded IR (880 nm) LED diodes each, were used as a source of illumination. This setup allowed nonintrusive observations of the nocturnal and diurnal behavior of the fish. A total of 10 colonies was videotaped. Two 3-h-long recordings were obtained from each colony at arbitrary times: one during the day and the other at night.

Individual tracks of sleep-swimming fish in the corals were analyzed from a randomly selected 10-min interval for each of the three fish species. The tracks were obtained by continuously recording the position of the fish's eye during that interval. Tracks were obtained only for fish that were clearly identifiable throughout the interval. In total, we tracked 4 *D. marginatus,* 4 *D. aruanus,* and 7 *C. viridis.*

The probability of a *D. marginatus* passing a random

point along the gap between two neighboring branches of *S. pistillata* was estimated for each of the seven corals as follows. Fifteen lines were plotted on a transparent sheet overlying the coral image, so that each line crossed the interbranch gap nearest to a randomly positioned point, followed by measurements of the time it took a fish to cross that line, starting at a randomly selected time in the record.

Stroke frequencies of the dorsal, pectoral, and caudal fins were compared between ''normal swimming'' outside the coral during the day and ''sleep swimming'' while holding position inside the coral at night. Because the fish could not be identified individually, we considered the inhabiting coral to be our ''sampling unit.'' The motions were analyzed from the aforementioned video records using a total of four corals during each day and night. For each of the three fins, the motions were analyzed during five separate, randomly selected intervals, each 2–7 s long, using haphazardly selected fish.

In situ gypsum experiment—The effect of sleep-swimming fish on the motion of water in the inner parts of their host corals was assessed using the gypsum dissolution technique (Doty 1971). This technique provides a proxy of mass transfer and the thickness of the diffusive boundary layer, although it is inaccurate in estimating the speed of the current (Porter et al. 2000).

Ten *S. pistillata* inhabiting natural groups of *D. marginatus* were selected for this experiment. The corals varied in their size, morphology, and the number of resident fish. The average diameter (± 1 SD) of the corals was 32.5 ± 5.5 cm. The number of fish per coral ranged from 3 to 20. The average branch diameter was 0.7 cm. Each experiment started at least 2 h after sunset and ended 8.5 h later, before dawn. The experiment was replicated during six nights—the first three nights with the fish sleeping in the coral, followed by three nights without fish. The fish were removed after the third night using the anesthetic Benzocaine, and their number was recorded. The experiments were carried out during October–November 2001. A large cage made with 5-mm mesh thin-nylon net was deployed over each coral during the day to block fish from resettling. The net was removed each evening before the start of the experiment. Visual inspections at the beginning and end of each experiment verified the absence of fish in the coral.

The gypsum casts were prepared according to the methods of Doty (1971) and Jokiel and Morrissey (1993). Casts were made from Alabaster gypsum that contained 98% $CaSO_4 \times 1/2H_2O$ (Gesher Gypsum), mixed with double-distilled water in a weight ratio of 1.3 : 1. The slurry was injected with a syringe into 0.5-ml polymerase chain reaction (PCR) tubes (cast diameter 0.6 cm, length 2.7 cm) in which a ~20 cm long, 0.1-mm metal wire had already been threaded. The wire protruded ~7 cm from each side of the cast. After molding, the gypsum casts were left to dry in open air for 48 h, removed from the PCR tubes, and dried for at least another 48 h, to ensure complete drying. The dry weight of each cast was measured before and after the experiment using an analytical scale (0.1 mg precision).

To account for the variation in the current regime within the coral, we placed four gypsum casts at four distal spots, one in each quarter of the coral and a fifth at its center. The five casts were carefully inserted between the coral branches, a few centimeters inside the edge. The wire was used to gently secure the cast by twisting it around the coral branches. To avoid dissolution outside the coral, the casts were inserted into 1.5-ml PCR tubes during transport to and from the reef. The casts were individually checked after retrieval, and damaged or broken casts were excluded from the analysis (<1%).

Because the ambient flow varied between different days and locations in the reef, the dissolution of the gypsum inside a coral was normalized to that just outside of it. The latter dissolution was measured simultaneously with five casts suspended on a $20 \times 20 \times 20$ cm metal frame placed <50 cm away from each coral, at the same height above the bottom and with similar intracast distances as those in the coral. Each frame was kept in a fixed position throughout the six nights during which the measurements were made. A pairwise dissolution index (DI) was calculated for each coral for each night by dividing the average weight loss of the five casts inside the coral with that of the five control casts.

