Predator recognition and social facilitation of predator avoidance in coral reef fish *Dascyllus marginatus* juveniles

Ilan Karplus[1],*, Ronit Katzenstein[2], Menachem Goren[2]

[1]Aquaculture Research Unit, Agricultural Research Organization, PO Box 6, Bet Dagan 50250, Israel
[2]Department of Zoology, Tel-Aviv University, Tel-Aviv 69978, Israel

ABSTRACT: Predator recognition was studied in *Dascyllus marginatus*, a small Red Sea pomacentrid that forms mixed-size schools associated with branching corals of the genera *Acropora* and *Stylophora*. The reactions of variously sized *D. marginatus* to sudden exposure to a live predatory fish (*Epinephelus fasciatus*), a non-predatory fish (*Acanthurus nigrofuscus*), and an empty cell were monitored in the laboratory. Adult fish (49 to 60 mm) discriminated between predatory and non-predatory fish, whereas juveniles (13 to 17 mm) could not. The responses of single juveniles, pairs of juveniles, and juvenile/adult pairs to sudden exposure to a predator were compared. Juveniles paired with adults avoided the predator more than single or paired juveniles. A mechanism in the reef habitat of social facilitation of predator recognition and avoidance among mixed-sized school pomacentrids is suggested. The relevance of the findings of this study to the low survival of reef fishes shortly after settlement and their preference for coral heads inhabited by conspecifics is discussed.

KEY WORDS: Predator recognition · Social facilitation · Predator avoidance · *Dascyllus marginatus* · Recruitment · Survivorship

INTRODUCTION

The ability of an individual to recognize its predators is of crucial importance for its survival and for cost-effectively regulating its activities. An individual should feed, reproduce, and carry out a variety of maintenance activities without disturbance in the presence of non-predatory species. However, it should flee, retreat into shelter, or display a variety of anti-predatory behaviors in the presence of a predator. The extent of its avoidance behavior, at a cost of stopping its other activities, should be directly related to its vulnerability to a particular predator (Stein 1979). The recognition of predators by reef fishes has been well documented, based on field observations and controlled experiments. Several field studies of reef fishes observed specific anti-predatory behaviors that were displayed only in the presence of piscivorous fishes, in contrast to a lack of response to non-piscivorous ones. These behaviors included: retreat into shelters by pomacentrids, gobies, and jaw fishes (Colin 1971, Hurley & Hartline 1974, Karplus 1979, Coates 1980a); school formation by pelagic pomacentrids (Myrberg et al. 1967); mobbing by pomacentrids (Fricke 1975, Ishihara 1987); and the emission of tactile and visual warning signals by gobies (Karplus 1979, Smith & Smith 1989). Some of these studies used controlled experiments to demonstrate that coral reef fish react differently to different species (Myrberg & Thresher 1974, Thresher 1976), especially in differentiating between piscivorous and non-piscivorous fishes (Fricke 1975, Karplus 1979, Coates 1980a). Little research has been carried out on the differential ability of adult and juvenile reef fishes to discriminate between species and, particularly, to recognize their predators. Juvenile reef fishes have been reported to be less able than adults to differentiate between the cleaner fish *Labroides dimidiatus* and its mimic the ectoparasitic *Aspidontus taeniatus* (Wickler 1963). Work by Almany, cited by Webster (2002), demonstrated that settlers did not

respond to cues from caged predators on Bahamian coral reefs.

Juvenile reef fishes suffer heavy mortality, especially shortly after settlement, and the mortality rate is inversely related to size (Doherty & Sale 1985, Sale & Ferrel 1988, Hixon 1991, Schmitt & Holbrook 1999, Steele & Forrester 2002). Controlled experiments have shown that predation is the major cause of this mortality; the experiments involved the removal of predators (Hixon 1991, Carr & Hixon 1995, Webster 2002), predator exclusion by cages (Dohery & Sale 1985, Steele 1999, Holbrook & Schmitt 2002, Steele & Forrester 2002), and direct day and night remote monitoring of predation with video cameras (Holbrook & Schmitt 2002). Several hypotheses have been advanced to explain the high vulnerability of small juveniles to predation: (1) their small size renders these fish particularly vulnerable to a wide array of small piscivores, including generalist micro-carnivores such as wrasses (Shulman 1985, Steele 1999); (2) the small juveniles have lower swimming speeds and reduced visual acuity compared with adults, which make their capture by predators easier (Shulman 1985, Sweatman 1985); (3) the smallest and most recently recruited juveniles are also lowest in the social hierarchy in mixed-size groups and are, through interference competition for refuge, pushed into the periphery of the shelter (e.g. coral or sea anemone) by larger and more dominant individuals, thus becoming more vulnerable to predation (Shulman 1985, Schmitt & Holbrook 1999, Holbrook & Schmitt 2002); and (4) young juveniles are naïve and more susceptible to predation than larger and more experienced fish (Hixon 1991).

