

Juvenile-adult associations in sea urchins *Strongylocentrotus franciscanus* and *S. droebachiensis*: Is nutrition involved?

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ABSTRACT: Juvenile-adult associations (i.e. juvenile sheltering) in sea urchins of the genus *Strongylocentrotus* provide an example of an important post-settlement behaviour in benthic invertebrates. It has been suggested that these associations provide a nutritional advantage to juveniles by facilitating access to kelp. We examined this hypothesis in a series of growth experiments involving 2 sea urchin species, *Strongylocentrotus franciscanus* and *S. droebachiensis*, which show high and low levels of juvenile sheltering, respectively. Juvenile sea urchins (7.73 ± 0.09 mm [mean \pm SE] test diameter) of both species had lower growth rates in the presence versus absence of adults, regardless of food type, though the effect was more pronounced in *S. franciscanus* (0.2 ± 0.1 vs 1.2 ± 0.3 mm mo⁻¹) than in *S. droebachiensis* (0.8 ± 0.5 vs 1.2 ± 0.7 mm mo⁻¹). This relationship was not evident in the absence of food, which leads us to conclude that the reduction in growth is due to intercohort competition. Hence, other post-settlement factors (e.g. predation and hydrodynamic disturbance) are likely responsible for maintaining the juvenile-adult associations observed in *S. franciscanus*. Species-specific strategies in juvenile sheltering indicate that behavioural processes are important for the recruitment of benthic invertebrates with mobile juvenile stages.

KEY WORDS: *Strongylocentrotus* · Intercohort competition · Post-settlement · Sea urchin · Juvenile strategies

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INTRODUCTION

Recruitment plays an important role in the population dynamics of benthic marine invertebrates (Gaines & Roughgarden 1985, Sutherland 1990), and is influenced by 3 factors (Cameron & Schroeter 1980): (1) larval supply, which refers to the density of competent larvae ready to settle in a given area (Gaines & Bertness 1992); (2) larval settlement, which affects the transition from the larvae in the water column to metamorphosis on the substrate (Gaines & Roughgarden 1985); and (3) post-settlement survival, which includes factors that influence the growth and survival of benthic juveniles after metamorphosis (Connell 1985, Hunt & Scheibling 1997). Although there are examples of settlement and post-settlement processes from sessile

species (Gaines & Roughgarden 1985, Gaines & Bertness 1992, Toonen & Pawlick 1994), only recently has attention turned to organisms with mobile juvenile stages (Moksnes et al. 2003, Hiddink 2003). The early life-history of mobile invertebrates may be more complex than for sessile invertebrates due to behavioural responses, which affect growth and survival.

Many mobile benthic marine organisms aggregate and potentially benefit from the presence of conspecifics (Shepherd 1986, Childress & Herrnkind 2001). It is clear that aggregation behaviour may confer several advantages, including collective detection of predators, increased vigilance, group defense, and a dilution effect (see Mauck & Harkless 2001 for review). The cost of close associations is often an increase in competition for resources (Werner & Anholt 1993). Consequently, onto-

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genetic changes in aggregation behaviour may exist, and include: (1) the aggregation of vulnerable juvenile stages with older and larger conspecifics for protection; (2) the dispersion of individuals as they attain some size refuge from mortality (due to predation); and (3) the aggregation of adults for reproductive purposes (Butler et al. 1999). Sea urchins are interesting in this regard, as aggregation in many species is independent of size (Andrew & Choat 1985, Himmelman 1986), whereas aggregation in other species (i.e. red sea urchin *Strongylocentrotus franciscanus*) is a function of size, as small juveniles aggregate under much larger adult conspecifics (Low 1975, Tegner & Dayton 1977, Breen et al. 1985, Sloan et al. 1987). These associations may lead to intercohort competition, although examples of this type of interaction are rare (Fletcher 1988, Szabo 2002). It would be appropriate, therefore, to determine: (1) whether competitive interactions exist between recently recruited juveniles and adults under which they aggregate; and (2) whether, and how, abiotic factors such as water motion affect these interactions, especially with respect to food resources.

Sea urchins in the genus *Strongylocentrotus* provide a model system for examining the role of post-settlement processes as there are species-level differences in the degree of juvenile sheltering. For example, *S. franciscanus* juveniles have been reported to shelter at high frequencies under adults (Low 1975, Tegner & Dayton 1977, Breen et al. 1985, Sloan et al. 1987) whereas *S. droebachiensis* show size-independent aggregation (Hagen & Mann 1994), which is typical of many classes of echinoderm (Warner 1979). Aggregation behaviour may provide a nutritional advantage to juveniles (Tegner & Dayton 1977), although intercohort competition has also been suggested in some *S. franciscanus* populations (Low 1975, Tegner & Dayton 1977). Regardless of this, adult sea urchins appear to aggregate on algae (Vadas et al. 1986), making these aggregations a possible source of suspended and dissolved nutrients for juveniles, as adult feeding liberates much organic matter. Moreover, these aggregations may reduce fluctuations in water velocity, allowing juveniles to utilize particulate matter and waterborne nutrients released from adult feeding activities. A comparison of the nutritional relationship in juvenile *S. franciscanus* and *S. droebachiensis* should provide information on how different sheltering strategies affect post-settlement growth and survival of mobile benthic invertebrates. The primary purpose of this study is to examine the potential nutritional advantages afforded by different levels of juvenile sheltering in *S. franciscanus* and *S. droebachiensis*. Furthermore, we also investigated the effects of water flow and kelp form on these processes in a series of controlled growth experiments in the laboratory.

MATERIALS AND METHODS

What form of kelp is utilized by juvenile sea urchins? Although the primary focus of the study was to examine the nutritional advantage of juvenile sheltering, we first needed to ascertain the forms of kelp utilized by small juvenile sea urchins. An experiment was, therefore, undertaken to determine what forms of kelp *Macrocystis integrifolia* are utilized by juvenile urchins; whole pieces, particulate, or dissolved organic material produced from the feeding activities of adults. Juvenile *Strongylocentrotus franciscanus* were obtained 41 to 186 d post-metamorphosis from an experimental hatchery (Island Scallops, Qualicum Beach, British Columbia, Canada) and used in the growth experiment over 2 mo (26 September to 19 November 1999). Juvenile *S. droebachiensis* were obtained 61 to 128 d post-metamorphosis from the same hatchery, and were used in an experiment lasting 1 mo (8 November to 13 December 2000). Juvenile *S. franciscanus* were grown on 1 of 4 diets: (1) whole blades of the kelp *M. integrifolia* (~40 g wet weight); (2) *M. integrifolia* (~40 g plus 250 ml of seawater) ground in a blender; (3) kelp exudates from around adult urchins (250 ml seawater collected from under the feeding adult, which included ~40 g of material, presumably faeces, produced by adult red urchins fed *M. integrifolia*); and (4) not fed (1 mm filtered seawater, no food). All kelp and kelp exudates were replaced twice a week. Much of the ground kelp and kelp exudate circulated within the growth chamber as water was supplied to the bottom of the container via plastic tubing (1.5 cm diameter) at ~2.4 l min⁻¹ and exited through a small opening at the top of the container, which was covered with Nitex[®] mesh (500 µm). Containers were kept on a light:dark cycle that ranged from 8:16 h to 12:12 h, which mimicked natural light conditions. Each treatment was run in a 500 ml container (16 cm height × 8 cm diameter) with 15 juveniles each, and was replicated 3 times (thus 45 juveniles per treatment and a total of 180 juveniles used for the experiment). Juvenile *S. droebachiensis* were grown under similar treatments, except that the kelp exudates were not used (a total of 135 juveniles for the experiment).

