

Possible effects of downwelling on the recruitment of coral reef fishes to the Eilat (Red Sea) coral reefs

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Abstract

We compared water current measurements with data on the recruitment of reef fishes to a coral reef in Eilat, Red Sea for two consecutive recruitment seasons. There was a clear correlation between the daily number of recruits and the magnitude of the downwelling flow, suggesting that an increase in offshore (near bottom) flow induces higher recruitment. The higher recruitment may be the result of larval swimming against the flow. Although the exact mechanism explaining this correlation is unclear, it may involve odor transport from the reef by the downwelling currents, which reaches competent larvae in deeper water and directs them to potential settlement sites.

The life cycle of most reef fishes starts with a pelagic larval stage, at the end of which they recruit to the reef where they will remain throughout the benthic (major) part of their lives. High variation in the timing and intensity of fish recruitment is common and probably affects the overall fish community assemblage (and especially the short-lived species), mainly over short time scales (Doherty 1991; Doherty and Williams 1988). Spatial and temporal differences in coral-reef fish recruitment are well documented and can be explained by ecological factors such as changes in reproduction magnitude, food availability, and predation during the pelagic stage, or by physical factors

like currents, tides, freshwater input, and wind during the pelagic and recruitment stages (*see* review by Cowen 2002).

The physical and biological processes operating during the larval stage do not affect the timing of recruitment, but they do generate high fluctuations in its magnitude and decouple between reproduction and recruitment (Danilowicz 1997; Robertson et al. 1988; Sponaugle and Pinkard 2004). Tides, currents, and winds all affect the ability of juveniles to successfully complete recruitment. However, the role of each factor and to what extent it affects the end number of larvae that will survive and recruit is not fully understood (Cowen 2002).

Upwelling and downwelling are among the currents commonly recorded at various coastal sites. These currents are usually driven by wind, which is one of the three principal agents controlling the movement of larval fish and invertebrates on the continental shelf (Epifanio and Garvine 2001). Evidence indicates that these currents might affect the recruitment of invertebrates such as crabs (Blanton et al. 1995; Wing et al. 1995; Shanks 1998), clams (Weissberger and Grassle 2003; Ma 2005; Shanks and Brink 2005), sea urchins (Wing et al. 1995), annelids (Verdier-Bonnet et al. 1997), and others, although the association with the vertical current might be weak (e.g., Shanks 1998). However, only a few studies have explained the differences found in the recruitment intensity of fish as due to upwelling or downwelling flow (Reiss and McConaughy 1999; Miller and Shanks 2005), and none of these have referred to coral-reef fishes. Since upwelling and downwelling currents are usually wind-driven (but can also

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The facilities and the Acoustic Doppler Current Profiler (ADCP) data of the IUI were used for this study. Tide data were provided by the Israel Limnological & Oceanographic Research Center. Sea temperature profiles were provided by the Israel Monitoring Program of the Gulf of Eilat.

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result from thermohaline forces), it is possible that some studies that found a correlation between the abundance of fish larvae and their transport to the reef by winds (Shenker et al. 1993; Milicich 1994; Kingsford and Finn 1997) were in fact dealing with up- and downwelling currents (Shenker et al. 1993).

The effect of such currents on the larval supply to the reef depends on the location of the larvae in the water column (Shanks 1998; Garland et al. 2002; Shanks and Brink 2005), and the local topography (McCulloch and Shanks 2003; Queiroga et al. 2006). Upwelling and downwelling are characterized by flow to different (mostly opposite) directions near the bottom and at the surface. Thus, passive or nearly passive larvae that are situated at different depths might be transported to different directions (on- or offshore; Roughgarden et al. 1991; Blanton et al. 1995; Wing et al. 1995), although there is evidence that even very weak swimming larvae will not necessarily be carried by the on- and offshore currents (Shanks and Brink 2005). However, unlike most other larvae, reef-fish larvae have well-developed swimming abilities (Stobutzki and Bellwood 1994; Stobutzki and Bellwood 1997) and hearing and olfactory senses (Sweatman 1988; Atema et al. 2002; Lecchini et al. 2005a) that can help them to find their settlement site while proceeding against the flow. On the other hand, the contribution of weak flow (such as downwelling or upwelling flows) to the transport of such larvae as pre-settled fish is not clear.

In this study, we examined the relationship between vertical (notably downwelling) and cross-shore currents in Eilat (at the northern tip of the Gulf of Aqaba, Red Sea) and their possible relation to the magnitude of fish recruitment, using a combination of extensive physical and ecological observations. In most cases up- and downwelling currents are wind-generated and relatively weak (compared to horizontal currents). Downwelling flow is common in Eilat during winter (Genin and Paldor 1998). However, Monismith et al. (2006) recently described a temperature-driven current, the so-called “thermal siphon,” which occurs at night and is likely to play an important role in the vertical flow of the northern Gulf of Aqaba.

Materials and methods

The Gulf of Aqaba is a deep and narrow strip of water connected to the main body of the Red Sea through the Straits of Tiran. The tide in the gulf is associated with the internal waves that are generated at these straits (Monismith and Genin 2004). Vertical variations in water density are determined mainly by temperature. Similar to oceanic regions, a mixed layer convectively driven by sea-surface cooling seasonally changes depth between <50 m in summer and >500 meters in winter, although this varies between years (Genin et al. 1995; see Fig. 7). The shore of the northern tip of the Gulf of Aqaba is steeply inclined with narrow patches of fringing coral reefs along its coast. Our study took place mainly near Eilat’s marine laboratory at the Interuniversity Institute for Marine Sciences of Eilat (IUI) on the western side of the gulf (~29°30’N, 34°55’E).