Five different species of small planktivorous pomacentrids, all living in mixed-size groups and sheltering inside branching corals, were reported to prefer to settle from the plankton into corals inhabited by conspecifics rather than into empty corals (Sweatman 1983, 1985, 1988, Jones 1987, Booth 1992). Several reasons have been advanced to account for this preference: (1) choice of a coral head inhabited by conspecifics ensures a continuous and adequate supply of food (Sweatman 1983, 1985, Booth 1992), (2) choice of an inhabited coral head ensures availability of proper mates in the future (Sweatman 1983, 1985), and (3) choice of an inhabited coral head provides the fresh recruits with the increased vigilance and the dilution effect of a larger school (Sweatman 1985).

The aims of the present study were to determine whether small juveniles and large adult individuals of *Dascyllus marginatus*, a pomacentrid living in mixed-size groups in branching corals (Holzberg 1973), differ in their ability to recognize predators, and whether juveniles benefit from being exposed to a predator in company with an adult. Resolving these 2 issues may

contribute to our understanding of the low survival of newly settled reef fishes and of the attraction of recruits living in mixed-sized schools to coral heads inhabited by conspecifics.

MATERIALS AND METHODS

Expt 1: Effect of size on predator recognition. Thirty-three adult (49 to 60 mm) and 35 juvenile (13 to 17 mm) *Dascyllus marginatus* were collected in the northern Red Sea from the upper slope of the coral reef (3 to 15 m depth) in front of the H. Steinitz Marine Biological Laboratory (29° 30' N, 34° 56' E). The size of this species in the Red Sea ranges between 10 and 59 mm, with a mean of 39 mm (Holzberg 1973). The 2 collected size classes were kept in separate large plastic containers ($50 \times 50 \times 100$ cm) with a seawater inflow of 8.5 l min^{-1} and with dead branching corals of the genera *Stylophora* and *Acropora* as shelters. Water temperatures ranged between 25 and 27°C. The fish were fed daily on *Artemia* and exposed to ambient light levels. *Epinephelus fasciatus* is a small grouper which feeds on crustaceans and fishes, including the size range of adult and juvenile *D. marginatus* (Karplus 1978, I. Karplus pers. obs.). *Acanthurus nigrofuscus* is a surgeon fish which feeds exclusively on brown, red, and green algae (Fishelson et al. 1987). These 2 species, which are both very common in the vicinity of the collected *D. marginatus*, were selected as representative of a piscivore and non-piscivore. Groupers and surgeon fish ranging in size from 25 to 30 cm total length (TL) were collected with hand nets and maintained in a large pool on diets of *Atarina* and *Ulva*, respectively. Fish collection and handling during the study were approved by the Israeli Nature Conservation authorities.

The effects of the size (i.e. large or small) of a *Dascyllus marginatus* individual on its avoidance behavior in 3 treatments—the presence of a much larger piscivore, the presence of a much larger non-piscivore, and no fish—were studied in a completely randomized factorial experimental design. The testing apparatus was divided into 2 unequal sections by a transparent glass partition that allowed only the passage of visual cues. The smaller section—$30 \times 10 \times 20$ cm—held a large predatory or non-predatory fish, and was empty in the control treatment (Fig. 1A). The larger section—$100 \times 10 \times 20$ cm—served for monitoring the response of the test fish (Fig. 1B). Inside the larger section and close to the transparent separating partition the releasing chamber (Fig. 1C) was installed, which comprised only 3 parts: a small upper plate (5×10 cm), to which an elongated white opaque plate (10×40 cm) and a net partition of the same size were attached. The opaque

plate prevented the test fish from seeing the adjacent large fish, and the net partition restrained it from moving outside the cell. A ruler attached to the elongated section of the apparatus enabled determination of the position of the test fish. The test apparatus was positioned on a table inside a small room, and a video camera was positioned outside the room to observe the behavior of the fish via a hole in the wall. The test fish was introduced into the releasing chamber and, after a 5 min acclimatization period, the chamber was lifted slowly by a pulley system, enabling the test fish to see into the small section of the apparatus while giving it access to the elongated section of the test apparatus, which allowed an avoidance response. Fish behavior was monitored for 4 min.

