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BEHAVIORAL RESPONSES OF THE SEA URCHIN *TETRAPYGUS NIGER* TO PREDATORS AND FOOD

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To test the importance of predators and food availability in determining patterns of aggregation and movement in the urchin *Tetrapygus niger*, we studied the behavioral responses of animals with different body sizes under laboratory conditions. Experiments were carried out on a square platform in tanks with circulating water. Twelve sea urchins of three size ranges were placed following a uniform spatial distribution on the platform and maintained in the presence or absence of: (a) one predator (the fish *Pinguipes chilensis* or the asteroid *Meyenaster gelatinosus*), or (b) food (fronds of the brown kelp *Lessonia nigrescens*). The experiments were followed with a video camera. The movement patterns of the sea urchins, the number and size of aggregations, and the dispersion patterns were quantified. To determine the importance of aggregation as a defensive mechanism, artificial aggregations of large sea urchins were created on the platform in the presence or absence of predators. Behavioral responses were followed and analyzed as described above. Individuals of *T. niger* recognize the presence of predators, and respond with increased mobility (e.g., number of sea urchins moving or average speed of movement; i.e., escape responses) but do not increase the number or size of aggregations. Moreover, the increased mobility of sea urchins would account for the random spatial distribution of individuals at the end of the experiments with predators. The escape responses were specially marked in the presence of the starfish *M. gelatinosus*. In this case, the aggregations were unstable, suggesting that the aggregations of *T. niger* would not have a protective function against this starfish. By contrast, sea urchins aggregated in the presence of food. It is concluded that the generation of aggregations in this species would be more related to feeding patterns (or to other factors related to spatial heterogeneity; e.g., substrate topography) than to responses to predators. The escape behavior of sea urchins to starfish is also described.

Keywords: *Tetrapygus*; sea urchin; aggregation; movement; predators; food

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INTRODUCTION

Sea urchins are one of the most important components of coastal marine ecosystems throughout the world, often playing a fundamental ecological role in intertidal and shallow subtidal environments (Lawrence, 1975; Harrold and Pearse, 1987). For several decades aggregation behavior in sea urchins has been implicated as a causal agent in the destruction of macroalgal assemblages and has been observed to produce other secondary effects in those communities (Breen and Mann, 1976; Bernstein and Mann, 1982; Bernstein *et al.*, 1983). Aggregation behavior has been largely associated with behavioral defense mechanisms against predation (Pearse and Arch, 1969; Bernstein *et al.*, 1981; Tegner and Levin, 1983). However, the importance of food and spatial heterogeneity have also been highlighted (Garnick, 1978; Vadas *et al.*, 1986). The existence of escape responses of sea urchins to predators (mainly asteroids) has been widely described (Duggins, 1983; Schroeter *et al.*, 1983). Escape responses are considered to be effective defensive mechanisms for sea urchins, when they decrease the detection rates and/or successful attacks by predators (Parker and Shulman, 1986).

Tetrapygus niger (Molina, 1782) is a conspicuous arbacioid occurring along the temperate Pacific coast from northern Peru to the Strait of Magallanes (Southern Chile), extending from the intertidal zone to 40 m depth (Larrain, 1975). Despite this species being the most abundant sea urchin on the central Chilean coast, little quantitative information has been gathered on key aspects of its biology and ecology. *Tetrapygus niger* in the shallow subtidal zone off the central Chilean coast has an aggregated distribution pattern, with small individuals (< 25 mm test diameter (TD)) mainly found in crevices or along the shallowest edge of beds of the macroalgae *Lessonia trabeculata* (Rodríguez and Ojeda, 1993). Also, small *T. niger* are frequently associated with adult spine canopies of the sympatric sea urchin *Loxechinus albus*, or to small depressions and interstices of rocks and cobble inside conspecific adult aggregations (personal observations).

It is apparent that several factors could be involved in aggregation behavior. Most commonly this behavior is thought to be related to defense, but other factors such as food and reproduction cannot be ignored. Here we examine two hypotheses related to aggregation behavior: defense mechanisms against predators and the presence of food. The aim of this study was to determine whether aggregation and movement patterns of *Tetrapygus niger* are affected by the presence of predators and food (under laboratory conditions) and whether this varied with body size. We also describe the escape response of *Tetrapygus niger* to seastars.

MATERIALS AND METHODS

This study was carried out in the Estación Costera de Investigaciones Marinas (ECIM) of the Pontificia Universidad Católica de Chile in Las Cruces (33° 30' S, 71° 30' W) on the central Chilean coast. Experiments were carried out on a wooden platform of 100 × 90 cm placed in tanks of 1000 l with constantly circulating aerated seawater. The platform was covered with sky-blue plastic to simulate the color of the holding tanks where the sea urchins and predators were acclimatized before the experiments. The platform was divided into 10 cm² units to facilitate the measurement of sea urchin movements.