Current regime data were obtained from an Acoustic Doppler Current Profiler (ADCP; 600 KHz Workhorse, RD Instruments) which is permanently positioned at a 30-m depth and ~90 m offshore from the IUI. Additional current data were obtained from another ADCP deployed at Katza, 3.5 km north of the IUI site at the same depth and ~130 m offshore, from June–December 2005. The ADCPs were set to sample profiles from the bottom to the sea surface every 10 min. The obtained data were used to plot progressive vector diagrams (PVDs) for depths of 3 m, 13 m, and 23 m. Strictly speaking, because the flow is not spatially uniform, the PVD cannot be used to calculate the trajectories of the larvae even though they resemble Lagrangian trajectories. However, PVDs can give a rough estimate of the residual or time-averaged currents at specific locations. Similar PVDs plotted from data obtained from different sites indicate that these estimates are more accurate and less site-specific. PVDs were drawn in three resolutions: (1) lags of lunar month quarter (=7 d or 8 d) that were plotted for the entire recruitment seasons; (2) lags of 24 h that were plotted for four major recruitment events; and (3) lags of 1 h for selected days. In order to obtain units with a full night we started our “days” at 19:00 h the previous day (e.g., 01 Aug starts at 19:00 h on 31 July and terminates at 18:50 h on 01 Aug). The main near-shore flow in Eilat is along shore (~30° or ~210°). Downwelling flow was identified when the near-surface currents had an onshore component and changed to be <30° or >210°, and the near-bottom currents had an offshore component and were >30° or <210° (see Genin and Paldor 1998).

The quality of the ADCP data obtained was examined in three ways. First, the instrument’s data-quality control feature was used. This built-in data control parameter is termed “correlation.” This correlation differs from the statistical correlation, and we refer to it here as ACo (ADCP’s Correlation) to avoid confusion with the statistical term. The ACo magnitude data gave the magnitude normalized echo autocorrelation at the lag used for estimation of the Doppler phase change. The ADCP programmed this magnitude using a linear scale of 0–255, where 255 was perfect ACo. ACo values <64 were considered unreliable (“uncorrelated”; RDI Principles of Operation booklet). Second, the possible effect of extreme values (which might be false data) was examined by comparing the PVD to the median multiplied by the number of readings (n). The PVD is actually an average reading multiplied by n . We found the median of the data sets and multiplied it by n as well. The difference between the PVD and the median data represents the effect of extreme values. Third, the proportion of readings with large differences in the current magnitude and/or direction were ascertained from both the previous and the subsequent readings. “Large difference” was defined as a change of $\geq 30\%$ in magnitude and $\geq 45^\circ$ in direction. Such readings have a good chance of being false and their frequency is an indicator of the data quality. The two latter approaches were applied only when the first indicated that data quality might be problematic.

For each of the two years we deployed a fixed transect along which we tagged 398 branching corals in 2004 and

348 in 2005. All the tagged corals were of the species and sizes that are usually selected for settlement by the studied species recruits. The recruitment to these corals of two Pomacentrids (Damsel-fishes), *Chromis viridis* (Cuvier, 1830) and *Dascyllus marginatus* (Rüppell, 1829), was censused daily throughout the entire recruitment season (June–December) of the study years. The number of recruits at each tagged coral colony was counted (or estimated when there were too many recruits) and the change in the number of fish (Δ) from the previous day was calculated. This Δ consisted of the number of recruits that had joined the coral the previous night plus or minus the number of fish that had migrated to or from this colony during the previous day minus mortalities. Since we did not have an estimate of or data on migration and mortalities, we considered Δ to be the net recruitment to this colony. The daily sum of all Δ s from colonies in the transect was calculated and served as the basis for comparison of recruitment intensity.

Data regarding the recruiting fish were obtained from otolith readings. Young fish were collected from the reef of the IUI a few days after recruitment. One lapilar otolith was removed from each fish and its increments were counted. Average pelagic larval duration (PLD) and total age were calculated based on three independent readings for each otolith. Otoliths with a coefficient of variance greater than 5%, for either age (PLD or total) were discarded. Recruitment dates were back-calculated from post-settlement ages and collection dates. Average PLDs were calculated for each species and recruitment event. We particularly searched for different (higher or lower) PLDs on the days of relatively high recruitment in order to identify both early and delayed recruits.

Based on these data, we defined periods in which recruitment occurred, termed “recruitment events.” A recruitment event was considered to have begun when the first recruits were identified among the tagged corals (pauses in the recruitment, which are described in the results, together with high growth rate of the recruiting fish, allow easy identification of the first recruits of each recruitment event), and to have ended when the daily sum of all Δ s was negative. We allowed three consecutive days with negative daily sums in order to ensure that recruitment had indeed terminated and that the negative daily sums observed was not a temporary reduction in recruitment.

Fluctuations in the intensity of recruitment were compared within each species and then to the PVDs in order to identify any links between the current and the larval supply to the reef. In order to distinguish between major and minor effects, comparisons between currents and recruitment intensity were performed for the entire recruitment event level, a weekly level, and a daily level. To examine the relationship between cross-shore flow and recruitment, we isolated the cross-shore component (120° and 300°) of the current from the total current using trigonometry $\sin(\text{current direction}-30^\circ) \times$ the current magnitude; the same was done for the currents measured at 3-m and 23-m depths. Forward stepwise multiple regression was used to examine the effect of the cross-

shore current on daily recruitment intensity. A total of four independent variables were introduced into the model. Net displacement (km) during the day (08:00–22:00 h) and night (22:00–08:00 h), was measured at depths of 3 m and 23 m, with positive values corresponding to offshore flow. To test whether these currents have a delayed effect, we ran separate analyses for the 24 h leading up to recruitment and for each of the two days that preceded it (a lag of 0 d, 1 d, and 2 d).

Results

Downwelling started to take place at the end of the summer of both study years, as described previously (Genin and Paldor 1998; Monismith et al. 2006), with sporadic events of downwelling in September and more events from mid-October onward (Fig. 1).

During the downwelling period the magnitude of the offshore and onshore flow fluctuated from day to day (Fig. 2). Downwelling occurred mainly at night and in the morning (~22:00 to 08:00–10:00 h), whereas the currents throughout most of the day were usually along shore, like in the summer (Fig. 2). The PVDs obtained from both ADCPs (separated by 3.5 km along the coast) during 2005 were usually very similar (Fig. 3). Even when differences in the alongshore component of the current were observed, the cross-shore components were similar in both data sets at all depths.

Examination of the data quality revealed that the ACo's of all the data obtained from 23 m and 13 m were above 120. Reductions in ACo were identified at a 3-m depth during the day time, but only once (21 Oct 2004) did the ACo drop to the threshold of 65. Because of these drops at 3 m, we reexamined the data for this depth. Comparison of the median of the 3-m data for all four recruitment events to the PVD of the same time showed differences $<2\%$. Detection of extreme flow changes revealed that $<0.1\%$ of the readings showed sharp changes in the current magnitude. Approximately 1.5% of the data showed large changes in current direction, but more than 90% of these had occurred when the current was very weak ($<2 \text{ mm s}^{-1}$). Elimination of these latter changes left 0.14% of the readings showing a sharp change in direction. The readings showing a large change in direction and those showing a large change in current magnitude corresponded at a rate of 56%. Distribution of these data between day and night was similar.

