RESEARCH ARTICLE

Juvenile–adult associations in sea urchins (*Strongylocentrotus franciscanus* and *S. droebachiensis*): protection from predation and hydrodynamics in *S. franciscanus*

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Abstract Juvenile red sea urchins, *Strongylocentrotus franciscanus*, aggregate under adult conspecifics, whereas sympatric juvenile green sea urchins, *Strongylocentrotus droebachiensis*, are typically more solitary and dispersed. Neither the potential advantage of juvenile sheltering nor the differences in post-settlement behavior between the two species has been demonstrated experimentally, but may be related to protection from predators and/or hydrodynamics. In predation experiments, juvenile vulnerability differed in the two species as the seastar *Pycnopodia helianthoides* consistently chose juvenile *S. franciscanus* over *S. droebachiensis* (100% vs. 0%). When associated with adults, juvenile mortality decreased dramatically in *S. franciscanus* (90% alone vs. 5% with adults), but very little in *S. droebachiensis* (85% vs. 75%). Not surprisingly, juvenile behavioral responses in the two species reflect this difference in vulnerability. Juvenile *S. franciscanus* sheltered under adults when predation risk was high, but not when risk was low (44% vs. 13%), whereas sheltering in *S. droebachiensis* was infrequent and not related to predation risk (7% for high risk versus 5% for low risk). From a hydrodynamic perspective, the presence of an adult led to the creation of a hydrodynamic refuge for juveniles, where average water velocities were reduced by > 60% around the adult urchin. Again, striking differences in sheltering rate were apparent in *S. franciscanus* (52% vs. 13% for high flow and low flow, respectively), but not *S. droebachiensis* (5% for high flow versus 4% for low flow). Sheltering behavior was also species-specific as juveniles did not shelter at high rates under adults of the opposite species ($\leq$ 16%). A field survey confirmed these finding in that juvenile *S. franciscanus* abundance was associated with both adults and water motion ($R^2 = 0.80$, $P = 0.008$, best-subsets regression). These results suggest that sheltering confers juvenile *S. franciscanus* with a degree of protection from predators and water motion, and that species-specific differences in this post-settlement behavior may be related to the differences in the protection afforded by adults.

Communicated by R.J. Thompson, St. John´s.

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Introduction

Studies of recruitment dynamics in benthic invertebrates often focus on processes such as larval supply and/or settlement because larval settlement has been

directly related to larval flux (e.g., Gaines and Rough-garden 1985; Jonsson et al. 2005). Yet, in many organisms, including those with mobile juvenile stages, recruitment patterns do not necessarily reflect larval supply or settlement (Harris and Chester 1996; Hunt and Scheibling 1997). This is due, in part, to high mortality rates during early juvenile stages (see Gosselin and Qian 1997; Hunt and Scheibling 1997 for review) and the possibility of the migration of juvenile stages to 'preferred' habitats (Bouma et al. 2001; Gillanders et al. 2003; Nishizaki and Ackerman 2005). Unfortunately, the factors influencing post-settlement mortality and/or migration are not well understood (Hunt and Scheibling 1997).

Sea urchins in the genus *Strongylocentrotus* provide an opportunity to examine post-settlement processes, as species-specific differences in recruitment have been noted. Although larval settlement appears to occur in response to habitat cues (i.e., coralline algae), it is not apparent how these cues relate to conspecifics (Cameron and Schroeter 1980; Lambert 2000). There are, however, clear differences in distribution during the early juvenile stage. *Strongylocentrotus franciscanus* juveniles aggregate under the spine canopy of adults (Low 1975; Tegner and Dayton 1977), whereas juvenile *S. droebachiensis* are solitary and well dispersed (Scheibling and Hatcher 2001). It has been suggested that differences in juvenile distribution for these closely related sea urchin species may be a consequence of juvenile post-settlement behavior related to predator avoidance (Breen et al. 1985; Rowley 1989, 1990; Hagen and Mann 1994), yet the selective pressure underlying such behavior remains speculative and has not been demonstrated experimentally.

There are several possible explanations for the role of juvenile-adult associations in sea urchins: (1) The *predation hypothesis*—that the risk of predation is lower under adult urchins. (2) The *hydrodynamic hypothesis*—that water velocity is moderated under adults. (3) The *food availability hypothesis*—that food such as macroalgae is more accessible to juveniles under adults. Recent evidence indicates that juvenile *S. franciscanus*, and to a lesser degree, juvenile *S. droebachiensis*, experience competition rather than nutritional gains when sheltering under adults (Nishizaki and Ackerman 2004). Consequently, the influence of predation and hydrodynamics on juvenile–adult associations warrants investigation. This study, therefore, examines the vulnerability of juvenile *S. franciscanus* and *S. droebachiensis* to predation and hydrodynamics in an effort to assess whether adult sheltering provides juvenile with 'protection' from these factors.

Materials and methods

Adult red urchins, *S. franciscanus* (A. Agassiz, 1863) (75–161 mm test diameter) and green urchins, *S. droebachiensis* (O.F. Müller, 1776) (66–87 mm test diameter) were fed macroalgae (*Macrocystis integrifolia*) and kept in flowing seawater at the Bamfield Marine Sciences Centre (BMSC), Bamfield, British Columbia, Canada. Similarly, juvenile *S. franciscanus* and *S. droebachiensis* (5.5–10.1 mm test diameter) were maintained in flowing seawater and fed benthic diatoms. Sunflower stars, *Pycnopodia helianthoides* (Brandt, 1835) [140 ± 30 (mean $\pm$ SE) mm], were used as predators. All experiments were supplied with unfiltered seawater via the BMSC seawater system (range in temperature = 8.8–13.2°C, salinity = 25.9–34.7 ppt, pH = 7.5–8.3, dissolved oxygen = 43–100% saturation). Adult sea urchins and seastars were collected by BMSC divers and juvenile sea urchins were obtained from Island Scallops, Vancouver Island, BC (2000–2002) or collected from Bamfield Inlet (2005).

