Gimme Shelter: factors influencing juvenile sheltering in the red sea urchin *Strongylocentrotus franciscanus*

Michael T. Nishizaki & Josef Daniel Ackerman
University of Northern British Columbia, Prince George, Canada and
The Bamfield Marine Station, Bamfield, Canada

ABSTRACT: Many benthic marine invertebrates disperse during an obligate, planktonic larval phase and subsequent recruitment into the adult population is often unpredictable in both time and space. Thus, the common occurrence of juvenile sea urchins "sheltering" under adults is peculiar given that they possess a pelagic larval stage. An explanation for this pattern cannot be provided by models based on larval transport or larval settlement and it is most probable that post-settlement processes (i.e. behaviour and/or mortality of juveniles) influence this sheltering phenomenon. Laboratory experiments were conducted to determine the relationship between juvenile sheltering in the red sea urchin *Strongylocentrotus franciscanus* and three factors, water motion, risk of predation, and nutrition. Juvenile sea urchins (6.50 ± 0.11 mm TD; test diameter) in a laboratory aquarium exhibited a significant increase ($p < 0.001$) in the percentage of sheltering juveniles under high energy water conditions (speed, U = 3.22 cm/s) compared to low energy conditions (U = 1.71 cm/s). Likewise, the proportion of juveniles sheltering was significantly increased ($p = 0.003$) using water passed over a starved predator *(Pycnopodia helianthoides)*. A nutritional benefit for sheltering was also evident in recently settled urchins (1.41 ± 0.02 mm TD), which had significant growth ($p = 0.013$) when provided with kelp *(Macrocystis integrifolia)* blades, whereas growth was not significantly different from controls when urchins were fed ground kelp or kelp processed by adults. These results indicate that juvenile movements related to post-settlement processes is a possible mechanism to explain the association between juvenile and adult sea urchins.

1 INTRODUCTION

1.1 *Background*

Marine benthic invertebrates with planktonic larvae experience high mortality during dispersal, settlement, and the early juvenile stage (Gosselin & Qian, 1997, Pechenik, 1999). Sea urchins are no exception given that juvenile mortality has been reported at 70-80% during the first 24 days (Rowley, 1990). Yet juvenile red urchins (*Strongylocentrotus franciscanus*) have been found under the spine canopy created by aggregations of adults, often at remarkably high frequencies (e.g. 90%) (Low, 1975, Tegner & Dayton, 1977, Breen et al. 1985, Sloan et al. 1987). This would appear to be an unlikely association for an organism with pelagic larvae and, therefore, it would be appropriate to examine the potential benefits of this association for recruitment into adult populations.

Although a number of studies have reported juvenile urchins residing under the adult spine canopy (Tegner & Dayton, 1977, Breen et al. 1985, Sloan et al. 1987), few have concentrated on the mechanisms underlying this interaction, particularly: (1) why are juvenile urchins found under the spines of adults?; and (2) how does this association occur? Not surprisingly, several possible advantages have been forwarded to explain why juvenile urchins reside under adults. For example, it has long been suggested that juvenile sheltering is a strategy to avoid predators such as the sunflower star *Pycnopodia helianthoides* (Tegner & Dayton, 1977, Breen et al. 1985, Sloan et al. 1987). There may also be a hydrodynamic advantage afforded by the spine canopy as water motion is known to influence the morphology and mobility of adult urchins (Lissner, 1983, Rogers-Bennett et al. 1995; Kawamata, 1998). Moreover, Pace (1975) reported that water motion could imposed a metabolic demand exceeding the capacity of aerobic metabolism in adult urchins. Another possibility is that juveniles under the spine canopy gain a nutritional advantage compared to juveniles found elsewhere. Tegner & Dayton (1977) noted that juvenile urchins appeared to be "sharing" food with the adults under which they resided. In addition, the spine canopy may reduce water velocities and hence the dispersion of water-borne nutrients liberated by adult feeding activities. This would be especially

be especially important if juveniles retain the ability to absorb dissolved organics from the larval stage (Kempf & Todd, 1989).

