

Harbouring the enemy: kelp holdfasts protect juvenile sea urchins from predatory crabs

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ABSTRACT: Predation is an important agent of post-settlement mortality of sea urchins that is mediated by the availability and suitability of spatial refuges, particularly during the vulnerable juvenile stage. In laboratory and field caging experiments, we show that holdfasts of a dominant kelp, *Saccharina latissima*, provide a spatial refuge for juvenile sea urchins *Strongylocentrotus droebachiensis* (<20 mm, test diameter) from crabs *Cancer borealis* and *C. irroratus*, considered to be the dominant predators of sea urchins in kelp-bed ecosystems in the northwestern Atlantic. In treatments with individual crabs of either species, the presence of holdfasts reduced predation on juvenile sea urchins by ~20 to 30% compared to treatments with no refuge. Crabs consumed juveniles (from 5 to 19 mm) in each of three 5 mm size classes in proportion to their abundance, regardless of treatment. In kelp beds in St. Margarets Bay, Nova Scotia, Canada, the number of juvenile sea urchins per holdfast ranged from 0.3 to 0.9, with juveniles in holdfasts accounting for two-thirds of the total urchin population density at one site. Up to 4 juveniles occurred within a single holdfast, and there was a significant positive relationship between juvenile size (but not number) and holdfast volume. Small adult sea urchins were not found within holdfasts in kelp beds and rarely occupied holdfasts presented to them in laboratory cages. Our findings indicate an ontogenetic shift in sea urchin–kelp interactions, whereby kelp facilitates recruitment of its major grazer.

KEY WORDS: *Strongylocentrotus droebachiensis* · Sea urchin · Kelp bed · Predation · Spatial refuge · Cancrid crab

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INTRODUCTION

Ecosystem-level phase shifts from luxuriant kelp beds to an alternative sea urchin barrens state, characterized by a reduction in productivity, habitat complexity, and biodiversity, have been documented on temperate rocky reefs worldwide (Steneck et al. 2002, Filbee-Dexter & Scheibling 2014). The ecological and economic consequences of this 'collapse' to a barrens state, generally brought about through destructive grazing of kelp beds by sea urchins (North & Pearse 1970, Breen & Mann 1976, Hagen 1983, Johnson et al. 2005), underscores the importance of understanding the mechanisms that deter-

mine sea urchin abundance and the resilience of the kelp state (Filbee-Dexter & Scheibling 2014). Population outbreaks of sea urchins resulting in a shift to the barrens state have been attributed to release from predation due to overfishing, which results in a trophic cascade (reviewed by Scheibling 1996, Steneck et al. 2004, Estes et al. 2010). Alternatively, high settlement rates associated with environmental anomalies (e.g. warm sea temperature) may lead to recruitment pulses of sea urchins that overwhelm predatory controls (Hart & Scheibling 1988, Hernández et al. 2010), leading to the eventual formation of destructive grazing aggregations (Lauzon-Guay & Scheibling 2010).

Sea urchins, like most benthic marine invertebrates, are subject to high rates of mortality at early life-history stages, as evidenced by order of magnitude declines in abundance following settlement of planktonic larvae (Rowley 1989, Scheibling & Raymond 1990, Hunt & Scheibling 1997). Predation is thought to be an important source of post-settlement mortality of sea urchins (Scheibling & Hamm 1991, McNaught 1999, Hereu et al. 2005, Scheibling & Robinson 2008, Jennings & Hunt 2010, Bonaviri et al. 2012, Clemente et al. 2013), although it is inherently difficult to study in the field, and these dynamics remain poorly resolved. Juvenile sea urchins are prey to a variety of benthic invertebrates and demersal fish (Keats et al. 1985, Scheibling & Hamm 1991, McNaught 1999, Scheibling & Robinson 2008, Jennings & Hunt 2010), while adults generally are vulnerable only to large-bodied predators such as sea otters, large fish and decapod crustaceans (Duggins 1980, Tegner & Dayton 1981, Hagen & Mann 1992, Shears & Babcock 2002). Post-settlement predation rate is mediated by the availability of spatial refuges, including biogenic (e.g. macroalgal turfs, mussel beds, adult spine canopies) and physical (e.g. pits, crevices, undersides of boulders, interstices of cobbles) microhabitats, which can vary with sea urchin size and life-history stage (Tegner & Dayton 1977, Harrold & Reed 1985, Keats et al. 1985, Witman 1985, Himmelman 1986, Scheibling & Raymond 1990, Ojeda & Dearborn 1991, Scheibling & Hamm 1991, Dumont et al. 2006, Clemente et al. 2013).

Along the Atlantic coast of Nova Scotia, Canada, destructive grazing by green sea urchins *Strongylocentrotus droebachiensis* drives a phase shift from a kelp-bed to a barrens state that potentially is stable on a decadal scale (Mann 1977, Scheibling et al. 1999). A reverse shift back to kelp beds occurs when outbreaks of disease cause mass mortality of sea urchins, enabling kelps and other seaweeds to recolonize the rocky subtidal zone (Scheibling 1986, Scheibling et al. 2013). The reestablishment of sea urchin populations within emergent kelp beds following these mass mortality events occurs mainly through recruitment via the planktonic larval stage (Balch & Scheibling 2000). Predation on juvenile sea urchins is broadly considered to be a major determinant of recruitment success and the expansion of sea urchin populations within these kelp beds (reviewed by Scheibling 1996, Scheibling & Hatcher 2013; but see also Feehan & Scheibling 2014).

Predation of *S. droebachiensis* in the northwestern Atlantic is mediated by the availability and suitability of spatial refuges from a variety of predators, includ-

ing small-mouthed fish (e.g. sculpin *Myoxocephalus octodecemspinosus*, cunner *Tautoglabrus adsperses*), decapod crustaceans (e.g. crabs *Cancer borealis*, *C. irroratus*) and sea stars (e.g. *Asterias vulgaris*) (Scheibling 1996, Scheibling & Hatcher 2013). Mortality due to predation is thought to be particularly high during the late juvenile and early adult phase of the benthic life history, when sea urchins outgrow small spatial refuges, such as crevices and interstices of cobbles, and move onto exposed rock surfaces to graze kelp (Himmelman 1986, Scheibling & Raymond 1990, Scheibling & Hamm 1991). Larger adult urchins reach a size refuge from most predators (Scheibling 1996). Bimodal size distributions observed for populations of *S. droebachiensis*, and other sea urchin species in temperate regions (e.g. *S. franciscanus* in California), have been attributed to high levels of predation on intermediate-sized sea urchins (Tegner & Dayton 1981, Tegner & Levin 1983, Scheibling & Hamm 1991). The ontogenetic transition between juvenile and adult habitats, with high associated mortality, can create a bottleneck that limits the growth rate of the sea urchin population and confers resilience to the kelp-bed state (Feehan & Scheibling 2014). Recent evidence indicates that large decapods, specifically cancrid crabs, have become the apex predators of sea urchins in the northwestern Atlantic because of overfishing of higher trophic level predators, such as large demersal fish (Steneck et al. 2004, 2013).