Oxygen measurements—We hypothesized that sleep swimming augments ventilation in the inner coral zone. The extent of water replenishment in that zone was assessed by measuring the oxygen concentration, a commodity that can be fully exhausted by the coral respiration during the night (Shashar et al. 1993; Kühl et al. 1995).

Seven *S. pistillata* (average diameter 14 cm, average branch diameter 0.8 cm) were used. Each colony was transferred from the reef to the dark laboratory at the beginning of the night of the experiment. Resident crabs (*Trapezia* spp.) were removed, and the coral was placed in a laboratory aquarium (80 liters) with freshly collected seawater at a constant temperature (26°C). Oxygen concentrations between the coral branches, 5–10 cm inside from its edge and ~1 mm away from the polyps, were measured every 10 s using a Clark-type O_2 electrode (1.1 mm tip diameter, OXN; Unisense). The ambient oxygen concentration was concurrently measured every 10 min ~30 cm away from the coral using an O_2 electrode (Oxi 323-B; WTW). Each run consisted of three consecutive parts: the first part, which lasted 40 min, started immediately after a coral without fish was placed in the aquarium. The second part, which also lasted 40 min, started immediately after two fish (*D. marginatus*) were introduced to the coral. The fish were randomly selected from the aforementioned stock. The third part, which lasted 20 min, started immediately after the removal of the two fish from the aquarium. The coral and fish were video recorded using the aforementioned black-and-white video camera and IR LED illumination, to verify that the fish remained among the coral branches throughout each run and that the coral polyps remained extended. The two oxygen electrodes were calibrated three times during each run on the basis of a three-point linear regression curve. Discrete water samples were taken from chambers with seawater at minimum (nitrogen flushed), maximum (fully aerated), and intermediate (~80% saturation; collected from the aquarium) oxygen levels (all at 26°C). Oxygen concentrations were measured using the

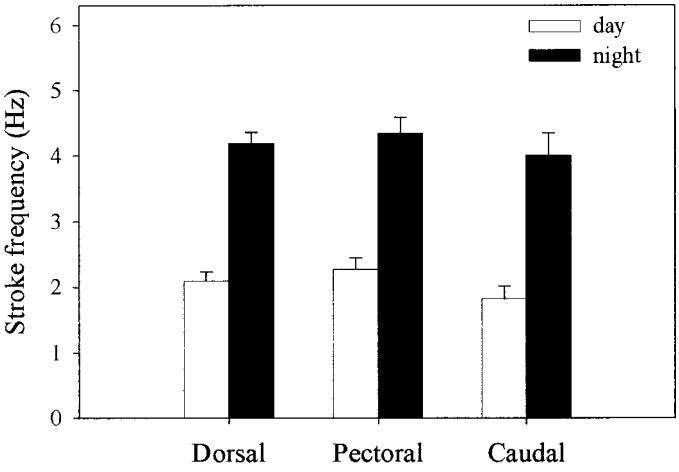

Fig. 2. In situ stroke frequencies (average ± SE) of the dorsal, pectoral, and caudal fins of *D. marginatus* inhabiting the coral *S. pistillata* during ''normal swimming'' (outside the coral during the day) and ''sleep swimming'' (between the coral branches during the night). The difference of the stroke frequencies between the normal and sleep swimming was significant (ANOVA, $P < 0.05$).

Winkler iodometric titration technique (Strickland and Parsons 1972).

Statistical analyses—The effects of time (day vs. night) on the stroke frequency by the dorsal, pectoral, and caudal fins were tested using three-way repeated-measures analysis of variance (ANOVA; time, fin type, and record). The effect of the presence of fish during consecutive nights on DI was tested using two-way repeated-measures ANOVA (treatment and consecutive nights were the repeated-measure factors). The difference between water motion inside and outside the coral was tested using Student's *t*-test of mean DI against constant reference (DI = 1, equal dissolution of gypsum inside and outside the coral). The effect of the presence of fish on the oxygen concentration between the coral branches was tested using one-way repeated-measures ANOVA. Repeated-measure analyses were made after verifying a compliance with the sphericity assumption. All statistical analyses were conducted using Statistica (version 6.0 for Windows; StatSoft).