The other issue that has been a posed is how juvenile sea urchins come to dwell under adults. Cameron and Schroeter (1980) proposed three mechanisms that could influence juvenile recruitment: (1) larval supply; (2) larval settlement; and (3) juvenile mortality. Harris & Chester (1996) reported that sea urchin recruitment was not associated with larval supply. Furthermore, Cameron and Schroeter (1980) indicated that urchin larvae did not settle preferentially in response to adult-associated cues. The lack of evidence for the larval supply or larval settlement model implies that urchin recruitment may be a consequence of early juvenile behaviour and/or mortality.

Given the potential importance of adult sheltering in the early life history of sea urchins, we investigated the mechanism responsible for juveniles residing under the adult spine canopy, and how they get there.

2 MATERIALS AND METHODS

2.1 *Association Experiment*

Laboratory experiments were undertaken to compare the association of juvenile urchins with adults (i.e. sheltering under spines) under different flow conditions, and with or without the presence of a predator under these same conditions. If the spine canopy provides protection it would be expected that juveniles would more likely shelter under adults at high flows and when predators were present.
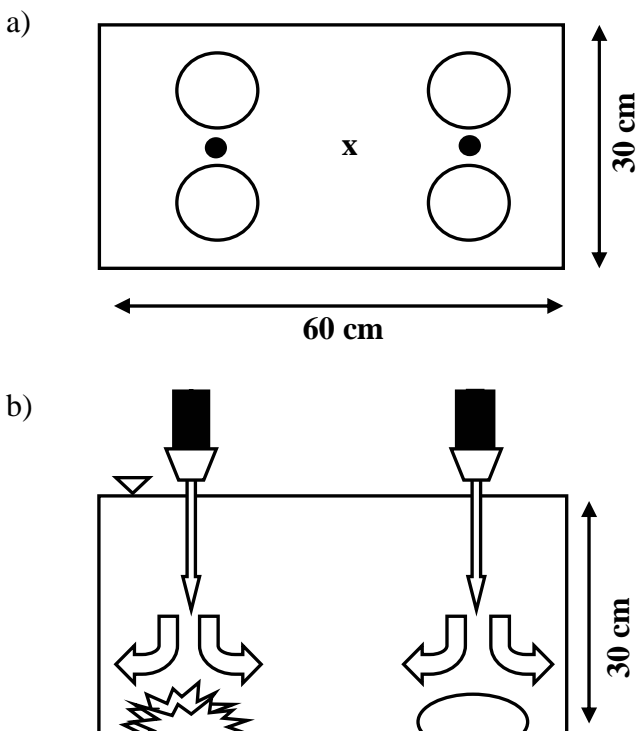
a)

b)

Figure 1. Experimental design for juvenile association experiment. a) Top-view of the aquarium with four cages indicated by large circles, release point for juveniles represented by the x, and the location of the two inlet nozzles indicated by the dark circles, b) Side-view of the aquarium with adult urchin (left) and rock (right). Open arrows indicate direction of flow.

All experiments were conducted in a glass aquarium (60 cm × 30 cm × 30 cm) using water from the Bamfield Marine Station seawater system, that provided unfiltered seawater from a depth of 25 meters at a constant temperature of 11°C throughout all of the experiment. Water flow was supplied via two nozzles, with one nozzle placed above the left and right sides of the aquarium (see Figure 1). Two water flow conditions (low and high) were used during the experiment. Under low flow each nozzle provided water at a rate of 1.5 L/min, and at high flow provided water at 15 L/min per nozzle.

Water velocities were measured 1 cm above the bottom in the middle of the aquarium using an Acoustic Doppler Velocimeter (Sontek, San Diego, CA). Water velocities used in this experiment (Table 1) were consistent with field measurements (i.e. average velocities between 2 and 23 cm/s, maximum velocities of 85 cm/s) from urchin habitats in the vicinity of Bamfield (Levitan, 1998).

Table 1. Water velocities under low and high flow conditions measured in the aquarium (see Figure 1). Velocities were measured in the x, y, and, z directions at 1 cm above the bottom (e.g. U_x, U_y, U_z; ± standard error). Recorded at 25 Hz for 180 seconds, N = 4.