Four response behaviors of the test fish were extracted from the video recordings; three were related to its initial escape response, and one to its position. The initial escape response was defined as its movement away from the small section of the test apparatus until it stopped or changed direction. The 3 relevant behaviors concerned: (1) escape time—the duration of the initial escape response, (2) escape distance—the distance covered by the test fish during the initial
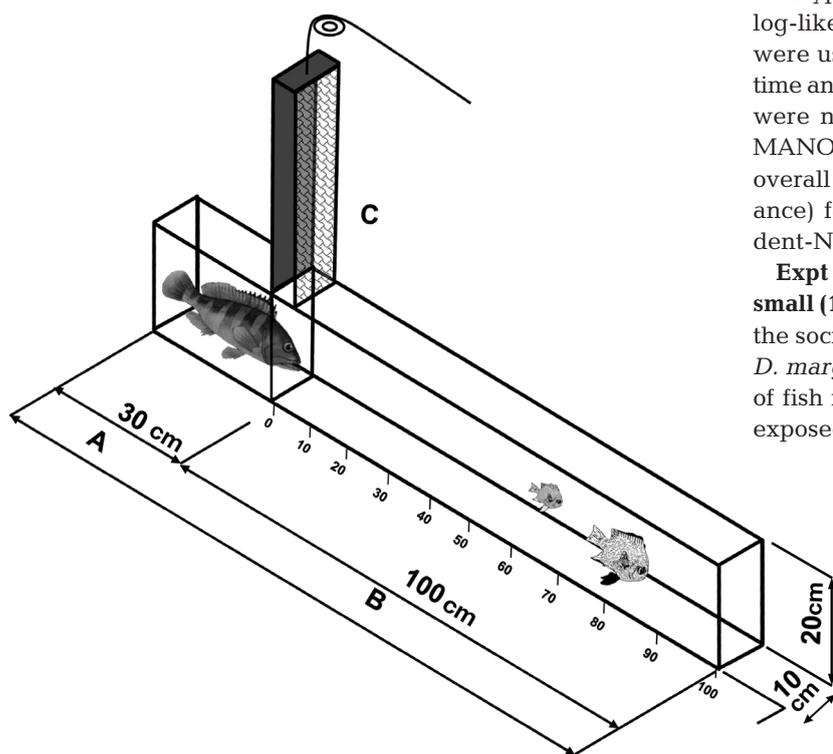

Fig. 1. Apparatus used for testing predator recognition and social facilitation of predator avoidance in *Dascyllus marginatus*: (A) small cell for large stimulus fish, (B) elongated cell for monitoring test fish response, and (C) the releasing chamber

escape response, and (3) escape velocity—the velocity of the test fish during the initial escape response. The average position was the mean distance between the test fish and the glass of the stimulus cell (monitored every 10 s) over the 4 min exposure period. All tests were carried out between 05:00 and 08:00 h under low light levels ranging from 50 to 56 µE m^{-2} s^{-1}, as measured with a QSI-140 light meter (Biospherical Instruments). Due to the increase in the foraging activity of piscivore fishes at low light levels in the early morning, the study was limited to these hours. The water temperature in the testing apparatus ranged from 25 to 27°C. The apparatus was drained, rinsed, and filled with fresh seawater after each trial, to eliminate any possible residual chemical cues from previously tested fish. Fish were tested within 1 wk of capture, but after a post-capture period of least 48 h. Each fish was tested only once and was then returned to the sea to suitable vacant living corals.

The data were analyzed with a SAS Instutite (1989) statistical software package, following transformations that provided compliance with normality (nonsignificant deviation from normality according to the Shapiro-Wilks tests) and homogeneity of variances (Bartlett's tests). Data were transformed following a search for Box-Cox type transformations that also yielded near-optimal log-likelihood results. The following transformations were used: $\log(x + 0.5)$ for escape distance and escape time and $\log(x + 2)$ for escape velocity. Only location data were not transformed. The results were subjected to MANOVA (multivariate analysis of variance) to reveal overall effects and to 2-way ANOVA (analysis of variance) for the individual parameters, followed by Student-Newman-Keul's test for multiple comparisons.