During a diving survey of populations of *Strongylocentrotus droebachiensis* in kelp beds in St. Margarets Bay, Nova Scotia, in June 2010, we observed juvenile sea urchins (<20 mm test diameter, Meidel & Scheibling 2001) inhabiting holdfasts (anchoring structures) of the dominant kelp *Saccharina latissima*. Previous studies at sites with more wave exposure off adjacent headlands showed that kelp (*Laminaria digitata* and *S. latissima*) holdfasts provide a microhabitat for a variety of epifaunal and cryptofaunal invertebrates, including bivalves, sea stars, brittle stars and polychaetes (Schmidt & Scheibling 2006, Knip & Scheibling 2007, Scheibling & Lauzon-Guay 2007). Although juvenile *Strongylocentrotus droebachiensis* were not recorded within kelp holdfasts in these studies, young post-settlers (2 to 6 mm test diameter) have been observed on branched and undercut crustose coralline algae *Lithothamnion glaciale* (Keats et al. 1985, Scheibling & Raymond 1990) or turfs of finely branched arborescent coralline algae *Corallina officinalis* (R. E. Scheibling pers. obs.) in sea urchin barrens. It has been suggested that these macroalgal microhabitats provide

juvenile sea urchins with a spatial refuge from predators (Keats et al. 1985, Scheibling & Robinson 2008).

Here, we examine the hypothesis that holdfasts of the dominant kelp (*Saccharina latissima*) are a spatial refuge for juvenile *Strongylocentrotus droebachiensis* from cancrid crabs (*C. borealis* and *C. irroratus*) using caging experiments in both field and laboratory settings. These crabs are abundant in Nova Scotian kelp beds and other macroalgal habitats (Schmidt & Scheibling 2007, Kelly et al. 2011) and have long been considered important predators of sea urchins (Bernstein et al. 1981, Scheibling & Hamm 1991). We also document the abundance and size distribution of sea urchins within kelp holdfasts in St. Margarets Bay and examine the relationship between holdfast size (volume of available space) and the number and size of resident sea urchins. Our findings indicate that holdfasts are indeed an important microhabitat and spatial refuge for juvenile sea urchins and indicate an ontogenetic shift in sea urchin-kelp interactions, whereby kelp facilitates recruitment of its major grazer.

MATERIALS AND METHODS

Sampling of sea urchins in kelp holdfasts

To measure the abundance and size distribution of sea urchins *Strongylocentrotus droebachiensis* within kelp holdfasts, we used SCUBA to haphazardly sample adult sporophytes of the dominant species *Saccharina latissima* (>1 m blade length) in kelp beds at 8 to 12 m depth from 2 sites located ~2 km apart (linear distance) in St. Margarets Bay, Nova Scotia (The Lodge: 44° 33.552' N, 64° 01.869' W; Birchy Head: 44° 34.473' N, 64° 02.491' W) in July 2010 and June and August 2011 (Table 1). Holdfasts were carefully loosened from the substratum using a dive knife, and the kelp blade and stipe were excised ~4 cm above

the junction with the holdfast. Holdfasts were placed in separate plastic bags and transported to the laboratory, where they were dissected, and the associated sea urchins were counted and measured (test diameter, 0.1 mm accuracy) using vernier calipers.

We examined the relationship between the refuge space within a kelp holdfast and the number and size of associated sea urchins at both sites in June 2011. We estimated the available refuge space (V_{refuge} , ml) by subtracting the volume occupied by the haptera ($V_{haptera}$, ml) from the volume of a cone that approximated the shape of a holdfast (simplified from Jones 1971):

$$V_{refuge} = 1/3 \pi r^2 h - V_{haptera} \tag{1}$$

where r (mm) is the radius of the holdfast (average of the minimum and maximum diameter at the base divided by 2) and h (mm) is the height of the holdfast (measured parallel to the stipe). $V_{haptera}$ is measured as the volume of water displaced by the holdfast (excluding the stipe). Simple linear regression was used to examine a relationship between size or number of associated sea urchins and holdfast volume.

To estimate the proportion of the sea urchin population inhabiting holdfasts within a kelp bed, we compared the estimated density within holdfasts to the total density of sea urchins measured in a haphazard sample of 1 m² quadrats at The Lodge in June 2010 (n = 8). Density in holdfasts was calculated by multiplying the mean number of individuals per holdfast, based on our sample in July 2010, by the average density of mature sporophytes of *S. latissima* measured in a sample of 1 m² quadrats in June 2010 (n = 4).

The Kolmogorov-Smirnov 2-sample test was used to examine whether the size-frequency distribution of sea urchins in kelp holdfasts (pooled over samples collected in 2010 and 2011) differed from that of the total sea urchin population in the kelp bed (in all microhabitats, including holdfasts) at The Lodge in 2010.

Table 1. Dates and sites of sampling of holdfasts of *Saccharina latissima* (>1 m blade length), indicating depth (m) of sample, sample size (n, number of holdfasts), total number of sea urchins *Strongylocentrotus droebachiensis* within holdfasts, number of sea urchins per holdfast (pooled or as a range for each site and sampling date), mean (± SD) test diameter (TD, mm) of sea urchins within holdfasts and mean (± SD) holdfast volume (ml). ND: no data

Date	Site	Depth (m)	Sample size (n)	Total no. of urchins	No. of urchins per holdfast Pooled Range	Urchin TD (mm)	Holdfast volume (ml)
30 Jul 2010	The Lodge	8–12	110	58	0.53 0–4	9.8 ± 3.5	ND
23 Jun 2011	The Lodge	8–12	35	16	0.46 0–3	6.0 ± 4.8	90 ± 92
30 Jun 2011	Birchy Head	12	10	9	0.90 0–4	5.8 ± 1.6	48 ± 26
24 Aug 2011	The Lodge	8–12	59	17	0.29 0–4	9.6 ± 4.8	ND

Laboratory experiments

To determine whether kelp holdfasts provide a spatial refuge to sea urchins from predatory crabs, we conducted laboratory experiments testing the survival of juvenile sea urchins (<20 mm) enclosed with a single crab (Jonah crab *Cancer borealis* or Atlantic rock crab *C. irroratus*) in 2.3 l hemispherical (25 cm diameter) plastic cages with or without holdfasts of *S. latissima* as 2 levels of a refuge treatment (Fig. 1A). The cages were constructed from kitchen colanders that were slotted and perforated to provide 2 mm wide openings to permit water flow. For each unit, a second (top) colander served as a weighted lid for the cage (Fig. 1B). The cages were placed in seawater tables such that the water line (~12 cm depth at center) was level with the top of the bottom colander, preventing

sea urchins from fleeing onto the lid during the experiment. This hemispherical cage design eliminated refuge space for sea urchins in corners while enabling the crab to access the entire curved bottom area.

