

T. Liberman · A. Genin · Y. Loya

## Effects on growth and reproduction of the coral *Stylophora pistillata* by the mutualistic damselfish *Dascyllus marginatus*

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**Abstract** Although coral dwelling fishes are common on coral reefs, the nature of their effect on the host corals is poorly understood. The present study, conducted in the Gulf of Eilat (Red Sea) between July 1989 and August 1990, demonstrated that the branching coral *Stylophora pistillata* (Esper) benefits, in two components of coral fitness, from the presence of the damselfish *Dascyllus marginatus* (Rüppell), an obligate coral dweller. The growth rate of damselfish-inhabited corals was significantly higher than that of corals without damselfish. This was observed, using two growth assessment methods, in long-term (>7 mo) comparisons between: (1) corals where the damselfish were experimentally removed versus corals with unaltered fish groups; and (2) naturally inhabited versus non-inhabited corals. The presence of damselfish did not affect the coral's specific (per surface area) reproductive output, whether it was assessed by the number of female gonads per polyp or by the number of planulae released  $\text{cm}^{-2}$  surface area  $\text{d}^{-1}$ . However, the more rapid increase in branch size in damselfish-inhabited corals resulted in an apparent increase in the total reproductive output, with age, in growing corals. These findings demonstrate that the association between the damselfish *D. marginatus* and its host coral, *S. pistillata*, is mutualistic.

### Introduction

In coral reefs, numerous species of fish live in close association with branching corals. Some fish live most of the time between the coral branches, whereas others forage in the immediate vicinity of the coral and use the coral for shelter, as a sleeping ground, and an egg-laying substrate (Fishelson 1963; Sale 1971 a, b; Holzberg 1973; Fishelson et al. 1974; Patton 1974; Luckhurst and Luckhurst 1976; Lassig 1977; Kuwamura et al. 1994). In most instances, the fish is an obligate coral dweller and relies on the coral for protection against predators (Coates 1980).

Although coral-fish associations in tropical reefs are widespread, surprisingly, the nature of the relationship between corals and fish is poorly understood. The majority of the studies looked at the biology of coral dwelling fish and treated the coral only in terms of a habitat (Fishelson 1963; Sale 1971 a, b; Holzberg 1973; Fishelson et al. 1974; Patton 1974; Luckhurst and Luckhurst 1976; Lassig 1977; Kuwamura et al. 1994). These studies did not look at the possible interaction between the coral and fishes.

One large scale study researching fish interaction with corals was a study on the grunts, *Haemulon flavolineatum* and *H. plumieri*, where hundreds of grunts rested above coral heads during the day and foraged at night in seagrass beds (Meyer et al. 1983; Meyer and Schultz 1985 a, b). Meyer and Schultz (1985 b) demonstrated that *Porites furcata* colonies above which the grunts rested had significantly more coral tissue  $\text{cm}^{-2}$  of branch surface area. On the other hand, the coral *Acropora palmata* did not exhibit such an effect. In a smaller system of a single coral head and a few small resident fish, one study reported that the damselfish, *Dascyllus aruanus*, attacked the coral predator *Acanthaster planci*, although a direct benefit to the coral was not shown (Weber and Woodhead 1970). Sale (1971 a) assumed that the relationship between *D. aruanus* and its host corals was not even commensal.

We focused on the coral *Stylophora pistillata* (Pocilloporidae), which is widely distributed throughout the Indo-Pacific and Red Sea (Veron 1986). In the Gulf of Eilat,

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T. Liberman<sup>1</sup> · Y. Loya  
Department of Zoology, The George S. Wise Faculty  
of Life Sciences, Tel-Aviv University, Tel-Aviv 69978, Israel

T. Liberman · A. Genin  
The H. Steinitz Marine Biology Laboratory, P.O. Box 469,  
Eilat 88103, Israel

A. Genin  
Department of Evolution, Systematics and Ecology,  
The Hebrew University, Jerusalem 91904, Israel

<sup>1</sup> Present address (✉): Department of Biological Sciences, State University of New York at Buffalo, Buffalo, New York 14260, USA

*S. pistillata* is one of the most abundant corals (Loya and Slobodkin 1972), and the coral is often inhabited by *Dascyllus marginatus*.