Initially, juvenile *Strongylocentrotus franciscanus* test diameters (TD) averaged 1.42 ± 0.02 mm (mean ± SE) and juvenile *S. droebachiensis* were 2.57 ± 0.07 mm. There were no differences in initial TD among treatments for the different species ($F_{3,176} = 0.03$, $p > 0.99$, $F_{2,132} = 0.14$, $p = 0.87$, respectively). Survivorship and test diameters were recorded throughout the experiment on a weekly basis and a 1-way ANOVA was used to compare the final change in test diameter among treatments using each container as a replicate.

Does sheltering increase access to kelp for juvenile sea urchins? A separate experiment was undertaken to determine whether the growth and survival of juvenile urchins was influenced by juvenile sheltering. It was anticipated that juveniles with adults would have higher growth rates and survivorship than unsheltered juveniles, and it was also expected that water motion, algal form, and urchin species would influence the juvenile-adult association. Specifically, we predicted that juvenile growth rates would be higher: (1) with adults, as sheltered juveniles would have greater access to kelp; (2) for sheltered *Strongylocentrotus franciscanus* compared to *S. droebachiensis* as the longer spines of adult *S. franciscanus* could enable more efficient capture and retention of kelp; (3) for sheltered juveniles under high water motion as adults would reduce fluctuations in water motion; and (4) for sheltered juveniles when whole kelp rather than ground kelp is provided due to the retention of whole kelp blades under adults.

Juvenile urchins were cultured in controlled laboratory conditions to determine whether juveniles show nutritional gains when associated with adults. The experiment consisted of 24 plastic tanks (77 cm height \times 46 cm diameter) with plastic false bottoms 25 cm below the top of the tank upon which both adult and juvenile urchins were placed (there was no access below the false bottom). Tanks were housed in a caged area with an aluminum ceiling and were exposed to ambient fall/winter light levels. Tanks typically received little direct light, and flashlights were often employed to locate juveniles in daylight hours. Water temperatures varied from 8.8 to 13.2°C (9.61 ± 0.03), pH from 7.7 to 8.1 (7.85 ± 0.00), and salinity from 26.02 to 30.70 ppt (27.91 ± 0.04) throughout the 4 mo-long experiment (Table 1). Water was supplied to the bottom of each tank via plastic tubing (1.5 cm diameter) at either low ($1.87 \pm 0.01 \text{ l min}^{-1}$) or high ($7.17 \pm 0.06 \text{ l min}^{-1}$) flow. In the former case, the flow in the container was laminar with little visible mixing, whereas under high flow there was noticeable water motion and mixing, especially evident when the ground kelp was added (see below). Water velocities measured near the outlet of each tube using an Acoustic Doppler Velicometer (Sontek) were $<1 \text{ cm s}^{-1}$ for low flow and $5.03 \pm 0.14 \text{ cm s}^{-1}$ for high flow. Macroalgae *Macrocystis integrifolia* was collected in the field and maintained in a flowing seawater table. Kelp was presented to juvenile urchins either as 50 g intact pieces, which included the blade, stipe and bulb, or as a 'ground' ration of the same mass (ground in a blender). Kelp was added 3 times per week, and tanks were cleaned of faeces and any microalgal film before each feeding.

Six treatments were undertaken with *Strongylocentrotus franciscanus* and 2 with *S. droebachiensis* juve-

Table 1. *Strongylocentrotus franciscanus* and *S. droebachiensis*. Experimental design for the growth experiment. (a) Summary of treatments and comparisons. (b) Measures of water quality (mean \pm SE). Period A corresponds to the first 8 wk of the experiment, Period B to the remaining 11 wk

| (a) Treatments | | | | |
|-------------------|------------------|----------------|---------------------|----------------|
| Urchin species | Adults | Water flow | Kelp form | |
| Red | Present | Low | Whole | |
| Red | Absent | Low | Whole | |
| Red | Present | High | Whole | |
| Red | Absent | High | Whole | |
| Red | Present | High | Ground ^a | |
| Red | Absent | High | Ground ^a | |
| Green | Present | High | Whole | |
| Green | Absent | High | Whole | |
| (b) Water quality | | | | |
| Period | Temperature (°C) | Salinity (ppt) | pH | Oxygen (% sat) |
| A | 10.3 ± 0.1 | 27.0 ± 0.1 | 7.8 ± 0.0 | 73.1 ± 0.5 |
| B | 9.2 ± 0.0 | 28.4 ± 0.0 | 7.9 ± 0.0 | 91.2 ± 0.3 |

^aTreatment where urchins were not fed in Period B

niles (Table 1). In each case, 5 juveniles ($7.73 \pm 0.09 \text{ mm}$, $0.21 \pm 0.01 \text{ g}$ wet weight) were placed in each tank on 27 October 2000. Differences in the initial size of juvenile urchins (*S. franciscanus* and *S. droebachiensis*) were not detected ($F_{23,95} = 0.22$, $p > 0.99$) among treatments. The 8 treatments were paired, in that each involved the comparison of juveniles grown in the presence or absence of adults; 2 adult *S. franciscanus* ($146 \pm 3 \text{ mm}$) or 4 adult *S. droebachiensis* ($TD = 50 \pm 1 \text{ mm}$) corresponding to 1.6 ind. m^{-2} , which is the density observed in the field (Sloan et al. 1987). The *S. franciscanus* treatments involved a comparison of growth on whole kelp at low and high flow, and ground kelp at high flow, which was considered as a control for the whole kelp treatment, in that kelp remained scattered along the bottom of the tank and would be available to all juveniles regardless of the presence of adults. The *S. droebachiensis* treatment was undertaken at high flow using whole kelp. The 8 treatments were replicated 3 times (a total of 24 tanks, see Table 1) and juveniles were measured each week for 8 wk during the first phase of the experiment (Period A). In order to determine whether the ground kelp treatments conferred a nutritional benefit to juveniles, 2 treatments were modified after Week 8, and these urchins were not fed for the final 11 wk of the experiment (Period B). The remaining 6 treatments were not altered in Period B.