Velocity	*Source*	U_x (cm/s)	U_y (cm/s)	U_z (cm/s)
Average	Low Flow	1.71 ± 0.5	0.6 ± 0.6	1.0 ± 0.2
	High Flow	-3.2 ± 1.0	1.4 ± 0.6	0.5 ± 0.2
Maximum	Low Flow	19.1	-26.1	7.4
	High Flow	-34.2	32.4	13.1

Cages were constructed using eight pieces of wood (13 cm x 0.5 cm) protruding from the floor of the aquarium to prevent adult urchin movement. One cage was placed in each of the four quadrants of the aquarium (large circles in Figure 1a). For each trial, two cages contained adult red urchins (*Strongylocentrotus franciscanus*) that had been starved for three to four days with test diameters (TD) of 80 mm. The remaining two cages contained rocks of similar size. The placement of adults and rocks was altered between runs so that all possible configurations were tested. To begin each trial (fifteen trials per treatment) five juvenile urchins (6.50 ± 0.11 mm TD; mean ± standard error) were placed in the centre of the aquarium floor ("x" in Figure 1a). The position of each juvenile was noted after 12 hours (i.e. under adult spines, under/on rock, on bottom of

aquarium, on glass walls of aquarium, or on wood cages).

The experiment was repeated using water that had passed over a predator (*Pycnopodia helianthoides*), which had been starved for one week. Predators were kept in a conditioning chamber and water from the seawater system was run through the chamber before entering the experiment. A Model I two-way analysis of variance was employed to determine the effect of flow and risk of predation on the percentage of juveniles sheltering.

2.2 Growth Experiment

Experiments were undertaken to determine whether juvenile urchins in the early developmental stages would benefit from the presence of kelp (*Macrocystis integrifolia*). Some variation in the presentation of kelp was necessary for several reasons. To begin with, it is not known when juveniles develop functional jaws and are able to feed on kelp. Secondly, it is not known whether juveniles could absorb dissolved organic material, which would be produced from the scraping and ripping of kelp as adult urchins feed. It was expected that ground or kelp processed by the adults would be a food source for juvenile urchins. To test these ideas, juveniles were reared in the laboratory using kelp presented in different ways.

Juvenile red urchins were obtained in one shipment from Island Scallops (Qualicum Beach, BC) 41-186 days after larval settlement and were maintained in flowing water (11°C) over the course of two months (Sept. 26 to Nov. 19, 1999). Juveniles were grown under the following nutritional conditions: (1) control group - 1 μm filtered seawater only; (2) kelp blades - blades of *M. integrifolia* (~ 40 grams each); (3) ground kelp - *M. integrifolia* (~ 40 grams plus 250 ml of seawater) ground in a blender; and (4) adult exudates – exudates (~ 40 grams of material produced by adult red urchins fed *M. integrifolia* plus 250 ml seawater collected from under the feeding adult). Each treatment was replicated in 3 separate 500 ml containers (16 cm tall x 8 cm diameter; 12 containers total) and 15 juveniles were placed in each container resulting in 45 juveniles per treatment (total of 180 juveniles for entire experiment). Juveniles were inspected for the presence of jaws at the beginning of the experiment and test diameters were also measured at that time. At the beginning of the experiment, juveniles averaged 1.42 ± 0.02 mm TD and there were no statistical differences in initial TD between treatments ($F_{(3, 176)} = 0.03$, p = 0.995). Survivorship and test diameters were recorded throughout the experiment. A Model I one-way analysis of variance was used to compare change in test diameter between treatments using the results from each container as a replicate.

2.3 Movement Experiment

Experiments were conducted to determine the response of juvenile and adult urchins to chemical cues from: (1) conspecifics; (2) predators (*P. helianthoides*); and (3) food (*M. integrifolia*). Results from these experiments would help to identify whether chemoreception is a mechanism through which juvenile sheltering occurs. Moreover, it was expected that juveniles might migrate towards adults only under the threat of predation.