*Dascyllus marginatus* is endemic to the Red Sea, Gulf of Aden, and the Gulf of Oman (Allen and Randall 1980). It occurs at depths of 4 to 30 m (Holzberg 1973; Fricke 1977, 1980; Allen and Randall 1980). *D. marginatus* inhabits the different branching corals *Stylophora pistillata*, *Acropora hemprichi*, *A. humilis*, *A. scandens*, *Seriatopora spinosa*, and *Pocillopora danai* (Holzberg 1973; Fishelson et al. 1974; Fricke 1980). Different coral species, characterized by different branch spacing, may be inhabited by different developmental stages of the same fish species (Fricke 1980). In addition, the number of damselfish occupying a coral is positively correlated with the coral size and its structural complexity (Fricke 1980; Shpigel and Fishelson 1986).

During the day, *Dascyllus marginatus* forages in the water column within approximately 80 cm of its host coral (Fishelson 1963; Holzberg 1973). It retreats between the coral branches when predators approach (Fishelson 1963; Shpigel and Fishelson 1986). At night, the fish sleep between the branches of the coral. These obligate coral dwellers inhabit only live corals (personal observation). On the other hand, not every *Stylophora pistillata* is inhabited by *D. marginatus*.

The objective of our study was to determine if the branching coral *Stylophora pistillata* benefits from the presence of the resident damselfish, *Dascyllus marginatus*. Benefits investigated included a comparison of growth rate and reproductive output between corals with and without resident damselfish.

## Materials and methods

The present study was conducted between July 1989 and August 1990 in the northern Red Sea (Gulf of Eilat) along 1 km of fringing coral reef in front of the H. Steinitz Marine Biology Laboratory, Eilat, Israel.

### Coral growth

The growth rate of *Stylophora pistillata* (Esper) with resident *Dascyllus marginatus* (Rüppell) was compared to that of corals without damselfish by a damselfish-removal experiment and by in situ measurements on non-manipulated corals.

### Damselfish-removal experiment

In order to focus on a possible damselfish presence effect, a growth experiment was conducted using 12 *Stylophora pistillata*, all initially inhabited by *Dascyllus marginatus*. The corals chosen occurred as isolated colonies ( $\geq 5$  m from the nearest damselfish-inhabited coral), so that visits by damselfish from nearby corals were unlikely. In addition to the presence of *D. marginatus*, the fish fauna inhabiting each *S. pistillata* colony usually consisted of one *Pseudochromis olivaceus*, two to four *Gobiodon citrinus*, and one juvenile Scorpaenidae (Lieberman 1991). In terms of both size and number, *D. marginatus* dominated. All 12 corals had between four to six *D. marginatus*. The corals were divided into six pairs in which the corals of each pair were on the same substrate and at the same depth. Three

pairs (A, B, C) were located at depths ranging from 7.5 to 12 m surrounded by coarse sand. Pairs D, E and F, were situated at depths ranging from 8.0 to 14.0 m on beach rock.

Since this was a manipulation experiment with a small sample size, an accurate, and yet partially destructive (branches were cut from the colony), growth measuring method was employed. Each *Stylophora pistillata* was stained with Alizarin Red-S. Prior to staining, all associated fish fauna were removed using quinaldine. The fish were held in a mesh cage (height 61 cm, top 21×21 cm, base 40×40 cm, mesh size 1 mm) adjacent to their coral. A coral was covered by a 20-liter plastic bag into which 0.3 g of Alizarin Red-S was introduced. The bag was removed after 12 daylight h, and the fish fauna was returned to the coral. Four corals were marked each day over three consecutive days. For one randomly chosen coral from each pair, *Dascyllus marginatus* was not returned. Thus, each coral pair consisted of one coral with all associated fish fauna including *D. marginatus* while the second coral had all the original fish fauna excluding *D. marginatus*. Hereafter, we define corals that were inhabited by *D. marginatus* and other associated fish fauna as corals "with damselfish," while corals that had no *D. marginatus* but had other fish fauna are defined as corals "without damselfish."