Does sheltering provide protection from predators?

Feeding-choice experiments were conducted to examine whether there were species-specific vulnerabilities of juvenile sea urchins to predation. Individual predators (*Pycnopodia helianthoides*) were presented a choice between one juvenile *S. franciscanus* and one juvenile *S. droebachiensis* of similar test diameter (13 ± 4 and 12 ± 4 mm; difference in test diameter size between paired juveniles $\leq 3.7\%$) in tanks measuring 170 cm long $\times$ 72 cm wide $\times$ 12 cm deep. Controls were run to determine the feeding rate of each species by presenting only one juvenile at a time. Each predator was starved between 1 and 2 weeks and trials were run until one of the juveniles was eaten (10 min to 72 h). Preference by *P. helianthoides* for either juvenile species was tested using a two-tailed binomial test with the null hypothesis being that each species has an equal chance of being eaten.

A second experiment was run to determine whether adult sheltering provides juveniles with protection from predation. Using the same tank design described above, batches of five juvenile *S. franciscanus* (TD = 14 ± 1 mm) were presented to two starved sea stars (*Pycnopodia helianthoides*) either (1) alone or (2) with four adults (TD = 143 ± 4 mm). Similarly, five juvenile *S. droebachiensis* (TD = 15 ± 2 mm) were presented to *P. helianthoides* either (1) alone or (2) with 14 adults (TD = 66 ± 4 mm). The greater number of adult *S. droebachiensis* was used to maintain a similar density of adult-sheltered habitat in the two treatments

(based on area covered by adults). Trials were run for 15 days and a two-way ANOVA was employed to analyze the results. The data were analyzed using Levene's test for homogeneity of variances and the Kolmogorov–Smirnov test for normality. All statistical analyses were undertaken using SPSS 13.0 for Windows© software (SPSS Inc., Chicago, IL, USA).

Does sheltering provide hydrodynamic protection?

Water flow around an adult urchin was examined in a flow chamber that measured 162 cm long, 20.5 cm wide, and was filled to a water depth of 18 cm. Water was supplied at constant head from a 180 L header tank through a 7.6 cm diameter pipe into the chamber via gravity and controlled by a ball valve on the inlet pipe. The test section extended from 120 to 150 cm downstream from the collimators of the chamber. The experiment focused on *S. franciscanus* given the aforementioned strength of the juvenile–adult association reported in this species. The underside of an adult *S. franciscanus* (TD = 60 mm) was relaxed in menthol for ~30 min such that tube feet and spines on the underside of the body were immobile and the spines on the sides and top of the body remained erect. This held the adult urchin stationary for > 1 h allowing measurements of hydrodynamic conditions that would be experienced by juvenile sea urchins. To approximate naturally occurring hydrodynamic conditions, the chamber was adjusted to an average streamwise velocity of 9.14 ± 0.03 cm s^{-1} measured 130 cm downstream and 1.80 cm from the bottom using an acoustic Doppler velocimeter (ADV; Sontek/YSI Inc., San Diego, CA, USA). The chamber Reynolds number (*Re*) was 18,000 based on the hydraulic diameter, which corresponded to turbulent conditions. With the urchin in place, the water velocities were measured with the ADV in three dimensions (i.e., *u*, *v*, and *w* velocity in *x*, *y*, and *z* directions, respectively) on a 2×2 cm^2 horizontal grid of points 1.8 cm above the bottom of the flow chamber. Data were recorded for 180 s at a sampling frequency of 25 Hz (i.e., 4,500 observations) at each grid point. The turbulence intensity (TI) of the streamwise velocity was determined from the quotient of the root mean square *u* velocity (u_{RMS}) and the average *u* velocity measured at each point in the grid.

Juvenile behavioral responses

Experiments were undertaken to determine whether juvenile behavior (i.e., sheltering under adult spines) was independent of hydrodynamics, predation risk, and species of adult. Cages preventing adult urchin movement were located in each of the four corners in an aquarium ($60 \times 30 \times 30$ cm^3) (for full details see Nishizaki and Ackerman 2001). Five juveniles [either *S. franciscanus* (TD = 8.0 ± 1.1 mm) or *S. droebachiensis* (TD = 8.4 ± 0.8 mm)] were placed in the center of the aquarium and given a choice between two caged adult urchins (*S. franciscanus* [TD = 81 ± 13 mm] or *S. droebachiensis* [TD = 84 ± 3 mm]) and two cages containing rocks of similar size to the adult urchins. The proportion of juveniles sheltering under adults after 12 h for each treatment was recorded. Water flow was supplied via nozzles above the left and right sides of the aquarium resulting in mean water velocities 1 cm above the bottom of the aquarium of 1.7 and 3.2 cm s^{-1} as measured by the ADV.

