

# Aggregative feeding behavior in sea urchins leads to destructive grazing in a Nova Scotian kelp bed

C. Feehan<sup>1,\*</sup>, R. E. Scheibling<sup>1</sup>, J. S. Lauzon-Guay<sup>2</sup>

<sup>1</sup>Biology Department, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

<sup>2</sup>Fisheries and Oceans Canada, Institut Maurice-Lamontagne, Mont-Joli, Quebec G5H 3Z4, Canada

**ABSTRACT:** Grazing aggregations of the sea urchin *Strongylocentrotus droebachiensis* drive the transition between alternative ecosystem states in Nova Scotia, from productive kelp beds to less productive barrens. This transition can be initiated by the formation of gaps within a kelp bed, containing dense aggregations of sea urchins. We examined the importance of local density of sea urchins and pre-existing gaps in a kelp canopy in mediating the formation of destructive grazing aggregations of sea urchins in a kelp bed. We transplanted 14 000 adult sea urchins from a barrens on the Atlantic coast of Nova Scotia into ~4.5 m<sup>2</sup> plots within a nearby kelp bed, at densities above and below a predicted threshold value for destructive grazing, and simulated disturbance to the kelp bed by removing the kelp canopy in half of the plots. Sea-urchin abundance and gap formation and expansion (as loss of kelp canopy cover) were monitored in and around plots weekly for 9 wk. Grazer-mediated gap formation began 3 wk after sea urchins were introduced, and increased for the remainder of the experiment. Our results indicate a direct linear relationship between sea-urchin abundance and increase in gap area within undisturbed treatments. Gaps expanded in the kelp bed at sea-urchin densities below the putative threshold for destructive grazing, indicating that the kelp bed was less resilient to grazing than predicted. Our findings provide insights into mechanisms controlling the stability of the kelp-bed ecosystem state and mediating shifts from kelp beds to barrens in Nova Scotia.

**KEY WORDS:** Alternative states · Destructive grazing · Aggregation · *Strongylocentrotus droebachiensis* · Kelp beds

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## INTRODUCTION

Transitions between alternative ecosystem states often are considered catastrophic events because they cause abrupt changes in ecosystem structure and function that can lead to loss of ecosystem services to humans (Scheffer et al. 2001). Understanding the mechanisms that drive shifts between contrasting community configurations is critical to judicious management and conservation of these ecosystems (Scheffer et al. 2001, Beisner et al. 2003). To restore or maintain an ecosystem state that is ecologically or economically desirable, we must first understand

feedback mechanisms that stabilize a given state and the factors that reduce its resilience.

Population outbreaks of sea urchins have repeatedly led to destructive grazing of kelp beds in temperate coastal regions (North & Pearse 1970, Breen & Mann 1976b, Hagen 1983, Johnson et al. 2005), with dramatic implications for ecosystem productivity and services (Mann 1982). Kelps create 3-dimensional structure and provide food and habitat for a diverse fauna, including many ecologically or economically valuable species, such as fish, lobsters, and sea otters (Dayton 1985). Along the Atlantic coast of Nova Scotia, grazing by high-density aggregations (fronts)

\*Email: colette.feehan@dal.ca

of sea urchins *Strongylocentrotus droebachiensis* at the offshore margin of kelp beds drives transitions between alternative community states, from kelp beds to sea-urchin barrens, on a decadal scale (Johnson & Mann 1988, Scheibling et al. 1999, Brady & Scheibling 2005, Lauzon-Guay & Scheibling 2007a). Previous studies provide evidence of a threshold biomass of sea urchins ( $\sim 2 \text{ kg m}^{-2}$ ) for destructive grazing of kelp beds in Nova Scotia (Breen & Mann 1976a,b, Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007a). At this threshold, sea urchins undergo a shift in feeding behavior, from passive feeding on drift algae and grazing coralline substrata to gregarious feeding that enables them to effectively weigh-down and consume kelp blades (Breen & Mann 1976b, Lauzon-Guay & Scheibling 2007a). Lauzon-Guay et al. (2008) expressed this threshold as a ratio of sea urchin to kelp biomass (1:2) in a model of the formation and propagation of grazing fronts that showed strong concordance between predicted and observed results.

