

# Habitat patchiness and predation modify the distribution of a coral-dwelling damselfish

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**Abstract** Fish abundance is often better predicted by microhabitat variables on continuous reefs than on isolated patch reefs. Although this was suggested to stem from reduced post-recruitment relocation, this has not been shown experimentally. We found the relationship between the presence of a coral-dwelling fish, *Dascyllus marginatus*, and the size of its coral host to differ between corals on continuous reefs and the sparsely distributed corals on sandy bottoms. Empty transplanted corals were colonized exclusively by new recruits when on the sandy bottom, and both by new recruits and post-recruitment dispersal of adults when on the continuous reef. New recruits settled predominantly into small corals, although analyses of recruitment patterns were confounded by low recruitment in the studied years. Both tank experiments and field survey data suggest that the presence of recruits in small corals is at least partially driven by predation by the dottedback, *Pseudochromis olivaceus*, which lives predominantly in large corals within both habitats. Consequently, we suggest that the relationship between fish presence and coral size differs between the habitats due to coral size dependent

predation on recruits and variability in the importance of direct recruitment to replenish fish populations.

## Introduction

Coral reefs can be composed of continuous reef tracks, isolated reef patches, and a variety of intermediate forms. Owing to their small size and the ease of experimental manipulations most research on coral reef fish ecology has been limited to isolated reef patches (Ault and Johnson 1998a; but see Webster 2003; Sandin and Pacala 2005). Nevertheless, ecological processes on isolated reefs may differ from continuous reefs. For example, predictability of fish abundance by microhabitat variables on continuous reefs is higher than on patch reefs (Ault and Johnson 1998a) and fish abundance is higher and less regular on isolated patches (Nanami and Nishihira 2002, 2003; Belmaker et al. 2007a). It is still unclear what mechanisms cause fishes on reefs with dissimilar degrees of isolation to respond differentially to microhabitat variables.

Accumulated evidence suggests that predation by piscivorous fish can have a significant effect on the abundance and the diversity of coral reef fishes (e.g., Carr and Hixon 1995; Beets 1997; Holbrook and Schmitt 2003; Almany and Webster 2004; Hixon and Jones 2005). As many coral reef fishes use the reef matrix as shelter from predation, fish might avoid traversing large stretches of unsuitable medium with high predation pressure (e.g., Hixon and Beets 1993). Therefore, predation risk might force fish settling onto isolated patches to stay in a suboptimal habitat. In contrast, on continuous reefs higher shelter-density might reduce predation risk associated with movement, thereby facilitating post-recruitment dispersal into alternative habitats of higher quality. This may lead to enhanced

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predictability of fish abundance by microhabitat variables on continuous reefs (Ault and Johnson 1998a).

Differences in fish distribution between habitats are frequently mediated through differential predation, which is strongest during the first few days on the reef (Doherty et al. 2004; Almany and Webster 2006; Holmes and McCormick 2006). Predation pressure may vary with reef spacing and between isolated and continuous reefs (e.g., Overholtzer-McLeod 2004; Belmaker et al. 2005; Overholtzer-McLeod 2006), potentially leading to dissimilar fish distributions. Intraspecific agonistic interactions may also contribute to differences between habitats that differ in spatial organization (Levin et al. 2000).

Coral size plays a pivotal role in many of the life history parameters of coral-dwelling fish, including adult size and abundance (Kuwamura et al. 1994), mating system (Fricke 1980; Wong et al. 2005) and reproductive success (Kuwamura et al. 1996). In this study, we examine how the relationship between a coral-dwelling fish and its host-coral size changes between two reef habitats that differ in coral cover: sandy bottom, which contains isolated corals embedded within a shelter-free sandy substrate, and a continuous reef with relatively dense coral cover as well as other shelter-providing microhabitats. Using a combination of observations and manipulative experiments we ask: (1) does the relationship between a coral-dwelling fish and its host-coral size differ between habitats? (2) if so, what processes can explain the observed difference?