Divers collected juvenile sea urchins from urchin barrens and collected crabs (males, 75 to 120 mm carapace width) and holdfasts of *S. latissima* (>1 m blade length) from kelp beds at sites between Halifax Harbour and St. Margarets Bay between May and August 2013. Crabs and sea urchins were maintained in laboratory aquaria with flowing oxygenated ambient seawater prior to use in experiments and fed ad libitum on kelp and crushed adult sea urchins, respectively. Sea urchins and other associated fauna (e.g. brittle stars, polychaetes, bivalves) were removed from holdfasts before holdfasts were used in experiments.

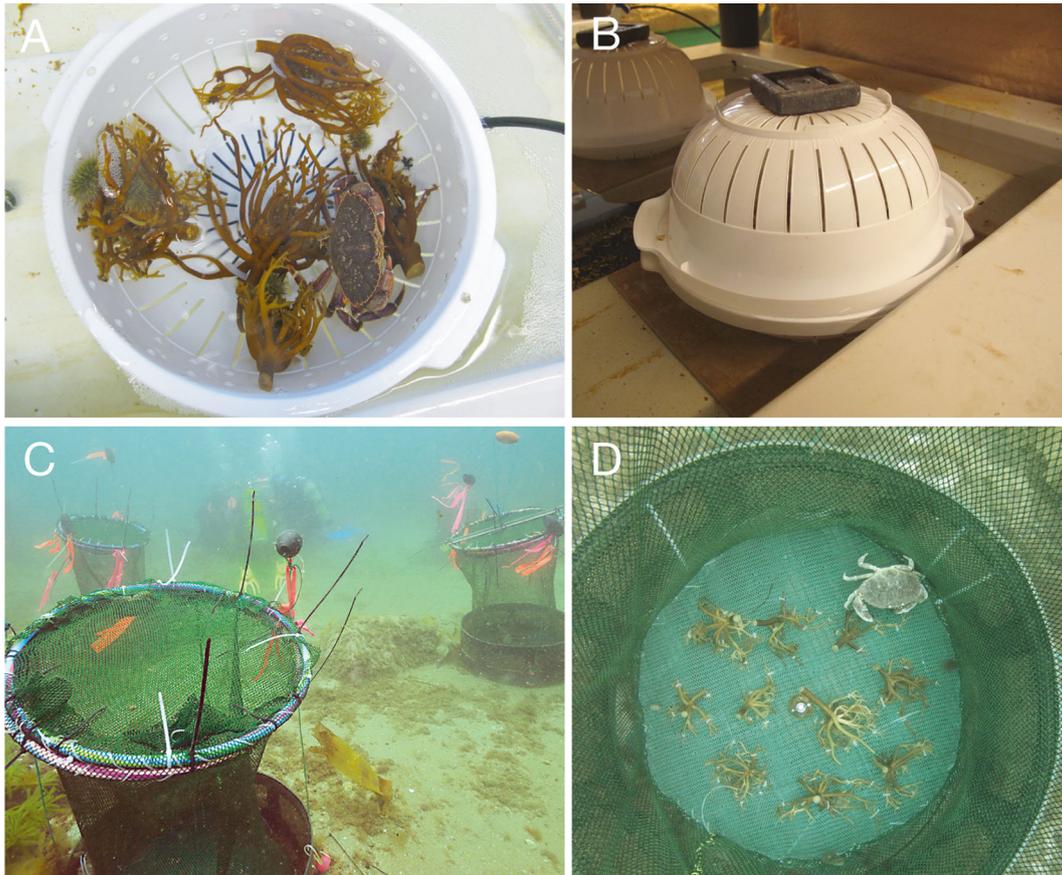


Fig. 1. Refuge treatment of the laboratory (A) and field (D) experiment showing juvenile sea urchins *Strongylocentrotus droebachiensis* and a crab *Cancer irroratus* (A) or *C. borealis* (D) amid attached holdfasts of the kelp *Saccharina latissima*. (B) Laboratory cages constructed from two 25 cm diameter plastic colanders, one stacked on top of the other and held in place by a lead weight, used to enclose juvenile sea urchins with a predatory crab and with or without holdfasts as a spatial refuge. The bottom colander was immersed (~12 cm depth at the center) in a flow-through seawater table, providing a barrier to sea urchins at the air-water interface. (C) Field cage (50 cm diameter, 100 cm height, 5 mm mesh) used to enclose sea urchins with a predatory crab and with or without holdfasts as a spatial refuge. Cages were placed in a linear array on a level sand patch within a kelp bed at Birchy Head, St. Margarets Bay

For each experiment with a given species of crab, we conducted 4 or 5 trials blocked in time in a replicated block design (Table 2). For each trial, 12 cages, each containing 5 juvenile sea urchins from 3 size classes (1 urchin, 5–9 mm; 3 urchins, 10–14 mm; 1 urchin, 15–19 mm), were placed in ~140 l seawater tables with flowing (~3 l min⁻¹) ambient seawater. For the refuge treatment, we attached 5 holdfasts of *S. latissima* (stipe excised ~4 cm above junction with holdfast) in each of 4 cages by pinning individual haptera to the bottom hemisphere of the cage with 10 cm (length) plastic cable ties to mimic attachment to a rocky substrate (Fig. 1A). This represents a density of 50 thalli m⁻² (based on surface area of the hemispherical cage bottom), which approximates the upper range of mean kelp density at Mill Cove in St. Margarets Bay (12 to 42 thalli m⁻²) and the midpoint of this range at Little Duck Island in neighbouring Mahone Bay (40 to 60 thalli m⁻²), recorded during intervals between defoliation events caused by an invasive bryozoan from 1992 to 2002 (Scheibling & Gagnon 2009).