Expt 2: Social facilitation of predator avoidance in small (15 to 18 mm) *Dascyllus marginatus*. The effect of the social environment on predator avoidance by small *D. marginatus* was studied by comparing the behavior of fish in 3 different social groups that were suddenly exposed to a predator. These groups comprised: (1) a single small fish (n = 11), (2) 2 small fishes (n = 12), and (3) a small and a large conspecific fish (n = 24). The overall lengths of the large and small tested fish were 35 to 48 and 15 to 18 mm, respectively. The testing apparatus and the testing procedure were as in Expt 1, except that the fish response was tested only with respect to exposure to a piscivore, and, in some of the trials, instead of a single fish, 2 fish were tested simultaneously. The position of the small fish in a social group of 2 small fishes was computed as the mean of their positions.

Data were transcribed as detailed for Expt 1. However, records were also made

of: whether the 2 fish were separated by < 15 cm, a situation designated 'associated'; movement of the 2 fish in the same direction while associated, termed 'led'; and the identity of the leader. The distance of 15 cm (about 3 body lengths of the large fish) was selected because almost all joint movements of 2 similar or differently sized fish in our study were within this distance. We assumed one fish to lead and the other to follow because that movement pattern occurred both when moving away from or towards the predator. Moreover, when one fish sped up the other increased its speed as well. Statistical analysis was carried out following data transformation as for Expt 1. Results were subjected to MANOVA and 1-way ANOVA, followed by Student-Newman-Keul's test for multiple comparisons. The frequencies of 'associated' and 'led' behavior in differently sized pairs were compared by means of the non-parametric Mann-Whitney U-test (with χ^2 approximation).

Expt 3: Social facilitation of predator avoidance in very small (8 to 12 mm) post-settlement *Dascyllus marginatus*. The third experiment was similar to the second, except that the tested fish were much smaller, with overall lengths of only 8 to 12 mm. These fish were collected 2 to 3 d following settlement. In this experiment fish were tested in only 2 social environments: (1) 2 small fishes (n = 24) and (2) a small and a large conspecific fish (n = 12).

RESULTS

Expt 1: Effect of size on predator recognition

MANOVA revealed an overall significant effect of treatment on fish responses (Wilk's test statistic, $W_{8,114}$ = 0.548; p < 0.0001), a lack of a size effect ($W_{4,57}$ = 0.940; p > 0.4), but a significant treatment × size interaction ($W_{8,114}$ = 0.712; p < 0.02). The main effects of treatment and fish size on escape time were nonsignificant, but the size × treatment interaction was significant (Table 1). The duration of the escape response of small test fish from both the predatory and non-predatory fishes was about 8 s and that from the empty cell about 2 s. Large test fish maintained their escape from the predator for twice as long as from the non-predator, and their escape time from the empty cell was intermediate (Fig. 2A). The escape distance was significantly affected only by treatment; the effects of size and of size × treatment interactions were nonsignificant (Table 1). Overall, irrespective of size, the test fish covered the longest distance (47.7 ± 43 cm) when confronted by the predator, the shortest

Table 1. Results of 2-way ANOVA (*F*-values) of the effect of size of *Dascyllus marginatus* (large and small) and treatment (piscivore, non-piscivore, and empty aquarium) on the initial escape response, and mean location of *D. marginatus* (*p < 0.05, **p < 0.01, ***p < 0.001)

Effect	df	Escape time	Escape distance	Escape velocity	Mean location
Size	1,60	0.014	1.417	1.286	0.03
Treatment	2,60	2.626	14.393***	3.521*	16.17***
Size × Treatment	2,60	4.189*	0.872	6.484**	3.38*

(6.7 ± 4.4 cm) when confronted by the empty compartment, and intermediate distances (24.1 ± 31 cm) in avoiding the non-predator. The escape velocity was not affected by size, but the effects of treatment and of the size × treatment interaction were significant (Table 1): overall, irrespective of size, the test fishe escaped from the predator at the highest speed (6.3 ± 4 cm s^{-1}), from the empty cell at the lowest (4.1 ± 6.3 cm s^{-1}), and from the non-predator at an intermediate speed (5.6 ± 5 cm s^{-1}). Large test fish escaped at a similar speed from both stimuli fishes and at less than a third of that speed from an empty cell. Small test fish escaped at a similar speed from stimuli fishes (about half the speed of large test fish), and an empty cell (Fig. 2B)

There was a highly significant main effect of treatment on the average location of *Dascyllus marginatus* in the testing apparatus (Table 1). Overall, irrespective of their size, fish were located closest (26.7 ± 24.4 cm) to the empty cell, more than twice as far (58.5 ± 68 cm) from the predator, and an intermediate distance from the non-predator. Fish size had no significant effect on mean position, but there was a significant size × treatment interaction, indicating that the responses differed among different-sized fish (Table 1). Large test fish avoided the vicinity of the predator: they stayed about 80 cm from it, compared with less than half that distance from the non-predator, and stayed closest to the empty cell (Fig. 2C). The small fish maintained similar intermediate distances from both the predator and the non-predator, and a smaller distance, but not significantly so, from the empty cell (Fig. 2C).