Experiment 1

Twelve sea urchins of three size classes (four large: 50–60 mm TD, four medium: 35–45 mm TD, and four small: 20–30 mm TD) were placed following a uniform spatial distribution pattern along the platform (Fig. 1). Sea urchins were maintained in the absence (control) or presence of one predator (i.e., the fish *Pinguipes chilensis* or the starfish *Meyenaster gelatinosus*). Each treatment was triplicated. In *M. gelatinosus* experiments, the starfish was placed in a corner of the platform. In *P. chilensis* experiments, the urchins were distributed along a platform previously placed in a tank holding the predator. In both cases, predators were allowed to move freely. Sea urchins and predators (captured from the intertidal and subtidal of the central Chilean coast), were acclimatized for 14 days before being tested. Observations were made over a 30 min period using a CANON L1 video camera equipped with a 15 × zoom lens. The camera was programmed to film at 10 s intervals. The video allowed the movement pattern of sea urchins and their behavior under the different treatments to be followed with ease. In each experiment the number of individuals moving and the average speed for each size class was recorded. The speed of movement was standardized according to body size (TD) to allow comparisons among individuals of different size classes. This was done by dividing the total run distance by the average body size of individuals of a determined size class (i.e., 55 mm for large; 40 mm for medium; and 25 mm for small sea urchins). Also recorded, at 5 min intervals were (1) the number and size (number of individuals present) of aggregations, (2) the size class of sea urchins observed in the aggregations, (3) the duration of the aggregations, and (4) the number of solitary urchins. An aggregation was defined as two or more individuals sufficiently close to be within presumed tactile detection range (i.e., touching spines).

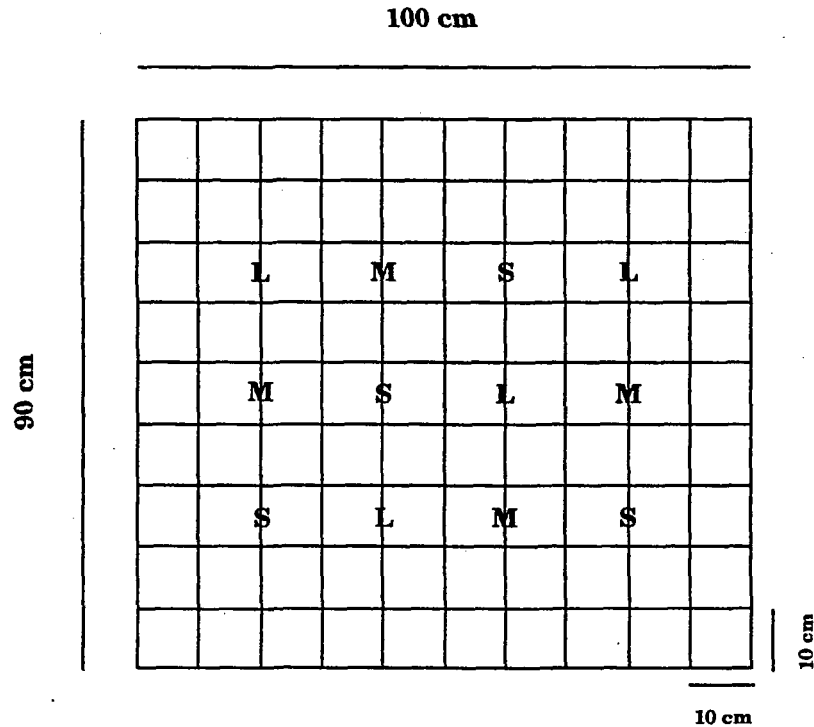


FIGURE 1 *Tetrapygus niger*. Experimental wooden platform, in which behavioral patterns of sea urchins were followed. L, M, and S indicate the initial position of large (50–60 mm TD), medium (35–45 mm TD), and small (20–30 mm TD) individuals, respectively (Experiments 1 and 2). Twelve sea urchins were used in each treatment.

of one another and remaining in this situation for more than 5 min. This use of the term association is similar to that of Vadas *et al.* (1986). Finally, in each experiment a dispersion index was calculated to determine the spatial distribution of sea urchins at the beginning and end of the experiments (see Russo, 1979). The index used was

$$R = \left(\sum r_1 / \sum r_2 \right),$$

where r_1 = distance from a random coordinate to the nearest sea urchin, and r_2 = distance from that sea urchin to its nearest neighbor. A value of 0.88 indicates a random distribution, higher than 0.88 an aggregated distribution, and less than 0.88 a uniform distribution (Russo, 1979). The measurements were carried out using 35 random coordinates since this was the approximate number of points at which the dispersion index value reached a plateau. In each experiment the index was calculated using a new

set of random coordinates. To determine whether the duration of the experiments (i.e., 30 min) played an important role in the number and size of the aggregations observed, a control treatment was followed for 2 h using video. The number of aggregations, the time the aggregations were sustained, the size class of the individuals present in the aggregations, and the index of dispersion at the beginning and end of the experiment were recorded and calculated.