## Materials and methods

### Study species

*Dascyllus marginatus* (Rüppell 1829), like many of its congeners, lives exclusively within branching corals (Fishelson et al. 1974). Based on its life history and by comparison with similar-sized tropical Pomacentrids this species is likely to live for up to 8 years, with most individuals younger than 3 (Fowler 1990; Fowler and Doherty 1992). In the northern Red Sea, most *D. marginatus* individuals inhabit the coral *Stylophora pistillata* (78%) and to a lesser extent *Acropora* spp. (Shpigel and Fishelson 1986; Kent et al. 2006). Group size is partially determined by coral size, although preference for smaller groups may result from intraspecific competition for food (Kent et al. 2006).

Some species of dottybacks (*Pseudochromis* spp.) are vicious predators of small fish (Beukers and Jones 1998; McCormick and Meekan 2007). *P. olivaceus* (Rüppell 1835), a common Red Sea species, is found mainly in large branching corals from the genera *Stylophora* and *Pocillopora* (Belmaker et al. 2007b). *P. olivaceus* has been observed to prey upon several species of small fish, including

*D. marginatus* recruits (J.B. personal observation). In addition, juvenile *P. olivaceus* were seen attacking and chasing heterospecifics too large for them to consume. *P. olivaceus* has a limited home range and can be seen within a single coral 96% of the time (Belmaker et al. 2007b).

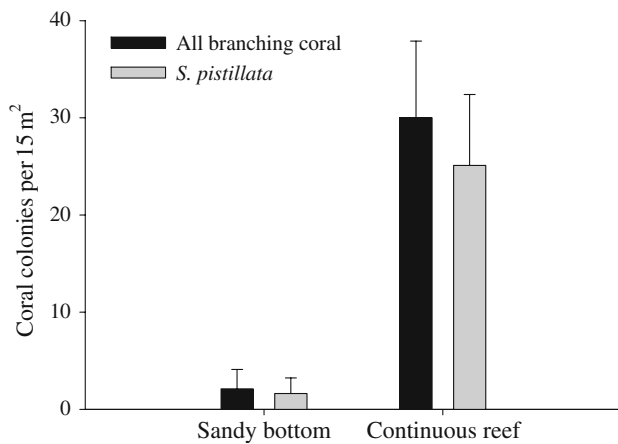
### Surveys

#### Pre-recruitment surveys

We first examined whether the relationship between adult *D. marginatus* presence and the size of its coral host is habitat-dependent. Two habitats were compared: (1) sandy bottom, where coral growth is limited to sparsely distributed coral heads and (2) continuous reef track composed of coral pavement with a relatively dense cover of living corals (Fig. 1). The surveys were conducted at least half a year after recruitment ceased and all fishes reached the size of sexual maturity (>3 cm; Shpigel and Fishelson 1986). Surveys were conducted near the Inter-University Institute for Marine Science (IUI) on the Israeli coast of the Gulf of Aqaba, northern Red Sea. Five sites were surveyed, three on sandy bottom and two on continuous reef tracks. Several (5–20) 15 × 1 m belt transects were surveyed in each site, depending on coral cover, such that sites with low coral cover were sampled more intensively. In addition, several more coral heads were surveyed haphazardly at sites with low coral density. Analyses were performed on all corals in each habitat combined, as no site-specific pattern was detected within each habitat in the proportion of occupied coral (likelihood ratio test on a contingency table,  $P > 0.5$  in both habitats). Therefore, transects and sites describe the way coral heads were surveyed, but were not factored into the analyses. All *S. pistillata* corals with a diameter larger than 5 cm within the belt transect were examined. Coral diameter was estimated as the geometric mean of the length, width and height (Loya 1976). For each coral, we recorded the number and size of *D. marginatus*, visually estimated to the nearest 0.5 cm using a UW measuring tape, as well as presence of the predatory fish *P. olivaceus*.