Three experiments were conducted to examine the effects of hydrodynamics, predation risk, and adult species on juvenile sheltering: (1) *Hydrodynamics*—this experiment examined the influence of water motion [low (1.7 cm s^{-1}) versus high (3.2 cm s^{-1}) flow] on juvenile sheltering rates in *S. franciscanus* and *S. droebachiensis*. (2) *Predation*—this experiment examined the influence of predator risk on sheltering behavior in *S. franciscanus* and *S. droebachiensis*, under low flow conditions, using water passed over a starved *P. helianthoides* versus untreated water. (3) *Species Interaction*—this experiment presented five juvenile *S. franciscanus* (or *S. droebachiensis)* with a choice between two caged adult urchins (either two *S. franciscanus* or two *S. droebachiensis)* and two adult-sized rocks. The experiment, which was run under high flow conditions, provided a fully crossed design in terms of juvenile and adult sea urchin species. Data (*x*) were transformed by taking the arcsin-square root of the sum (*x* + 0.01) to achieve normality and homoscedasticity (Kolmogorov–Smirnov test, > 0.05 and Levene's test, $P > 0.05$ after transformation). When the assumptions of the general linear model could not be met, the Kruskal–Wallis test was used to analyze the data.

Juvenile sea urchins in the field

A field survey for juvenile urchins was conducted in Barkley Sound, British Columbia, between January and March 2001 to ascertain the relationship between urchins, predators, and water motion. Three sites of differing levels of wave exposure were examined including: (1) a wave-sheltered site (Dixon Island; 48 49.551°N; 125 11.819°W); (2) a moderately wave-exposed site (Ohiat Island; 48 51.328°N; 125 11.000°W); and (3) a wave-exposed site (Taylor Island; 48 49.647°N; 125 11.839°W). At each site, SCUBA divers set three vertical transect lines spaced at a

distance of 10 and 15 m apart. A 1 m^2 quadrat was placed adjacent to each transect line at each of three depths [~1.0 m (0.98 ± 0.23 m), ~3.0 m (3.05 ± 0.14 m), and ~4.7 m (4.69 ± 0.21 m) below chart datum]. This provided three replicates at each of three depths for the three sites (27 quadrats total). Depth was recorded as distance below chart datum (Canadian Hydrographic Service Harmonic Station at 48 50°N; 125 8°W). The presence and abundance of benthic organisms were recorded in each quadrat (see below). An airlift equipped with a 335 μm mesh (Nitex, Sefar, Rüschlikon, Switzerland) holding bag was used to vacuum the surface of each quadrat and a 33 cm long nylon brush (Justman Brush Co. Omaha, NE, USA) was used to gently dislodge material from the bottom of the quadrat for the vacuum. All material within the vacuum bag, including juvenile urchins, was transported to the laboratory for identification.

Water motion was measured at each depth at each site using the dissolution rate of plaster of Paris cubes. The cubes were poured into a $3 \times 3 \times 4$ cm^3 mould using one part plaster and two parts cold water, and were allowed to dry for 24 h. The dissolution rate of the cubes was measured in the flow chamber described above by suspending them 5 cm above the bottom of the chamber and measuring the mass loss over 24 h. Linear regression analysis was used to determine the relationship between water velocity and the dissolution rate. In the field, cubes were fixed at 5 and 20 cm above the bottom of each leg of a tripod constructed from steel rebar and deployed at each depth within a site for 24 h. This technique was designed to integrate the energy in the water column directly above and near the seafloor (e.g., 5 and 20 cm, respectively), recognizing its limitations (e.g., Porter et al. 2001).

The abundance of the twenty invertebrate and four algal groups (collapsed into coralline and fleshy functional groups in the analysis) was recorded along with the substrate type, depth, water motion (at 5 and 20 cm above substratum), and site location (Table 1). Three

Table 1 Variables used to analyze the factors determining juvenile *Strongylocentrotus franciscanus* abundance

Type	Category
Invertebrates	Adult *S. franciscanus*, Juvenile *S. franciscanus*, *S. purpuratus*, *S. droebachiensis*, Anemones, Nematodes, Abalone, Polychaetes, Chitons, Limpets, Nudibranchs, Other Gastropods, Clams, Mussels, Scallops, Crabs, Sea Stars, Sea Cucumbers, Brittlestars, Finfish
Algae	Coralline, Fleshy
Physical	Substrate, Water motion (5 cm), Water motion (20 cm), Depth

quadrats (one each at 1.0, 3.0, and 4.7 m depth for Ohiat site) were missing measurements of water motion, so replacement values based on average values from the same depth within the same site were used. These measured variables were reduced to four nontrivial dimensions using principal components analysis (PCA). Juvenile *S. franciscanus* abundance was compared against each of the four principal components (PC) mentioned above using: (1) four separate simple linear regressions and (2) a stepwise linear regression.

Results

Does sheltering provide protection from predation?

When exposed to a predator, juvenile *S. franciscanus* typically displayed some levels of movement throughout the trials, whereas juvenile *S. droebachiensis* often showed little or no movement. When presented alone, juveniles of both species experienced high mortality [100% for *S. franciscanus* ($N = 10$) vs. 80% for *S. droebachiensis* ($N = 10$); Fig. 1a]. In choice trials, predatory *Pycnopodia helianthoides* were observed to explore the tank, even coming into contact with both species (even passing mouth region over juveniles) before attacking. Although contact was often made with both species, *S. franciscanus* juveniles were always preyed upon first (i.e., 100% mortality) by *P. helianthoides* ($N = 14$, $P < 0.05$, binomial test; Fig. 1a). Thus, the null hypothesis that predation choice is independent of juvenile species was rejected.