Experiment 2

To determine the importance of food in the distribution patterns of *Tetrapygus niger*, combinations of twelve sea urchins (three size classes, described above) were maintained without food for 7 days and then placed, following a uniform spatial distribution pattern, on the experimental platform, to the center of which whole fronds of the brown kelp *Lessonia* sp. had been attached. Because of the initial distribution of urchins (Fig. 1) and the position of food, two individuals (i.e., a large and a small) were under the kelp canopy at the start of the experiment. The number and size class of sea urchins under the algal canopy, the number of urchins feeding, and the dispersion pattern at the end of the experiment was recorded. The experiment was triplicated.

Experiment 3

To determine the importance of aggregations as a defensive mechanism against predators, seven large sea urchins were placed in the middle of the platform in an aggregated distribution in the absence (control) or presence of one predator (fish or starfish). Experiments were carried out in triplicate and followed for 10 min. The number of individuals remaining in the initial aggregation was registered at five-minute intervals.

As preliminary observations in the control treatments of Experiment 1 showed that individuals tended to remain in an aggregation once formed, seven large sea urchins were uniformly distributed on the platform and the percentage of individuals moving was registered at five-minute intervals. These results were contrasted with the control treatments of this experiment (i.e., movement of sea urchins starting aggregated).

Experiment 4

Finally, to characterize the attack behavior of the starfish *Meyenaster gelatinosus* and the escape responses of *Tetrapygus niger*, 18 sea urchins of the three size classes (i.e., six large, six medium and six small individuals) were

placed in the presence of three starfish (two large and one small: 52.3, 49.3 and 21.6 cm of diameter – starfishes were measured as if they were the diameter of a circle). The starfishes were maintained without food for 48 h before the experiment. The experiment was followed for 70 min using video. The number of attacks, the size class of the individuals being attacked, and the escape speed of sea urchins was registered. The sustained pursuit of a sea urchin by a starfish or the capture of a sea urchin was considered to be an attack. Likewise, a sudden change in the velocity of a sea urchin (generally associated with a sudden change in the movement direction) as consequence of a starfish proximity was considered to be an escape response.

All experiments were carried out sequentially in the same tank. After each experimental trial, the seawater was completely replaced and a different group of urchins was placed on the platform for the next trial. The same spatial arrangement of the urchins described in Fig. 1 was used for all trials in Experiments 1 and 2. To test whether the number of sea urchins moving (i.e., totals and per size class; Experiment 1), the type of aggregations observed (i.e., in terms of number of sea urchins involved and their size classes; Experiment 1), the participation of the different size classes in the aggregations (i.e., Experiment 1), and the number of sea urchins remaining in the aggregation (i.e., Experiment 3) of replicates were homogeneous, for each experiment we first computed G_H (Heterogeneity G). Since we did not detect statistical differences among the replicates in any of the experiments done, data were pooled for further analysis. The data were then statistically tested using chi-square contingency table analysis (Sokal and Rohlf, 1995). In case of significant differences in frequencies, the contingency tables were subdivided to detect the variables responsible (Zar, 1974, p. 65). The average speed of sea urchins, the average time the sea urchins remained aggregated and the number of solitary individuals in the different treatments were compared using the Kruskal-Wallis (H) non-parametric test followed by the Mann-Whitney (Z) posteriori test (Siegel and Castellan, 1988). All data in the text are expressed as means \pm 1 standard error.

RESULTS

Experiment 1

The control treatment showed that a high number of large sea urchins moved in comparison to medium and small individuals (i.e., 91.7 ± 8.3 , 41.7 ± 8.3 and $33.3 \pm 22.1\%$ for large, medium and small sea urchins, respectively; $\chi^2 = 6.75$ with 1 df, $p = 0.009$ for medium individuals, and