For 13 mo, a weekly census was conducted to determine the number of *Dascyllus marginatus* in the six corals that contained damselfish and to insure that no *D. marginatus* settled in the other six corals. During the first month of the study, individual adult *D. marginatus* immigrated to the corals without damselfish and these damselfish were promptly removed.

After 13 mo, four branches, haphazardly selected from the central part of the coral, were cut from each *Stylophora pistillata*. Tissue from the collected coral branches was detached using a Water Pik. Branches were dried, and the skeleton below the alizarin line was removed using a wire cutter and sandpaper. The length ( $l$ ), height ( $h$ ) and width ( $w$ ) of the newly grown skeleton were measured with calipers ( $\pm 0.1$  mm). Surface area ( $S$ ) was determined as accurately as possible by the sum of the area of the hemispherical tip,  $S = \pi(h^2 + r^2)$ ,  $r = [(l+w)/4]$ , where  $r$  = radius (Rinkevich and Loya 1983) and the cylindrical body  $S = 2\pi r h$  (Falkowski and Dubinsky 1981; Rinkevich and Loya 1983). In addition, the new skeletal growth was weighed ( $\pm 0.001$  g) and its volume determined by water displacement ( $\pm 0.1$  ml) (Meyer and Schultz 1985 b). Measured parameters were compared between the coral pairs utilizing the Wilcoxon's Signed-Ranks Test (Sokal and Rohlf 1981).

The density of polyps in *Stylophora pistillata* with and without damselfish was determined by counting the number of polyps in a  $0.25$  cm<sup>2</sup> area below the spherical tip in the corals collected for the alizarin experiment.

### Non-manipulated corals

In addition to the damselfish-removal manipulated experiment, we compared non-manipulated, naturally occurring corals with and without damselfish found on the reef. We measured and marked with plastic tags 51 *Stylophora pistillata* colonies with *Dascyllus marginatus* and 65 corals without *D. marginatus*. The corals were randomly distributed in 10×10 m census plots with additional corals with *D. marginatus* chosen at random from the reef in order to increase the sample size. Coral dimensions were determined using a sliding ruler, which resembled an oversized caliper. The height, from the base of the coral ( $h$ ), length ( $l$ ) and width ( $w$ ) of each coral were measured ( $\pm 0.1$  cm). The geometric mean radius (GMR) was calculated using the formula:  $\bar{r} = (l w h)^{1/3} / 2$  (Loya 1976 c). None of the corals had any large dead areas and all exceeded 4.0 cm GMR. The GMR measurement of size was chosen because it allowed measuring a large sample size while causing no damage to the corals.

Every week, for 7 mo, a census was conducted on all 116 tagged *Stylophora pistillata* to monitor the presence or absence of *Dascyllus marginatus* within the corals. Any coral that originally was without damselfish but later acquired *D. marginatus*, or a coral that lost its damselfish during this period, was omitted from the analysis. Corals which died or were broken during the 7-mo period were also omitted. The final number of corals in this analysis was 40 corals with damselfish and 46 corals without damselfish. Corals were meas-

ured at the beginning and end of the study. The difference in GMR was calculated. A one-way ANOVA determined if a difference existed in the initial size of corals with and without damselfish. An ANCOVA was employed to determine if a significant difference existed in the change in GMR between corals with and without damselfish taking into account initial coral size (Sokal and Rohlf 1981).