In the second experiment, juveniles in the absence of adults displayed no consistent pattern of movement in response to a predator. Some individuals in both species moved away from predators while others remained stationary. When juvenile *S. franciscanus* were held together with adults, however, they sheltered under the adults throughout the experiment. For *S. droebachiensis*, both adults and juveniles were observed throughout the tank, with the majority on either the sides of the tank near the air-water interface or in the corners of the tank. When juveniles were exposed to a predator without adults, mortality in both species was high (90 and 85% for *S. franciscanus* and *S. droebachiensis*, respectively; $N = 4$ batches of five juveniles in each treatment in Fig. 1b). When associated with adults, juvenile mortality rates for *S. franciscanus* decreased dramatically to 5%. In contrast, juvenile *S. droebachiensis* mortality decreased only slightly to 75% when presented with adults. Both 'species' and 'adult presence' were significant factors ($F_{(1, 12)} = 13.70$, $P = 0.003$ and $F_{(1, 12)} = 29.27$, $P < 0.001$,
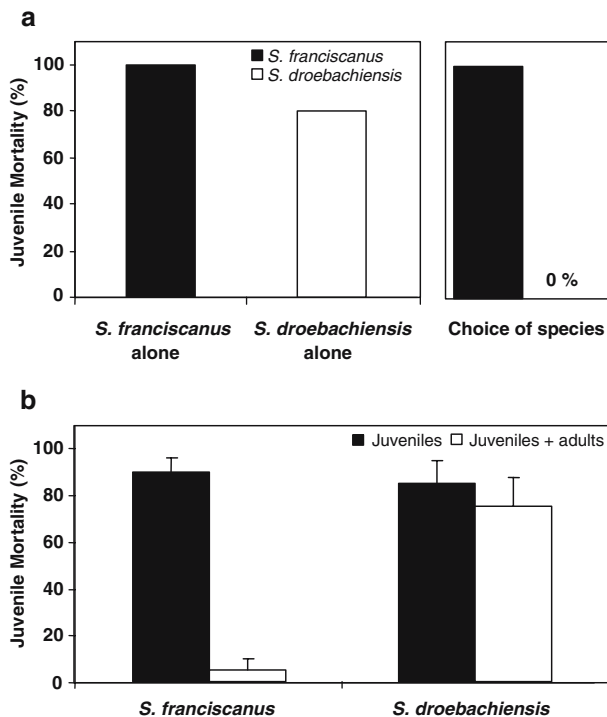
Fig. 1 Results from predation experiments using juvenile urchins. **a** Vulnerability of juvenile urchins to *Pycnopodia helianthoides* when presented either alone (*Strongylocentrotus franciscanus* [*Test Diameter, TD* = 13 ± 4 mm] alone and *S. droebachiensis* [TD = 12 ± 4 mm] alone; *N* = 10 for each) or together as a choice of species for the predator (*N* = 14). **b** Vulnerability of juvenile *S. franciscanus* (TD = 14 ± 1 mm) and *S. droebachiensis* (TD = 15 ± 2 mm) to *P. helianthoides* when presented either alone or with adults. Each run consisted of five juveniles, *N* = 4 runs for each treatment

respectively) influencing juvenile mortality. There was a significant 'species' × 'adult presence' interaction ($F_{(1, 12)}$ = 18.24, *P* = 0.001) given the different outcomes noted above.

Does sheltering provide hydrodynamic protection?

The velocity field around an adult *S. franciscanus* is shown in Fig. 2. Contours of the velocity (cm s^{-1}) and TI (proportion; i.e., u_{RMS}/mean[u]) measured 1.8 cm from the bottom in the immediate vicinity of the adult urchin are presented (note the total cross-stream distance = 20.5 cm). Mean streamwise velocities (i.e., u) were reduced markedly within ~5 cm of the adult urchin to > 20 cm downstream where velocities were generally under 3 cm s^{-1} (Fig. 2a). A small region on the centerline, directly downstream of the adult urchin, was found to have a negative average velocity of −0.40 ± 0.03 cm s^{-1}, indicating an area of recirculation. Turbulence intensities were generally low throughout the test section with the exception of a
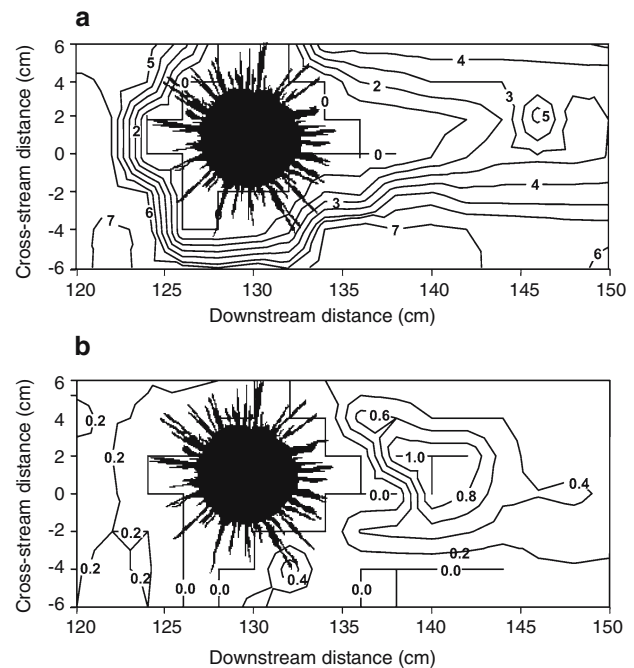

Fig. 2 Contour maps of hydrodynamic fields measured around an adult *Strongylocentrotus franciscanus* (in silhouette) at a height of 1.8 cm above the bottom of a flow chamber. **a** Mean streamwise velocity (i.e., u in the x direction; cm s^{-1}). **b** TI of u (proportion; u_{RMS}/mean[u])

region 5–20 cm downstream of the urchin (Fig. 2b). In this region, alternating regions of high and low turbulence downstream indicate eddies produced by Von Karman vortex streets being shed by the urchin body (*Re* = 5,700 calculated using urchin test diameter). Mean velocities in the cross-stream and vertical directions were much lower than velocities in the streamwise direction (i.e., < 10% of u, data not presented), indicating that the flow was largely two dimensional in the chamber.