$\chi^2 = 8.711$ with 1 df, $p = 0.003$ for small sea urchins); but that the average speed was similar for the three size classes (i.e., 0.175 ± 0.04 , 0.312 ± 0.1 and 0.193 ± 0.09 times the test diameter/min for large, medium and small sea urchins, respectively; $H = 1.843$ with 2 df, $p = 0.398$). The last result means that small individuals travelled relatively short distances in comparison to larger sea urchins (i.e., the speed of movement was standardized according to body size). Regardless of the size class of sea urchins, a larger number of individuals moved in presence of the starfish than in the control and fish treatments (i.e., 91.7 ± 4.2 , 66.7 ± 11.8 and $55.6 \pm 11.6\%$ for the starfish, fish and control treatments, respectively; $\chi^2 = 6.82$ with 1 df, $p < 0.01$ for the fish and $\chi^2 = 12.08$ with 1 df, $p < 0.001$ for the control). The analysis per size class showed that there was no change in the number of large individuals moving among the three treatments (i.e., 91.7 ± 8.3 , 83.3 ± 16.7 and $100 \pm 0\%$ for the control, fish and starfish treatments, respectively; $\chi^2 = 2.18$ with 2 df, $p = 0.336$) (Fig. 2(a)), but that their average speeds increased in the presence of predators (i.e., from 0.18 ± 0.04 in control to 0.31 ± 0.05 and 0.40 ± 0.08 times the test diameter/min in the fish and starfish treatments respectively; $H = 6.423$ with 2 df, $p = 0.04$, $Z = -2.253$, $p = 0.024$ for the fish and $Z = -2.031$, $p = 0.042$ for the starfish) (Fig. 2(b)). On the other hand, the number of medium sea urchins moving showed a significant increase in the presence of predators (i.e., from $41.7 \pm 8.3\%$ in the control to 91.7 ± 8.3 and $100 \pm 0\%$ in the fish and the starfish treatments, respectively; $\chi^2 = 6.75$ with 1 df, $p < 0.005$ for the fish, and $\chi^2 = 9.88$ with 1 df, $p < 0.005$ for the starfish) (Fig. 2(a)), but their average speeds did not change among the treatments (i.e., 0.31 ± 0.09 , 0.22 ± 0.05 and 0.37 ± 0.09 times the test diameter/min for the control, fish and starfish treatments, respectively; $H = 1.651$ with 2 df, $p = 0.438$) (Fig. 2(b)). Finally, the number of small sea urchins moving showed a significant increase in the presence of the starfish (i.e., from 33.3 ± 22.1 and $25 \pm 0\%$ for the control and fish treatments, respectively, to $75 \pm 0\%$ in the starfish treatment; $\chi^2 = 4.19$ with 1 df, $p < 0.05$ for the control and the fish treatments) (Fig. 2(a)), but their average speed in this treatment was significantly lower than in the fish treatments (i.e., 0.087 ± 0.04 and 0.329 ± 0.09 times the test diameter/min for the starfish and fish treatments, respectively; $Z = -2.149$ with 1 df, $p = 0.03$) (Fig. 2(b)).

A total of 21 aggregations were observed in the experiments. There were no major differences between treatments in the number of aggregations formed: six in control treatments, eight in experiments with *P. chilensis*, and seven in experiments with *M. gelatinosus*. Likewise, the frequency of the different type of aggregations observed as well as the participation in