Results

The fish of all three species (*D. marginatus*, *D. aruanus*, and *C. viridis*), which seek nocturnal shelters between the branches of living corals, move their fins during the entire night, even when they are holding fixed positions (*see* video clip, 30 s long, of fish motions in a single coral during the night in Web Appendix 1 http://www.aslo.org/lo/toc/vol_49/issue_5/1832a1.html). The motions of the dorsal, pectoral, and caudal fins were especially vigorous. The frequency of fin strokes during sleep swimming was about twice that during normal daytime swimming outside the coral (ANOVA, $F_{1,1} = 174.3$, $P < 0.05$; Fig. 2).

Our direct visual and video observations indicated that the polyps of fish-inhabiting corals remained extended throughout the night, with no apparent effect of the fish motion on polyp contraction. Individuals within a group maintained quasi separated swimming zones most of the time, with minimal overlap between individuals and maximal coverage of the coral area (Fig. 3). Some fish, however, did penetrate into neighboring zones for short intervals (Fig. 3A). For corals inhabited by *D. marginatus*, the probability that a fish would pass a random point within the coral at least once every 30 s was >50%.

The presence of *D. marginatus* in a coral during the night significantly (ANOVA, $F_{1,5} = 13.15$, $P < 0.02$) enhanced the dissolution of gypsum in situ (Fig. 4). The DI values indicated that without fish the coral formed an effective barrier to flow, with slower gypsum dissolution within the colony than outside, as indicated by DI < 1.0 (average ± SE = 0.82 ± 0.02, $n = 28$; *t*-test, $P < 0.001$). With fish, the DI values (0.97 ± 0.03, $n = 26$) were not significantly dif-

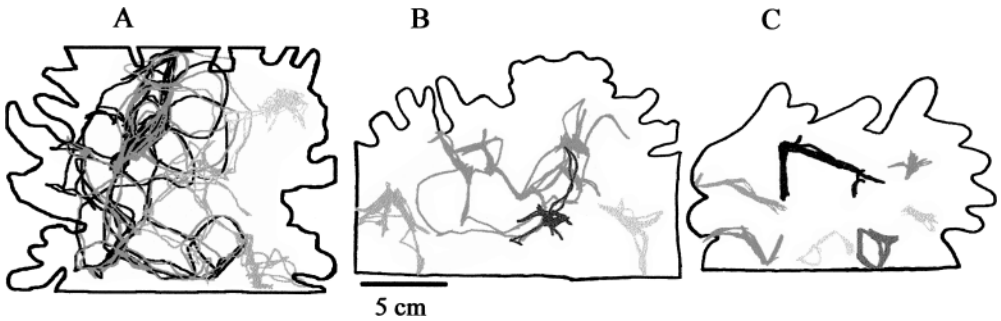

Fig. 3. Examples of in situ tracks of neighboring sleep-swimming fish in a coral. (A) Tracks of four of the total six *D. marginatus* sleep swimming in *S. pistillata.* (B) Four of seven *D. aruanus* in *S. pistillata.* (C) Seven of 15 *C. viridis* in *A. humilis.* Tracks were obtained by continuously plotting the position of the fish eye on the video image during a randomly selected 10-min interval for each coral. Different gray scales indicate different fish. Black line: outline of the coral image on the video screen. The presented tracks were obtained for the fish best seen in the video records. The remaining fish swam mostly in the regions of the coral left blank in the plots, exhibiting minimal overlap between the fish. See Web Appendix 1 (http://www.aslo.org/lo/toc/vol_49/issue_5/1832a1.html) for a color version of this figure, with improved resolution of the individual fish tracks, and a video clip, 30 s long, of fish motions in a single coral during the night.