#### Surveys during recruitment

Sixty-one *S. pistillata* corals from a single sandy bottom site and 260 corals from one continuous reef track were chosen for detailed surveys to determine patterns of *D. marginatus* recruitment. Corals were marked, measured and surveyed weekly during the recruitment season (August–September) for the presence of new *D. marginatus* recruits as well as for the presence of *P. olivaceus*. For analysis, a fish species (*D. marginatus* or *P. olivaceus*) was considered to be present within a specific coral if it was sighted at least once during the surveys.



**Fig. 1** The average ( $\pm$ SD) number of corals per 15 m<sup>2</sup> in the two habitats: continuous reef and sandy bottom. (gray bars) only *Stylophora pistillata*, (black bars) total coral cover (all branching coral species)

### Coral transplantation

Nineteen corals were removed from nearby locations, matched for size, and half were planted on the continuous reef (10 corals) and half planted on the sandy bottom (9 corals). Transplanted corals were at least 12 m from each other and at least 1 m away from another coral occupied by *D. marginatus*. The corals in the natural surveys were usually spherical, enabling easy underwater estimation of their size from their length, width and height (Loya 1976). However, as we had relatively few transplanted coral we chose to use a more accurate method to estimate coral size in which coral volume was calculated as the sum of the volumes of the simple geometric shapes (column, cube, sphere, etc.) of which they were composed. This allowed better estimation of the size of the few transplanted corals that deviated from a perfect sphere or ellipsoid. Coral volume ranged from 2,300 to 13,500 cm<sup>3</sup>. The corals were surveyed for the presence of *D. marginatus* every fortnight for 6 months (12 surveys were completed). *D. marginatus* individuals were assigned as either new recruits or previous year adults, based on size (< or >1.5 cm). To examine whether the relationship between *D. marginatus* presence and coral volume changes between habitats we performed a binomial regression. The dependent variable was the number of times a *D. marginatus* was present within a coral (successes) out of the total number of surveys (12). The independent variables were log<sub>10</sub> transformed coral volume and habitat (continuous reef vs. sandy bottom).

### Tank experiments

We examined the preference of *D. marginatus* recruits for large versus small corals and explored whether this preference is dependent on the presence of *P. olivaceus*. Eight

pairs of large (mean volume 2,860 cm<sup>3</sup>  $\pm$  1,019 SD) and small (mean volume 503 cm<sup>3</sup>  $\pm$  181 SD) corals were placed in plastic containers (75  $\times$  52  $\times$  40 cm). Three *D. marginatus* recruits, freshly collected from the nearby reef, were placed in the middle of each container. After a day of acclimatization, the presence of the fish in each of the corals was monitored hourly (9:00–17:00) to establish their preference for the large versus small coral. During the afternoon (~13:00) a single juvenile *P. olivaceus*, too small to consume *D. marginatus*, was placed in half of the tanks, whereas the other half served as a control. The preference of *D. marginatus* for each of the corals was monitored hourly for another day and a half. Six additional temporal replications were conducted using the same fish and corals by completely reshuffling the corals (breaking up pairs) and fish among treatments. *D. marginatus* preference for large coral was calculated as number of fish in the large coral divided by the total number of fish within each container (i.e., 3). This value was averaged over all hourly surveys to obtain a single value per tank for each section of the experiment (before and after the addition of *P. olivaceus*).

This difference between tanks with and without *P. olivaceus* was examined by first calculating the difference in preference between the first and second parts of the experiment (preference before the addition of *P. olivaceus* to any of the tanks minus preference after). This difference was compared among tanks with and without *P. olivaceus* addition using a *t* test. Data were angular transformed prior to analysis. Because we hypothesized that *P. olivaceus*, which lived predominately within large corals (Belmaker et al. 2007b, see also “Results” section below), may drive *D. marginatus* individuals towards small coral we used an one-tailed test.

All experiments and fish/coral collections were performed under a special permit from the Israeli Nature Reserve Authority.