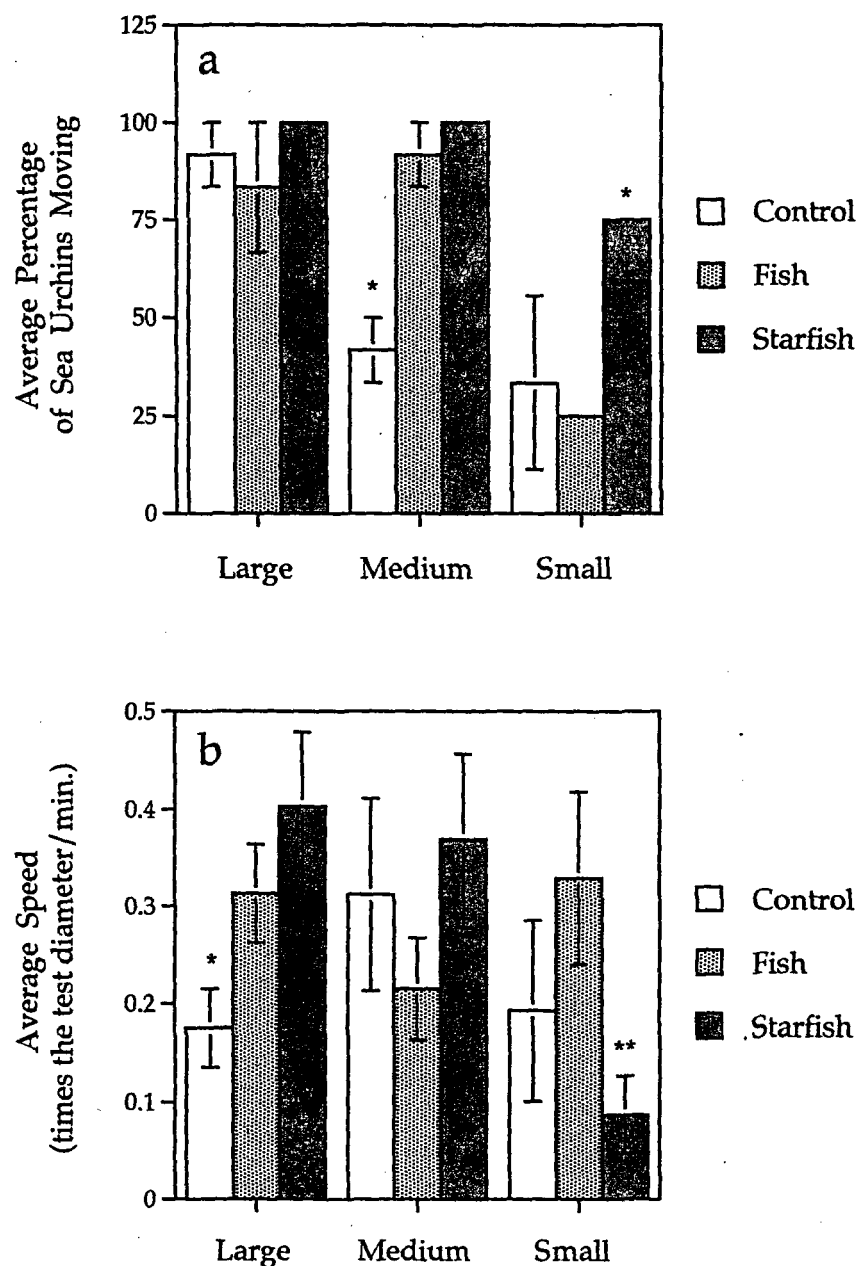


FIGURE 2 *Tetrapygus niger*. (a) Percentage of individuals moving, and (b) speed of movement of sea urchins of distinct size classes in the three experimental treatments (means \pm 1 SE). Asterisks show the treatments being different in each size class. * $p < 0.01$, ** $p < 0.05$.

aggregations of the different size classes were independent of the treatments ($\chi^2 = 15.65$ with 14 df, $p = 0.335$ for the type of aggregations, and $\chi^2 = 1.43$ with 4 df, $p = 0.839$ for the participation in aggregations of the different size classes). However, regardless of the treatments, the participation of sea urchins in aggregations was dependent of the size class ($\chi^2 = 10.19$ with 2 df, $p < 0.01$). In this sense, large and medium sea urchins were observed in $76.9 \pm 11.4\%$ and $79.6 \pm 8.2\%$ of the aggregations formed, respectively; while small individuals were observed in $30.6 \pm 13.3\%$ of them ($\chi^2 = 8.00$ with 1 df, $p < 0.005$ and $\chi^2 = 6.22$ with 1 df, $p = 0.013$, for large and medium individuals, respectively). Likewise, most of the aggregations were composed of two sea urchins ($82.4 \pm 7.4\%$). Of these aggregations, $61.1 \pm 11.5\%$ were formed between large and medium sea urchins. Aggregations of three and four individuals were observed in only $13.9 \pm 7.3\%$ and $3.7 \pm 3.7\%$ of the aggregations, respectively. The small size of the aggregations (most of them consisting of two sea urchins) seems not to be determined by the duration of the experiments, since aggregations of more than four individuals were never observed in the long-term control (2 h). Moreover, most aggregations (three out of five) were formed by two sea urchins (mainly between large and medium individuals).

The average time the sea urchins remained aggregated was significantly less in presence of *M. gelatinosus* than in the controls (8.3 ± 2.0 min and 20.2 ± 3.7 min in starfish and control treatments, respectively; $H = 6.031$, $p = 0.049$; $Z = -2.103$, $p = 0.035$). Moreover, the average number of solitary individuals was significantly higher in the presence of the starfish than in the controls (10.2 ± 0.4 and 8.6 ± 0.3 solitary sea urchins in starfish and control treatments, respectively; $H = 6.485$, $p = 0.039$; $Z = -2.349$, $p = 0.019$). The time the sea urchins remained aggregated and the average number of solitary individuals in the fish treatment reached values intermediate between the control and the starfish treatment. The long duration of aggregations and the few solitary urchins found at 5 min intervals in control treatments, suggest that *T. niger* remains aggregated once aggregations have been formed. To test this hypothesis, large sea urchins were placed in aggregated and uniform distribution patterns and the number of individuals moving was recorded. This experiment showed that although the average speed reached by sea urchins was no different between the aggregated and uniform distribution ($Z = -1.862$, $p = 0.063$), $71.4 \pm 8.2\%$ of the dispersed urchins showed movement, compared to only $14.3 \pm 8.2\%$ of the aggregated urchins.

Finally, the dispersion index showed a uniform distribution pattern at the beginning of all experiments ($R = 0.65 \pm 0.07$). At the end of control

experiments, the sea urchins' spatial distribution pattern was aggregated ($R=1.08 \pm 0.19$) while it was random in the experiments with predators ($R=0.87 \pm 0.07$ for fish, and $R=0.87 \pm 0.19$ for starfish). The dispersion index in the short-term controls (30 min) seems not to be determined by the duration of these treatments, since a similar index was found in the long-term control lasting 2 h ($R=0.98$).

Experiment 2

In experiments with food, 17 sea urchins ($47.2 \pm 2.7\%$ of the total) were under the *Lessonia* sp. canopy at the end of the experiment ($64.5 \pm 2.2\%$ of these moved to food and $35.5 \pm 2.2\%$ started in this position). Of those sea urchins moving to food, seven were medium individuals, three were large sea urchins, and only one was a small individual. Of those individuals that ended up associated with *Lessonia*, $41.1 \pm 4.9\%$ were feeding. The final distribution pattern of *T. niger* was aggregated, reaching a value higher than in controls ($R=1.33 \pm 0.10$).