Several recruitment events recorded during the two seasons of observations differed in their duration, timing relative to the lunar cycle, and recruitment intensity (Fig. 4). The intervals between the recruitment events were also of different durations and timing relative to the lunar and tidal cycles. Massive recruitment of many fishes (>30 species; Ben-Tzvi et al. unpubl. data), including the studied species, was documented for four of these events (Table 1). High fluctuations in recruitment intensity were recorded both between and within recruitment events (Table 1 and Fig. 4, respectively). The ratios between the numbers of recruits of the different species differed between recruitment events (Table 1). However, the daily relative number

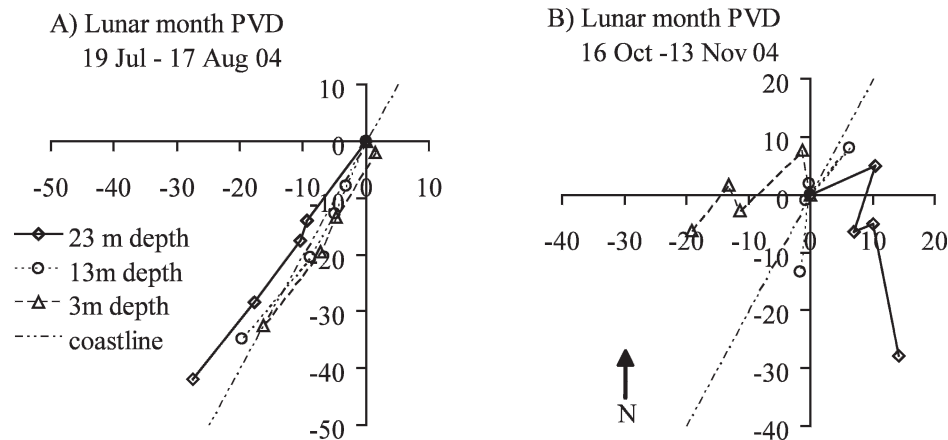


Fig. 1. PVDs depicting the typical currents at the IUI in (A) summer and (B) fall. Each PVD depicts the currents of one lunar month. Each lag represents one lunar month quarter (scale in km). Negative values represent the distances to the west and the south while positive values represent distances to the north and east. The current flow along the shoreline ($\sim 30^\circ$) during the summer months at all depths is seen on the left. During October the surface current starts flowing toward the coast, and the near-bottom current flows from the coast, while at the mid-depth the current continues to flow along the coastline. The data were obtained from ADCP deployed at a 30-m depth at the IUI. The coastline mark represents the approximate coastline direction.

of recruits of *D. marginatus* and *C. viridis* during the same recruitment event changed respectively (except for the second event of 2005 in which very few *D. marginatus* recruited, probably due to the late season). These changes included four to six spikes of high Δ per recruitment event in three of the documented events. These spikes usually lasted one day in which the Δ of both species were more than twice the average of the other days at the same event. In October–November 2004 we documented one peak of high recruitment that lasted several days (Fig. 5).

Our estimates of the number of fish in corals with many recruits were compared to counts of the fish taken from photographs. Photos of four coral colonies with schools of 150–350 *C. viridis* recruits were taken. The estimates differed from counts taken from the photos by -9.7% to $+2.1\%$. Since all field counts and estimates were made by the same diver, a similar error could be expected in all estimated figures.

Association between recruitment magnitude and presence and the magnitude of downwelling was observed at different resolutions. The late recruitment events of both years, which occurred during the downwelling period, were more intense than the early events (Table 1). Almost all spikes in recruitment during all four recruitment events followed a spike in the downwelling magnitude with a one-day lag. Hourly resolution PVDs revealed downwelling even on days where it was not seen on the daily resolution PVD, due to changes in the current direction and magnitude during the day (e.g., 26 Oct 05; Fig. 2C). The early event of 2004, which occurred before clear downwelling had been identified, was different. Here only near-bottom offshore current was identified in the PVD and only on a few days. No conclusive association of recruitment with the downwelling was observed for this event. At least one recruitment spike did not follow offshore current, and

there were days with offshore currents that were higher than normal but with no higher recruitment following them.

Since downwelling occurred only at night and early morning (Fig. 2A,C; Monismith et al. 2006), we compared the correlations of the recruitment intensity of *C. viridis* to that of all-day (24 h) PVDs and to that of night (22:00–08:00 h the following day, approximately equal to the downwelling hours) PVDs. The correlations to the night PVDs were higher at all recruitment events for both examined depths (Fig. 6). The differences between the correlations between the sum of daily recruitment Δ s to 24 h-PVDs and night-PVDs cannot be explained by the reduction in data quality during the day since that occurred only on a few days and only at a 3-m depth, and its effect on the results was minimal.

The multiple regression results (Table 2) reveal that nighttime, cross-shore currents measured at a 23-m depth explained much of the variation in recruitment intensity; especially when allowing for the one-day delay (Table 2; note the higher r^2 values of the 1-day lag models, as well as the fact that a significant model was found for each of the four dates considered). The positive relationship ($\beta_1 > 0$) implies that stronger recruitment followed nights with a relatively large offshore current displacement.

Only during October to November 2004 was the contribution of the onshore, 3-m-depth flow significant (and thus also entered in the regression model; Table 2). This event is the only one for which a significant correlation of the recruitment magnitude to the flow of the same day and of two days before was obtained as well. The onshore flow was found to be significant on the same day and the offshore flow was significant with a two-day lag.