Juvenile response to hydrodynamics

The effects of hydrodynamic conditions on juvenile sheltering rates were species-specific. Juveniles of both species typically sheltered at low rates under low flow (13 ± 4% and 4 ± 4% for *S. franciscanus* and *S. droebachiensis*, respectively; *S. franciscanus* data from Nishizaki and Ackerman 2001; Fig. 3a). Under high flow conditions, juvenile *S. franciscanus* sheltered at higher rates (52 ± 7%), whereas the response of juvenile *S. droebachiensis* was similar to low flow (5 ± 2%). Both 'species' and 'flow' were significant factors influencing juvenile sheltering ($F_{(1, 50)}$ = 20.19, *P* < 0.001 and $F_{(1, 50)}$ = 5.41, *P* = 0.024, respectively). There was a marginally significant ($F_{(1, 50)}$ = 84.00, *P* = 0.051)
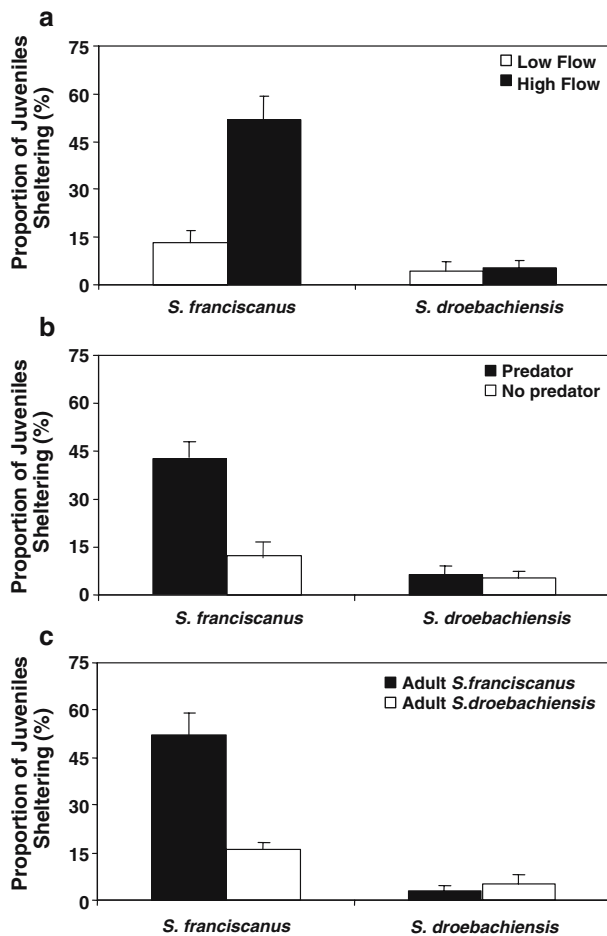
a

b

c

Fig. 3 Proportion of juvenile sheltering in relation to hydrodynamics, predation, and adult species. **a** A comparison of juvenile sheltering under low (1.7 cm s^{-1}) versus high (3.2 cm s^{-1}) water flow. $N = 15$ for all treatments except the low flow treatment for *S. droebachiensis* ($N = 9$). **b** Juvenile sheltering with and without predators ($N = 15$). **c** Juvenile sheltering when exposed to adults of either species ($N = 15$). All data are means ± 1 SE. Juvenile *S. franciscanus* data from Nishizaki and Ackerman (2001)

'species' × 'flow' interaction (Fig. 3) because high water flow led to significant increases in juvenile sheltering in *S. franciscanus*, but not in *S. droebachiensis*.

Juvenile response to predators

Increased predation risk appeared to have different effects on sheltering rates for the two species of urchin (Fig. 3b). In the absence of a predator, juveniles of both species exhibited low rates of sheltering (13 ± 4% for *S. franciscanus* and 5 ± 2% for *S. droebachiensis; S. franciscanus* data from Nishizaki and Ackerman 2001). With the addition of a predator, juvenile *S. franciscanus* sheltered at a much higher rate (44 ± 6%) relative to *S. droebachiensis* (7 ± 3%).

Both 'species' and 'predator presence' were significant factors influencing juvenile sheltering ($F_{(1, 56)} = 34.85$, $P < 0.001$ and $F_{(1, 56)} = 16.26$, $P < 0.001$, respectively). There was a significant 'species' × 'predator presence' interaction ($F_{(1, 56)} = 12.56$, $P < 0.001$, Fig. 3b) because the presence of the predator led to significant increases in juvenile sheltering in *S. franciscanus*, but not in *S. droebachiensis*.

Juvenile responses to interspecific adults

There were clear differences in sheltering behavior between juveniles *S. franciscanus* and *S. droebachiensis* when presented with adults of the opposite species (Fig. 3c). Juvenile *S. droebachiensis* exhibited low levels of sheltering regardless of the adult species present (5 ± 2% with adult *S. droebachiensis* and 3 ± 2% with adult *S. franciscanus*). Conversely, juvenile *S. franciscanus* sheltered at a rate of 52 ± 7% when placed with adult *S. franciscanus* (*S. franciscanus* data from Nishizaki and Ackerman 2001) and at a relatively low rate (16 ± 5%) when placed with adult *S. droebachiensis*. Similar patterns were also observed for sheltering under adult-sized rocks, with 7% and 1% for intra and interspectific comparisons for *S. droebachiensis* versus 9% and 20%, respectively, for *S. franciscanus*. Note that this incorrect choice in *S. franciscanus* juveniles occurred at low levels when adult *S. franciscanus* were present (i.e., 9% vs. 52%). The species of adult urchin presented to juveniles significantly increased juvenile sheltering for *S. franciscanus* ($P = 0.004$, Kruskal–Wallis), but not for *S. droebachiensis* ($P = 0.340$, Kruskal–Wallis).