After an acclimation period of 8 to 24 h (we observed that sea urchins took at least 8 h to enter and remain within holdfasts in the absence of a predator), we randomly assigned a single crab to each of 4 replicate cages in both the refuge (with holdfasts) and the no-refuge (no holdfasts) treatment. An additional 4 cages with sea urchins but without a crab or holdfasts acted as a control for other sources of sea urchin mortality (e.g. disease or stress). To reduce

variability due to recent feeding history, crabs were starved for 48 h before use in each trial. Sea urchin mortality (proportion out of 5 urchins) in each cage was measured 48 h after crabs were added to the treatment cages. Two-way ANOVA was used to test for an effect of refuge (fixed factor, 2 levels: holdfasts, no refuge) and trial (random factor, 4 to 5 levels) on the proportion of sea urchins consumed by crabs (in separate tests for each crab species). At termination of each trial, the carapace width of crabs and test diameter of the surviving sea urchins were measured using a plastic measuring tape (1 mm accuracy). A chi-squared goodness-of-fit test was used to examine differences between observed and expected frequencies of 3 size classes of sea urchin (5–9, 10–14, 15–19 mm test diameter) surviving in cages with crabs (*C. borealis* or *C. irroratus*) at 2 levels of a refuge treatment (holdfast refuge, no refuge). Expected frequencies were based on the null hypothesis of no size-selective predation. Data were pooled over trials in separate analyses for each crab species.

Individual crabs were used in a maximum of 2 trials and were allowed to acclimate for at least 1 wk in the laboratory before each trial. Reusing crabs in different trials could potentially introduce a bias if larger and/or more voracious crabs were consistently used within a particular treatment. To minimize this risk, crabs were randomly assigned to cages within each trial. Inspection of the mean carapace width of crabs within treatments suggests no bias in crab size among treatments within trials (Table 2).

Table 2. Summary of field and laboratory experiments investigating kelp holdfasts as a refuge for juvenile sea urchins *Strongylocentrotus droebachiensis* from predatory crabs *Cancer borealis* and *C. irroratus*, indicating the number of experimental trials, start date of trials in 2013, mean (\pm SD) seawater temperature ($^{\circ}$ C), mean (\pm SE) carapace width of crabs (CW, mm) and mean (\pm SE) predation rate of crabs (urchins crab⁻¹ d⁻¹) in cages at 2 levels of a refuge treatment (holdfasts, no refuge) (n = 4)

Expt	Trial no.	Start date	Water temp. ($^{\circ}$ C)	CW of crabs (mm)		Predation rate (urchins crab ⁻¹ d ⁻¹)	
				Holdfast	No refuge	Holdfast	No refuge
Laboratory							
<i>C. borealis</i>	1	24 May	8.1 \pm 0.4	86 \pm 3	85 \pm 4	1.0 \pm 0.6	1.9 \pm 0.6
	2	11 Jun	6.2 \pm 0.1	99 \pm 2	84 \pm 5	1.0 \pm 0.5	1.5 \pm 0.4
	3	26 Jun	8.1 \pm 0.1	91 \pm 6	101 \pm 2	1.5 \pm 0.5	2.0 \pm 0.4
	4	17 Jul	10.2 \pm 0.3	101 \pm 3	105 \pm 3	1.0 \pm 0.4	1.5 \pm 0.4
	5	25 Jul	10.4 \pm 0.3	103 \pm 3	104 \pm 6	0.5 \pm 0.4	1.1 \pm 0.5
<i>C. irroratus</i>	1	29 Jul	9.7 \pm 0.4	83 \pm 1	83 \pm 3	0.8 \pm 0.6	1.8 \pm 0.6
	2	10 Aug	8.8 \pm 0.3	85 \pm 4	80 \pm 2	0.6 \pm 0.6	0.8 \pm 0.3
	3	24 Aug	8.9 \pm 0.4	79 \pm 3	86 \pm 1	0	1.4 \pm 0.5
	4	27 Aug	10.3 \pm 0.2	78 \pm 3	81 \pm 1	0.4 \pm 0.4	1.3 \pm 0.7
Field							
<i>C. borealis</i>	1	31 Jul	11.4 \pm 0.9	103 \pm 2	103 \pm 3	2.3 \pm 0.5	3.2 \pm 0.5
	2	13 Aug	8.6 \pm 0.7	99 \pm 4	100 \pm 2	1.4 \pm 0.3	2.2 \pm 0.6
	3	24 Aug	7.3 \pm 0.8	97 \pm 8	90 \pm 6	2.2 \pm 0.6	3.7 \pm 0.6

For the experiment with *C. irroratus*, seawater temperature was continuously recorded (1 h intervals) with a temperature logger (StowAway TidbiT Temperature Logger, Onset Computer) placed within one of the seawater tables. For the experiment with *C. borealis*, we used temperature records provided by the Aquatron, Dalhousie University (laboratory seawater source), for the May trial. For the trials in June and July, we obtained temperatures recorded at 7 to 8 m depth in Bedford Basin (~5 km from the Aquatron intake and at the same depth; J. Hackett pers. comm.), which we adjusted for warming (+1°C) during transfer to our laboratory. The experimental array was illuminated by natural light from a large north-west-facing window.

To examine size-specific utilization of kelp holdfasts as refuge/habitat by sea urchins, we measured the tendency of sea urchins in 5 size classes (juveniles: 5–9, 10–14, 15–19 mm test diameter; small adults: 20–24, 25–29 mm) to enter and reside within holdfasts of *S. latissima* in our experimental cages. In each of 3 trials blocked in time, we introduced 1 sea urchin from each of the 5 size classes to each of 4 cages with 5 attached holdfasts (1 holdfast per sea urchin, 1 urchin per size class per cage) in an unreplicated block design. Cages were maintained in seawater tables with flowing (~3 l min⁻¹) ambient seawater. After 24 h, we measured the proportion of sea urchins (out of 4) within each size class that were within a kelp holdfast. One-way ANOVA was used to examine differences among size classes (fixed factor, 5 levels) in the proportion of sea urchins residing within holdfasts. Tukey's HSD test ($\alpha = 0.05$) was used to compare means among levels of size class.

Field experiment

To examine whether kelp holdfasts provide a spatial refuge to sea urchins from predatory crabs under ambient conditions in the field, we conducted an experiment testing the survival of juvenile sea urchins (<20 mm) enclosed with a single crab (*C. borealis*) in 200 l cylindrical cages (5 mm aperture nylon mesh) with or without holdfasts of *S. latissima* as 2 levels of a refuge treatment (Fig. 1C,D). A cylindrical cage design (diameter = 50 cm, height = 100 cm) was used to minimize refuge space for sea urchins in corners. The bottom of each cage was reinforced with plastic-coated steel mesh to allow for attachment of holdfasts and bolted to a round plastic base (diameter = 75 cm) that was anchored to the seafloor with an iron weight (Fig. 1C). The mesh was

attached to a hollow plastic ring ('hula hoop') at the top of the cage and suspended with small floats (Fig. 1C). The lid of the cage was fashioned from another plastic ring covered with mesh and attached to the cage top with plastic cable ties to allow divers access for observation (Fig. 1C). Crabs, sea urchins and kelp for the field experiment were collected from the same sites and over the same period as for the laboratory experiments (see above). Water temperature was recorded at 10 min intervals using a temperature logger (StowAway TidbiT Temperature Logger, Onset Computer) at 8 m depth at The Lodge (<2 km south-southwest of Birchy Head).