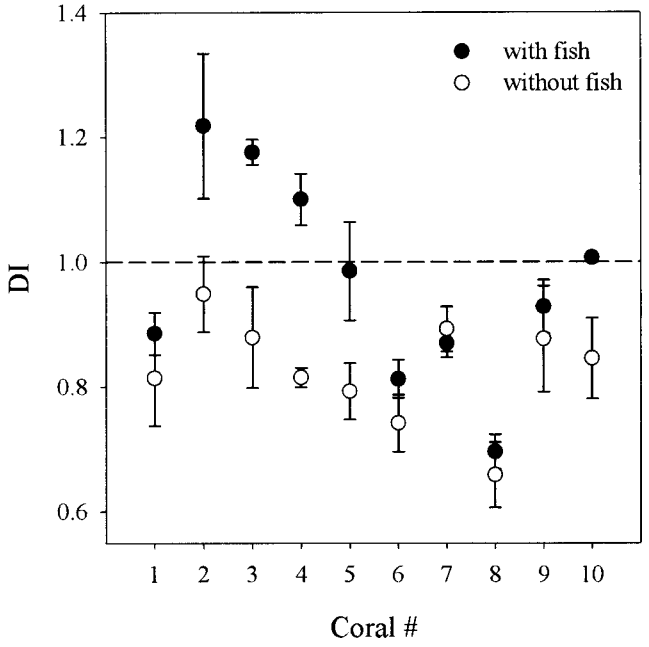

Fig. 4. The in situ effect of fish (*D. marginatus*) on gypsum dissolution between the branches of *S. pistillata.* Each point indicates the average (±SE) DI during the three nights before the removal of fish and the three nights after the removal of fish. Overall, the presence of sleep-swimming fish significantly ($P < 0.02$) augmented the dissolution by ~17% compared with colonies without fish. The horizontal line (DI = 1.0) indicates equal dissolution of gypsum inside and outside the coral.

ferent from 1.0 (*t*-test, $P > 0.4$), with values >1.0 (faster dissolution within the coral than outside) observed in 11 of the 26 measurements.

In the laboratory experiment, the oxygen concentration in corals without fish gradually declined (Fig. 5B) from the artificially aerated conditions (caused by our handling of the coral), reaching levels near hypoxia (<20% saturation). Such levels prevailed until the introduction of the fish, at which time oxygen concentrations rapidly (<30 s) increased (Fig. 5A). The presence of fish significantly (ANOVA, $F_{2,12} = 25.5$, $P < 0.001$) increased the oxygen concentration between the coral branches (at the measuring height; ~1 mm). Without fish, the average oxygen level was 31 ± 20% (average ± SD) of ambient. For about three quarters of the time, the oxygen levels were <40% of ambient, and they were rarely (<5% of the time) >60% of ambient. With fish, oxygen remained high at a quasi steady state of 69 ± 8.7% ambient; they were almost always (89% of the time) >60% of ambient and almost never (<0.1% of the time) <40% ambient. Oxygen time series data (Fig. 5) showed much higher frequency variations with fish than without. However, a power spectrum analysis indicated no dominant frequency in the fish activity.

The oxygen measurements were made within the diffusive boundary layer, in which the concentration of a dissolved gas or nutrient decreases linearly until it reaches zero (in *S. pistillata*, this is 0.5 mm above tissue; Shashar et al. 1993). We calculated the oxygen flux according to Fick's law,