Otolith readings revealed a consistency in the PLDs of fish of the same species that recruited to the IUI reef during

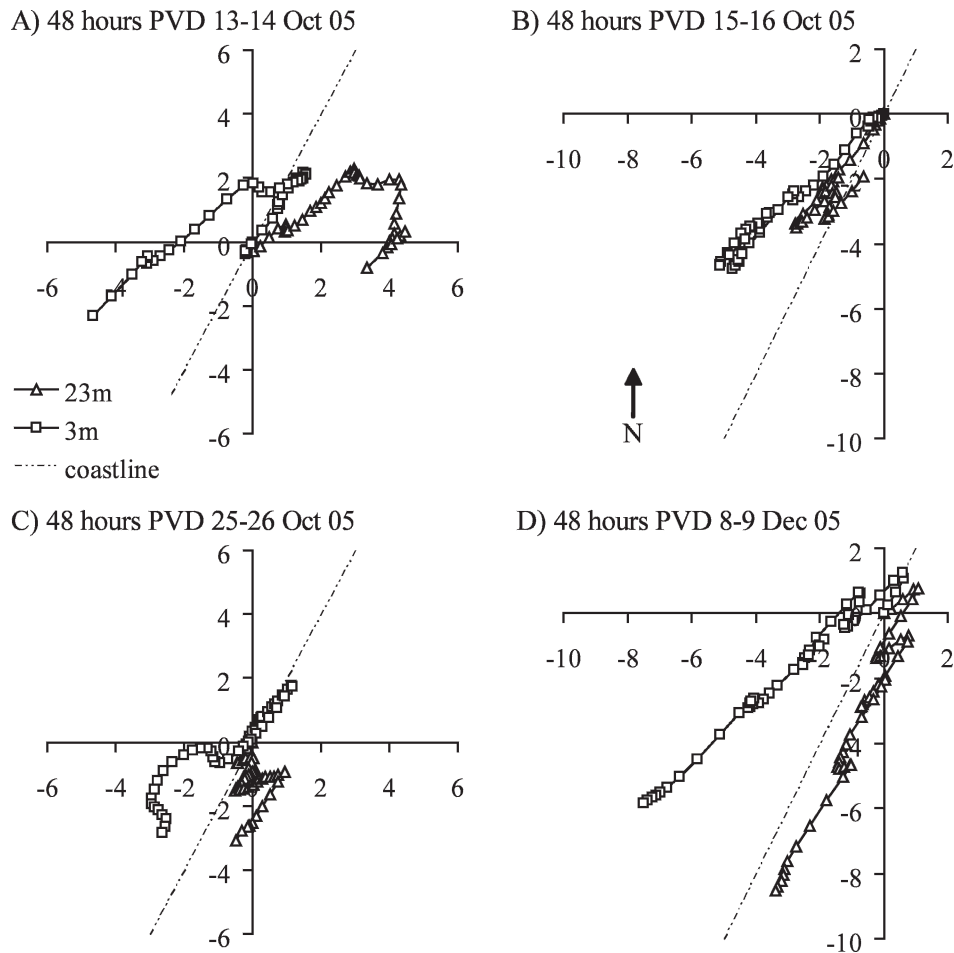


Fig. 2. PVDs of 48 h with 1-h resolution (scale in km). Each PVD starts at 19:00 h (evening before the first date) and lasts a complete two nights and two days. (A), (B), and (C) depict days during October 2005. In (A) and (C) downwelling is seen on the second night while no downwelling is seen in (B). In (C) the current changed direction after the downwelling (the next morning), thus the downwelling that is seen here is not clearly identified (Fig. 5); (D) shows days with no strong downwelling during the recruitment event of December 2005. Weak downwelling existed throughout the entire recruitment event; distance between the two PVDs on the cross-shore vector is ~ 5 km. The coastline mark represents the approximate coastline direction.

the same recruitment event (for *C. viridis* at all recruitment events; Table 3). This consistency was recorded throughout each recruitment event. No differences in the PLD were documented between days of high and low recruitment.

Supporting data

Vertical water-temperature profiles for the study period were obtained from the Israel Monitoring Program of the Gulf of Eilat (Fig. 7). They were obtained by conductive-temperature-depth (CTD) casts made approximately once a month from a vessel in the middle of the Gulf (~ 3 km from the coast) from the surface down to the bottom.

Sea level (tide) data were provided by the Israel Limnological and Oceanographic Research Center. These data were obtained from an instrument located at the IUI study site. Due to technical problems, usable sequential data were obtained only for 2004 (Fig. 8).

Discussion

Many studies from different seas have noted an association between the existence and magnitude of coral-reef fish recruitment and lunar or tidal cycles (reviewed by Cowen 2002). In the present work, however no such association was clearly identified, and recruitment events seems to occur at different times in the lunar cycle (Fig. 8). Because the lunar and tidal cycles in the Gulf of Aqaba are coupled with high tides during new and full moon periods (Fig. 8), and because the tide is generated by internal waves (Monismith and Genin 2004), it can be argued that there is also no effect of the internal waves on recruitment. The recruitment of many fish species was documented during the same recruitment events, whereas practically no fish recruited in the intervals between these events (Ben-Tzvi et al. unpubl. data). The causes for these nearly complete pauses in recruitment are not yet known. Here we discuss

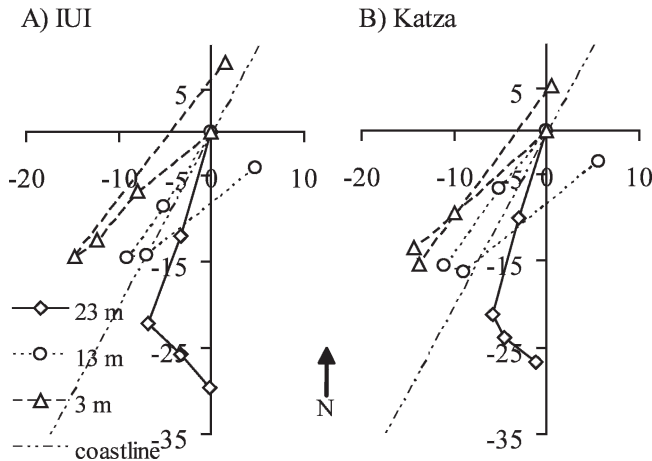


Fig. 3. PVDs of the same lunar month (05 Sep–03 Oct) at the (A) IUI and (B) Katza (distance of ~ 3.5 km). The currents at depths of 3 m, 13 m, and 23 m are plotted for each site. Scale in km. The coastline mark represents the approximate coastline direction.

several possible explanations for the differences in recruitment among the periods in which it occurred. The changes in recruitment intensities observed during a recruitment event included one to several spikes of one to a few days. These spikes also had no association with the tidal or lunar cycles (Fig. 8).