Expt 2: Social facilitation of predator avoidance in small fish (15 to 18 mm)

Small *Dascyllus marginatus* spent most of the time associated when exposed in pairs to a predatory fish. The level of association did not differ significantly (χ^2 = 0; df = 1; p > 0.99) when associated with either a small or a large fish (54.2 ± 51.9 and 67.2 ± 33.1%, respectively). The frequency of movement of the 2 fish in the

same direction (i.e. led) while associated did not differ statistically between matched and unmatched pairs ($\chi^2 = 1.041$; df = 1; p > 0.3), although fish tended to lead more often in the latter (14.4 ± 17.3 and 6.3 ± 6.2%, respectively). The larger fish was the leading partner 2.7 times as often as the small one.
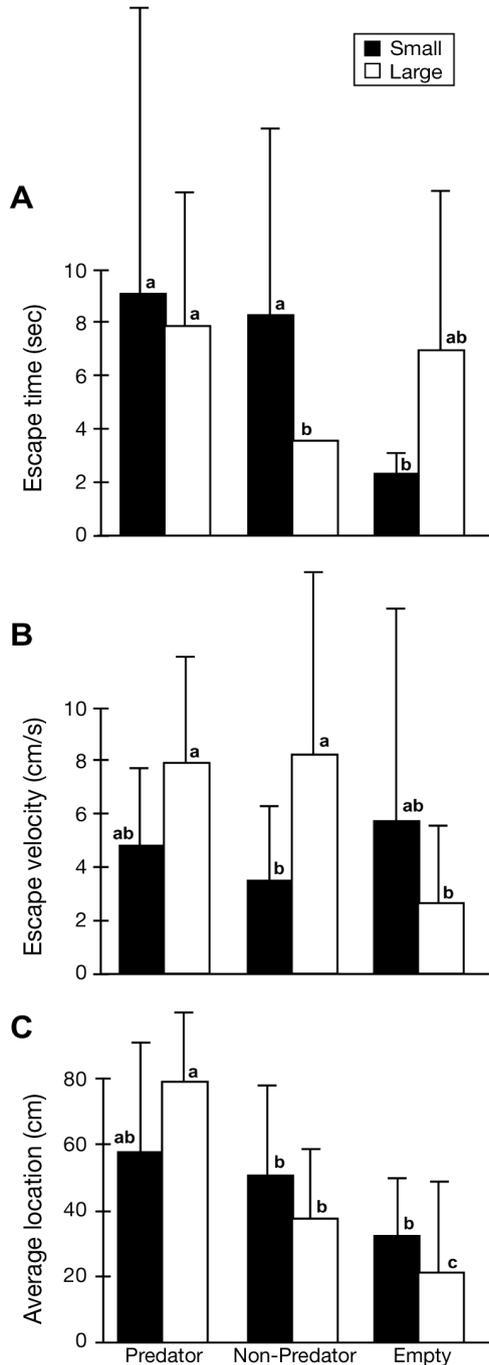

A

Escape time (sec)

■ Small
□ Large

B

Escape velocity (cm/s)

C

Average location (cm)

Predator   Non-Predator   Empty

Fig. 2. *Dascyllus marginatus.* Responses of large (49 to 60 mm) and small (13 to 17 mm) fish to sudden exposure to a predator, a non-predator, and an empty cell. Columns not sharing letters are significantly different (p < 0.05). Error bars indicate standard deviation

MANOVA revealed an overall significant effect of group composition ($W_{8,76} = 0.609$; p < 0.02) on the responses of small fish when exposed to a predator. Group composition had significant effects on the following 4 tested parameters: escape time ($F_{2,42} = 10.838$; p < 0.001), escape distance ($F_{2,42} = 15.955$; p < 0.001), escape velocity ($F_{2,42} = 3.983$; p < 0.03), and mean location ($F_{2,44} = 5.630$; p < 0.01). The escape time of a small fish paired with a large one was >6 times as long as that while it was paired with a small one and almost twice as long as that of a single fish (Fig. 3A). The escape distance of a small fish paired with a large one was >2.5 times that of a single small fish and >10 times that of a pair of small fishes (Fig. 3B). The escape velocity of a small fish paired with a large one was almost twice that of a single small fish or of a pair of small ones (Fig. 3C). The average location of a small fish paired with a large one during the 4 min of testing was twice as far from the predator as that of a single small fish or of a small fish paired with another small one (Fig. 3D).