## Results

### Surveys

#### *Pre-recruitment surveys*

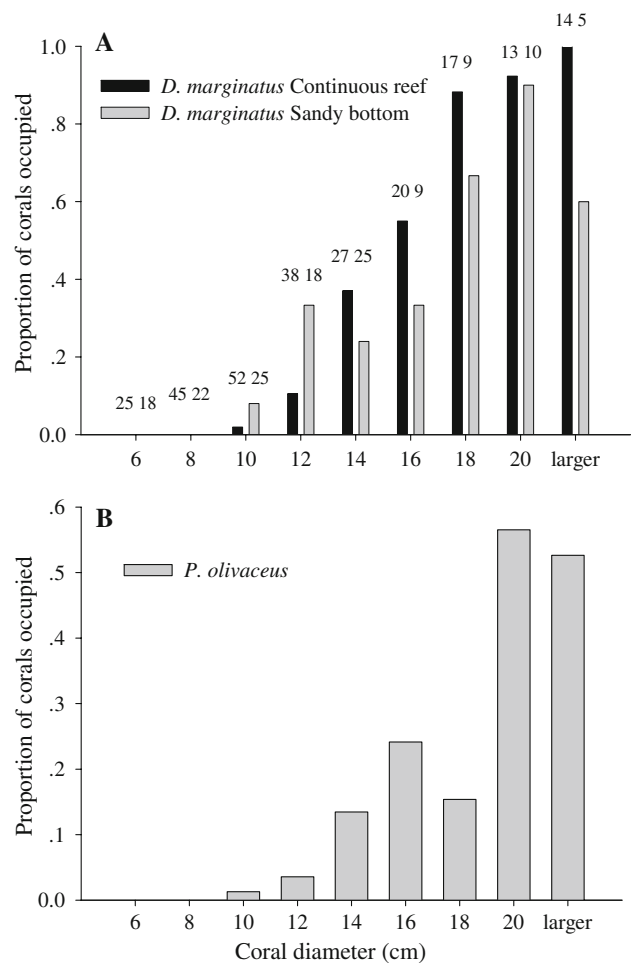
The sandy bottom had a lower density of total branching coral colonies in general and of *S. pistillata* in particular than the continuous reef (Fig. 1). There was no difference in average coral diameter between the habitats (*t* test, *P* = 0.75). To examine whether coral size had similar effects on *D. marginatus* occurrence in both habitats a logistic regression was performed, with coral diameter and habitat as a continuous predictor and a categorical

predictor, respectively. The full model was highly significant (Table 1). *D. marginatus* presence was positively related to coral size and, importantly, we found a significant interaction term between habitat and coral diameter (Table 1), indicating differences between habitats in the fish–coral relationship. The proportion of corals occupied by *D. marginatus* was higher on the sandy bottom compared with the continuous reef for small corals (<13 cm); while lower for large coral (>13 cm; Fig. 2). Although *P. olivaceus* presence was positively related to coral size, it was not different between sandy bottom and continuous reef habitats and the interaction term was not significant (Table 1).

Surveys during recruitment

In the study year (2007), *D. marginatus* recruitment was low and only 12 corals received recruits (7 and 5 on sandy bottom and continuous reef, respectively). Owing to the small number of recruits, we could not perform a full factorial analysis. Combining both habitats, the presence of new recruits (at least once during the survey period) had a negative relationship with coral diameter (Table 1). When including in the analysis only corals without sightings of *P. olivaceus* ( $n = 111$ ) we did not find a relationship between coral diameter and the presence of recruits (Table 1). In addition, in the range of coral diameters occupied by new recruits (9.0–14.9 cm) we found a significant negative relationship between a sighting of *P. olivaceus* and the presence of *D. marginatus* recruits ( $P < 0.01$ , Fisher exact test).

As in the previous surveys, *P. olivaceus* presence was positively related to coral size ( $P < 0.05$ ) but was not different between habitats and the interaction term between habitat and coral size was not significant (Table 1).