In the late 1960s, Mann (1972) observed gaps in the kelp bed, with high densities of sea urchins, in St. Margarets Bay, a large semi-protected embayment near Halifax, Nova Scotia. These gaps gradually expanded and coalesced, resulting in a loss of  $140 \text{ km}^2$  of kelp bed in the bay and a shift to the barrens state by 1973 (Breen & Mann 1976b, Mann 1977). Since those pioneering studies, destructive grazing by sea urchins has been recorded repeatedly within St. Margarets Bay (as it has elsewhere in Nova Scotia) at the deep margin of kelp beds (Scheibling et al. 1999, Lyons & Scheibling 2008), although the transition to the barrens state was interrupted in each case by outbreaks of disease that eliminated the sea urchins. To our knowledge, the initial formation of gaps within a kelp bed, attributed to sea-urchin grazing, has not been recorded in the NW Atlantic.

To explore the possibility that sea-urchin aggregations within a kelp bed could lead to a shift to the barrens state, Lauzon-Guay & Scheibling (2010) developed a coupled map lattice model to simulate the spatial dynamics of kelp and sea-urchin abundance over time, under different sets of conditions relating to urchin movement, spatial variability in recruit density, localized sea-urchin aggregation, and localized disturbance that creates gaps in the kelp bed. For example, their model shows that pre-existing gaps in a kelp bed can catalyze the shift to barrens by causing sea urchins to aggregate along the perimeter of the gap and graze outwards. This requires that sufficient numbers of sea urchins inhabit the kelp bed when gaps are formed, and that sea urchins migrate to the gap perimeter as they forage. The model also

shows that a localized aggregation of sea urchins within a kelp bed can result in destructive grazing leading to gap formation. As these gaps expand, an influx of sea urchins from a background population within the kelp bed maintains sea-urchin density along the gap margin.

The Lauzon-Guay & Scheibling (2010) model not only indicates that formation of sea-urchin grazing aggregations and consequent canopy loss within a kelp bed are theoretically possible, but also yields predictions that can be used to inform manipulative field experiments to test causal mechanisms. The present study experimentally examines 2 factors that can potentially trigger destructive grazing within kelp beds and mediate the transition to a barrens state: local density of sea urchins and pre-existing gaps in a kelp canopy. Based on the results of previous grazing experiments, we predicted that gaps within a kelp bed would form in areas where sea-urchin biomass exceeded the established threshold (Breen & Mann 1976a,b, Scheibling et al. 1999). Also, because sea urchins tend to aggregate along a kelp-barrens interface (Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007a), we predicted that manually clearing kelps to create artificial gaps within the kelp bed would catalyze the formation of grazing aggregations and expand these cleared patches. We examined potential interactive effects on destructive grazing of local sea-urchin density and presence of pre-existing gaps in a kelp canopy by manipulating these factors concurrently in a factorial experiment at a site where Breen & Mann (1976a) first documented the phenomenon between 1968 and 1973. Our findings provide insight into mechanisms that reduce resilience of the kelp-bed state and drive shifts to the alternative and less productive barrens state.

## MATERIALS AND METHODS

### Study site and experimental design

Our study site at The Lodge ( $44^{\circ} 33.491' \text{ N}$ ,  $64^{\circ} 01.493' \text{ W}$ ) is located on the western shore of St. Margarets Bay (Fig. 1). At the time of the experiment, the shallow subtidal zone was covered by a dense kelp canopy (mainly *Saccharina longicruris* and scattered *Agarum clathratum* and *Laminaria digitata*) with a turf understory of coralline (*Corallina officinalis*), foliose (*Chondrus crispus*), and filamentous (*Polysiphonia lanosa*, *Bonnemaisonia hamifera*) red algae. The substratum is a gradually sloping field of granitic boulders and cobble, which grades to sand at