Expt 3: Social facilitation of predator avoidance in very small post-settlement fish (8 to 12 mm)

Very small *Dascyllus marginatus* differed in the times they spent associated with a similar-sized fish or with a large one ($\chi^2 = 18.264$; df = 1; p < 0.001). When paired with another small fish they spent almost the entire time (99.0 ± 1.8%) associated with it, compared with less than half of the time with a large one (47.2 ± 33.9%). The frequency of movement of the 2 fish in the same direction (i.e. led) while associated did not differ statistically between matched and unmatched pairs ($\chi^2 = 2.460$; df = 1; p > 0.1), although leading tended to happen more often in matched than in unmatched pairs (11.5 ± 9.9 and 4.8 ± 5.5%, respectively). In unmatched pairs the larger fish was the leading partner 1.6 times more often than the small one.

MANOVA revealed an overall significant effect of group composition ($W_{4,29} = 0.680$; p < 0.03) on the responses of post-settlement fish when exposed to a predator. Group composition had significant effects on 2 of the 4 tested parameters: the escape distance ($F_{1,32} = 6.632$; p < 0.02) and the escape velocity ($F_{1,32} = 11.394$; p < 0.02). The escape distance of a very small fish when paired with a large fish was about 3 times as long as that when it was paired with a small one (Fig. 4A); and the escape velocity of a very small fish was more than twice as great when it was paired with a large fish as when it was paired with another very small one (Fig. 4B). There were non-significant effects of pair composition on the escape time ($F_{1,32} = 0.120$; p > 0.7) and average location ($F_{1,34} = 1.28$; p > 0.2) of very small fish.
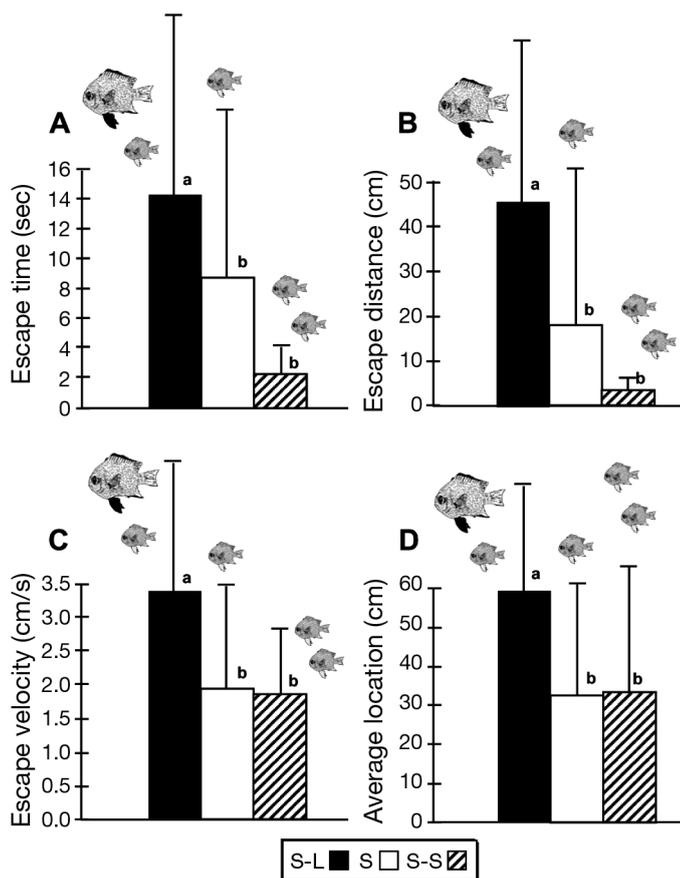
Fig. 3. *Dascyllus marginatus*. Responses of small (15 to 18 mm) fish to sudden exposure to a predator while isolated (S) or paired with a small (S-S) or large conspecific (S-L). Columns not sharing letters are significantly different (p < 0.05). Error bars indicate standard deviation

DISCUSSION

This study revealed that, whereas adult *Dascyllus marginatus* are able to discriminate between predatory and non-predatory fishes, juveniles are unable to do so, and this inability to recognize predators may contribute to the greater vulnerability of juveniles to predation. The difference in predator recognition capability was particularly evident in its effect on the mean position of the test fishes, less so in its effects on the various components of the initial escape response. The intensity of the initial avoidance response of a test fish when exposed very close to a much larger hetero-specific one was independent of whether or not that large fish was a piscivore. However, a large test fish was probably able to practice discrimination after examination of the large hetero-specific from a greater distance. Some of the avoidance responses of the test fish may represent a general fright response due to confinement in a small space prior to testing and the movement of the opaque partition while lifting the releasing chamber.