Juvenile sea urchins in the field

Strongylocentrotus franciscanus and *S. droebachiensis* juveniles were generally found in low density and only through vacuum filtration of the bottom; divers did not locate them at the time of sampling even though they had received laboratory training and searched for them intensively. The average density of juvenile *S. franciscanus* (TD = 23 ± 3 mm) was 0.7 ± 0.4 individuals m^{-2}, which was greater than that of juvenile *S. droebachiensis* (TD = 26 ± 4 mm; 0.3 ± 0.2 individuals m^{-2}). There was an average of 5 ± 1 adult *S. franciscanus* m^{-2} (TD = 102 ± 0.4 mm) observed, but no adult *S. droebachiensis* were found (juveniles found in the field were cultured in the lab to confirm their identity). Interestingly, an average of 0.5 ± 0.5 adult m^{-2} (TD = 40.6 ± 0.7 mm) of the third sympatric *Strongylocentrotus* species, *S. purpuratus*, were observed, but no juveniles were recovered. Adult *S. franciscanus* were found in 25 of 27 quadrats, representing 93% of the total area

examined whereas juvenile *S. franciscanus* occurred in 6 of 27 quadrats.

The algal community was composed primarily of coralline red algae (often 100% coverage) with less brown algae (up to 50% coverage) and no fleshy red or green algae (0% each). The areal coverage of coralline red algae tended to increase with wave-exposure ($57 \pm 14\%$, $67 \pm 14\%$, and $69 \pm 14\%$ for sheltered, moderately sheltered, and exposed sites, respectively), but was more consistent among depths ($67 \pm 13\%$, $61 \pm 16\%$, and $66 \pm 15\%$ for the shallow, mid, and deep depths, respectively). The abundance of brown algae did not vary systematically among sites ($7 \pm 6\%$; $4 \pm 6\%$; and $6 \pm 6\%$ for sheltered, moderately sheltered, and exposed sites, respectively), but showed a marginally significant decrease with depth (($P = 0.058$, Kruskal–Wallis; $17 \pm 8\%$, $1 \pm 1\%$, and 0%, respectively, for shallow, mid, and deep depths).

The distribution of most animal groups (anemones, brittlestars, polychaetes, other gastropods, nematodes, and all urchin species) was patchy, with high numbers of individuals found in a low number of quadrats (Fig. 4). Other Gastropods (range = 2–$223\ \text{m}^{-2}$), hermit crabs (0–$17\ \text{m}^{-2}$), nematodes (0–$29\ \text{m}^{-2}$), and adult *S. franciscanus* (0–$28\ \text{m}^{-2}$) were the most common ani-

mals among the three sites. Mobile organisms, such as seastars ($1.1\ \text{m}^{-2}$), polychaetes ($1.1\ \text{m}^{-2}$), and fish ($0.4\ \text{m}^{-2}$), were found at similar low densities among depths. In contrast, the abundance of other gastropods, adult *S. franciscanus*, mussels, brittlestars, and anemones decreased with depth (66 vs. $29\ \text{m}^{-2}$, 7 vs. $4\ \text{m}^{-2}$, 4 vs. $0\ \text{m}^{-2}$, and 2.4 vs. $1.6\ \text{m}^{-2}$, 2.6 vs. $0\ \text{m}^{-2}$ for 1 and 4.7 m depths, respectively), whereas the abundance of clams, hermit crabs increased with depth (0.3 vs. $3\ \text{m}^{-2}$, and 2.3 vs. $3.8\ \text{m}^{-2}$, respectively).

Twenty-six measured variables were reduced to the four PC presented in Table 2. Measured variables with one or fewer observations were discarded from the analysis, though their inclusion/exclusion did not alter the conclusions reached from either the principal component analysis or subsequent regression analysis. The first principal component (PC1) was interpreted to represent water motion as both 5 and 20 cm above the substratum loaded highly (i.e., variable loading ≥ 0.91). Physical features such as site and substrate were most closely related to the PC2 (i.e., variable loading ≥ 0.81). The PC3 represented benthic grazers, including adult *S. franciscanus* (variable loading ≥ 0.65), whereas PC4 was interpreted to represent predators (i.e., variable loading = 0.68).

Fig. 4 Mean abundance of major animal groups observed at different depths across sites in the field study. Note that the gastropods category includes taxa not listed separately
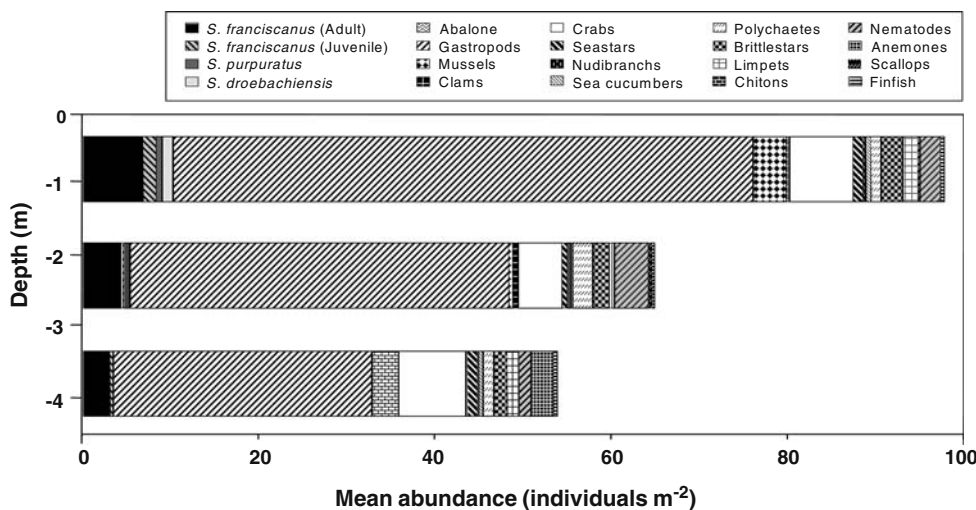