#### Coral reproduction

Specific reproductive output ( $\text{area}^{-1}$ ) of *Stylophora pistillata* was evaluated by the number of female gonads  $\text{polyp}^{-1}$  and the number of planulae released  $\text{cm}^{-2}$  of coral surface area  $\text{d}^{-1}$ . Gonadal histology was conducted on haphazardly selected branches from the 12 alizarin marked, manipulated corals. An additional 16 non-manipulated corals with ( $n=8$ ) and without ( $n=8$ ) *Dascyllus marginatus* were sampled. Because reproductive maturity is uniform throughout each colony (Rinkevich and Loya 1979b), a single branch was sampled from each coral. Tissue samples were embedded in wax and serial sections 6- $\mu\text{m}$  thick were stained with Mayer's hematoxylin and eosin (Rinkevich and Loya 1979a). Intact polyps were followed through the serial slides. Female gonads were counted, and the average number of female gonads  $\text{polyp}^{-1}$  calculated.

To determine the number of planulae  $\text{d}^{-1}$   $\text{cm}^{-2}$  of coral surface area, equal numbers of coral branches ( $n=10$ ) were cut from non-manipulated *Stylophora pistillata* with and without *Dascyllus marginatus*. Branches were brought to the laboratory and placed in separate, aerated seawater basins. For seven consecutive days, planulae released in each basin were collected and counted. The surface area of the branches was determined by projecting them on a leaf-area image analyzer (Muscatine et al. 1989) and multiplying the resulting number by  $\pi$  (Falkowski and Dubinsky 1981). This area method was employed, as opposed to measuring the dimensions of each branch with a caliper, since it gave a fast, easy and sufficient way, for this experiment, of measuring the numerous branches collected from each colony. Parameters of reproductive output were compared using the Mann-Whitney *U*-test (Sokal and Rohlf 1981).

## Results

### Coral growth

#### Damselfish-removal experiment

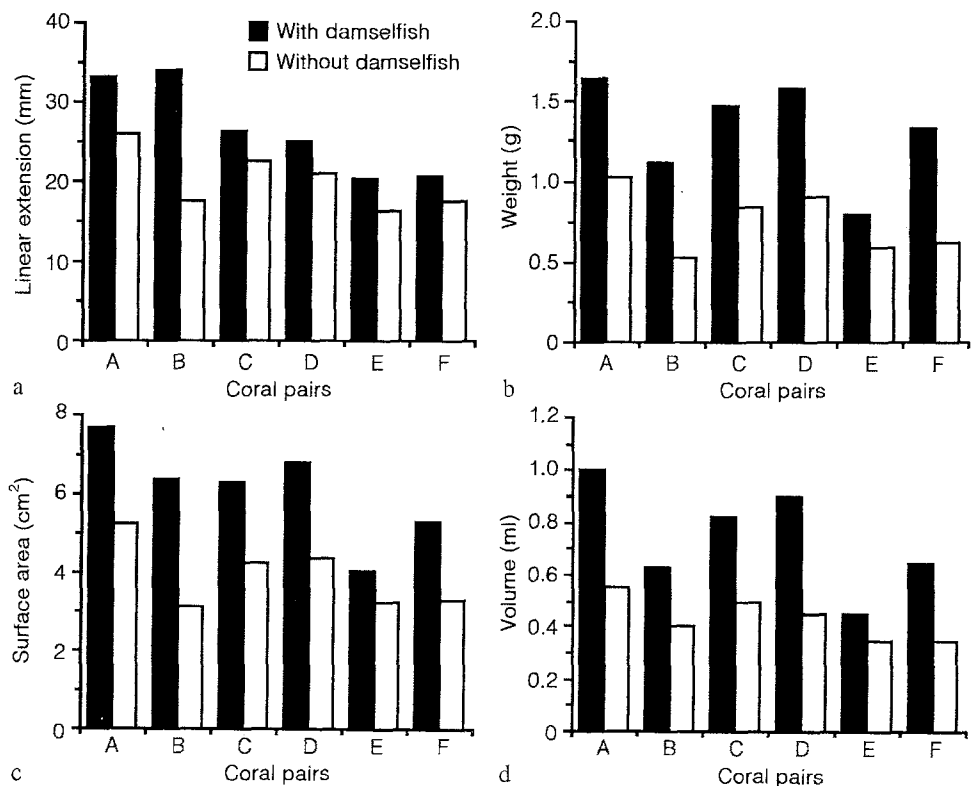
Measurements taken 13 mo after the alizarin staining showed that corals with *Dascyllus marginatus* grew significantly more than corals from which damselfish had been removed (Wilcoxon's Signed Rank Test,  $P < 0.03$ , Fig. 1). Increases in linear extension were accompanied by increases in weight, surface area and volume of the new coral skeleton (Wilcoxon's Signed Rank Test,  $P < 0.03$ , Fig. 1).