We conducted 3 trials blocked over time in a replicated block design (Table 2). For each trial, 13 cages, each containing 10 juvenile sea urchins from 3 size classes (2 urchins, 5–9 mm test diameter; 6 urchins, 10–14 mm; 2 urchins, 15–19 mm), were deployed in a linear array at 8 m depth on a level sand patch within a kelp bed at Birchy Head. In each of 6 cages, we attached 10 kelp holdfasts (stipe excised ~4 cm above junction with holdfast) to the cage bottom (using the same method of attachment as in the laboratory experiments) for the holdfast refuge treatment (Fig. 1D). This represents a density of 50 thalli m⁻² (based on surface area of the circular cage bottom), like that of our laboratory experiments. We manually placed sea urchins inside of holdfasts in the refuge treatment. We then added a single *C. borealis* (males, 70–120 mm carapace width) randomly assigned to each of the 6 replicate cages in both the refuge (with holdfasts) and the no-refuge (no holdfasts) treatment. A single cage with sea urchins but no holdfasts or crab acted as a control for other sources of sea urchin mortality. Crabs were starved for 48 h before use in the field experiment to standardize recent feeding history. Individual crabs were used in a maximum of 2 trials and were allowed to acclimate in the laboratory for at least 1 wk before each trial.

Video cameras (GoPro Hero2, Woodman Labs), with an extra battery pack (GoPro BacPac) to extend the battery life of the camera to 4.5 h, were mounted to the inside lid of cages of the refuge treatment to monitor sea urchin and crab behavior at 30 s intervals (time-lapse recording). Predation was not observed during the first 4.5 h of the field experiment in time-lapse video of the holdfast refuge treatment, likely because crabs were still acclimating to the cages. Juvenile sea urchins were frequently observed moving into and out of holdfasts, suggesting that they also were acclimating to their surroundings during this period. Attempts by larger juveniles to move into holdfasts were sometimes unsuccessful. At the end of

each trial, carapace width of crabs (mm) and test diameter (mm) of the surviving sea urchins were measured using a plastic measuring tape. Sea urchin mortality (proportion out of 10 urchins) in each treatment and control cage was measured 48 h after crabs were added to the treatment cages. Two-way ANOVA was used to test for an effect of refuge (fixed factor, 2 levels: holdfasts, no refuge) and trial (random factor, 3 levels) on the proportion of sea urchins consumed. A chi-squared goodness-of-fit test was used to examine differences between observed and expected frequencies of 3 size classes of sea urchin (5–9, 10–14, 15–19 mm test diameter) surviving in cages with crabs at 2 levels of a refuge treatment (holdfast refuge, no refuge). Expected frequencies were based on the null hypothesis of no size-selective predation. Data were pooled over trials for the analysis.

All statistical tests were run with Statistica 8 (Stat-Soft). Assumptions of homoscedasticity for ANOVA were tested using Cochran's C-test ($\alpha = 0.05$).

RESULTS

Field observations

The number of *Strongylocentrotus droebachiensis* per holdfast of *Saccharina latissima* ranged from 0.29 to 0.90 in samples from kelp beds in St. Margarets Bay in summer 2010 and 2011 (Table 1). Up to 4 sea urchins occurred within a single holdfast. The mean test diameter of *S. droebachiensis* in these samples ranged from 5.8 to 9.8 mm (Table 1) about a grand mean of 8.8 mm (Fig. 2A). Sea urchins >20 mm (approximate size at sexual maturity; Meidel & Scheibling 2001) were not observed in holdfasts (Fig. 2A). There was a significant positive relationship between the mean test diameter of sea urchins within a holdfast and holdfast volume (Fig. 3) but no relationship between the number of sea urchins within a holdfast and holdfast volume (Table 1). The mean \pm SD density of adults of *S. latissima* (>1 m blade length) at The Lodge in summer 2010 was 6.8 ± 4.0 sporophytes m^{-2} , giving an estimated mean density of sea urchins within holdfasts of 3.6 ± 2.1 urchins m^{-2} , two-thirds of the total population density in the kelp bed (5.5 ± 6.8 urchins m^{-2}). The majority (~98%) of the sea urchin population within the kelp bed in summer 2010 was composed of juveniles (<20 mm) (Fig. 2B). The size-frequency distribution of sea urchins in kelp holdfasts (pooled over samples collected in 2010 and 2011) did not differ from that of

the total sea urchin population in the kelp bed (in all microhabitats, including holdfasts) at The Lodge in 2010 (Kolmogorov-Smirnov 2-sample test: $D_{44,100} = 0.071$, $p > 0.10$) (Fig. 2). Sea urchin density at The

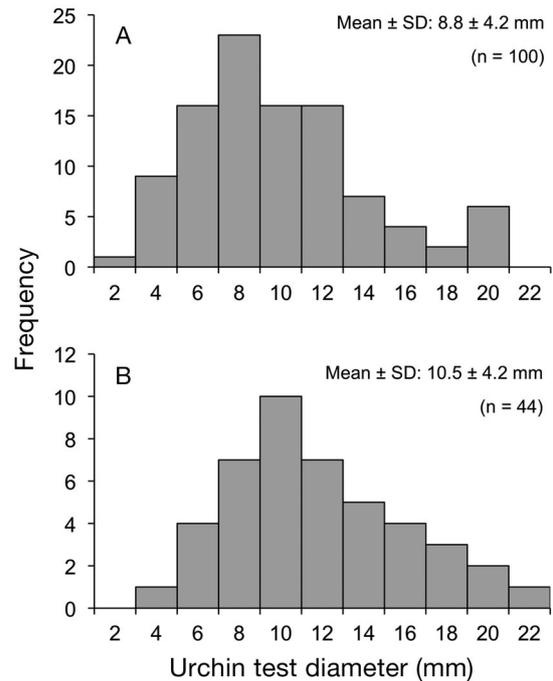


Fig. 2. Size-frequency (test diameter, mm) distributions of sea urchins *Strongylocentrotus droebachiensis* sampled in (A) holdfasts of *Saccharina latissima* in kelp beds in St. Margarets Bay, Nova Scotia, in summer 2010 and 2011 (see Table 1 for sample sites and dates); and (B) all microhabitats in a kelp bed at The Lodge, St. Margarets Bay, in June 2010

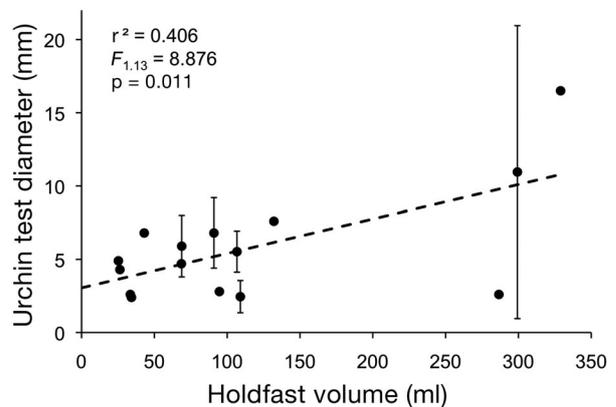


Fig. 3. Relationship between size of sea urchins *Strongylocentrotus droebachiensis* (test diameter, mm) and kelp *Saccharina latissima* holdfast volume (ml). Data are from a sample of 15 holdfasts from kelp beds in St. Margarets Bay in June 2011 (Table 1). Error bars are SD of mean test diameter for holdfasts with 2 to 4 sea urchins

Lodge in 2010 approximated the grand mean (5.0 ± 3.3 urchins m^{-2}) for kelp beds at 10 sites (including The Lodge) sampled throughout St. Margarets Bay at that time (Feehan & Scheibling 2014).