Treatment effects (juvenile sheltering, water motion, algal form, and urchin species) on juvenile survival were examined using separate nonparametric Mann-Whitney *U*-tests. Likewise, 3 separate 2-way ANOVAs were used to examine the effect of: (1) adult urchins (presence vs absence of adults) and kelp form (whole

pieces vs ground); (2) adult urchins (presence vs absence of adults) and water flow (high vs low); and (3) and urchin species (*Strongylocentrotus franciscanus* vs *S. droebachiensis*) on juvenile growth measured both as changes in test diameter and as body mass (per month). Data were tested for heteroscedasticity using a homogeneity-of-variance test (Levene's test). Adult test diameters were also measured 3 times during the experiment (beginning, near the end of Period A, and near the end of Period B) and analyzed using 2-way ANOVA.

Sheltering behaviour in the growth experiment. Behavioural experiments were undertaken to further examine whether nutrition influences juvenile-adult interactions. Comparisons were made of the frequency that juveniles sheltered under and/or were in contact with (1) adults or (2) kelp on a weekly basis under low versus high water motion, whole kelp versus no kelp, and *Strongylocentrotus franciscanus* versus *S. droebachiensis*. Each week, we recorded the position of each juvenile as: (1) sheltering under the spines/test of an adult or in direct contact with an adult though not entirely under the spines; (2) in the open; or (3) in direct contact with kelp. Sheltering data were arcsin square-root transformed and comparisons among treatments were made using a 1-way ANOVA (for each time period) with least significant difference (LSD) pairwise multiple comparison tests. Kelp data could not be transformed to satisfy the general assumptions for Student's *t*-tests (i.e. normality and homoscedasticity), thus Mann-Whitney *U*-tests were employed.

Crawling speeds in the growth experiment. A comparison of juvenile crawling speed was made to examine whether juvenile behaviour affected growth rates among the different treatments. Juveniles were placed in the middle of the chambers and their movement was tracked over 3 h. Comparisons of crawling speeds under different juvenile sheltering (sheltered vs unsheltered) and kelp form (whole kelp vs no kelp) treatments were made using Kruskal-Wallis tests.

RESULTS

What form of kelp is utilized by juvenile sea urchins?

On Day 0 of the experiment, 100% of the small *Strongylocentrotus franciscanus* juveniles and 100% of the *S. droebachiensis* juveniles had visible jaws. Survivorship of juvenile *S. franciscanus* (pooled within containers) was relatively high for whole and ground kelp treatments and was lower for exudates and unfed treatments (see Fig. 1). Survivorship for *S. droebachiensis* showed similar patterns, although the rates were higher than for *S. franciscanus* (Fig. 1A), possibly

due to their larger initial size. Although there was a 3-fold difference in survival among treatments, significant differences were not detected among treatments for *S. franciscanus* ($F_{3,8} = 2.14$, $p = 0.17$) or *S. droebachiensis* ($F_{2,6} = 0.74$, $p = 0.52$).

The highest growth rates were observed for juveniles provided whole pieces of kelp, which for *Strongylocentrotus franciscanus* were 0.28 mm mo^{-1} in 1999 and 0.37 mm mo^{-1} in 2000, and 0.35 mm mo^{-1} for *S. droebachiensis* in 2000. *S. franciscanus* in the ground kelp treatment exhibited almost no growth (0.00 mm mo^{-1}), whereas growth in *S. droebachiensis* was much higher (0.17 mm mo^{-1}), again possibly due to the greater initial size. In contrast, *S. franciscanus* provided with the kelp exudates showed moderate growth (0.11 mm mo^{-1}). Growth for unfed juvenile *S. franciscanus* (control) was not statistically different from 0 (-0.04 mm mo^{-1}), and was appreciably less than for unfed *S. droebachiensis* (0.12 mm mo^{-1}). Differences in growth rate were noted among treatments for *S. franciscanus* ($F_{3,8} = 6.97$, $p = 0.01$; Fig. 1B) in that the whole kelp treatment differed from the unfed treatment (LSD test, $p < 0.05$). The results for *S. droebachiensis* were also significant ($F_{2,6} = 8.19$, $p = 0.02$) in that growth in the whole kelp treatment was higher than either the ground kelp or unfed treatments (LSD tests, $p < 0.05$).

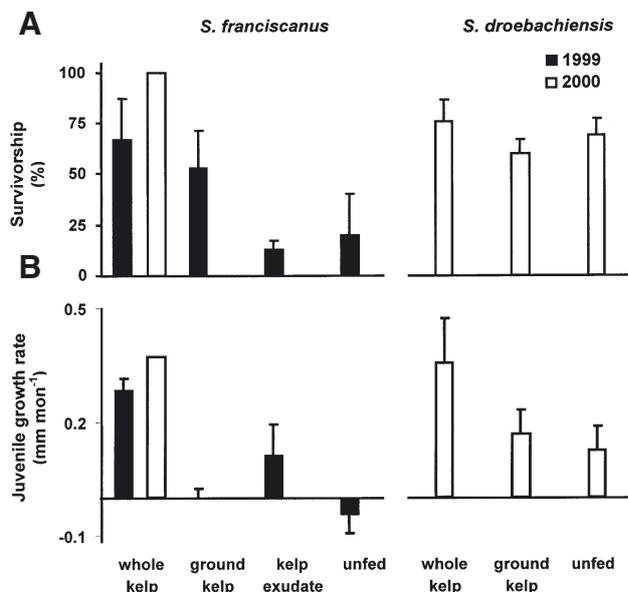


Fig. 1. *Strongylocentrotus franciscanus* and *S. droebachiensis*. Survivorship and growth rates of *S. franciscanus* ($1.42 \pm 0.02 \text{ mm}$) and *S. droebachiensis* ($2.57 \pm 0.07 \text{ mm}$) provided with different forms of kelp *Macrocystis integrifolia*. Data are means ± 1 SE for 3 replicate containers, except the *S. franciscanus* 2000 treatment, which consisted of 1 replicate (each container started with 15 juveniles). (A) Survival rates (%) of juvenile urchins in the growth experiment. (B) Growth rate (change in test diameter) of juvenile sea urchins. The 1999 data are from Nishizaki & Ackerman (2001)

Does sheltering increase access to kelp for juvenile sea urchins?