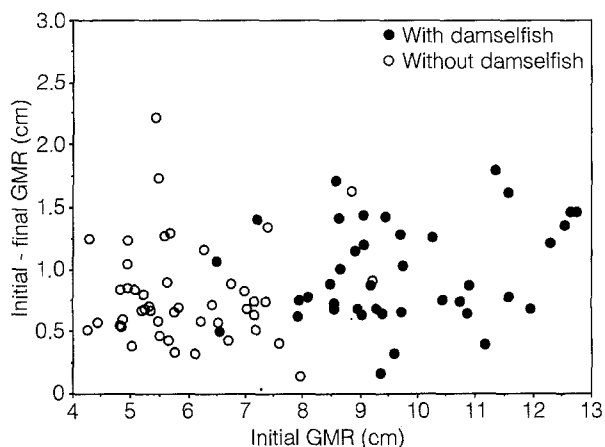
The higher skeletal growth rate of *Stylophora pistillata* with damselfish did not alter polyp distribution. Polyp density in the new growth areas did not differ significantly between corals with damselfish ( $39.05 \pm 1.72$  polyps  $\text{cm}^{-2}$ ,  $n=6$ ) and without damselfish ( $39.00 \pm 1.90$  polyps  $\text{cm}^{-2}$ ,  $n=6$ ) (Mann-Whitney *U*-test,  $P > 0.8$ ). The significant differences between corals with and without damselfish in the damselfish-removal experiment were also apparent in the non-manipulated corals.

#### Non-manipulated corals

The GMR of corals measured in situ ranged from 4.2 to 12.8 cm, with the majority of the larger corals inhabited by *Dascyllus marginatus* (Fig. 2). The initial size (GMR) of

**Fig. 1** *Stylophora pistillata*. **a** Linear extension, **b** weight, **c** surface area and **d** volume over a 13-mo period for pairs of *S. pistillata* with and without resident *Dascyllus marginatus*. Values are median of new skeletal growth from four branches of each colony





**Fig. 2** *Stylophora pistillata*. Initial Geometric Mean Radius (GMR) of corals with and without *Dascyllus marginatus* versus the change in GMR in a 7-mo period

**Table 1** *Stylophora pistillata*. One-way ANOVA and ANCOVA on non-manipulated corals with and without *Dascyllus marginatus*. (GMR Geometric Mean Radius; IGMR Initial Geometric Mean Radius)

Groups	df	MS	F	P
Damselfish presence vs IGMR				
Between	1	295.965	155.2	0.0001
Within	84	1.907		
ANCOVA of change in GMR vs damselfish presence with IGMR as a covariant				
Fish presence	1	1.200	7.145	0.009
IGMR	1	66.185	394.042	0.000
Error	84	14.109	0.168	

corals with damselfish was significantly larger than that of corals without damselfish (Table 1). Since we measured a naturally occurring situation, we could not control the size distribution of corals with and without damselfish. A test of the homogeneity of slopes found the change in GMR per change in initial size not to differ between corals with and without damselfish ( $F_{1,83} = 0.586$ ,  $P = 0.446$ ). Therefore, the assumptions of an ANCOVA were met. The ANCOVA analysis demonstrated that there was a significant effect of damselfish presence on change in GMR (Table 1). Seven months after the initial measurements, corals with *Dascyllus marginatus* increased their GMR by 0.972 cm (SD=0.4,  $n=40$ ), compared with only a 0.796 cm increase for corals lacking *D. marginatus* (SD=0.4,  $n=46$ ).