Experimental results

In laboratory experiments with predatory crabs, we found significantly lower mortality of juvenile sea urchins in treatments with kelp holdfasts than in those with no refuge, for both *Cancer irroratus* and *C. borealis* (Table 3, Fig. 4). Similarly, in a field experiment with *C. borealis*, we found significantly lower mortality of juvenile sea urchins in cages with kelp holdfasts compared to cages with no refuge (Table 3, Fig. 5). Most of the surviving sea urchins were found within holdfasts at the end of each experimental trial: available data indicate that >99 and $86 \pm 13\%$ (SD) of surviving sea urchins were within holdfasts at the end of trials 1 to 3 in laboratory and field experiments with *C. borealis*, respectively. Predation by both species of crab resulted in broken sea urchin test fragments within cages. We observed no mortality of sea urchins in control treatments without holdfasts or a crab in both the laboratory and field experiments.

Table 3. Two-way ANOVA of the effect of refuge (fixed factor, 2 levels: holdfasts, no refuge) and trial (random factor, 3 to 5 levels) on the proportion of sea urchins *Strongylocentrotus droebachiensis* consumed by a crab after 48 h in laboratory cages (*Cancer borealis* or *C. irroratus*) or field cages (*C. borealis*). Refuge and Trial were tested against the pooled interaction (Refuge \times Trial) and error MS. **Bold** values are significant at $\alpha = 0.05$. Data for all tests conform to the assumptions of normality and homoscedasticity (Cochran's C-test, $\alpha = 0.05$)

Expt	Source of variation	df	MS	F	p
Laboratory					
<i>C. borealis</i>	Refuge	1	0.576	4.604	0.039
	Trial	4	0.149	1.187	0.334
	Refuge \times Trial	4	0.009	0.060	0.993
	Error	30	0.141		
<i>C. irroratus</i>	Refuge	1	0.845	5.465	0.027
	Trial	3	0.113	0.733	0.541
	Refuge \times Trial	3	0.085	0.520	0.672
	Error	24	0.163		
Field					
<i>C. borealis</i>	Refuge	1	0.380	6.160	0.019
	Trial	2	0.177	2.87	0.072
	Refuge \times Trial	2	0.020	0.314	0.733
	Error	30	0.065		

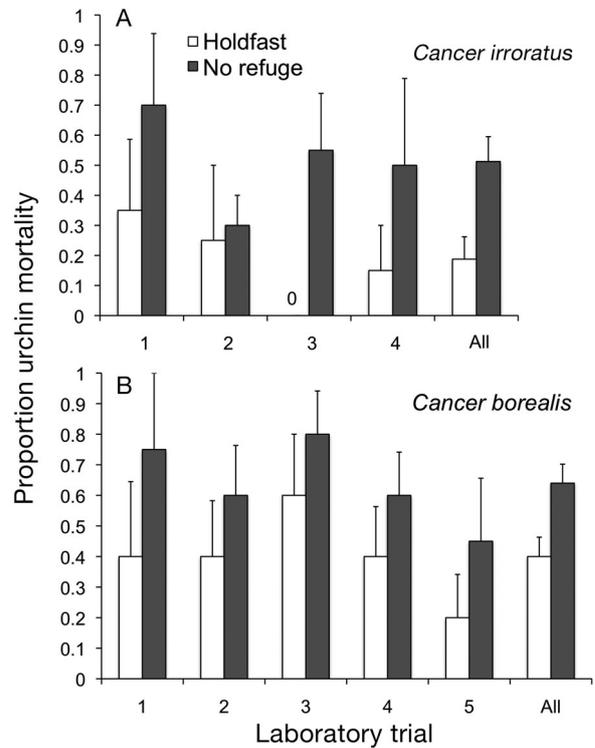


Fig. 4. Proportion of mortality of sea urchin *Strongylocentrotus droebachiensis* juveniles (out of 5) exposed for 48 h to a single crab, (A) *Cancer borealis* or (B) *C. irroratus*, in laboratory cages at 2 levels of a refuge treatment (5 kelp holdfasts, no holdfasts). Data are mean (+ SE) for 4 replicate cages for each of 4 or 5 experimental trials and grand mean (+ SE) for all trials

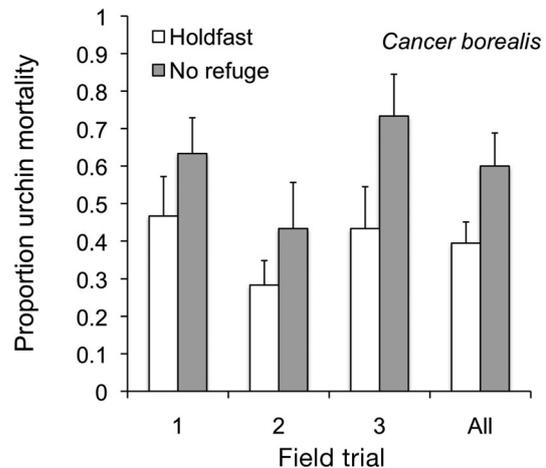


Fig. 5. Proportion of mortality of sea urchin *Strongylocentrotus droebachiensis* juveniles (out of 10) exposed for 48 h to a single crab, *Cancer borealis*, in field cages at 2 levels of a refuge treatment (10 kelp holdfasts, no holdfasts). Data are mean proportion of urchin mortality (+ SE) for 6 replicate cages for each of 3 experimental trials and a grand mean (+ SE) for all trials