The magnitudes of downwelling correlated to the recruitment intensity on both the daily and overall recruitment event scales are shown in Tables 1 and 3. The number of recruits of *C. viridis* was higher during the later recruitments events of both years (i.e., during early winter when downwelling is more common; Fig. 8). The reproduction volume of *C. viridis* at the relevant hatching time for the later recruitment in these years was much lower than that observed at the relevant time for the earlier

recruitment for both years. Reproduction volume of *D. marginatus* at the Eilat reefs diminished in mid-September and terminated one month later (Ben-Tzvi et al. unpubl. data). Such discrepancy between magnitude of reproduction and recruitment of reef fishes is well known (e.g., Robertson 1990; Robertson et al. 1993) and assumed to be a consequence of several physical and biological factors (Cowen 2002). The possible downwelling effect we documented in Eilat is an additional factor that may play a role in determining recruitment magnitude. Thus, based on the differences between the magnitudes of the entire recruitment events alone, we cannot argue that downwelling is the major factor affecting the number of fish larvae that reach the reef. However, the actual role of the downwelling flow gains greater importance upon examination of the daily changes in recruitment.

Our study revealed that most of the recruitment spikes occurred one day following strong (relative to the season) downwelling currents, and vice versa. Most “downwelling nights” documented during the recruitment periods were followed by a night of high recruitment. Of 13 documented spikes only two (the last two of August–September 2004) did not match with downwelling in the previous night. The strong correlations obtained between fluctuations in the recruitment magnitude of *C. viridis* and the cross-shore currents of the previous nights (Table 2) indicate that changes in the downwelling explain much of the change in the recruitment intensity of this fish. The major exceptions were the significant correlations obtained for the same day and with a two-day lag in October–November 2004, which can be explained by sequential days with both relatively high recruitment and relatively strong downwelling (Fig. 5). Thus, a shift of one day backward or forward does not greatly change the recruitment–downwelling correlation. Another exception occurred in the correlation with the daytime cross-shore current in October 2005. The hours we have defined as “night” are those in which most

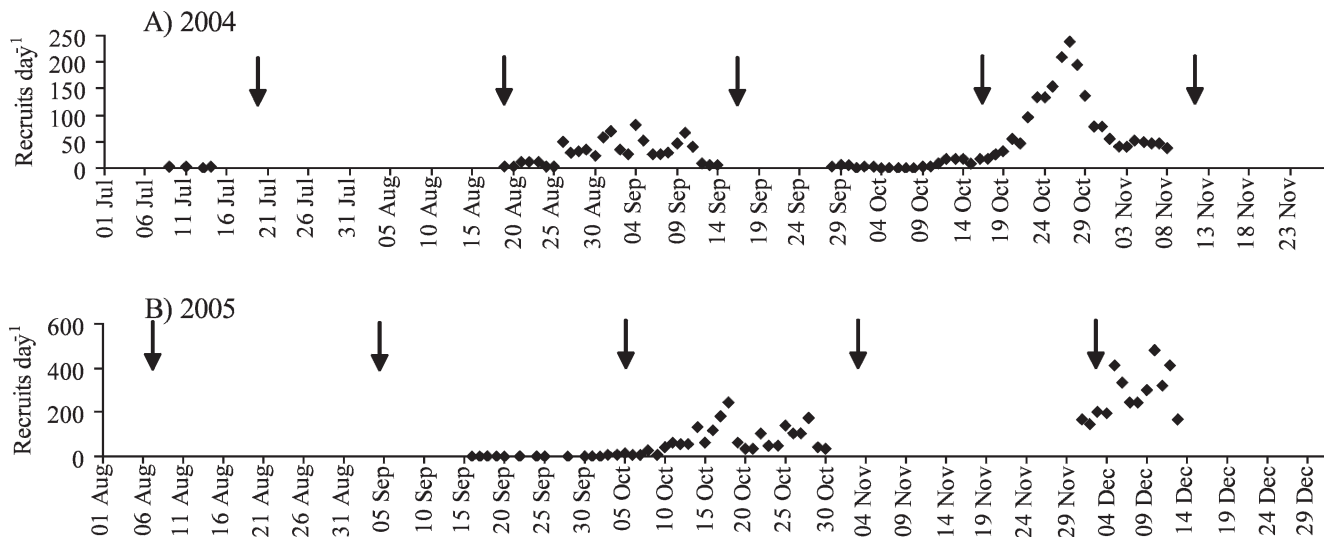


Fig. 4. The recruitment events during (A) 2004 and (B) 2005 observed throughout the entire study seasons are represented by the recruitment intensity of *C. viridis*. Each point represents the sum of daily observed Δ s in the number of recruits. The arrows indicate a new moon. No recruitment was documented before and after the presented periods.

Table 1. Differences in the number of recruits per day between the major recruitment events of 2004 and 2005 as shown by the average number of recruits per day \pm SD as recorded for the entire transect. The total number of tagged corals and the proportion of *Acropora* spp. (which attracted most of the recruits) in the transect differ between the years and both were lower in 2005, hindering comparison of the figures between years. It is also probable that the figures for 2005 are relatively lower than they would have been had the transect been the same as that of 2004.

	No. of days	<i>D. marginatus</i>	<i>C. viridis</i>
Aug–Sep 04	27	27.88 \pm 19.83	30.15 \pm 22.59
Oct–Nov 04	42	5.97 \pm 6.82	50.35 \pm 62.03
Oct 05	29	31.25 \pm 25.81	72.78 \pm 62.54
Dec 05	13	4.62 \pm 2.36	279.08 \pm 106.99

downwelling occurred. However, there were differences in the downwelling hours, and thus, on corresponding days, “tails” of downwelling remained before or after the night hours. These tails, if long enough, could have resulted in the correlation obtained. The fluctuations in the relative magnitude of daily recruitment of *D. marginatus* were similar to those for *C. viridis*, except for December 2005, when very few larvae of the former recruited (Table 1). Thus, it can be argued that downwelling similarly affects more than one fish species.

Although the coupling between downwelling flow and fish recruitment in the Eilat reefs is fairly clear, two major questions still remain: (1) what is the actual role that downwelling flow plays in enhancing recruitment? and (2) assuming that the downwelling currents do govern the observed recruitment spikes, what is the reason for the one-day lag found between downwelling and a recruitment spike?

First, the onshore surface currents may theoretically help in transporting the recruits to the reef (*see* review by Cowen 2002) as occurs with invertebrate larvae (*see* review by Epifanio and Garvine 2001). We have no clear picture at present of the location of pre-recruitment larvae of the study species in the water column. (As far as we know no such data exist for the study species or for of fish larvae depth distribution in the Red Sea.) However, based on previous works, we assume that most of these are located at depths of 15–60 m (Cha et al. 1994; Cowen 2002).