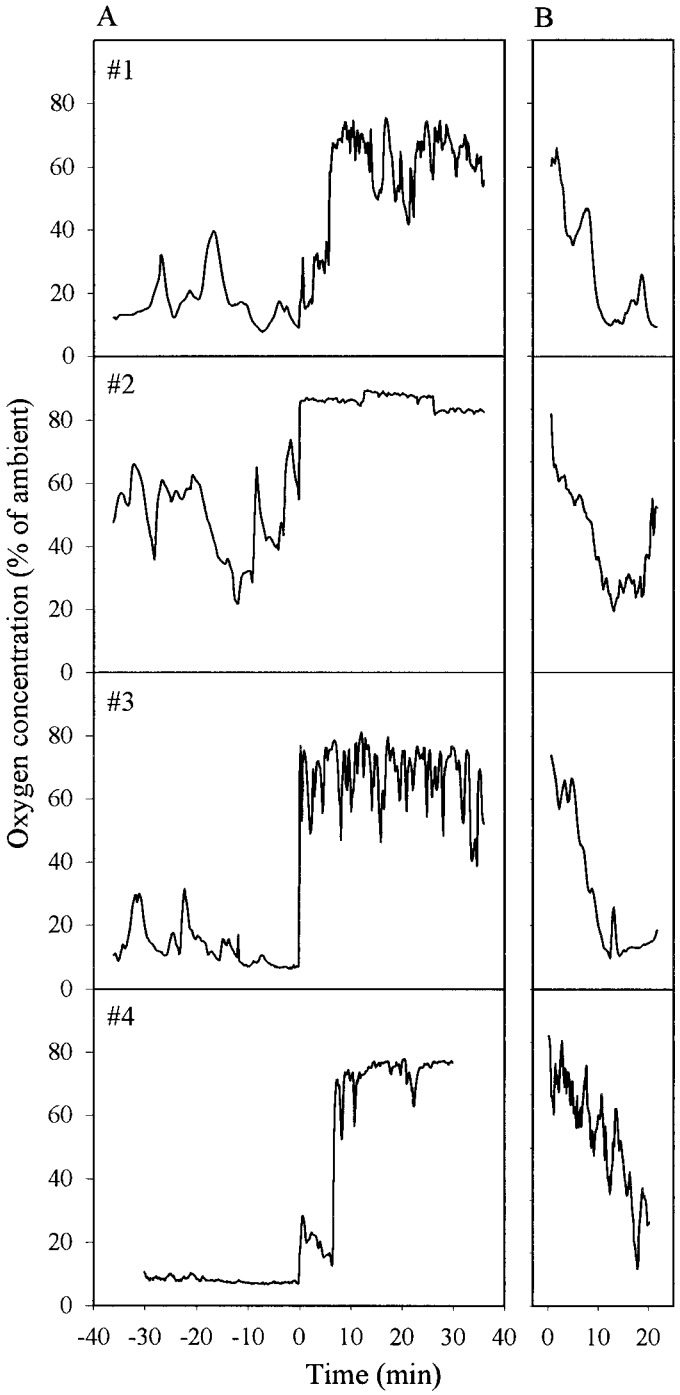

Fig. 5. Changes in oxygen concentration during the night before the introduction (negative time in A), during the presence (positive time in A), and after the removal (B) of pairs of *D. marginatus* in four different *S. pistillata* (1–4) in laboratory aquaria. Time zero in panel A indicates the introduction of the fish. Oxygen concentrations are presented as the percentage of ambient. The presence of fish doubled (or more) the oxygen concentration between the coral branches (ANOVA, $P < 0.001$).

$$F_z = -D\frac{\partial C}{\partial z} \cong -D\frac{C_0}{z} \quad (1)$$

where F_z is the flux rate, D is the molecular diffusion coefficient (2.02×10^{-5} cm^2 s^{-1}; Kühl et al. 1995), C_0 the concentration at the measurement point, and z is the distance to zero concentration (0.5 mm). The average oxygen flux with fish was about twice that without fish ($6 \times 10^{-5} \pm 1 \times 10^{-5}$ and $3 \times 10^{-5} \pm 2 \times 10^{-5}$ μmol O_2 cm^{-2} s^{-1}, respectively).

Discussion

The three fish species we studied, all of which spend the night exclusively in living corals, exhibited an unusual mode of continuous sleep swimming, aerating the inner parts of their host corals. The faster dissolution of gypsum indicated that the presence of fish increased the motion of water between the coral branches in the reef, enhancing the effect of ambient currents. This enhanced dissolution could result from increased shear and turbulence produced by the fish, an equivalent of stirring, as well as from enhanced exchange with ambient waters. A substantial rate of exchange was indicated by the maintenance of a quasi steady state of high oxygen at the measuring height when fish were present (Fig. 5). The fish actively modulated the hydrodynamic conditions in their host corals. The ensuing augmentation of mass transfer is expected to enhance the rates of respiration, primary production (Patterson et al. 1991), calcification (Dennison and Barnes 1988), nutrient uptake (Atkinson and Bilger 1992; Thomas and Atkinson 1997), and coral growth and survival (Jokiel 1978). Indeed, colonies of *S. pistillata* hosting *D. marginatus* grow faster and reproduce more than colonies without fish (Liberman et al. 1995). In addition, the enhancement of flow and mass transfer by sleep-swimming fish may improve the coral survival (Nakamura and Van Woesik 2001) and their recovery from bleaching (Nakamura et al. 2003).