Predation rate on sea urchins tended to be higher for *C. borealis* than for *C. irroratus* in the holdfast refuge treatment in the laboratory experiments (grand mean \pm SE of trials: 1.0 ± 0.2 vs. 0.5 ± 0.2 urchins crab⁻¹ d⁻¹, respectively; $t_7 = 2.35$, $p = 0.051$) but did not differ among species in the no-refuge treatment (1.6 ± 0.2 vs. 1.3 ± 0.2 urchins crab⁻¹ d⁻¹, respectively; $t_7 = 1.07$, $p = 0.32$) (Table 2). The mean size (carapace width) of *C. borealis* was greater than that of *C. irroratus* in both treatments (holdfast refuge: $t_7 = 3.75$, $p < 0.01$; no refuge: $t_7 = 2.46$, $p = 0.044$) (Table 2). Predation rates by *C. borealis* were significantly higher in the field than in the laboratory in both treatments (holdfast refuge: 2.0 ± 0.3 vs. 1.0 ± 0.2 urchins crab⁻¹ d⁻¹, respectively; $t_6 = 3.26$, $p = 0.017$; no refuge: 3.0 ± 0.4 vs. 1.6 ± 0.2 urchins crab⁻¹ d⁻¹, respectively; $t_6 = 3.70$, $p = 0.010$) (Table 2). There was no difference in the size of *C. borealis* in field and laboratory experiments ($t_{14} = 0.727$, $p = 0.48$) (Table 2). Predation rates of crabs do not appear to be related to seawater temperature during each experiment (Table 2). In both the laboratory and field experiment, the size-frequency distribution of surviving sea urchins (in three 5 cm size classes, pooled across all trials) in cages with crabs (*C. irroratus* or *C. borealis*) did not differ from the expected size-frequency based on the null hypothesis of no size-selective predation (i.e. consumption by crabs was proportional to initial abundance in a size class) in either treatment (holdfast refuge, no refuge) (Table 4).

There was a significant difference among size classes in the proportion of sea urchins residing within holdfasts after 24 h of enclosure in laboratory

Table 4. Chi-squared goodness-of-fit (χ^2) test for difference between observed and expected frequencies of 3 size classes of sea urchins *Strongylocentrotus droebachiensis* (5–9, 10–14, 15–19 mm test diameter) surviving in cages with crabs *Cancer irroratus* or *C. borealis* at 2 levels of a refuge treatment (holdfast refuge, no refuge). Expected frequencies were based on the null hypothesis of no size-selective predation. Data are pooled over 2 to 5 trials for each analysis; N = total number of surviving urchins

Experiment	Treatment	N	df	χ^2	p
Laboratory					
<i>C. borealis</i>	Holdfasts	59	2	0.407	0.816
	No refuge	36	2	1.962	0.375
<i>C. irroratus</i>	Holdfasts	65	2	0.154	0.926
	No refuge	39	2	1.812	0.404
Field					
<i>Cancer borealis</i>	Holdfasts	75	2	5.333	0.069
	No refuge	56	2	0.607	0.738

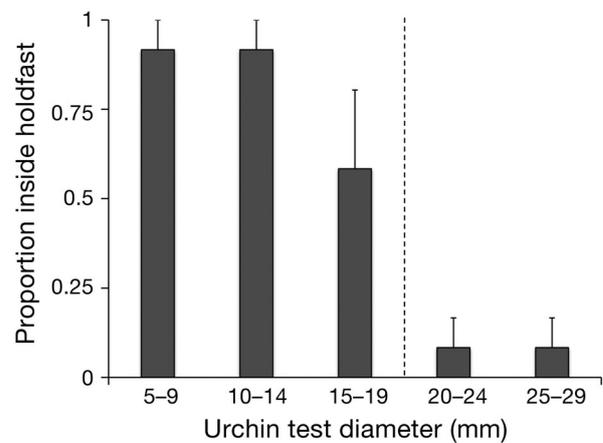


Fig. 6. Proportion of sea urchins *Strongylocentrotus droebachiensis* (out of 4) within each of 5 size classes (test diameter, mm) found within kelp holdfasts after 24 h in laboratory cages. The vertical line indicates approximate size at maturity of sea urchins (20 mm). Error bars are SE for $n = 3$ experimental trials

cages (1-way ANOVA: $F_{4,10} = 11.455$, $p < 0.001$) (Fig. 6). Two separate groups emerged, with a significantly higher proportion of sea urchins from smaller, juvenile size classes (<20 mm) within holdfasts compared to sea urchins from larger, adult size classes (20 to 29 mm) (Tukey’s test, $p < 0.001$, Fig. 6).

DISCUSSION

Kelp holdfasts as spatial refugia

We found that holdfasts of the dominant kelp *Saccharina latissima* act as an important refuge habitat to juvenile sea urchins *Strongylocentrotus droebachiensis* in Nova Scotian kelp beds. Kelp holdfasts reduced the vulnerability of juvenile sea urchins (<20 mm test diameter) to predation by cancid crabs (*Cancer borealis* and *C. irroratus*) by ~20 to 30% in field and laboratory caging experiments. Most surviving sea urchins exposed to a crab in the holdfast refuge treatment were found within holdfasts at the end of experimental trials in both the laboratory and field experiment, indicating that the holdfasts provided a spatial refuge from predation. These crabs currently are considered the dominant predators of *Strongylocentrotus droebachiensis* in kelp beds and other macroalgal habitats in the northwestern Atlantic (Scheibling 1996, Steneck et al. 2002) and can reach densities of 0.5 to 2.3 crabs m⁻² in the summer and fall in Nova Scotia (Schmidt & Scheibling 2007, Kelly et al. 2011). Any reduction in vulnerability to crab

predation afforded by kelp holdfasts (this study), or other biogenic or abiotic refuges (Keats et al. 1985, Witman 1985, Scheibling & Raymond 1990, Scheibling & Hamm 1991), is likely to greatly influence sea urchin recruitment rates.

The maximum size threshold of sea urchins that can effectively use kelp holdfasts as a spatial refuge occurs at ~20 mm test diameter. We did not observe adult sea urchins within holdfasts in the kelp beds that we sampled in summer 2010 and 2011. Similarly, we found that adult sea urchins (>20 mm) were less likely to move into and remain within holdfasts in our laboratory experiment that examined size-specific utilization of holdfasts. Time-lapse video of our field experiment showed that some large juvenile sea urchins (15 to 19 mm) that attempted to move into holdfasts were unsuccessful during the first 4.5 h in cages with crabs (*C. borealis*). However, there was no evidence of size-selective predation among the 3 experimental size classes of juvenile sea urchins in field or laboratory cages with crabs (*C. irroratus* or *C. borealis*), indicating that holdfasts likely provided protection from crab predation across the entire juvenile size range.