The currents recorded (using the ADCP at 30-m depth) during downwelling at the 13-m depth revealed almost no cross-shore current at this depth. (They were mainly along shore.) Further data were obtained from two additional ADCPs at the 46-m depth (~200 m from the coast) and at the 70-m depth (~300 m from the coast). These data indicate that the downwelling flow extends beyond 300 m offshore and that the near-bottom cross-shore flow increases with greater depth (Ben-Tzvi et al. unpubl. data). Reliable readings from the deeper ADCPs were obtained only up to the bottom of the “no cross-shore” zone, which was deeper than in the shallower sea-bottom area. Thus it is not known whether the shallow onshore current in the deeper sea-bottom area is also stronger.

If the pre-settlement larvae are indeed carried by the current rather than swimming against the flow, the larvae should consequently have been found at depths from which they could be transported by onshore currents. However, the results of our multiple regression tests revealed no

correlation between the near-surface, onshore flow and recruitment intensity (Table 2), suggesting that the role of larval transport by near-surface, onshore flow is negligible.

A second probable explanation of passive transport is that of the mechanism described by Shanks and Brink (2005). They argue that larvae that reside below the thermocline are carried shoreward during the upwelling events that follow downwelling events, as the nose of the bent thermocline and sub-thermocline water moves shoreward. However, the most intense recruitment events recorded in this study occurred from October onward (Figs. 4, 5). The thermocline at this time was already deep (especially in 2005, when recruitment was the highest; Fig. 7), making it improbable that the thermocline could have played any role in the larval transport at this status. Moreover, the recruitment intensity in the summer was much lower, even though the relevant reproduction was the highest. The mixed layer at this time was minimal (Fig. 7), and thus, if the thermocline had any effect on the recruitment intensity, it would have been a negative one. Blocking of the downwelling could have resulted in this negative affect. The temperature-driven downwelling is generated by minute temperature differences, which may have been overcome by the thermocline, thus reducing or even completely preventing offshore current.

Yet another possible explanation for the downwelling : recruitment correlation is that the bottom offshore current may enhance fish recruitment. This possibility is reinforced by the highly significant correlations obtained between recruitment and offshore flow (Table 2). Fish at the recruitment stage have been shown to be able to detect specific chemicals (Wright et al. 2005) and use them as cues to guide them to the reef (Atema et al. 2002) and for habitat selection (Sweatman 1988; Lecchini et al. 2005a,b). The advection of chemical-containing water from the reef toward the open sea might enhance the pre-settlers' ability to proceed in the right direction, against the flow, toward the potential recruitment sites. Locating the source of odor in a stream in order locate its source for the purpose of settlement is common in nature. Some evidence indicates that even larvae of small marine organisms use active plume-tracking in flow to reach their preferred settlement site (e.g., the nauplius of the barnacle *Trevathana dentate* [Pasternak et al. 2004]). Other solutions are utilized when swimming against the flow is not feasible. For example, the complex behavior of the blue crab (*Callinectes sapidus*) detects and differentiates among odors from different sources (e.g.,

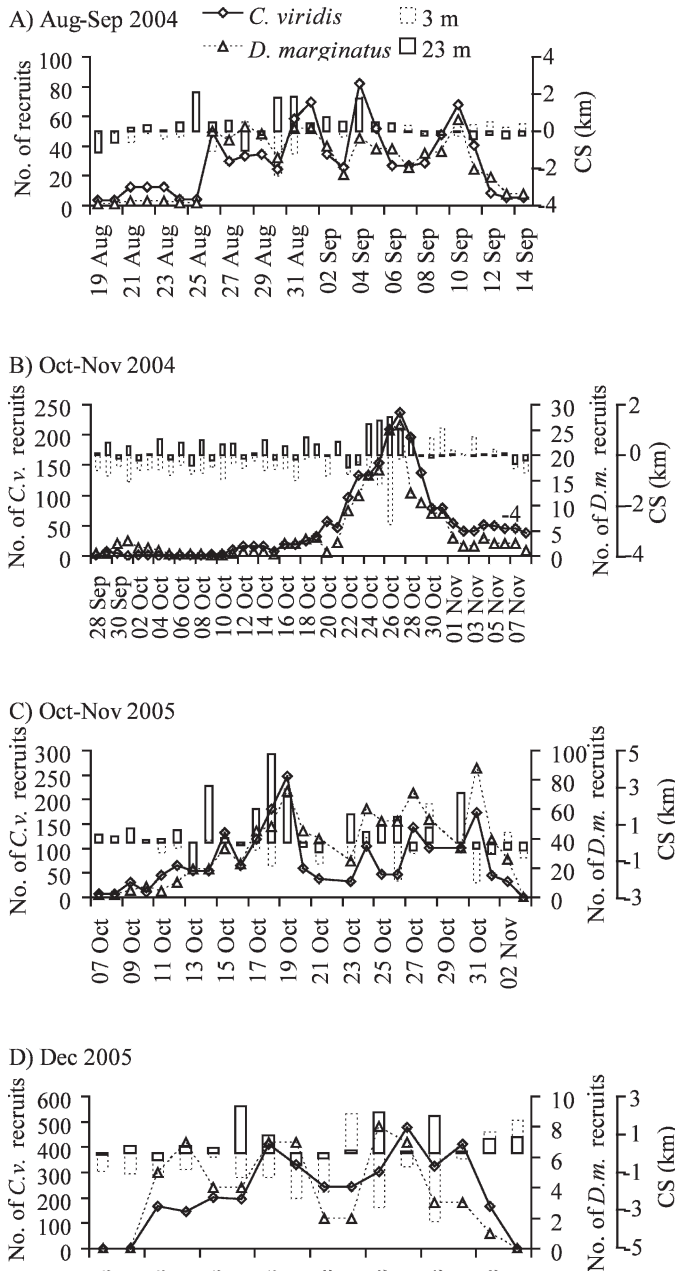


Fig. 5. Comparisons of the cross-shore components during (A) Aug–Sep 2004, (B) Oct–Nov 2004, (C) Oct–Nov 2005, and (D) Dec 2005 of 24-h PVDs and the fish recruitment during four recorded recruitment events in Eilat. The sum of daily Δ s in the number of two species' recruits during the events is represented by the lines. The Δ recruits is the summary of all the positive Δ s in the corals at the transect. Daily cross-shore PVDs (CS) of the current data at 3 m and 23 m as measured at the IUI is shown by columns (columns with solid line shows 23-m depth and broken line shows 3-m depth). Positive values represent the offshore (120°) flow and negative values represent the onshore (300°) flow. The PVD distances were calculated for each day starting at 19:00 h on the previous day and thus incorporate the data of one full night and one full day. Left Y axis: No. of recruits of *C. viridis* per day (panel A shows *D. marginatus* also). Right outer and inner Y-axis: No. of recruits of *D. marginatus* per day. PVD values are shown in km, respectively.