Juvenile survival was generally high ($\geq 73\%$) in all treatments except in the low flow, sheltered (i.e. with adults) treatment where survival rates were $\sim 60\%$ (first black bar in Fig. 2). Conversely, the low flow, unsheltered (i.e. without adults) treatment experienced no mortality in Period A and averaged $93 \pm 7\%$ survival by the end of Period B. In the high flow, whole kelp treatments with *Strongylocentrotus franciscanus*, juveniles grown with and without adults showed high rates of survival throughout the experiment (93 ± 7 and $87 \pm 7\%$ by the end of Period B), whereas the unfed treatments and *S. droebachiensis* treatments all showed lower survival rates (73 ± 7 to $93 \pm 7\%$) by the

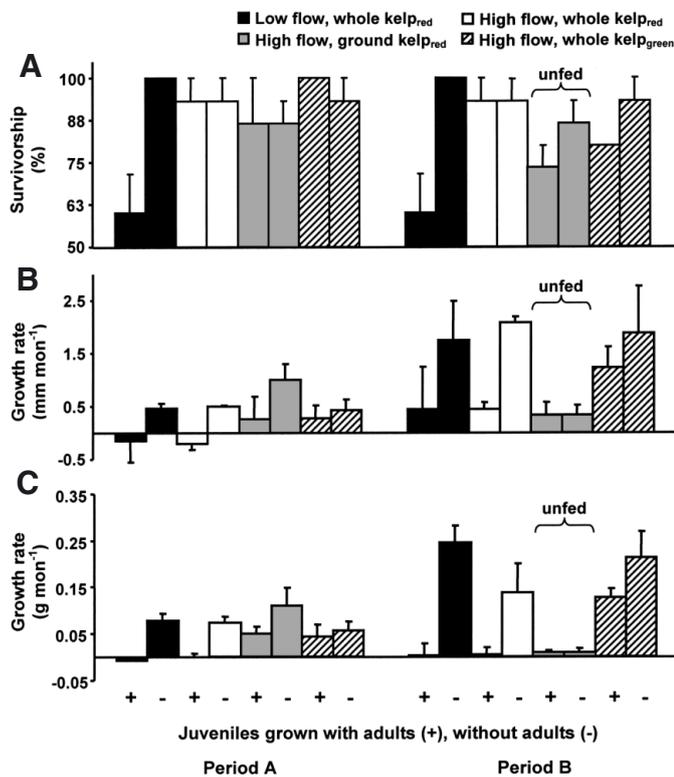


Fig. 2. *Strongylocentrotus franciscanus* and *S. droebachiensis*. Survivorship and growth rates for juvenile (7.73 ± 0.09 mm) grown with (+) and without (-) adults. (A) Survivorship (%), (B) growth rate (change in test diameter) and (C) growth rate (change in mass). Treatments include: (1) low flow, whole kelp treatments using *S. franciscanus* (black bars), (2) high flow, whole kelp treatments using *S. franciscanus* (open bars), (3) high flow, ground/unfed treatments using *S. franciscanus* (grey bars), and (4) high flow, whole kelp treatments using *S. droebachiensis* (hatched bars). Note that the ground kelp treatment was discontinued in Period B, when urchins were left unfed. Data are means ± 1 SE for 3 replicate containers (each container began experiment with 5 juveniles each). Period A = October to December 2000, Period B = January to March 2001

end of Period B (Fig. 2). There was significantly lower survival for juvenile *S. franciscanus* grown with adults in the low flow treatments than those without adults (Mann-Whitney, $Z = -2.12$, $p = 0.03$), but not in the remaining comparisons involving high flow ($Z < 0.01$, $p > 0.99$), ground kelp ($Z < 0.01$, $p > 0.99$), no kelp ($Z < 0.01$, $p > 0.99$), or *S. droebachiensis* ($Z < 0.01$, $p > 0.99$). Significant differences were not found between juveniles fed whole versus ground kelp ($Z = 0.47$, $p = 0.73$), but unfed juveniles tended to have lower survival than those fed whole kelp ($Z = 1.78$, $p = 0.08$).

Growth was higher in Period B (January to March) than in Period A (October to December) except in the unfed treatments in Period B (Fig. 2). In the presence of adults, *Strongylocentrotus franciscanus* growth averaged between -0.2 ± 0.1 and 0.3 ± 0.4 mm mo⁻¹ for Period A and between 0.3 ± 0.3 and 0.5 ± 0.1 mm mo⁻¹ for Period B. Conversely, in the absence of adults, juveniles grew much faster, ranging from 0.5 ± 0.1 to 1.0 ± 0.3 mm mo⁻¹ for Period A and from 0.3 ± 0.2 to 2.1 ± 0.4 mm mo⁻¹ for Period B. Growth for juvenile *S. droebachiensis* in the presence of adults ranged from 0.3 ± 0.3 mm mo⁻¹ in Period A to 1.2 ± 0.4 mm mo⁻¹ in Period B, whereas growth for juveniles grown without adults ranged from 0.4 ± 0.2 mm mo⁻¹ in Period A to 1.9 ± 0.9 mm mo⁻¹ in Period B. In terms of mass, the growth rates of juvenile *S. franciscanus* with adults ranged from -0.01 ± 0.002 to 0.05 ± 0.02 g mo⁻¹ in Period A and 0.00 ± 0.02 to 0.01 ± 0.01 g mo⁻¹ in Period B. In contrast, juveniles grown without adults grew an average of 0.07 ± 0.01 to 0.11 ± 0.04 g mo⁻¹ in Period A and 0.01 ± 0.01 to 0.2 ± 0.04 g mo⁻¹ in Period B (see Fig. 2). Juvenile *S. droebachiensis* grown with adults grew at a rate of 0.04 ± 0.03 g mo⁻¹ in Period A and 0.1 ± 0.02 g mo⁻¹ in Period B, whereas juveniles grown without adults showed growth rates of 0.1 ± 0.02 g mo⁻¹ for Period A and 0.2 ± 0.1 g mo⁻¹ in Period B.

A statistical analysis revealed that presence of adults led to lower juvenile growth rates (i.e. test diameter and body mass) in all *Strongylocentrotus franciscanus* treatments, but not in the *S. droebachiensis* treatments (see Table 2 for results of ANOVA). Conversely, water flow (high versus low) and species (*S. franciscanus* versus *S. droebachiensis*) were not significant factors in determining juvenile growth, although in Period B, *S. droebachiensis* tended to gain mass faster than *S. franciscanus* ($p = 0.06$, Table 2). Regardless of whether adults were present or not, juveniles fed ground kelp grew significantly faster than juveniles fed whole kelp (Table 2, Period A). In contrast, there was a significant interaction between juvenile sheltering and kelp form when ground kelp treatments were left unfed in Period B.