**Fig. 2** a The proportion of corals occupied by *Dascyllus marginatus* in the sandy bottom (gray bars) and continuous reef (black bars) at various coral diameter categories. The numbers above the columns indicate sample sizes. A higher proportion of coral are occupied on the sandy bottom at small coral size categories ( $\leq 13$  cm), while a lower proportion are occupied at larger coral size categories ( $> 13$  cm). b The corresponding proportion of corals occupied by *Pseudochromis olivaceus* (both habitats combined)

**Table 1** Logistic regressions relating the presence of *Dascyllus marginatus* and *Pseudochromis olivaceus* to coral diameter and habitat type in the two surveys: pre-recruitment and during recruitment

Survey	Species	Remarks	$R^2$	Total coral	Occupied coral	df	$\chi^2$	p	p-coral diameter	p-habitat	p-interaction
Pre-recruitment	<i>D. marginatus</i>		0.49	392	102	3	221	<0.0001	<0.0001	0.19	<0.01
	<i>P. olivaceus</i>		0.34	392	44	3	93	<0.0001	<0.0001	0.17	0.29
Recruitment	<i>D. marginatus</i>	All corals (both habitats combined)	0.14	301	12	1	14.2	<0.001	<0.01	NA	NA
		Only corals without <i>P. olivaceus</i> (both habitats combined)	0.03	111	12	1	2.3	0.13	0.16	NA	NA
	<i>P. olivaceus</i>		0.23	301	190	3	90	<0.0001	<0.0001	0.97	0.82

In the survey during recruitment *D. marginatus* presence was analyzed on the sandy bottom and continuous reef together, due to small sample size preventing a full factorial analysis

Coral transplantation

The presence of *D. marginatus* within transplanted corals differed between the habitats and a significant interaction term between habitat and coral volume (binomial regression, Table 2) indicates differences between the sandy bottom and the continuous reef in the fish–coral size relationship.

Combining both habitat types, the presence of *P. olivaceus* (sighted at least once during the periodic surveys) was negatively related to the presence of *D. marginatus* recruits (Table 3, 12 of 13 for corals without *P. olivaceus* and one of six for corals with *P. olivaceus*;  $P < 0.01$ , Fisher exact test), indicating a negative correlation between the presence of *P. olivaceus* and *D. marginatus*.

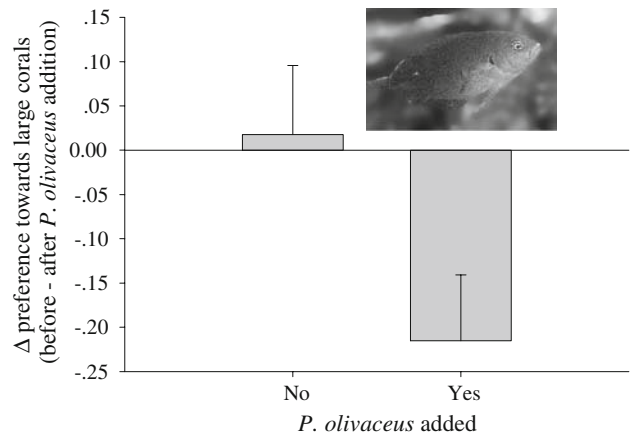
We next examined whether the proportion of corals with adult *D. marginatus* initially arriving as recruits was higher on the sandy bottom compared with the continuous reef. Because some corals might not be able to provide suitable habitat for adult *D. marginatus*, we only retained for analysis those corals that had been occupied at the end of the experiment by an adult fish (independent of whether it arrived as an adult or as a recruit which subsequently grew within the coral). Overall, seven corals on the continuous reef and four on the sandy bottom were occupied by adult *D. marginatus* (Table 3). Of these, only two corals (29%) on the continuous reef contained individuals arriving as recruits compared with all four coral (100%) on the sandy bottom (Table 3, Fisher exact test,  $P_{\text{one-tail}} < 0.05$ ). Consequently, it appears that post-recruitment movement is of higher importance for population replenishment on the continuous reef compared with the sandy bottom.