Movement experiments were conducted within a Y-shaped chamber (Figure 2) filled to a depth of 3.5 cm. Fluorescent dye was used to ensure that flow was equal on both sides of the chamber and water speeds were recorded as ~2 cm/s. Caged targets (i.e. five juvenile urchins, an adult urchin, a predator, or kelp) were placed alternately in one of the arms near the inlet end of the chamber (denoted by "T" in Figure 2). Subjects (i.e. three juveniles or one adult) were then placed on the centreline of the chamber 15 cm from the outlet end (on the "x") and the position of the subject was recorded after 45 minutes (adult test subjects) or 12 hours (juvenile test subjects). Trials were also conducted with an adult urchin in the opposite arm of the chamber to the predator, to test whether the presence of predators altered the behaviour of the juvenile.
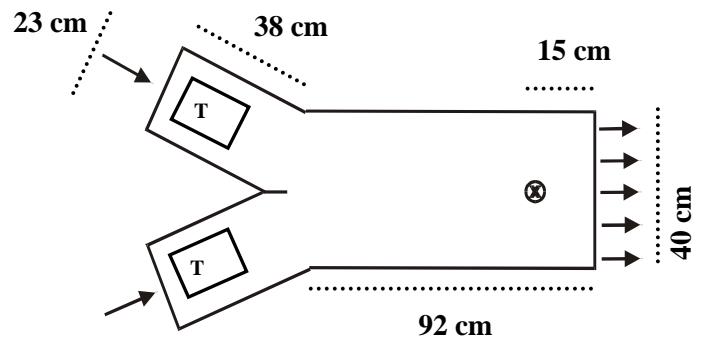

Figure 2. Drawing of Y-shaped flow chamber used in movement experiments (filled to 3.5 cm depth). Arrows indicate direction of water flow. "T" represents target areas. Individuals being tested were placed on the "x" at beginning of each trial.

Urchin movement was categorized under one of the following: (1) upstream and to the same side as the target; (2) downstream and to the same side as the target; (3) upstream and to the opposite side of the target; and (4) downstream and to the opposite side of the target. A Chi-squared test was used to test the null hypothesis that urchins would move equally in each of the four quadrants.

3 RESULTS

3.1 Association

At the beginning of each trial, juveniles moved about in a seemingly random manner using their

tube feet. Observations in the early part of the experiment (0 to 6 hours) indicated that juveniles were often found solidly attached in a variety of locations (i.e. in the open, on glass walls, on wood cages, under rocks, or under urchins). After 12 hours however, many juveniles were found sheltering under adults and these associations once formed, persisted over long periods (> 72 hours). Under low flow and without predators, only $13 \pm 4\%$ of the juvenile urchins were found sheltering under adults (Figure 3). At high flows however, the proportion of sheltering juveniles increased to ($52 \pm 7\%$). Interestingly, when water was passed over a predator, the percentage of juveniles remained at similarly high levels for both low ($44 \pm 6\%$) and high flow conditions ($59 \pm 7\%$). A significant difference was found in the proportion of juveniles sheltering under adults at different flow rates ($F_{(1, 56)} = 19.080$, $p < 0.001$) and in the presence or absence of a predator ($F_{(1, 56)} = 9.349$, $p = 0.003$). The interaction between the two factors was not significant ($F_{(1, 56)} = 3.864$, $p = 0.054$).

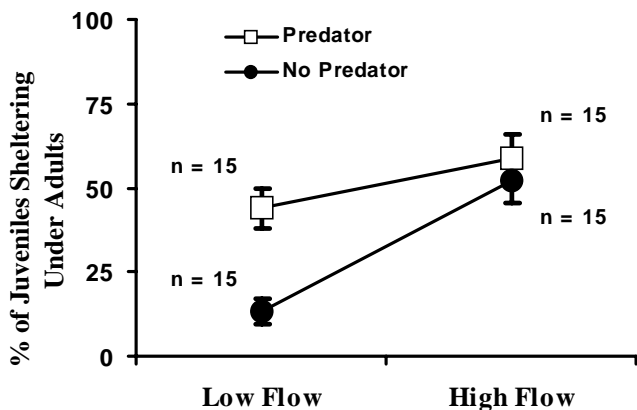

Figure 3. Mean percentage of juveniles sheltering under adults ($\pm$ standard error).

3.2 Growth

On day zero of the experiment, (41-186 days post-settlement) 100% of the juveniles had formed jaws. Growth of the juveniles over two months is presented in Figure 4 (below) as the average change in test diameter ($\pm$ standard error). Percentages above bars represent average juvenile survival.