There was 100% survival of adult sea urchins in all treatments. Growth rates for adult urchins were variable, but generally higher in Period A when test diameters in-

Table 2. *Strongylocentrotus franciscanus* and *S. droebachiensis*. Summary of 2-way ANOVA results for juvenile growth-rate comparisons. Effects of adult presence and either (1) algal form, (2) water flow or (3) urchin species on test diameter and body mass growth. Asterisk indicates significant results ($p < 0.05$). Period A corresponds to the first 8 wk of the experiment, Period B to the remaining 11 wk

| Period Source | Test diameter | | | Body mass | |
|-----------------|---------------|-------|--------|-----------|--------|
| | df | F | p | F | p |
| A | | | | | |
| Adult | 1 | 11.19 | 0.01* | 8.68 | 0.02* |
| Kelp | 1 | 5.42 | 0.05* | 3.64 | 0.09 |
| Adult × Kelp | 1 | 0.14 | 0.72 | 0.07 | 0.70 |
| Adult | 1 | 16.77 | 0.04* | 54.2 | <0.01* |
| Flow | 1 | 0.01 | 0.25 | 0.01 | 0.95 |
| Adult × Flow | 1 | 0.11 | 0.18 | 0.35 | 0.57 |
| Adult | 1 | 5.69 | 0.01* | 4.97 | 0.06 |
| Species | 1 | 1.55 | 0.95 | 0.42 | 0.54 |
| Adult × Species | 1 | 2.17 | 0.75 | 2.46 | 0.16 |
| B | | | | | |
| Adult | 1 | 13.08 | 0.01* | 3.97 | 0.08 |
| Kelp | 1 | 17.81 | <0.01* | 3.56 | 0.10 |
| Adult × Kelp | 1 | 17.78 | 0.01* | 4.14 | 0.08 |
| Adult | 1 | 60.05 | <0.01* | 23.2 | 0.01* |
| Flow | 1 | 0.79 | 0.40 | 1.85 | 0.21 |
| Adult × Flow | 1 | 0.79 | 0.40 | 1.96 | 0.20 |
| Adult | 1 | 5.69 | 0.01* | 6.22 | 0.04* |
| Species | 1 | 1.55 | 0.11 | 5.09 | 0.06 |
| Adult × Species | 1 | 2.17 | 0.24 | 0.30 | 0.60 |

creased in all treatments (see Fig. 3). However, by 5 February 2001 negative growth rates were observed for all treatments. Unfortunately, data were not available for the remaining portion of Period B, which would have included spring conditions more favourable for growth. For adult *Strongylocentrotus droebachiensis*, an increase in test diameter was observed between 3 November 2000 and 4 December 2000 (see Fig. 3). There were no differences in growth rates for adults among treatments in Period A ($F_{2,6} = 0.63$, $p = 0.56$) or Period B ($F_{2,6} = 1.04$,

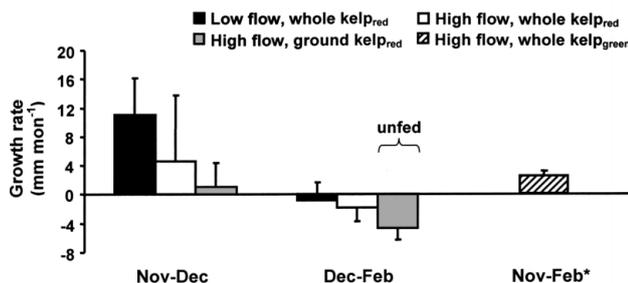


Fig. 3. *Strongylocentrotus franciscanus* and *S. droebachiensis*. Growth rates of adult *S. franciscanus* (146 ± 3 mm) and *S. droebachiensis* (50 ± 1 mm). Treatments as in Fig. 2. Note that the high flow, ground kelp treatment was discontinued in January, when urchins were left unfed. Data are means ± 1 SE for 3 replicate containers (2 adult red urchins per container, 4 adult green urchins per container)

$p = 0.41$) nor were there any differences between Period A and B in the low flow ($t_4 = 1.26$, $p = 0.27$), high flow ($t_4 = 1.13$, $p = 0.32$), and ground kelp/unfed ($t_4 = 1.57$, $p = 0.19$) treatments.

Sheltering behaviour in the growth experiment

There was a high degree of sheltering in *Strongylocentrotus franciscanus* (e.g. ~55 to 83%) compared to *S. droebachiensis* (e.g. ~25 to 30%, Fig. 4). Sheltering tended to be greater in the whole kelp treatments (e.g. low flow = $77 \pm 6\%$, high flows = 66 ± 10 to $72 \pm 3\%$), and whereas the sheltering increased in the whole kelp treatments in Period B ($83 \pm 4\%$ and $77 \pm 5\%$), it was considerably lower in the unfed treatment during Period B ($55 \pm 1\%$). Differences were found in the frequency of juvenile sheltering among treatments in Period A ($F_{3,8} = 5.77$, $p = 0.02$), with the juvenile *S. droebachiensis* sheltering less than the juveniles in any of the *S. franciscanus* treatments ($p < 0.01$ compared to low and high flow, $p = 0.02$ for ground kelp, LSD test). There was also a difference in sheltering for Period B ($F_{3,8} = 26.78$, $p < 0.01$), with juvenile *S. droe-*

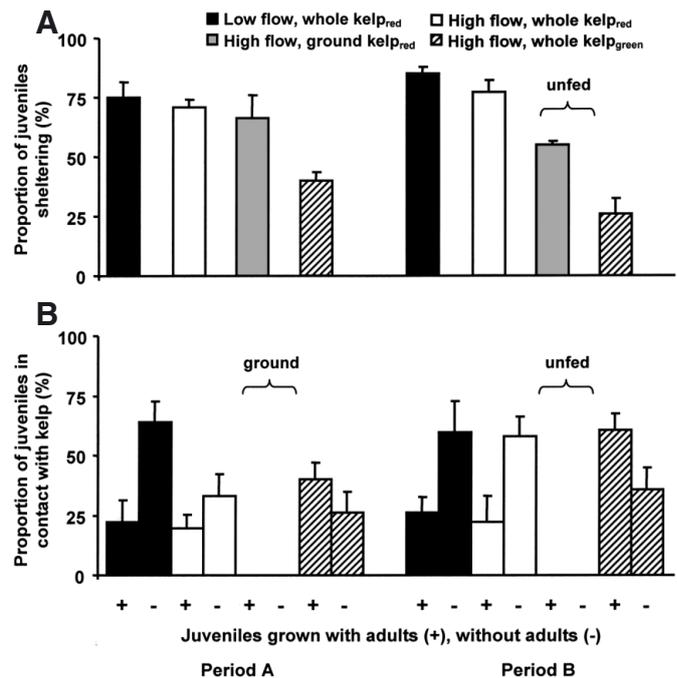


Fig. 4. *Strongylocentrotus franciscanus* and *S. droebachiensis*. Proportion of juveniles found (A) sheltering under adult urchins and (B) in contact with kelp. Treatments as in Fig. 2. Data are means ± 1 SE for 3 replicate containers (each container started with 5 juveniles). Period A = October to December 2000, Period B = January to March 2001. It was not possible to determine the proportion of juveniles in contact with kelp in the ground kelp and unfed treatments

bachiensis sheltering less than juveniles in any of the *S. franciscanus* treatments ($p < 0.01$ compared to low flow, high flow and unfed treatments). In addition, the unfed juveniles also sheltered less than the fed juveniles ($p = 0.02$ at high flow, $p < 0.01$ at low flow).