**Table 2** Binomial regressions relating the number of *Dascyllus marginatus* presences within the transplanted coral (out of 12 bi-weekly surveys) to coral diameter and habitat type

	Coefficient ( $\pm$ SE)	z value	Pr ( $> z $ )
Habitat (reef)	-144 ( $\pm$ 26)	-5.466	<0.001
Log <sub>10</sub> (coral volume)	-40 ( $\pm$ 8)	-5.23	<0.001
Interaction	42 ( $\pm$ 8)	5.46	<0.001

**Table 3** Summary of the coral transplantation experiment results

	Total coral	Corals with <i>D. marginatus</i> recruit sightings	Corals with <i>P. olivaceus</i>	Corals with <i>P. olivaceus</i> and <i>D. marginatus</i> recruits	Coral settled by adult <i>D. marginatus</i> at end of experiment (regardless of whether they arrived as recruits or adults)	Coral from the previous column with <i>D. marginatus</i> that have arrived as recruits
Sandy bottom	9	7	2	1	4	4
Continuous reef	10	6	4	0	7	2



**Fig. 3** The difference in the preference of *Dascyllus marginatus* recruits for large coral in the tank experiments between the beginning of the experiment (no *Pseudochromis olivaceus* in all tanks) and the end of the experiment (*P. olivaceus* in half of the tanks). Bars are 1 SE. Adding *P. olivaceus*, which settled in the large corals, significantly reduced recruit preference towards large corals compared with tanks in which the predator was not added ( $p_{\text{one-tail}} < 0.05$ ). Small picture—*P. olivaceus*

Tank experiments

Before the introduction of *P. olivaceus*, *D. marginatus* displayed a slight preference for large corals (average preference of 0.76, 0.57–0.94 CI,  $n = 14$ ). Adding *P. olivaceus* significantly altered the preference of *D. marginatus* toward small coral compared with tanks in which *P. olivaceus* was not added ( $t = 2.13$ ,  $P_{\text{one-tail}} < 0.05$ ; Fig. 3). Although *P. olivaceus* was free to move between corals, it remained exclusively within the larger coral.

Discussion

We found, both in surveys and when using coral transplantations, that the relationship between *D. marginatus* and the size of its coral host differed between habitats—continuous reef versus sandy bottom. This augments a number of recent studies that suggest that patchiness and isolation might influence coral reef fish population dynamics (Ault and Johnson 1998a; Nanami and Nishihira 2002, 2003).

By following patterns of colonization to empty transplanted corals, we showed that the source of *D. marginatus* population replenishment within *S. pistillata* corals differed between the habitats. Although corals on sandy bottom are mainly colonized through direct recruitment, corals on continuous reefs were colonized through a mixture of direct recruitment and post-recruitment relocation of older fish (Table 3). However, as sample size was small, these results should be interpreted prudently. Experimental and observational data showed that the presence of the predatory fish *P. olivaceus* in large corals reduces the ability of *D. marginatus* to successfully recruit, either by direct predation or agonistic interactions. Tank experiments indicated a shift towards the use of small corals in the presence of the predator (Fig. 3). Moreover, in natural corals the negative relationship between coral size and recruit presence disappeared when excluding corals with *P. olivaceus* (Table 1). Corroborating this notion, in *Acropora* spp., that seldom contain *P. olivaceus*, *D. marginatus* recruits are predominantly found in the larger corals (Ben Tzvi 2008).