#### Coral reproduction

Specific reproductive output (area<sup>-1</sup>) of *Stylophora pistillata*, measured by the number of female gonads polyp<sup>-1</sup> and the number of planulae released cm<sup>-2</sup> of coral surface area d<sup>-1</sup>, did not differ significantly for corals with and without damselfish (Table 2).

**Table 2** *Stylophora pistillata*. Reproductive output (mean±SD) in corals with and without *Dascyllus marginatus*. Numbers in parentheses designate number of corals sampled in each category

	With damselfish	Without damselfish	P
Female gonads polyp <sup>-1</sup>			
Alizarin marked corals	0.523±0.373 (6)	0.482±0.267 (6)	ns
Unmarked corals	0.608±0.386 (8)	0.691±0.538 (8)	ns
Planulae d <sup>-1</sup> cm <sup>-2</sup>			
	0.27 ± 0.14 (10)	0.26 ± 0.13 (10)	ns

#### Discussion

*Stylophora pistillata* with *Dascyllus marginatus* grew about 1.34 times faster than corals without damselfish over a 13-mo period. The faster growth rate of corals with fish did not alter polyp density, as there was no significant difference in the number of polyps cm<sup>-2</sup> in corals with and without damselfish. However, due to their enhanced growth rate, corals with damselfish increased their surface area on average by 6.37±1.6 cm<sup>2</sup> compared to an average increase of only 4.03±0.97 cm<sup>2</sup> in corals without damselfish. Therefore, corals with fish gained during a 13-mo period approximately 37% more polyps than corals without fish.

The in situ monitoring of naturally occurring *Stylophora pistillata* with and without *Dascyllus marginatus* revealed that, in the field, nearly all the large corals were inhabited by damselfish. Within the smaller size classes (4<GMR<9 cm), some corals were inhabited while others were not. This field observation could be the consequence of damselfish selectively inhabiting larger corals, damselfish settling in any coral and as a result of their presence the coral growing faster and attaining a larger size, or a combination of both factors. The observed significant increase in GMR of non-manipulated corals with damselfish could be a result of the damselfish presence or because *D. marginatus* may selectively inhabit specific corals that grow faster. Based on the damselfish removal experiments, we conclude that the observed faster growth of non-manipulated corals with damselfish occurred as a result of the damselfish presence.

In fact, previous studies of *Stylophora pistillata* stated that large corals grew more slowly than small corals (Loya 1976 a, b, 1985; Kuwamura et al. 1994). The corals defined as large in Loya's study (1976 a, b) had a GMR of 5.0 cm, which is a coral size at the lower range of the corals in our study. Kuwamura et al. (1994) used corals >15 cm in diameter and reported that growth rate was negatively correlated with size which may be due to destruction and/or partial death. Kinzie and Sarmiento (1986) found that growth rate in *Pocillopora damicornis* was independent of coral size. They obtained this result both by measurement of GMR and by measurements of linear extension from an alizarin mark. Damselfish presence therefore may be one of the factors that may either change the potential decrease in coral growth with size or increase and change the constant coral growth rate.

The effect of fish presence on coral growth on a larger scale has been previously reported for migrating grunts (*Haemulon flavolineatum* and *H. plumieri*) (Meyer et al. 1983; Meyer and Schultz 1985 b). In that study up to 760 grunts, each weighing up to 14.0 g dry weight, rested over coral heads during daylight hours (Meyer and Schultz 1985 a). The present study focused on a much smaller scale of a maximum of six *Dascyllus marginatus* per coral head, up to 1.0 g dry weight each (Lieberman 1991), that never left the close proximity (< 1 m) of their host coral (Fishelson 1963). Our study demonstrated that small numbers of closely associated fish significantly influence their host coral. In addition, the effect of resident damselfish on coral reproduction was examined for the first time.