In our laboratory experiments, *C. irroratus* and *C. borealis* exhibited similar predation rates on juvenile sea urchins in the no-refuge treatment; however, *C. borealis* was a more effective predator in the refuge treatment with holdfasts. We occasionally observed individuals of *C. borealis* severing the haptera of holdfasts using their claws, suggesting that the larger claw size of *C. borealis* may allow it to more easily extract sea urchins from holdfasts than *C. irroratus* of similar body size. It should be noted that this behavior could be an artifact of laboratory containment, given that crabs were not offered alternative prey that may have involved less handling effort (Wong & Barbeau 2006). Moody & Steneck (1993) also found that *C. borealis* exhibits different foraging tactics than *C. irroratus* on blue mussel *Mytilus edulis* (e.g. *C. borealis* utilized only crushing tactics, while *C. irroratus* was more dexterous and utilized a greater variety of tactics). We found that predation rate on sea urchins by *C. borealis* was 2-fold greater in field than in laboratory cages (Table 2). Given that crab size and water temperature were similar in field and laboratory experiments, we attribute this difference in predation rate to cage design or some other artifact of laboratory containment.

Kelp holdfasts have been shown to harbour a broad range of algal, invertebrate and fish species in kelp beds worldwide (Ghelardi 1971, Ojeda & Santelices 1984, Anderson et al. 1997, Christie et al. 2003,

Schmidt & Scheibling 2006, Knip & Scheibling 2007, Blight & Thompson 2008, Schaal et al. 2012). Studies in the northeastern and southeastern Pacific indicate that juvenile sea urchins frequently shelter within kelp holdfasts (Dayton 1975, Vasquez et al. 1984, Pearse & Hines 1987, Tegner et al. 1995). Pearse & Hines (1987) showed that juvenile *Strongylocentrotus* spp. in California, USA, move into kelp holdfasts once they have outgrown other spatial refuges, such as crevices. Dayton (1975) observed juvenile *Strongylocentrotus* sp. in holdfasts of *Laminaria* spp. in Alaska, USA, where sea urchin populations are strongly controlled by sea otter predation. He noted that sea urchins disappeared from a study site when the kelp canopy cover was removed, suggesting that kelp provides a refuge from predation by sea otters. Along the southwestern coast of South Africa, holdfasts of kelp *Ecklonia maxima* facilitate recruitment of juvenile conspecifics by providing a refuge from grazers such as sea urchins, abalone, limpets and gastropods (Anderson et al. 1997).

Christie et al. (2003) found a significant positive relationship between the total number of individuals within holdfasts of *L. hyperborea* in Norway (incorporating up to 77 faunal species, including sea urchins *Echinus esculentus* and *Psammechinus miliaris*) and holdfast volume. Although we did not observe a direct relationship between sea urchin abundance and holdfast volume of *Saccharina latissima*, there were numerous other invertebrates within the holdfast that were not considered. Knip & Scheibling (2007) recorded 15 taxa (family, genus or species level) from 6 phyla in holdfasts of *L. digitata* in a kelp bed along a headland (Splitnose Point) ~40 km east-southeast of St. Margarets Bay. *Strongylocentrotus droebachiensis* was not recorded, possibly because the haptera of *L. digitata* in wave-exposed habitats are tightly applied to the rock substratum, leaving less refuge space for juvenile sea urchins. These holdfasts are filled by small bivalves and by brittle stars and sea stars that can conform to small and irregular gaps among haptera.

We found that the size of sea urchins within holdfasts was directly related to the volume of space within a holdfast. Larger holdfasts can provide a spatial refuge to sea urchins in late juvenile or early adult stages that may be most vulnerable to predation, as they have outgrown smaller physical refuges (e.g. narrow crevices, interstices of cobbles) but have not yet reached a size refuge from small-mouthed fish and decapod predators (Scheibling & Hamm 1991). Mesopredators of juvenile sea urchins, such as sea stars and polychaetes, were rare within kelp

holdfasts in our study, with only single individuals of *Asterias* sp., *Nereis* sp., or *Polynoidae* observed in a total of 45 holdfasts sampled in June 2011. We observed no predatory decapods (e.g. juvenile cancrid crabs) within holdfasts. This suggests that predation pressure on juvenile sea urchins within holdfasts may be minimal.

Tegner et al. (1995) found that juveniles of *Strongylocentrotus purpuratus* and *S. franciscanus* graze holdfasts of giant kelp *Macrocystis pyrifera* in California, forming cavities that increase susceptibility of kelp to breakage during storms, thereby increasing kelp mortality. We found no evidence that juvenile *S. droebachiensis* cause appreciable damage to holdfasts of *Saccharina latissima*, likely because they are sustained by particulate algal detritus actively or passively trapped within the holdfast microhabitat (Bernstein et al. 1981, Rowley 1990, Scheibling & Hamm 1991, Dumont et al. 2004).

Facilitation of sea urchin recruitment by kelp: consequences for kelp-bed resilience

Positive feedback mechanisms within both kelp beds and barrens increase the resilience of each state to phase shifts, and these often involve facilitation or inhibition of sea urchin recruitment (reviewed by Filbee-Dexter & Scheibling 2014). For example, a higher cover of coralline algae in barrens compared to kelp beds may result in increased settlement of sea urchin larvae in barrens due to induction by coralline algae (Pearce & Scheibling 1990, Baskett & Salomon 2010). Conversely, the lower cover of coralline algae in kelp beds promotes persistence of kelp beds by reducing settlement rates of sea urchins (Baskett & Salomon 2010). Other feedback mechanisms stabilizing the kelp bed state include increased habitat available for benthic macroinvertebrates and demersal fish that prey on sea urchins; the whiplash effect of wave-driven kelp fronds, which impedes sea urchin grazing; and the production of detrital algae within the kelp bed, which promotes passive detritivory rather than destructive grazing by resident sea urchins (Filbee-Dexter & Scheibling 2014).

Adult sea urchins were rare in the kelp bed sampled in St. Margarets Bay in summer 2010, following an epizootic that caused a mass mortality of sea urchins the previous fall (Feehan & Scheibling 2014). Our results suggest that kelp holdfasts can act to facilitate the reestablishment of sea urchin populations in kelp beds after disease outbreaks by providing refuge to juvenile urchins from predators such as

cancrid crabs. These crabs are now considered apex predators in kelp beds in the northwestern Atlantic as a consequence of historical overfishing of higher trophic level predators, such as large demersal fish (Steneck et al. 2004). In a recent review, Filbee-Dexter & Scheibling (2014) conclude that while positive feedbacks that strengthen resilience of kelp-bed ecosystems are relatively well known, examples of negative feedbacks that could destabilize kelp ecosystems are generally lacking. Given that dense populations of *S. droebachiensis* destructively graze kelp beds in the northwestern Atlantic, our findings suggest a potentially important negative feedback mechanism whereby a dominant kelp facilitates recruitment of its major grazer. This also underscores the importance of considering ontogenetic shifts in predator-prey interactions that can govern ecosystem dynamics.

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