Predator recognition in this study was mainly based on visual cues, since there was no exchange of chemical cues between the stimuli and the test fish. However, one cannot rule out the transmission of acoustic cues through the glass partition that separated the fishes (Katzir 1981). The visual cues that enable predator recognition by adult *Dascyllus marginatus* are not known. A large number of facial features, e.g. size and shape of the eye and/or mouth, of reef fishes could theoretically serve as cues for discrimination (Karplus & Algom 1981). Adult *Chromis caeruleus* responded differently to complex 2-dimensional models of a grouper and a surgeon fish that differed in many parameters (Karplus et al. 1982). These were the same type of fish used in the present study. A study of the responses of *C. caeruleus* to simple models, which differed in only 1 parameter at a time — eye or mouth size, structure of the mouth, or distance between the eyes — revealed that mouth size and structure provided the cue for predator recognition (Karplus et al. 1982). In a preliminary study in which *Anthias squamipinis* were confronted with the same type of models, eye size and distance between the eyes were cues that enabled predator recognition (L. Fishelson pers. comm.). In view of the variation among species in the actual cues they use for predator recognition, only controlled experiments could reveal the cues that serve adult *D. marginatus* for this purpose. This study did not address the recognition of predators by chemical cues, and thus it cannot be ruled out that juveniles recognize piscivores by olfaction.

Juvenile fish that are not born with the ability to recognize their predators may acquire or refine that ability by 1 or more of 3 processes: (1) maturation of the sensory or neural system, which does not require exposure to a predator (Munz & McFarland 1973, Coss 1978, Blaxter 1986); (2) individual learning, which may be a dangerous process that involves the exposure of a naive fish to a predator (Csanyi & Doka 1993); and (3) social transmission, by which a naïve fish may learn to recognize predators through exposure to them in company with experienced individuals (Mathis et al. 1996, Vilhunen et al. 2004). Several recent studies have addressed the problem of social transmission of predator recognition with relation to stock rehabilitation programs and sea ranching of commercial edible fishes (reviewed by Suboski & Templeton 1989, Brown & Laland 2001), but none in connection with reef fishes. However, social transmission of information concerning the learning of twilight migration routes from more experienced conspecifics has been demonstrated for the reef fish *Haemulon flavolineatum* (Helfman & Schultz 1984).
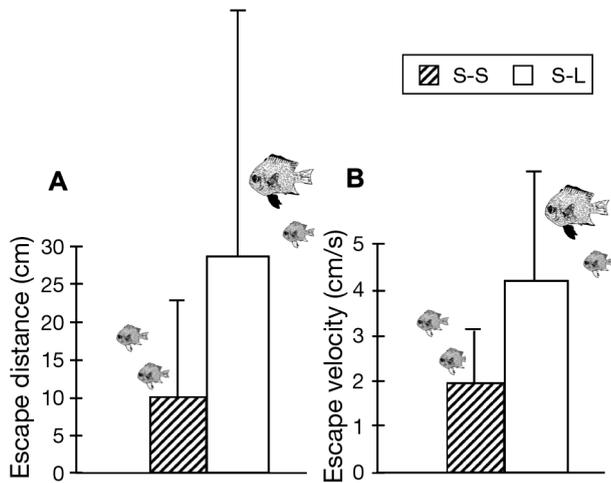
Fig. 4. *Dascyllus marginatus*. Response of very small (8 to 12 mm) post-settlement fish to sudden exposure to a predator while paired with a small (S-S) or a large conspecific (S-L). Error bars indicate standard deviation

In the present laboratory experiment, the exposure of a juvenile *Dascyllus marginatus* in the company of an adult to a piscivore elicited greater avoidance of the predator than exposure of 1 or a pair of juveniles, and the difference was attributed to the association with the adult, their joint movement, and, especially, the following of the adult by the juvenile. In the testing apparatus the very small, newly settled juveniles spent less time in association with an adult and were, therefore, less influenced by its behavior. Possibly, the body size of the very small fish acted as a constraint, making it harder for them to follow the much swifter adults.