The presence of adults tended to reduce the proportion of juveniles in contact with kelp in *Strongylocentrotus franciscanus* (19 to 26%) but not in *S. droebachiensis* (40 to 61%, Fig. 4), where the inverse was found. In contrast, in the absence of adults, a larger proportion of juvenile *S. franciscanus* were in contact with kelp (33 to 64%). Statistical analysis revealed that juvenile *S. franciscanus* grown without adults were in contact with kelp more frequently than juveniles grown with adults at both high flow (Mann-Whitney, $Z = -4.68$, $p < 0.01$,) and low flow (Mann-Whitney, $Z = -2.47$, $p = 0.02$). Juvenile *S. droebachiensis*, however, were found with kelp more frequently when grown with adults (Mann-Whitney, $Z = 2.69$, $p = 0.01$, Fig. 4).

Crawling speeds in the growth experiment

Crawling speeds were determined for the 59 juveniles that could be observed for the duration of the experiment (note that 28 sheltering juveniles were obscured from view under adults), 41 of which showed no appreciable movement during the course of the experiment. The average crawling speeds for sheltered juveniles were lower than the speeds for unsheltered juveniles (1.8 vs 2.9 cm h^{-1} ; data averaged across treatments in Fig. 5), but these differences were not significant ($p = 0.83$, Kruskal-Wallis). Crawling speeds were low in the presence of whole kelp regardless of the presence of adults (with adults = 0.4 cm h^{-1} and without adults = 0.4 cm h^{-1}). Conversely, unfed juveniles had higher crawling speeds (i.e. with adults = 3 cm h^{-1} and without adults = 5 cm h^{-1}), and these differences were significant ($p < 0.01$, Kruskal-Wallis).

Given the small sample size of juveniles observed in the presence of adults, (i.e. 15 individuals in total), a model was applied to examine the robustness of our conclusions regarding juvenile crawling speed (Fig. 6). In the model, we examined the effect of the potential movement of juveniles that were obscured from view on the statistical results described above. The assumed crawling speeds of obscured, unsheltered juveniles were combined with speeds for the observed, sheltered juveniles to render the modelled crawling speeds. In this model, crawling speeds for treatments without adults remained stable throughout the analysis (e.g. $\sim 3 \text{ cm s}^{-1}$) as no juveniles were obscured from view. In the situation when the obscured sheltered juveniles were assumed to not move (i.e. 0 cm h^{-1}), the modelled average crawling speed was significantly

lower (due to the increased sample size) than unsheltered juveniles. However, the modelled average crawling speed of obscured, sheltered juveniles was similar to those of unsheltered juveniles at assumed crawling speeds $< 8 \text{ cm h}^{-1}$. In a similar analysis for treatments with and without kelp (not presented), significant differences in the modelled average crawling speeds were only found when obscured, sheltered juveniles were assumed to move $< 10 \text{ cm h}^{-1}$. Given that speeds $> 8 \text{ cm h}^{-1}$ were not observed during the course of the experiment, we conclude that the results in Fig. 5 are reasonable estimates of juvenile crawling speed.

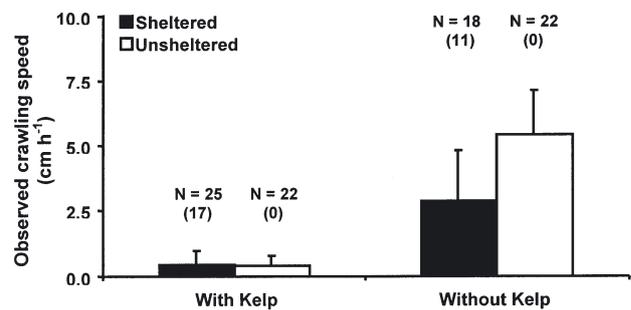


Fig. 5. *Strongylocentrotus franciscanus*. Juvenile crawling speeds in growth experiment. Black bars: treatments with juveniles and adults; open bars: treatments with juveniles alone. N: number of juveniles observed at the beginning; numbers in parentheses: juveniles that moved under adults during the observation period and thus obscured from view (not included in final analysis). Data are means ± 1 SE

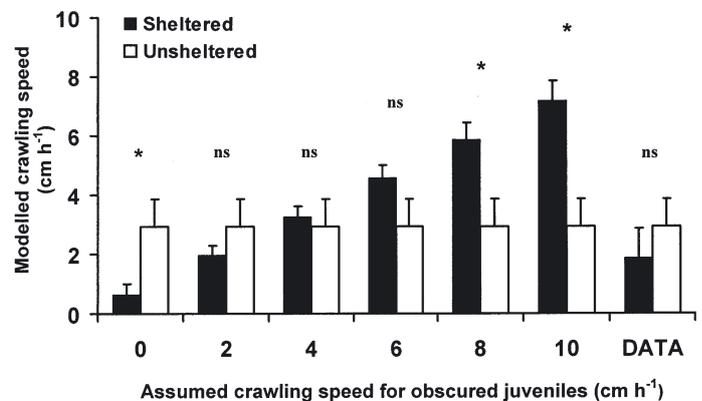


Fig. 6. *Strongylocentrotus franciscanus*. Potential effect of movement of obscured juveniles on the crawling speed reported in Fig. 5. Modelled crawling speeds were based on assumed crawling speeds for juveniles obscured from view in addition to those observed in the experiment. The original data ($n = 15$ for sheltered juveniles, $n = 44$ for unsheltered juveniles) are presented in the 'DATA' column at right. Asterisks indicate significant difference in crawling speed ($p < 0.05$) between sheltered and unsheltered treatments. ns: non-significant. Data are means ± 1 SE

DISCUSSION

Contrary to expectations (Tegner & Dayton 1977), juvenile sheltering does not appear to provide a nutritional advantage for juveniles. The fundamental finding here is that juveniles with adults consistently grew less, regardless of water flow, algal form, or urchin species, suggesting a competitive interaction between adult and juvenile sea urchins. The only exception to this pattern occurred in the absence of kelp, where both sheltered and unsheltered juveniles had low growth rates. Moreover, the lower growth of sheltered juveniles in the kelp treatments was not due to their inability to make use of food, as juveniles were able to utilize all forms of kelp (including ground kelp). It is more likely that adults limited the access of juveniles to food in the sheltered treatments. This competitive interaction was observed in both species, though the pattern was more pronounced for *Strongylocentrotus franciscanus* than for *S. droebachiensis*. This difference may reflect the fact that juvenile *S. droebachiensis* sheltered under adults less frequently than *S. franciscanus*, thus decreasing the impact of adults on juvenile growth. It could be argued that this type of intercohort competition would lead to higher recruitment in areas without adults, but other selective pressures (e.g. predation and hydrodynamic disturbance) may limit this possibility (Low 1975, Gosselin & Qian 1997, Hunt & Scheibling 1997). For example, juvenile shore crabs *Carcinus maenas* (<750 μm) avoid open areas lacking refuge even though food availability may be high (Moksnes et al. 2003). It is interesting to note that intercohort competition in sea urchins does not lead to size-related habitat/resource segregation (i.e. competitive exclusion of smaller individuals from optimal habitats) seen in other benthic marine organisms (Bollache et al. 2000, Szabo 2002).