The addition of sleep-swimming fish increased the oxygen flux to the corals' tissue in a way similar to that observed after increasing external flows (Patterson et al. 1991), reflected by a narrowing of the diffusive boundary layer. Our laboratory experiments were carried out under conditions of still water. Therefore, our findings of enhanced oxygen fluxes by the fish are relevant to in situ conditions of weak flows. The current measurements (Fig. 1) indicate that, indeed, the currents in the coral reef of Eilat are weak. Although the effect of the fish on oxygen fluxes should be most significant under weak ambient currents, the results of our in situ gypsum dissolution experiment (Fig. 4) indicated that sleep-swimming fish enhance mass fluxes between the coral branches, regardless of the ambient flow conditions. The absolute values of oxygen fluxes in the corals that we studied were similar to those reported by Reynaud-Vaganay et al. (2001; 0.16 μmol O_2 cm^{-2} h^{-1}) for *S. pistillata*, but lower than those for other corals (Patterson et al. 1991; Kühl 1995).

The trigger for the fishes' aeration movements is unclear. A lowering of oxygen concentration to <60% of ambient induces swimming, and consequently ventilation, in fish larvae (Weihs 1980). On the other hand, many coral reef fishes, including *C. viridis* and *D. aruanus*, can tolerate very low oxygen levels (<30% saturation; Nilsson and Östlund-Nilsson 2004). However, because of the coral's high respiration rate, oxygen concentrations between the branches can reach as low as 10% saturation (Shashar et al. 1993) or even 7% (this study). Aeration swimming may therefore be necessary for the fish. Nevertheless, oxygen deficiency does not seem to be the proximate cause for the unique sleep-swimming motions—in the laboratory, the fish exhibited identical motions between branches of dead, nonrespiring corals as well as during short retreats into the coral during the day (R. Goldshmid unpubl. data), in spite of supersaturating oxygen at that time (Shashar et al. 1993, 1996; Kühl et al. 1995; Gardella and Edmunds 1999). Oxygen deficiency between coral branches could nevertheless be the ultimate cause for the evolution of this behavior in the fish.

Sleep swimming could have also evolved as one of the several behaviors through which the fish benefit their host coral, including defense from predators, cleaning from sediments, and fertilization (Weber and Woodhead 1970; Meyer and Schultz 1985; Liberman et al. 1995). Of interest, our observations showed that zooplanktivorous fishes for which the association with living corals is not exclusive (e.g., *Pseudanthias squamipinnis* and *Neopomacentrus myriae*), which are similar to the fish we studied in size, food, and foraging activity, are motionless during sleep. This demarcation further strengthens the suggestion that sleep motions evolved by augmenting the fitness of fish that improved the quality and longevity of their shelter. The selective force is expected to be specifically strong in species for which the association between the fish and a single coral colony is long lasting (Sale 1971). Indeed, the three fishes we studied readily abandon corals that start to die (M. Shpigel pers. comm.). Dead corals provide short-term, unreliable shelter, because the bare skeleton is rapidly bio-eroded (Hutchings 1986), with the branches becoming about one-half their thickness and more brittle within a period of ~1 yr (A. Genin unpubl. data). Bare skeleton may also become unsuitable for fish because of fouling by algae, sponges, and sea anemones, which can fill the spaces between the dead coral branches (Bak and Steward-Van Es 1980).

While sleep swimming, the fish transverse almost the entire coral area; however, the individual fish retains quasi separated swimming zones within the coral (Fig. 3). This separation may be the outcome of intragroup competition for better-protected territories. Nocturnal predation is apparently a major cause of fish mortality (Holbrook and Schmitt 2002). The separation between swimming zones clearly indicates that the supposedly ''sleeping'' fish process sensory information. During that time, however, the fish do not respond to external stimuli such as light and the presence of predators (Holbrook and Schmitt 2002). Hence, the state of the fish can be defined an ''equivalent to sleep,'' an intermediate state between full sleep, such as that exhibited by most coral-reef fishes, and apparent wakefulness, such as that exhibited by many scombrids and sharks (Kavanau 1998).

We observed sleep swimming in three very common fish species residing in different branching corals. These fishes and other congeneric species are widely distributed in coral reefs throughout the Indian and Pacific Oceans. It is ex-

pected, but not yet known, whether sleep-swimming occurs outside the Red Sea. This common, yet so far overlooked, mutualistic relationship is unique by virtue of its effect, the active modulation of hydrodynamic conditions, and its operation during the sleep of the active animal.

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Received: 25 November 2003
Accepted: 8 April 2004
Amended: 29 April 2004