Growth for juveniles in the control group was not statistically different from zero (-0.04 ± 0.05 mm/month) and survivorship was low ($20 \pm 20\%$). In contrast, urchins that were provided blades of kelp throughout the experiment experienced increased growth (0.28 ± 0.03 mm/month) and had high survivorship ($67 \pm 20\%$). While the urchins in the ground kelp treatment experienced little growth (0.00 ± 0.04 mm/month), they had higher survival rates ($53 \pm 18\%$). Finally, juvenile urchins growing with the addition of adult-processed kelp had moderate growth rates (0.11 ± 0.08 mm/month) and low

survival rates ($13 \pm 4\%$). A significant difference ($F_{(3, 8)} = 6.971$, $p = 0.013$) was found in growth between treatments (Figure 4) and planned comparisons indicated that only the kelp blade treatment differed significantly from the control. Survivorship of juveniles was variable and there were no significant differences found between treatments ($F_{(3, 8)} = 2.142$, $p = 0.173$).
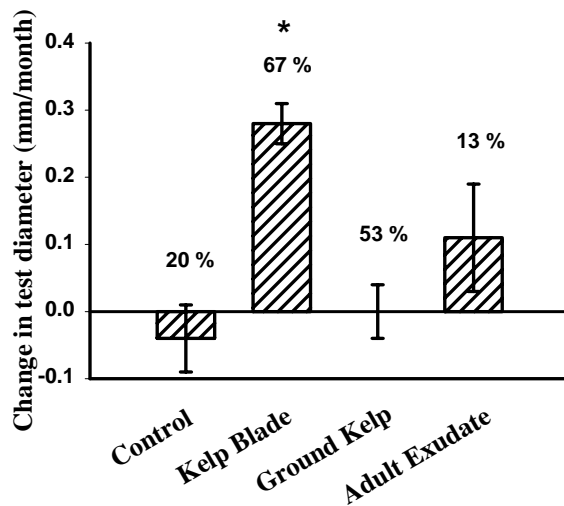

Figure 4. Average change in test diameter over two months ($\pm$ standard error). * indicates test diameter growth significantly different from control. Percentages represent average juvenile survival rates. Initial test diameters averaged 1.41 ± 0.02 mm and were statistically indistinguishable among all treatments.

3.3 Movement

Results of the movement experiments are presented in Table 2.

Table 2. Chi-square results from movement experiment (df = 3, DM = average distance moved, CV = coefficient of variation).

Subject	Target	N	χ^2, p value	DM (cm)	CV (%)
Juvenile	Adult	27	1.30, 0.73	32.64	88
	Predator + Adult	30	1.20, 0.75	32.69	69
	Kelp	24	27.67, < 0.01	61.12	70
Adult	Juvenile	20	1.20, 0.75	32.63	83
	Predator	23	10.91, 0.01	39.29	84
	Kelp	24	39.00, < 0.01	100.00	20

Juvenile urchins did not display directional movement towards or away from adults ($\chi^2 = 1.30$, $p = 0.73$) and the response was similar when given a choice between adults and predators ($\chi^2 = 1.20$, $p = 0.75$). However, when juveniles were presented kelp, they moved upstream to the side containing kelp ($\chi^2 = 27.67$, $p < 0.01$). Likewise, adult red ur-

chins did not move towards or away from juveniles ($\chi^2 = 1.20$, $p > 0.75$). However, they did respond to both predators ($\chi^2 = 10.91$, $p = 0.01$) and kelp ($\chi^2 = 39.00$, $p < 0.01$). For both adults and juveniles, the average distance traveled was significantly higher for the kelp treatment only ($F_{(2, 64)} = 23.12$, $p < 0.01$, and $F_{(2, 75)} = 5.01$, $p < 0.01$, respectively).

4 DISCUSSION

Research on sea urchins and other marine invertebrates has focussed on relationships between recruitment and processes affecting gametes (Levitan et al. 1992), larvae (Cameron & Schroeter, 1980, Ebert & Russell, 1988, Harris & Chester, 1996, Miller & Emlet, 1997), and adults (Wootton, 1999). While it has been recognized that the juvenile stage may be important for urchin recruitment (Pearse & Hines, 1987, Rowley, 1989), the advantages of juvenile sheltering remain unclear. The strong associations observed between juvenile and adult urchins in these experiments may be used to address two questions: (1) why are juveniles found under adults; and (2) how is this distribution achieved?