Experiment 3

It was found that the number of individuals remaining in the aggregation at different times (in the experiment with aggregated sea urchins) was dependent of the treatment ($\chi^2=15.07$ with 4 df, $p=0.005$). In this sense, an average of $19.0 \pm 12.6\%$ of large sea urchins remained aggregated after 5 min in presence of *M. gelatinosus*, and only $14.3 \pm 8.2\%$ remained after 10 min (Table I). On the other hand, in the presence of *P. chilensis*, 100% of the sea urchins remained in aggregations at the end of the experiment but $85.7 \pm 8.2\%$ were aggregated in the controls (Table I).

Experiment 4

Meyenaster individuals followed a common attack behavior pattern on urchins. During a pursuit, starfish usually moved with two arms in front with the tips raised. Podia in the tips of these arms were active. When a starfish made contact with a sea urchin, the tendency was to impede its prey's movement by gathering together the arm tips. Immediately afterwards, the starfish tended to hold the prey down by putting one of its arms over the sea urchin. Finally, the starfish started moving over the sea urchin until the prey reached the mouth. Of 13 attacks observed, eight (62%) were on large sea urchins and 5 (38%) on medium individuals. The

TABLE I *Tetrapygus niger*. Mean number and percentage (± 1 SE) of sea urchins that remain in the aggregation at different times in the three experimental treatments (control in the presence of fish, and in the presence of starfish)

Treatment	Mean number (± 1 SE) of sea urchins remaining in the aggregation at different times (%)		
	0 min	5 min	10 min
Control	7 (100)	6 ± 0.6 (85.7 ± 8.3)	6 ± 0.6 (85.7 ± 8.3)
Fish	7 (100)	7 (100)	7 (100)
Starfish	7 (100)	1.3 ± 0.9 (19 ± 12.6)	1 ± 0.6 (14.3 ± 8.3)

large starfishes (i.e., 52.3 and 49.3 cm of diameter) attacked large as well as medium sized sea urchins, whereas the small starfish (i.e., 21.6 cm of diameter) attacked only medium sized individuals. At no time was an attack on a small sea urchin observed. Indeed, starfishes would pass over them without causing any damage.

Faced with the presence of a starfish, sea urchins pursued a common escape strategy. Once the presence of a starfish was detected, the sea urchins actively moved their pedicellariae. The escape response, defined as an abrupt change in speed (and often in direction), was always generated in reaction to physical contact with the starfish, and was observed in only large and medium sized individuals. During the escape response the large and medium sized sea urchins reached an average velocity of 1.56 ± 0.15 and 1.80 ± 0.31 times the body's diameter per minute, respectively. In some escape attempts the sea urchins would climb over other urchins if these blocked their path. Likewise, sea urchins surrounded by the arms of a starfish often climbed over one of the arms to escape predation.

DISCUSSION

Individuals of *Tetrapygus niger* appear to be able to recognize the presence of predators, and respond with increased mobility (i.e., number of sea urchins moving or average speed of movement). However, the distinct size classes respond in different ways. Large sea urchins increased their speed of movement in the presence of predators, but the number of individuals moving was the same in these treatments as in controls. On the other hand, a larger number of medium sea urchins moved in the presence of predators than in the controls, but the average speed was not different among treatments (Fig. 2). Finally, in the starfish treatment, there was an increase in the number of small sea urchins moving but a decrease in the average speed of movement with respect to the fish treatment. Despite the

lack of difference in the number of aggregations formed between the control and predator treatments, the increased mobility of sea urchins was probably responsible for the random spatial distributions of sea urchins observed at the end of experiments involving predators.

The behavioral response of sea urchins in the presence of predators was specially marked in the starfish treatment. In this case, the number of sea urchins moving was high (92% of the total), and the larger sea urchins moved with a velocity which was significantly greater than that shown in the controls, reaching speeds of up to 1.56 times body diameter/min. Likewise, in the presence of this predator, the aggregations were more unstable. In this sense, both the average duration of aggregations and the average number of solitary individuals in the presence of starfish were significantly lower and higher, respectively, in comparison to the controls. This suggests that aggregations formed by *T. niger* in the present study would not have an important protective function against the starfish *Meyenaster gelatinosus* (one of this species' most important predators). Indeed, in rapid escape responses, large sea urchins tended to abandon aggregations when under attack from this asteroid (only 19% remained in the vicinity five minutes after the introduction of the starfish, Table I). The abandonment of aggregations by sea urchins in the presence of predators has also been reported for other species. For example, Duggins (1981) showed that the density of the sea urchin *Strongylocentrus purpuratus* and *S. droebachiensis* decreased to virtually zero in mixed aggregations of these species with *S. franciscanus*, when the starfish *Pycnopodia helianthoides* was introduced into the system. Hagen and Mann (1994) observed that the presence of the wolffish *Anarhichas lupus* reduced the size of aggregations of *Strongylocentrus droebachiensis* by triggering escape responses in its constituents.