Table 2 Principal components from individual counts ($N = 27$); three missing values of water motion were replaced by the average values at the same depth and site

Component	Eigenvalues	Cumulative Variance (%)	Variables loadings in component (loading)	Interpretation
1	4.61	38.45	Water Motion at 5 cm (0.92) and 20 cm (0.91)	Water motion
2	2.53	59.56	Site (0.93) and Substrate (0.81)	Physical features
3	1.91	75.46	Depth (0.95), Grazers (0.89), Fleshy Algae (0.73), Adults (0.65)	Herbivores
4	1.37	86.85	Predators (0.68)	Predators

Table 3 Simple linear regressions between principal components and the abundance of juvenile *Strongylocentrotus franciscanus*

	Beta	R^2	P-value
PCA 1—Water motion	0.695	0.260	0.161
PCA 2—Physical features	−0.124	0.008	0.816
PCA 3—Herbivores	1.004	0.542	0.024
PCA 4—Predators	0.241	0.031	0.649

The results of the linear regression analysis indicate that benthic grazers PC3 were the only component that had a statistically significant relationship with juvenile abundance ($R^2 = 0.54$, $P = 0.024$) (Table 3). Not surprisingly, the presence of adult sea urchins PC3 accounted for 54.2% of the variation in juvenile abundance, whereas water motion PC1 accounted for 26.0%, predators PC4 3.1%, and physical features PC2 < 1.0%. Similarly, the best-subsets multiple regression model contained only adult urchins PC3 and water motion PC1 as independent variables ($R^2 = 0.80$, $P = 0.008$; Table 4), reflecting the importance of both adults and hydrodynamics in the prediction of juvenile urchin abundance.

Discussion

These results represent the first experimental evidence that juvenile *S. franciscanus* and *S. droebachiensis* differ in their vulnerability to predators and protection afforded by the adult spine canopy, with *S. franciscanus* being the more vulnerable prey that benefits most from the adult spine canopy (Fig. 1). This is in contrast to field observations for adult urchins in which *S. droebachiensis* is the more vulnerable species on account of the size refuge attained by adult *S. franciscanus* (Duggins 1981) and the observation that adult *S. franciscanus* use their large spines to pinch the soft arms of *Pycnopodia helianthoides* (Moitoza and Phillips 1979). The mechanism underlying the difference in juvenile vulnerability is not known, nor was it expected given that differences in spine length between the two species in the early juvenile stage are minimal (Nishizaki, pers. obs.). It is possible that more effective use of pedicel-

laria by juvenile *S. droebachiensis* renders them less vulnerable (also see below). Regardless, juvenile *S. franciscanus* receive a high degree of protection from adult conspecifics, whereas juvenile *S. droebachiensis* are afforded much less (Fig. 1). Interspecific differences in sheltering behavior (Fig. 3), therefore, appear to be directly related to interspecific difference in the degree of protection afforded by adults.

It appears that juvenile-adult associations in *S. franciscanus* represent an important post-settlement strategy to escape predators such as *P. helianthoides*, which may be the most important predator of *S. franciscanus* in many regions of western North America between Oregon and the Gulf of Alaska (Duggins 1983). Conversely, adult *S. droebachiensis* do not provide the same degree of protection and their juveniles are often found in cryptic microhabitats (i.e., in crevices and under rocks) rather than under adult conspecifics (Duggins 1981). It remains unclear as to the role of aggregations in *S. droebachiensis* in terms of a defense from predators (Fig. 1) and in terms of access to food resources as these gatherings may lead to competitive interactions between juveniles and adults (Nishizaki and Ackerman 2004).

From a physical perspective, it has been long recognized that structural complexity in many natural systems can influence hydrodynamic flow (Nowell and Jumars 1984; Ackerman and Okubo 1993). Indeed, the use of hydrodynamic refugia has been reported in both freshwater (Cardinale et al. 2002) and marine systems (Arsenault and Himmelman 1996). For sea urchins, water motion has been demonstrated to impose a metabolic demand that can exceed the capacity of aerobic metabolism in adult *S. franciscanus* (Pace 1975). It is possible that hydrodynamic refugia around adults reduce the energetic requirements needed to maintain similar metabolic processes for juveniles. It is also evident that the spine canopy provides hydrodynamic protection by reducing mainstream velocities by > 60% (Fig. 2). Under higher velocities, juvenile *S. franciscanus* sheltered under the spine canopy, whereas juvenile *S. droebachiensis* tended to reside near the corners of the aquaria and under rocks. As indicated above, this is reminiscent of the tendency of *S. droebachiensis*

Table 4 Best-subsets multiple regression predicting juvenile abundance from the most parsimonious combination of eight principal components

Dependent	Step	Components	Interpretation	Cumulative R^2	P-value
Juvenile	1	3	Adult urchins	0.542	0.024
	2	1 + 3	Adult urchins + water motion	0.801	0.008

Stepwise criteria: probability of F to enter ≤ 0.05; probability of F to remove ≥ 0.10

to cluster in crevices during high wave-surge in the field (Scheibling and Hatcher 2001).