Coral reef fish may be more mobile than previously thought and capable of long distance movements (Frederick 1997; Lewis 1997). Nevertheless, low post-settlement dispersal seems to be characteristic of most Pomacentridae (McCormick and Makey 1997; Booth 2002; Lecchini and Galzin 2005) and there is little evidence that coral-dwelling *Dascyllus* traverse expanses of exposed sand (Sale 1972). Therefore, on the sandy bottom a fish recruiting to a coral, possibly avoiding large corals that contain the predator *P. olivaceus*, may be limited in its post-recruitment dispersal and nearly forced to remain in the coral to which it recruited. In contrast, the shelter-rich continuous reefs may allow enhanced post-recruitment movement of fish into alternative corals, e.g., dispersal into larger corals with increasing size, thereby enhancing the fish-microhabitat association. This can explain the larger proportion of small corals (e.g., 10 and 12 cm diameter) occupied by adult fish on sandy bottom reefs compared with continuous reefs, while the lower proportion found in the larger coral size categories (e.g., the >20 cm diameter category, Fig. 2). Nevertheless, if no inter-coral dispersal was present on the sandy bottom, we would expect mostly small corals to be occupied. As this is not the case and large corals are occupied at a higher rate than small coral in both habitats (Fig. 2), it is evident that some post-recruitment movement is taking place in the sandy bottom as well, though at a lower rate.

Adult fish were found predominantly in large corals (Fig. 2; Table 1; see ‘pre-recruitment survey’), while recruits were found predominantly within small corals, regardless of habitat (Table 1; ‘survey during recruitment’). This seems to indicate ontogenetic shifts in coral use, which may be common among reef fishes (McCormick and

Makey 1997; Booth 2002; Lecchini and Galzin 2005). But what is the motivation for post-settlement movement in *D. marginatus*, especially if predators are more common in the larger corals? In the case of *D. marginatus* small corals may provide limited shelter for adult fish that need larger branch spacing for effective shelter. In addition, the limited space in small coral may prevent the formation of social groups, that may entail important advantages such as accesses to mates (Fricke 1980; Kuwamura et al. 1996; Wong et al. 2005) or reduced predation risk (Karplus et al. 2006). Although *P. olivaceus* attacks and consumes recruits, it co-inhabits with adult *D. marginatus* (J.B. personal observations, see McCormick and Meekan 2007 for a similar phenomenon with a different dottyback species) so predation on large post-recruitment individuals within large coral may be minimal.

Few branching coral species apart from *S. pistillata* live on the sandy bottom (Fig. 1). Consequently, *D. marginatus* population replenishment may depend almost entirely on patterns of recruitment and survival within this coral species. However, on the continuous reef several other branching coral species exist, most notably *Acropora* spp. that may also provide suitable habitat for the fish (Kent et al. 2006). *D. marginatus* frequently recruit to *Acropora* spp. (Ben Tzvi 2008), presumably because they offer the small fish protection from predator with their densely-spaced branches (O. Ben Tzvi, personal communication). Therefore, *D. marginatus* demography on the continuous reef may be influenced by recruitment and post-recruitment movement patterns of individuals from other coral species, especially when recruitment to *S. pistillata* is low (as in the studied years).

The differences between habitats in fish distribution can also potentially originate from different habitat-specific recruitment patterns. Availability of recruits is not expected to differ over small spatial scales (Ault and Johnson 1998b). However, paucity of suitable habitat might favor less stringent microhabitat selection on isolated reefs, while on continuous reefs recruits may have more flexibility to select microhabitats among a suite of potential options. Therefore, the observed divergent fish–microhabitat relationships between habitats may originate from dissimilar recruitment patterns on top of size-specific predation and reduced post-recruitment relocation.

Differences in fish distribution between habitats are frequently mediated through differential predation (reviewed in Juanes 2007). However, in this system predation pressure by *P. olivaceus* is likely to be comparable between habitats as its prevalence within corals was similar (66% on the continuous reef, 52% on the sandy bottom). In addition, there is no reason to assume that predation efficiency, which is often mediated by habitat complexity (Almany 2004; Beukers and Jones 1998), differs between habitats as

coral shape and size were equivalent. We therefore suggest that even when predation pressure does not vary spatially, its effect on adult distribution pattern may depend on patch spacing. This is because of coral size dependent predation on recruits and variability in the importance of direct recruitment to replenish fish populations.

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