In this study social facilitation of predator avoidance has been demonstrated, but not the actual occurrence of learning. That would have involved the test exposure of unaccompanied juveniles that had previously been exposed to a predator in the company of an adult, to enable a distinction between being influenced by a conspecific and actual learning (i.e. the acquisition or modification of predator avoidance).

Laboratory studies on social facilitation of predator recognition in fishes often lack identity with the situation of free-ranging animals in the field. Social facilitation of predator avoidance, as studied by us in the laboratory, is probably practiced by fishes on the reef. Mixed-size schools of *Dascyllus marginatus* associated with branching

corals have a typical distribution pattern that facilitates transfer of information between school members. Immediately after settlement the very small juveniles occupy the inner space of the coral, and we found them to be only little affected by adults when jointly exposed to a predator. Larger juveniles venture out of the corals, and the adults occupy the space still further out (Shpigel 1982, R. Katzenstein unpubl.). An approaching piscivore is first encountered by the adults who rush into the coral and so induce retreat of the juveniles, which are closer to the coral. The repeated, selective withdrawal of adults upon the approach of a piscivore and their lack of response to an approaching non-predator could transfer the crucial knowledge of predator recognition to naïve juveniles (Fig. 5).

We suggest that branching corals inhabited by mixed-size fish could serve as permanent information centers, somewhat similarly to the role of large trees in relation to roosting or breeding birds (Ward & Zahavi 1973, Brown 1986, Krause & Ruxton 2002). In this role they would store information on predator recognition, e.g. the foraging times of different piscivores, and this information could be culturally transmitted from the experienced adults to the naïve juveniles. We predict that the survival of juvenile *Dascyllus marginatus* sharing corals with adults should be higher than that of juveniles occupying corals by themselves. Indeed, such a result was obtained for the related *D. aruanus*
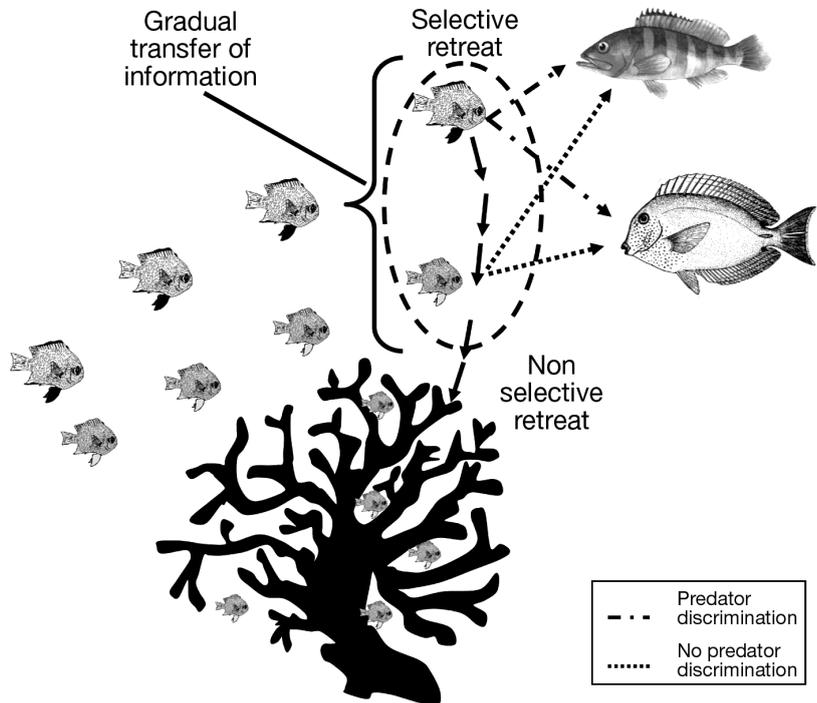

Fig. 5. *Dascyllus marginatus*. A graphic presentation of social transmission of information on predator recognition in mixed-size schools

(Jones 1987, Forrester 1990). Social transmission of predator recognition within schools of mixed-size fish that inhabit branching corals could be an additional reason for juveniles to prefer to settle into corals inhabited by conspecifics rather than into empty corals. The advantages of being associated with larger conspecifics more than counterbalance the cost of increased competition, which was found to manifest itself in reduced growth and slower maturation (Coates 1980b, Forrester 1990, 1991, Booth 1995).

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