Adult urchins tended to collect whole pieces of kelp in their spines and under their test, whereas pieces of ground kelp remained scattered throughout the tanks. This is also evident in the field, where both standing crop and drift kelp comprises a large portion of sea urchin diets (e.g. 68% in some species, Rodríguez 2003). In *Strongylocentrotus franciscanus*, drift kelp and other detritus may be their major food item (Low 1975). A benthic litter assessment on Vancouver Island showed that 41 g wet weight m^{-2} of drift kelp accumulated over 1 wk in the field (Smith & Foreman 1984), which is less than the 50 g wet weight of kelp (241 g wet weight m^{-2}) provided 3 times a week in our growth experiments. The results from this study however, indicate that sheltered juveniles have similar growth and survival rates as unfed juveniles, and it would appear unlikely that juveniles under all except the most food-limited conditions would benefit nutritionally from sheltering under adults.

Juveniles with adults did not move faster than those without adults (in some cases the opposite was true), indicating that reduced growth is not likely a result of juveniles expending more energy to locate adults. Moreover, lower growth is most probably a result of ecological (e.g. competitive) interactions between juveniles and adults for food. Despite reduced growth rates, however, a larger proportion of juvenile *Strongylocentrotus franciscanus* sheltered under adults than was the case for juvenile *S. droebachiensis*, which is similar to what has been observed in the field (Low 1975, Tegner & Dayton 1977). Our results suggest that juveniles of both species do not experience nutritional gains from adults and point, therefore, towards other factors (i.e. predation and hydrodynamic factors) as possible explanations for the adult-juvenile associations observed in nature.

In addition to the juvenile-adult interactions reported above, juvenile growth varied with the form of kelp presented. Specifically, small juveniles (1 to 2 mm) grew faster on whole kelp in the first experiment (Fig. 1), whereas larger juveniles (7 mm) grew faster on ground kelp in the second experiment (Fig. 2). It is likely that the larger juveniles in the second experiment were better able to search for and/or capture individual pieces of ground kelp than their smaller conspecifics in the first experiment, which were limited in mobility. In addition, the larger containers in the second experiment may have hindered juveniles from accessing whole pieces of kelp, which floated throughout the water column and on the water surface compared to the smaller containers used in the first experiment. It is likely that both juvenile and container size may have affected the results. It should also be noted that only one species of kelp (*Macrocystis integrifolia*) was used in our feeding experiments. In contrast, urchins in the field feed on a wide array of algae and invertebrates (Vadas 1977), and different diets in the laboratory can influence feeding, growth and survival rates (Scheibling & Anthony 2001). Moreover, it should be noted that juveniles in the whole kelp treatment sheltered at higher frequency and had lower crawling speeds than in treatments where food could not be monopolized by adults (e.g. ground kelp and no kelp treatments). This variability in behaviour suggests that juvenile sea urchins may be capable of assessing nutritive conditions in their environment, which is similar to other benthic marine invertebrates such as polychaetes (Dill & Fraser 1997).

Compared to juvenile sheltering, water flow had a negligible effect on juvenile growth rates (Fig. 2). There was little evidence that adults enhanced juvenile growth by reducing velocity fluctuations and/or retaining particulate matter and water-borne nutrients. Our experiment was limited to average velocities

Table 3. Comparison of juvenile growth for (a) *Strongylocentrotus franciscanus* and (b) *S. droebachiensis* from laboratory studies and field studies. NA: not available

| Location | Growth rate (mm mo ⁻¹) | Initial size (mm) | Density (ind. l ⁻¹) | Temp (°C) | Food type(s) | Source |
|---|---------------------------------------|----------------------|------------------------------------|--------------|--|------------------------------|
| (a) <i>S. franciscanus</i> | | | | | | |
| Lab | | | | | | |
| British Columbia, Canada | 0.1 | 1.6 | 60 | 11 | <i>Macrocystis integrifolia</i> | Present study |
| Unsheltered | 1.1 | 7.9 | 0.1 | 9.6 | <i>M. integrifolia</i> | Present study |
| Sheltered | 0.2 | 7.9 | 0.1 | 9.6 | <i>M. integrifolia</i> | Present study |
| California, USA | 0.5 ^a | 34.8 | 0.06 | 12.5–16.8 | 30% protein feed | McBride et al. (1998) |
| | 0.6 ^a | 36.2 | 0.06 | 12.5–6.8 | 40% protein feed | McBride et al. (1998) |
| | 0.5 ^a | 31.5 | 0.06 | 12.5–16.8 | 50% protein feed | McBride et al. (1998) |
| California, USA | 1.3 ^a | 0.40 | NA | NA | <i>Macrocystis pyrifera</i> | Rogers-Bennett et al. (1994) |
| Field | | | | | | |
| California, USA | 2.0 ^a | 17.6 | Field | Ambient | Natural flora | Rogers-Bennett et al. (1994) |
| California, USA | 2.0 ^a | 18 | Field | Ambient | Natural flora | Ebert & Russell (1993) |
| | 1.3 ^a | 30 | | | | |
| British Columbia, Canada | 0.1 ^a | 25 | 0.03 | Ambient | Natural flora | Low (1975) |
| Washington, USA | 2.0 ^a | 29 | 32 | Ambient | <i>Nereocystis leutkeana</i> | Swan (1961) |
| | 1.1 ^a | 50 | 32 | | | |
| Lab | 0.7 ± 0.2 | 18.7 ± 7.0 | 0.06–60 | 9.6–16.8 | | |
| Field | 1.3 ± 0.4 | 30.4 ± 6.9 | 0.03–32 | Ambient | | |
| Total | 0.9 ± 0.1 | 23.6 ± 4.3 | 0.03–60 | 9.6–16.8 | | |
| (b) <i>S. droebachiensis</i> | | | | | | |
| Lab | | | | | | |
| British Columbia, Canada | 0.2 | 2.6 | 60 | 11 | <i>M. integrifolia</i> | Present study |
| Unsheltered | 1.2 | 7.7 | 0.1 | 9.6 | <i>M. integrifolia</i> | Present study |
| Sheltered | 0.8 | 7.7 | 0.1 | 9.6 | <i>M. integrifolia</i> | Present study |
| Nova Scotia, Canada | 2.0 ^a | 45 | 0.5 | 3–17 | <i>Laminaria longicruris</i> , <i>L. digitata</i> , <i>Codium fragile</i> | Scheibling & Anthony (2001) |
| Maine, USA | 1.0 ^a | 15 | 0.5 | 2.3–17.8 | <i>Mytilus edulis</i> , <i>M. trossulus</i> , <i>L. longi-</i> <i>cruris</i> , <i>L. digitata</i> , <i>Litho-</i> <i>thamnium glaciale</i> , <i>Phymatolithon laevigatum</i> | Meidel & Scheibling (1999) |
| Nova Scotia, Canada | 0.2 | 0.5 | 100 | 3, 5, 16 | <i>L. glaciale</i> | Raymond & Scheibling (1987) |
| | 0.3 | 4.8 | 100 | 3, 5, 16 | <i>L. longicruris</i> , <i>L. glaciale</i> | Raymond & Scheibling (1987) |
| Washington, USA | 1.1 ^a | 38.4 | NA | 9–12.5 | <i>N. leutkeana</i> , <i>L. saccharina</i> , <i>Agarum</i> spp. | Vadas (1977) |
| Field | | | | | | |
| Nova Scotia, Canada | 0.8 ^a | 4.5 | 0.8 | Ambient | <i>L. longicruris</i> | Raymond & Scheibling (1987) |
| Maine, USA | -0.4 ^a | 4.8 | Field | Ambient | Natural flora | Russell et al. (1998) |
| Quebec, Canada | 0.2 ^a | 4.3 | Field | Ambient | Natural flora | Himmelman et al. (1983) |
| Nova Scotia, Canada | 0.7 ^a | 14 | Field | Ambient | Natural flora | Miller & Mann (1973) |
| Washington, USA | 1.9 ^a | 29 | 26 | Ambient | <i>N. leutkeana</i> | Low (1975) |
| New Hampshire, USA | 1.5 ^a | 9 | 87 | Ambient | <i>L. digitata</i> , | Low (1975) |
| | 1.3 ^a | 25 | 89 | | <i>Ascophyllum nodosum</i> | |
| | 0.7 ^a | 41 | 83 | | | |
| Lab | 0.7 ± 0.2 | 16.3 ± 6.8 | 0.1–100 | 2.3–17.8 | | |
| Field | 0.9 ± 0.2 | 21.9 ± 5.9 | 0.8–89 | Ambient | | |
| Total | 0.8 ± 0.2 | 19.7 ± 3.9 | 0.1–100 | 2.3–17.8 | | |
| ^a Estimates calculated from graphs or reported means | | | | | | |