In contrast to other echinoderms (Hendler et al. 1999), there was no evidence of strong interspecific juvenile-adult associations between *S. franciscanus* and *S. droebachiensis*. Juvenile *S. franciscanus* sheltered under adult *S. droebachiensis* infrequently and juvenile *S. droebachiensis* showed little sheltering behavior under adults of either species (Fig. 3). One potentially important difference between the two species is that juvenile *S. droebachiensis* tended to show greater tenacity and were less easily dislodged than juvenile *S. franciscanus* (Nishizaki, pers. obs.). Although Duggins (1981) suggests *S. franciscanus* facilitate the persistence of *S. droebachiensis*, the *S. droebachiensis* juveniles examined here showed no tendency to preferentially utilize the hydrodynamic shelter afforded by adult *S. franciscanus*.

Results from the field indicate that juvenile *S. franciscanus* abundances were positively associated with the presence of adults and water motion (Tables 2, 3, 4). Although juvenile association with adults has been observed in the field (Tegner and Dayton 1977; Breen et al. 1985; Sloan et al. 1987), this is, to the best of our knowledge, the first demonstration of the association between juvenile sea urchins and local water motion. We do acknowledge the limitations associated with using mass dissolution techniques as estimators of fluid motion (Porter et al. 2000; Ackerman and Hoover 2001), as well as the lack of long-term field data. Regardless, there are several plausible explanations for these observations in the field. For example, areas of higher water motion may limit the distribution of predators (i.e., decapods, sea stars; Gagnon et al. 2003) and/or deliver more drift algae, while juveniles are able to take advantage of hydrodynamic refuges under adults. Although algal food was not a significant predictor of juvenile abundance (Tables 3, 4), assessments of algal community composition in this study were limited due to the winter season.

At larger scales, Ebert (1983) proposed a 'latitudinal cline of recruitment' for urchins citing low recruitment in northern British Columbia compared to more frequent recruitment in southern California. A survey of published recruitment data for *S. franciscanus* supports Ebert's (1983) observation and indicates that recruitment rates decline with latitude from 47% in southern California to 1–18% in British Columbia (Fig. 5). Moreover, there is evidence of a similar pattern for juvenile-adult association with relatively high rates in southern California (81%) relative to lower rates in British Columbia (35–41%; Fig. 5). It should be noted that some of the variation in these patterns may be due
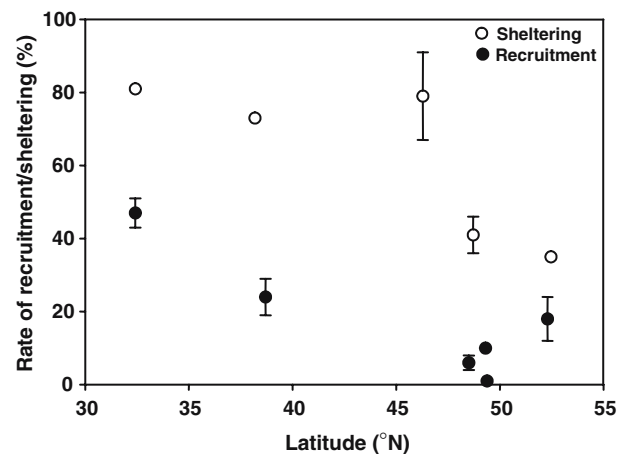

Fig. 5 Latitudinal variation in juvenile recruitment and juvenile-adult associations for *Strongylocentrotus franciscanus*. Data compiled from Low (1975), Tegner and Dayton (1977, 1981), Adkins et al. (1981), Breen and Adkins (1982), Breen et al. (1985), Sloan et al. (1987), Rogers-Bennett et al. (1995), and Morgan (1997)

to the variation in the definition of 'juvenile' [i.e., TD < 20 mm in California (Tegner and Dayton 1977) versus TD < 50 or 60 mm elsewhere (Breen et al. 1985; Sloan et al. 1987; Rogers-Bennett et al. 1995)]. It is also reasonable to suggest that some of these latitudinal differences in sheltering may be due to differences in predation pressure. In the northern regions, sea otters *Enhydra lutris* and *Pycnopodia helianthoides* are the important predators (Duggins 1981), whereas in southern sites, predators also include sheephead fish *Semicossyphus pulcher* and spiny lobster *Panulirus interruptus* (Cowen 1983; Tegner and Levin 1983). In an interesting comparison, Connolly et al. (2001) measured recruitment for sessile invertebrate species (*Balanus* sp., *Chthamalus* sp., and *Mytilus* sp.) directly, thus, minimizing the influence of post-settlement processes. Here, an inverse latitudinal cline for recruitment was found with higher recruitment in Oregon versus California. Whether post-settlement processes play a role in these divergent patterns remains an intriguing question and warrants further investigation.

There is a growing appreciation of the role of post-settlement processes in the recruitment of marine organisms (Gosselin and Qian 1997; Hunt and Scheibling 1997; Menge 2000). The present study supports the concept that post-settlement behavior in *S. franciscanus* contributes to their survival and hence explains the juvenile–adult associations observed in the field. It appears that juvenile *S. franciscanus* react to potential dangers such as predation and hydrodynamic disturbance by sheltering under adults. This confirms the suggestion that the adult spine canopy offers juvenile *S. franciscanus* a refuge from predators (Breen

et al. 1985), and also indicates that water motion is an importance physical factor for juvenile sea urchins. It is evident that behavioral outcomes, such as juvenile-adult associations in red sea urchins, which result in lowered post-settlement mortality and/or migration of the early life history of benthic marine invertebrates, are not consistent with predictions made for sessile species. Current models of recruitment should be revised accordingly.

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