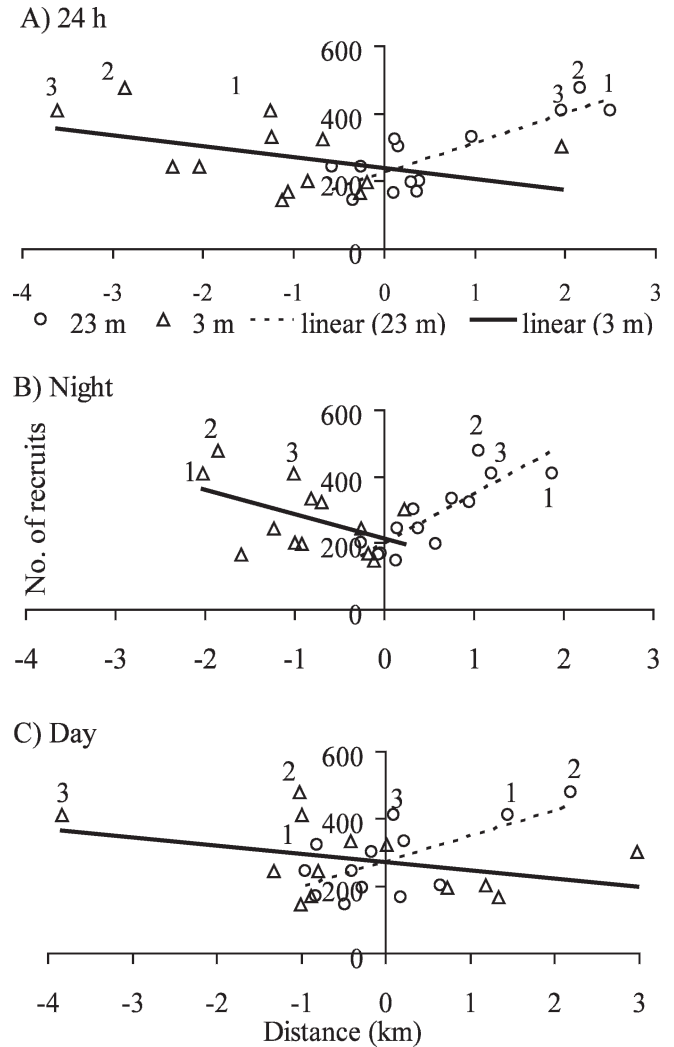


Fig. 6. The daily recruitment magnitude plotted against the PVD value of the cross-shore current of (A) the previous 24 h, (B) the previous night (22:00–08:00 h), and (C) the previous day (08:00–22:00 h). The data are from the recruitment event of December 2005. Linear regressions with the flow at 3-m and 23-m depths are presented. Positive values of the current represent offshore current (120°), and negative values represent onshore current (300°). Nos. 1, 2, and 3 indicate days with relatively strong cross-shore current which were followed by high recruitment. It should be noted that the downwelling hours are not always the same. In this season downwelling may start several hours before 22:00 h and/or terminate well after 08:00 h. The night PVD includes only the main downwelling hours and, thus, downwelling tails of different lengths are included in the day PVD and increase the correlation there (see Table 2 for statistics).

potential recruitment site or predator) and reacts to them (Forward et al. 2003a,b). But at the end it has to sink to the bottom to catch the landward flow from the gravitational circulation into the estuary (Epifanio and Garvine 2001). Hence, it is not surprising that fish that at this stage are capable of prolonged fast swimming (Stobutzki and Bellwood 1994, 1997) and have a developed olfactory sense, swimming against the odor flume toward their destination. Unlike less adept swimmers, the downwelling flow should

Table 2. Results of forward stepwise multiple regression of recruitment intensity on net cross-shore displacement (km). Independent variables considered include the net displacement during the day (d, 08:00–22:00 h) and night (n, 22:00–08:00 h), measured at depths of 3 m and 23 m (d3, d23, n3, and n23, respectively); with positive values corresponding to offshore flow. Separate analyses were conducted for each of four recruitment events, at time lags of 0 d, 1 d, and 2 d. Only significant models are provided, along with the unstandardized coefficient of the variable(s) entered (β_1) and its standard error (SE); as well as the model's *F* ratio, adjusted r^2 , and significance level. The program rejected three of the factors (currents) for most examinations and thus only the major factors are presented.

Date	Lag	Variable	β_1	SE	<i>F</i>	Adj. r^2	<i>p</i>
Oct–Nov 04	0	n3	−91.57**	30.710	8.89	0.28	0.006
Aug–Sep 04	1	n23	53.05***	11.69	20.59	0.45	<0.001
Oct–Nov 04	1	n23	68.26**	17.88	11.96	0.52†	<0.001
		n3	−65.99*	24.82			
Oct 05	1	n23	88.00***	12.93	33.90	0.75‡	<0.001
		d23	15.98**	5.54			
Dec 05	1	n23	148.15***	28.99	26.11	0.68	<0.001
Oct–Nov 04	2	n23	68.25**	21.05	10.51	0.33	0.005
Dec 05	2	d23	61.38*	20.02	9.39	0.43	0.012

* $0.05 \geq p > 0.01$; ** $0.01 \geq p > 0.001$; *** $p \geq 0.001$.
 † $\Delta r^2 = 0.16$ due to inclusion of n3.
 ‡ $\Delta r^2 = 0.09$ due to inclusion of d23.

not prevent them from proceeding from relatively a long distance up-current toward the odor sources in the reef. The suggested mechanism couples the olfactory and swimming abilities of the pre-settlement fish with the downwelling, which differentiates this mechanism from many others that explain the role of vertical currents in recruitment by passive transport.