under 0.05 m s^{-1} , which are adequate to disperse kelp particles, but may be inadequate to effect changes in juvenile-adult interactions. Specifically, water velocities of 0.3 to 0.4 m s^{-1} were found to limit the movement and feeding in *Strongylocentrotus nudus* (Kawamata 1998), which were much higher than the velocities used in this experiment.

Overall, the mortality rates of small juveniles observed in our study (~ 50 to 85%) are typical of early post-settlement benthic marine invertebrates, including sea urchins (Pearse & Hines 1987, Raymond & Scheibling 1987, Rowley 1990, Gosselin & Qian 1997). The growth rates for unsheltered juvenile *Strongylocentrotus franciscanus* and *S. droebachiensis* are consistent with those reported in the literature (Table 3). Juvenile *S. franciscanus* tended to grow faster than juvenile *S. droebachiensis* (e.g. 0.9 ± 0.1 vs $0.8 \pm 0.2 \text{ mm mo}^{-1}$, respectively, for $\sim 20 \text{ mm}$ test diameter). Moreover, field conditions are more conducive to growth than the laboratory (1.3 ± 0.4 vs $0.7 \pm 0.2 \text{ mm mo}^{-1}$ for *S. franciscanus*, 0.9 ± 0.2 vs $0.7 \pm 0.2 \text{ mm mo}^{-1}$ for *S. droebachiensis*), although size effects may be involved. A summary of both laboratory and field studies indicates that the highest size-specific growth rates exist for 10 to 30 mm juveniles (Fig. 7). These results are similar to other studies of size-dependent growth, which were conducted on field populations (Himmelman 1986, Ebert & Russell 1993, Russell et al. 1998). The lower growth rates at small sizes ($<10 \text{ mm}$) may be related to size-dependent sheltering behaviour, although this mechanism remains to be determined.

Recruitment for many marine invertebrates has been linked to larval supply and settlement (Gaines & Roughgarden 1985). Both settlement and post-settlement processes influence the distribution of sessile species (i.e. barnacles and ascidians), yet garnering equivalent information regarding mobile benthic species remains a challenge (Hunt & Scheibling 1997). Post-settlement processes, including mortality, can be as important as larval supply in influencing patterns of recruitment in sessile species (Delany et al. 2003). This appears to be the case for members of the genus *Strongylocentrotus*, where post-settlement mortality may be as high as 90% within the first year (Pearse & Hines 1987, Rowley 1990). Nutrition has been shown to affect post-settlement distribution in juvenile ophiuroids ($<1 \text{ mm}$ disk diameter, Turon et al. 2000), but our data do not support a nutritional advantage for juvenile *S. franciscanus* and *S. droebachiensis* sheltering under adults (Tegner & Dayton 1977, Rogers-Bennett et al. 1995). Whereas post-settlement mortality has been argued to be more important than other processes (i.e. dispersal) in sessile (Gaines & Roughgarden 1985) and mobile benthic invertebrates (Rowley 1990), our results demonstrate the importance of juvenile

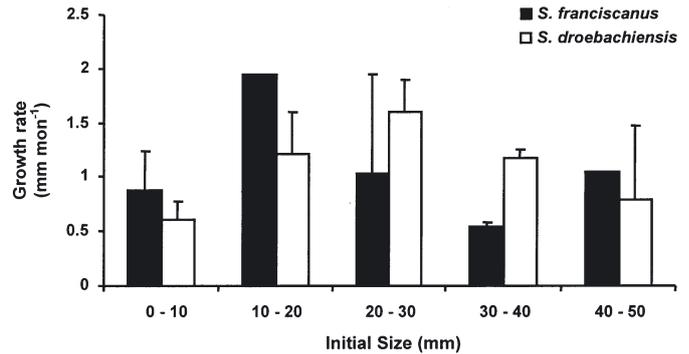


Fig. 7. *Strongylocentrotus franciscanus* and *S. droebachiensis*. Size-specific juvenile growth rates. The figure is based on the summary provided in Table 3. Data are means ± 1 SE

sheltering as a behavioural strategy in the early life-history of sea urchins. Clearly, additional research concerning the early life-history of mobile benthic organisms is needed to better understand the recruitment process of benthic marine invertebrates.

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