The lack of a difference in specific reproductive output per unit of surface area between *Stylophora pistillata* with and without *Dascyllus marginatus* indicates that the increased growth rate of corals with damselfish was not at the expense of reproduction. The fact that the reproductive output area<sup>-1</sup> was the same for the two groups implies that a growing *S. pistillata* with damselfish would increase its reproductive output faster than a coral without damselfish due to the larger acquired surface area and therefore greater number of polyps. Based on the counts of female gonads polyp<sup>-1</sup> and the growth rate for the 13-mo period, a coral with damselfish would bear 28 more gonads (26%) branch<sup>-1</sup>. The number of planulae released d<sup>-1</sup> by the coral section grown during that period would be 1.7 in corals with damselfish compared to only 1.1 in corals without damselfish.

The present study clearly demonstrated two benefits to *Stylophora pistillata* of having resident *Dascyllus marginatus*. An additional benefit to *S. pistillata* from its resident damselfish may be in the form of protection from corallivores. When a coral loses tissue and skeleton due to predation or other factors, it must allocate energy to regeneration. Regeneration can lower fecundity for more than 19 mo after breakage (Rinkevich and Loya 1989). Several researchers have documented fish protecting their coral. For example, *Dascyllus aruanus* attacked the predator *Acanthaster planci* when it approached its host, *Stylophora mordax* (Weber and Woodhead 1970). A similar behavior was observed for the damselfishes *Plectroglyphidodon dickii*, *Stegastes nigricans* and *S. acapulcoensis* while they defended their territory (Glynn and Colgan 1988; Gochfeld 1992). In the present study, we observed *D. marginatus* chasing away butterflyfishes (*Chaetodon* spp.), known coral predators (Reese 1977).

Alternatively, the coral may receive nutrients from the fish's excretions and feces (Webb et al. 1975; Meyer and Schultz 1985 a), which may increase coral growth (Meyer and Schultz 1985 b). We have observed that *Stylophora pistillata* is capable of absorbing ammonia excreted by *Dascyllus marginatus* although it has not been shown whether this ammonia benefits the coral in any way (Lieberman et al. in preparation).

Lastly, damselfish behavior (that of darting in and out of the coral and swimming between the coral branches) may in itself be beneficial for the coral and may increase

coral growth. The movement within the coral may provide mixing of the usually stagnant water in the middle of the coral (Chamberlain and Graus 1975). Dennison and Barnes (1988) demonstrated in a laboratory experiment that stirring the water with a magnetic stirrer significantly increased coral net photosynthesis. Calcification was also higher in stirred conditions, although not significantly so due to high variability (Dennison and Barnes 1988).

Stirring may also serve as a sediment clearing mechanism. *Stylophora pistillata* that was artificially covered with sediments was clear of sediments faster in the presence of *Dascyllus marginatus*. Occasionally a damselfish was observed carrying a pebble in its mouth and releasing it away from the coral (Lieberman personal observation). Direct links between all of these possible mechanisms and the observed benefits to the coral still remain to be determined.

However, irrespective of the mechanism, given that *Dascyllus marginatus* is an obligate coral dweller (Fishelson 1963; Holzberg 1973) and the present study's findings on increased coral growth and reproductive output, the specific association between *D. marginatus* and *Stylophora pistillata* should be regarded as mutualistic.

*Dascyllus marginatus* is a common fish which inhabits at least four species of corals other than *Stylophora pistillata* in the northern Gulf of Eilat (Fricke 1980). Approximately 40% of suitable coral colonies greater than 8 cm in diameter are inhabited (Genin personal communication). Therefore, the association of *D. marginatus* with these corals may make a significant contribution to coral growth and reproduction.

On the other hand, *Dascyllus marginatus* is not the only coral dwelling fish. Many fishes reside in and restrict their territory to a single coral head (Hiatt and Strasburg 1960; Fishelson 1963; Sale 1971 a, b; Sale 1972; Patton 1974; Luckhurst and Luckhurst 1976; Lassig 1977; Shpigel and Fishelson 1986). These fishes may also enhance coral growth and reproduction. If this is the case, then significant differences in components of coral fitness should be observed between corals with and without fish. In addition, factors affecting fish communities may affect the long-term structure and growth of coral reefs in ways previously not considered.

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