The second open question is that of why the enhanced recruitment occurs one night following the downwelling night. To the best of our knowledge there are no available data on the behavior of fish larvae during the final stages of their pelagic phase that might explain such a time lag between the flow-induced arrival of larvae at the reef and the appearance of recruits in the reef. One possible explanation is that the competent fish larvae improve their position and relocate themselves closer to a potential recruitment site shortly before they are due to recruit. This hypothesis is based on a recent finding that Pomacentrids that recruit to the same site at the same time have similar PLDs (Bay et al. 2006). Similar findings were obtained in the present study (Table 3). This inflexibility in recruitment age forces the larvae to arrive at the right place at the right time (age) or be lost. Since the assumed effect of downwelling on recruitment was seen one day after downwelling had occurred (Table 2), the hypothesis suggests that downwelling may help the larvae to locate themselves in the right position prior to actual settlement.

Table 3. Average PLD \pm SD as obtained from otolith readings. Each figure is an average of averages of three readings for each otolith. The number in parentheses is the sample size. No fish were collected during December 2005.

	<i>C. viridis</i>	<i>D. marginatus</i>
Aug–Sep 04	22.09 \pm 1.01 (17)	26.07 \pm 1.07 (14)
Oct–Nov 04	21.96 \pm 0.67 (106)	20.96 \pm 0.66 (26)
Oct 05	22.11 \pm 0.38 (33)	—

Evidence for reef fishes recruiting to their natal area (Jones et al. 1999; Swearer et al. 1999) and for the role of active behavior in achieving this is accumulating (Paris and Cowen 2004). We suggest that active swimming against the flow aids the young recruits in reaching their destination reef. However, additional studies are needed in order to better understand the behavior of the fish and the mechanism by which they are affected by downwelling. Monismith et al. (2006) suggested that the “thermal siphon” causing the downwelling might also be present at

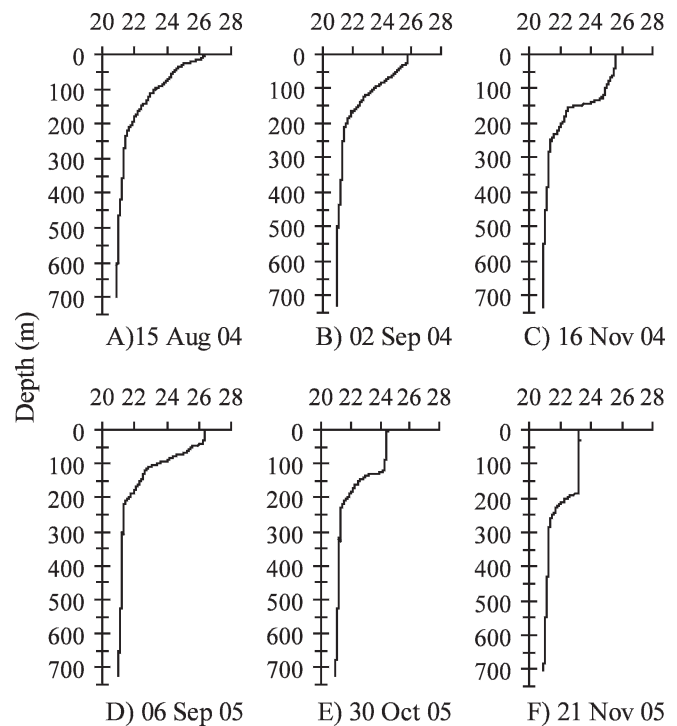


Fig. 7. Vertical temperature profiles of the water column in the deep center of the northern Gulf of Aqaba (between Israel and Jordan) obtained from CTD on (A) 15 Aug 04, (B) 02 Sep 04, (C) 16 Nov 04, (D) 06 Sep 05, (E) 30 Oct 05, and (F) 21 Nov 05.

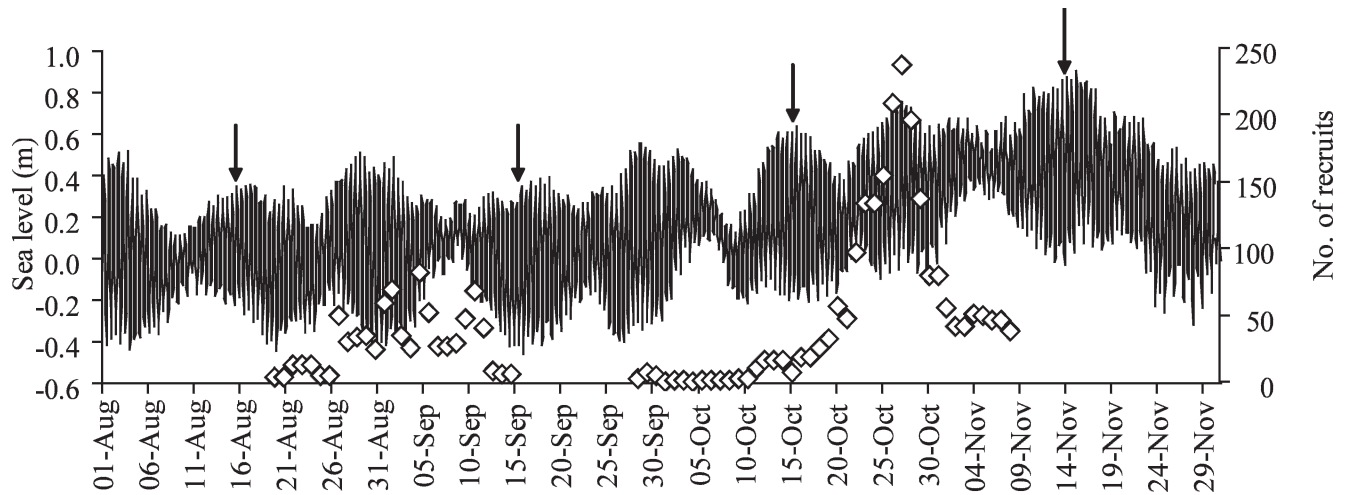


Fig. 8. Plot of the sea level measured at the IUI over 4 months (of the major recruitment) in 2004. The arrows indicate a new moon. The daily recruitment data of *C. viridis* during this period are shown (open diamonds) in order to demonstrate the relation between lunar phase and recruitment.

other coral reefs in addition to Eilat. If this is the case, downwelling flow may be one of the factors affecting the intensity of reef fish recruitment in many reefs, which underlines the importance of further studies of the mechanisms by which downwelling affects recruitment.

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