The food seems to be an important factor in the distribution pattern of *T. niger*. In the presence of *Lessonia* sp., nearly 50% of the sea urchins were beneath the macroalgal canopy at the end of the experiment, generating an even higher aggregated distribution than in controls ($R = 1.33$). As predicted from the mobility studies on small sea urchins, most movement towards the food source was seen in medium and large individuals (7 medium, 3 large and 1 small). Likewise, the experiments with *Lessonia* suggest that the association with the macroalga was formed not only in search of food but also probably in search of spatial refuge. In fact only 41% of those individuals found in association with *Lessonia* sp. were eating at the end of the experiment. These results agree with those of Russo (1979) who calculated the same index with *Strongylocentrotus franciscanus* in the presence and absence of food in laboratory experiments. He found that sea urchins with

food showed an aggregated spatial distribution while those without food were randomly distributed.

The results of the control treatment suggest that *T. niger* tends "naturally" to form aggregations. In this sense, the spatial distribution of sea urchins at the end of controls was aggregated ($R=1.08$). Likewise, in this treatment the aggregations were stable (i.e., remained formed for an extended time and the number of solitary individuals was low). This phenomenon was corroborated by the observation that more individuals moved when dispersed than when aggregated.

Different causes have been advanced for the formation and maintenance of aggregations and for the existence of aggregated spatial distributions in populations of different species. Pearse and Arch (1969) gave great importance to scototaxic (i.e., dark attraction) and thigmotaxic responses as being responsible for the formation and maintenance, respectively, of aggregations in the sea urchin *Diadema* sp. Garnick (1978) demonstrated experimentally that *Strongylocentrotus droebachiensis* formed aggregations in response to other sea urchins in a form of chemotaxis. The formation of aggregations as a defense mechanism has also been described in other sea urchin populations, e.g., *S. franciscanus* and *S. purpuratus* (Bernstein *et al.*, 1981; Tegner and Levin, 1983). In contrast, some authors have pointed out that aggregations of sea urchins may be induced not only by predators but also by a chemotaxic response in conspecifics to feeding individuals (Garnick, 1978). In this sense, Vadas *et al.* (1986) argued that aggregations of the sea urchin *Strongylocentrotus droebachiensis* formed only as a response to the presence of food or topographic features, and was linked to the presence of predators (conclusions questioned by Hagen and Mann, 1994). Scheibling and Hamm (1991) found that both juveniles and adults belonging to this same species formed aggregations around food sources, even when predators were present (see also Vadas *et al.*, 1986).

Interestingly, starfish in our experiments never attacked smaller sea urchins. While larger starfish (52.3 and 49.3 cm in diameter) attacked both medium and large individuals, smaller starfish (21.5 cm) only attacked medium-sized individuals. This agrees with our observation on the size of the sea urchins consumed by starfish in aquaria before their use in experiments. Of a total of 9 sea urchins consumed, 5 were large (an average of 53.3 mm TD) and 4 were medium sized (an average of 43.9 mm TD). Despite the availability of small sea urchins, starfish never consumed individuals less than 30 mm TD. This suggests that in contrast to the situation in other urchins, size provides no means of escape for *T. niger* against *M. gelatinosus*. A refuge in size has been observed in other sea urchin species

(e.g., *Strongylocentrotus franciscanus* against the starfish *Pycnopodia helianthoides*, Duggins, 1981; Tegner and Dayton, 1981). However, our observations corroborate those of Dayton *et al.* (1977) regarding the absence of escape through size by the sympatric sea urchin *L. albus* from *M. gelatinosus* along the Chilean coast.

In the present study the escape response of *T. niger* was always triggered by contact with the starfish. Likewise, individuals of *T. niger* were clearly capable of recognizing starfish in foraging modes. In holding aquaria, it was common to observe sea urchins in contact with passive starfish. The study of Dayton *et al.* (1977) is the only one carried out in Chile which considers the behavior patterns of the starfish *Meyenaster gelatinosus* during the foraging and escape actions of its prey. Our results are similar to those described by Dayton *et al.* (1977), with some exceptions. They suggested that the escape responses in the prey (e.g., the sea urchin *Loxechinus albus*) was triggered at a considerable distance (50–115 cm) from the starfish. On the basis of these observations they proposed that at least some of the prey would respond to vibrations generated by the ossicles when rubbed together during the starfishes' movement. However, in many cases, escape responses to asteroids are generated by contact; responses which are presumably caused by the detection of chemical compounds liberated by the predators in question (Dayton, 1975). The fact that sea urchins demonstrated an escape response only after physical contact with *M. gelatinosus*, suggests that the vibration detection hypothesis proposed by Dayton *et al.* (1977) is unlikely. In our experiments it seems that *T. niger* only responds to compounds liberated by the starfish when foraging. As a consequence of the behavior patterns described above, the distribution patterns of *T. niger* could be severely affected in areas with high densities of *M. gelatinosus*, as has been demonstrated with the sea urchin *Lytechinus anamesus* and the starfish *Patiria miniata* in California (Schroeter *et al.*, 1983).