With respect to the first question, it is clear that high-energy conditions result in a significant increase in the proportion of juveniles that shelter under adults (Figure 3). This is likely due to the protection offered by the spine canopy (i.e. relatively low flow under adults compared to outside the spine canopy). Juvenile urchins should benefit from slower water velocities under the spine canopy, which should reduce the energetic requirements needed to maintain metabolic processes (e.g. Pace, 1975).

The risk of predation also influences the frequency of juvenile sheltering in that juveniles exposed to predators were more likely to be found under adults than juveniles not exposed to predators (Figure 3). These results are consistent with previous field studies (Tegner and Dayton, 1977, Breen et al. 1985, Sloan et al. 1987), which suggest that the spine canopy offered a refuge for juvenile urchins from predators such as *P. helianthoides*. In this study, the frequency of juvenile sheltering under the risk of predation was near 50% (Figure 3), which is lower than the 80% reported by Breen et al. (1985).

The growth experiment addressed the effect of different food sources potentially available in the spine canopy on juvenile survival and growth. Firstly, it is important to note that jaws had appeared in 100% of the juveniles by the beginning of the experiment (i.e., 41 - 186 days post-settlement), thus confirming observations reported by Miller & Emlet (1999). Moreover, significant growth rates for juveniles in the kelp blade treatment (0.28 ± 0.03 mm/month) demonstrated the presence of functional jaws. Rowley (1990) reported similar growth rates

for *S. purpuratus* (0.29 to 0.45 mm/month) during the first 50 days after larval settlement. High survival rates (53%) for the ground kelp treatment indicates that juveniles may also absorb dissolved organic material, as is the case for larval urchins (Manahan et al. 1983). However, growth rates for the ground kelp treatment were zero (0.00 ± 0.04 mm/month). Furthermore, many individuals in the control experienced negative growth (-0.04 ± 0.05 mm/month), which supports a similar field observation by Ebert (1967). It is clear that juveniles use kelp very early after settlement, however, additional research is needed to determine whether kelp is more readily available under the spine canopy.

The second question as to how juveniles come to shelter under adults can also be addressed by these results. Juvenile urchins were observed to move under the spines of adults (Figure 3), which supports the idea that juvenile migration may account for the association of juveniles and adults (Breen et al. 1985). Presently, it is not known how juveniles detect predators or adult urchins to hide under, although one hypothesis is that juveniles might respond to chemical cues (Snyder & Snyder 1970, Mann et al. 1984, Vadas et al. 1986, Scheibling & Hamm 1991). While juveniles responded to predators in the association experiment, they did not respond to adult or predator effluent in choice experiments (Table 2). This result may be related to different mixing rates within the large area of the Y-shaped chamber (> 5000 cm^2) compared to the aquarium used for the association experiment (1800 cm^2). Both juveniles and adults were however, able to target kelp in the Y-shaped chamber. Scheibling and Hamm (1991) and Vadas et al. (1986) showed that chemical responses to predators were secondary to the response towards kelp in *S. droebachiensis*. This may support the notion that urchins are more sensitive to kelp than to predators and are, therefore, able to respond to kelp in the Y-shaped chamber, but only respond to predators when cues are confined to a smaller area as was the case for the association experiment (Figure 3). It is likely that juveniles are able to target adults and predators chemically over small distances.

Analysis showed that adults and juveniles moved significantly greater distances towards kelp (Table 2). The movement of juveniles to adults was more variable compared to movement towards adults and predators, or towards kelp. This differed from the adults, where the variability was similar when adults were exposed to juveniles and predators (Table 2). The significance of this variation is not clear, and further work is needed to determine the response of juvenile urchins to chemical cues.

The results of this study indicate that post-settlement processes play an important role in influencing the frequency of juvenile sheltering. While juvenile mortality cannot be eliminated as a possible

explanation for adult-juvenile associations, these results support the hypothesis that sheltering is a consequence of juvenile behaviour. This may be a strategy to: (1) avoid predators; (2) avoid high-energy water conditions; and (3) to obtain food. It appears that juveniles can move under adults over short distances, but further study is needed to determine the significance of this behaviour in the field. The early life history of benthic invertebrates should be investigated to understand how events during these stages influence recruitment.

5 ACKNOWLEDGEMENTS

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