There were no differences in the number of aggregations formed among the treatments. Moreover, the type of aggregations formed (i.e., in terms of number and size class of the sea urchins involved) as well as the participation of sea urchins of the different size classes, were independent of the treatments. However, regardless of the different treatments, small sea urchins rarely participated in aggregations. Only 30% of formed aggregations included small urchins, whereas 77% and 80% of formed aggregations included large and medium individuals, respectively. Hagen and Mann (1994) observed in laboratory experiments that large *Strongylocentrotus droebachiensis* were more likely to be found in aggregations than smaller individuals. Similarly, Scheibling and Hamm (1991) showed that in the

absence of food the juvenile *S. droebachiensis* tended to become cryptic and did not participate in the aggregations formed by adults. These authors also found the same behavior in the field, where juveniles tended to lead a solitary life between crevices and interstices, and the adults tended to live in aggregations in exposed environments. As reported for *S. droebachiensis*, this behavior would provide a partial explanation of why small individuals of *T. niger* in the field tend to be found alone in crevices, and not with large sea urchins in aggregations in exposed places (Rodríguez and Ojeda, 1993).

The most frequently formed aggregations were between two individuals (i.e., mainly between medium and large sea urchins). We suggest two main factors to explain why the aggregations formed in this study were so small: the density of sea urchins used and the lack of spatial heterogeneity (e.g., substratum topography). Despite the fact that the density of individuals in a certain area can also be important in determining the size of the aggregations formed (see Pearse and Arch, 1969; Berstein *et al.*, 1983), this explanation seems unlikely in this case because sea urchin densities in our experiments were similar to field densities for *T. niger* (i.e., 10 to 16 individuals/m²; see Rodríguez and Ojeda, 1993). On the other hand, it has been suggested that spatial heterogeneity (e.g., substrate topography) could play an important role in the formation of aggregations and in establishing an aggregated spatial distribution in populations of sea urchins (see Vadas *et al.*, 1986; recently called into question by Hagen and Mann, 1994). This explanation is likely, since field experiments have shown that bottom topography (together with food availability) is one of the most important factors determining the formation of large aggregations of *T. niger* (unpublished data).

The average speed of sea urchins was similar for the three size classes in the control treatment. This means that small sea urchins travelled relatively short distances in comparison to larger individuals. Schroeter *et al.* (1983) showed that small *Lytechinus anamesus* travelled relatively short distances in comparison to adults when exposed to the starfish, *Patiria miniata*. They concluded that small individuals were more vulnerable to predation than large sea urchins. Despite the fact that the present study shows that small sea urchins were not attacked by the starfish *M. gelatinosus*, their low mobility would make them potentially vulnerable to other predators. Small individuals of this species (< 15 mm TD) are preyed upon, for example, by some common fish of Central Chile, such as the "rollizo" *Pinguipes chilensis* or the "bilagay" *Cheilodactylus variegatus* (unpublished observations). Likewise, one of the most important predators of *T. niger*, the fish

Graus nigra (Moreno, 1982; Fuentes, 1982), preys on a wide range of sizes, including individuals of less than 20 mm TD (unpublished observations).

We conclude that individuals of *Tetrapygyus niger* are able to recognize the presence of predators, and respond with increased mobility (e.g., number of sea urchins moving or average speed of movement; i.e., escape responses) but without increasing the number or size of aggregations. Moreover, aggregations of individuals of *T. niger* do not seem to have a protective function against one of their main predators, the starfish *Meyenaster gelatinosus*. Indeed, large sea urchins in aggregations tend to abandon them by way of rapid escape when they are under attack from this asteroid. It is probable that the generation of aggregations is related more to feeding patterns or to other factors associated with spatial heterogeneity (substrate topography). In this sense, ongoing field experiments by one of the authors (S.R.R.) using geostatistical analysis in a large intertidal pool have shown that the position of *T. niger* is strongly associated with substratum irregularities. In the presence of drift algae, however (i.e., exogenous subsidies) they leave the crevices, depressions and interstices, increase their abundance near the algae, and form dense aggregations around the food (unpublished data).

The present study represents the first experimental description of the behavior of the black sea urchin *Tetrapygyus niger* in response to different stimuli such as food and predators. More extensive field studies will be necessary before these preliminary hypotheses can be confirmed or refuted. The study also throws light on the importance of these behaviors on the generation of patterns within populations of this species, and their possible consequences at community level.

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