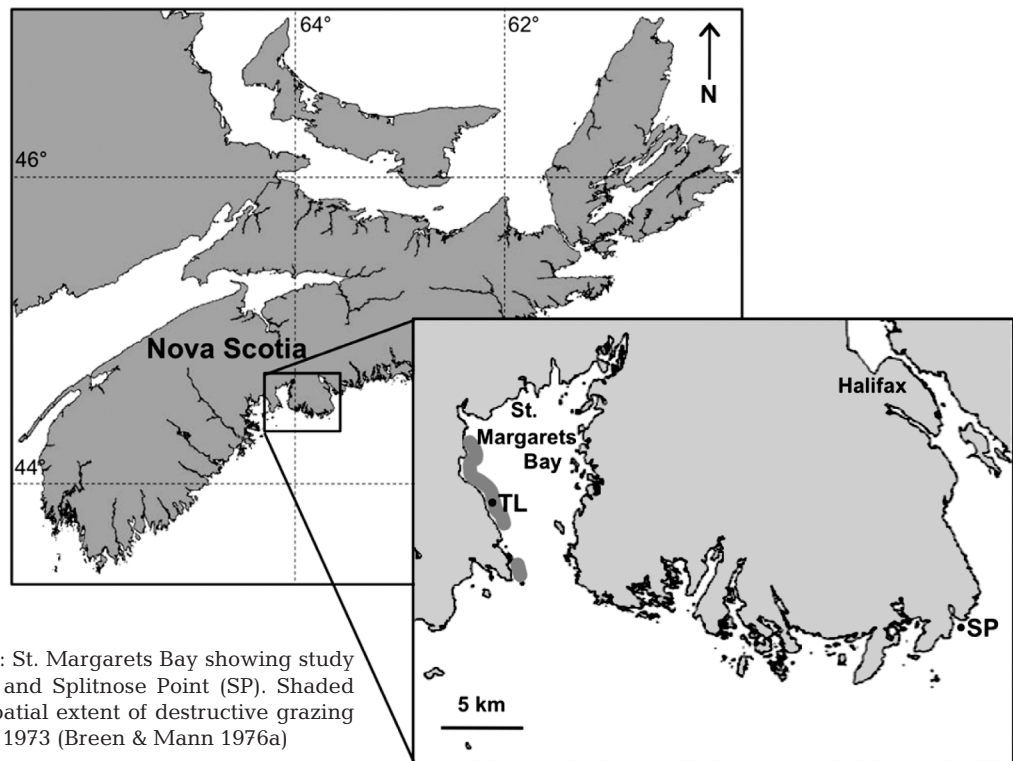


Fig. 1. Nova Scotia. Inset: St. Margaret's Bay showing study sites at The Lodge (TL) and Splitnose Point (SP). Shaded area along the coast = spatial extent of destructive grazing between 1968 and 1973 (Breen & Mann 1976a)

~18 m depth. A preliminary SCUBA-diving survey conducted in June 2009 indicated that adult sea urchins *Strongylocentrotus droebachiensis* (>20 mm test diameter) were rare at this site.

To examine the effects of local sea-urchin density and small-scale disturbance to the kelp bed on the formation of destructive grazing aggregations, we used SCUBA to collect 14 000 adult (42 to 61 mm test diameter,  $n = 20$ ) sea urchins from a feeding front at Splitnose Point (44° 28.609' N, 63° 32.741' W), 40 km east-southeast of The Lodge (Fig. 1), and transplant them into the kelp bed at The Lodge on 14 July 2009. Our experimental array consisted of 32 circular plots spaced 7 m apart and equally divided among 4 depth strata running parallel to shore from 7 to 10 m depth (chart datum). Each plot was marked with a central float anchored to the substratum with marine epoxy glue. SCUBA divers manually cleared all kelps by completely removing thalli at the holdfast within a 1.2 m radius of the center of half of the plots, as a disturbance treatment (hereinafter referred to as 'disturbed plots'). All cleared kelps were collected in mesh bags and subsequently discarded in deeper water, 100s of meters from our experimental site. Sea urchins were dispersed by divers within an ~1.2 m radius of the center of plots at 4 levels of density (0, 50, 100, and 200 sea urchins  $m^{-2}$ , or 0, 250, 500, and 1000 sea urchins  $plot^{-1}$ ). These densities were

selected to encompass values both below and above the putative 1:2 threshold ratio of sea urchin to kelp biomass required for destructive grazing to occur. One replicate of each treatment combination of sea-urchin density by disturbance was randomly allocated to each depth stratum. Depth was used as a blocking factor to account for variation in environmental conditions across a depth gradient (e.g. temperature, light, water motion) (Fig. 2a).

Kelp defoliation by physical or biological disturbance, such as extreme wave forces during hurricanes (K. Filbee-Dexter & R. E. Scheibling unpubl.) or outbreaks of an epiphytic bryozoan that causes extensive blade loss (Saunders & Metaxas 2008, Scheibling & Gagnon 2009), can create large gaps or cause major thinning in Nova Scotian kelp beds. The area that we cleared for the experiment was limited by logistical constraints of manipulation and monitoring, although this patch size is within the scale of disturbance resulting from storm events (Ebeling et al. 1985, R. E. Scheibling pers. obs.).

### Environmental conditions

Water temperature was recorded at 10 min intervals using a temperature logger (StowAway TidbiT Temp Logger, Onset Computer) at 8 and 12 m depth

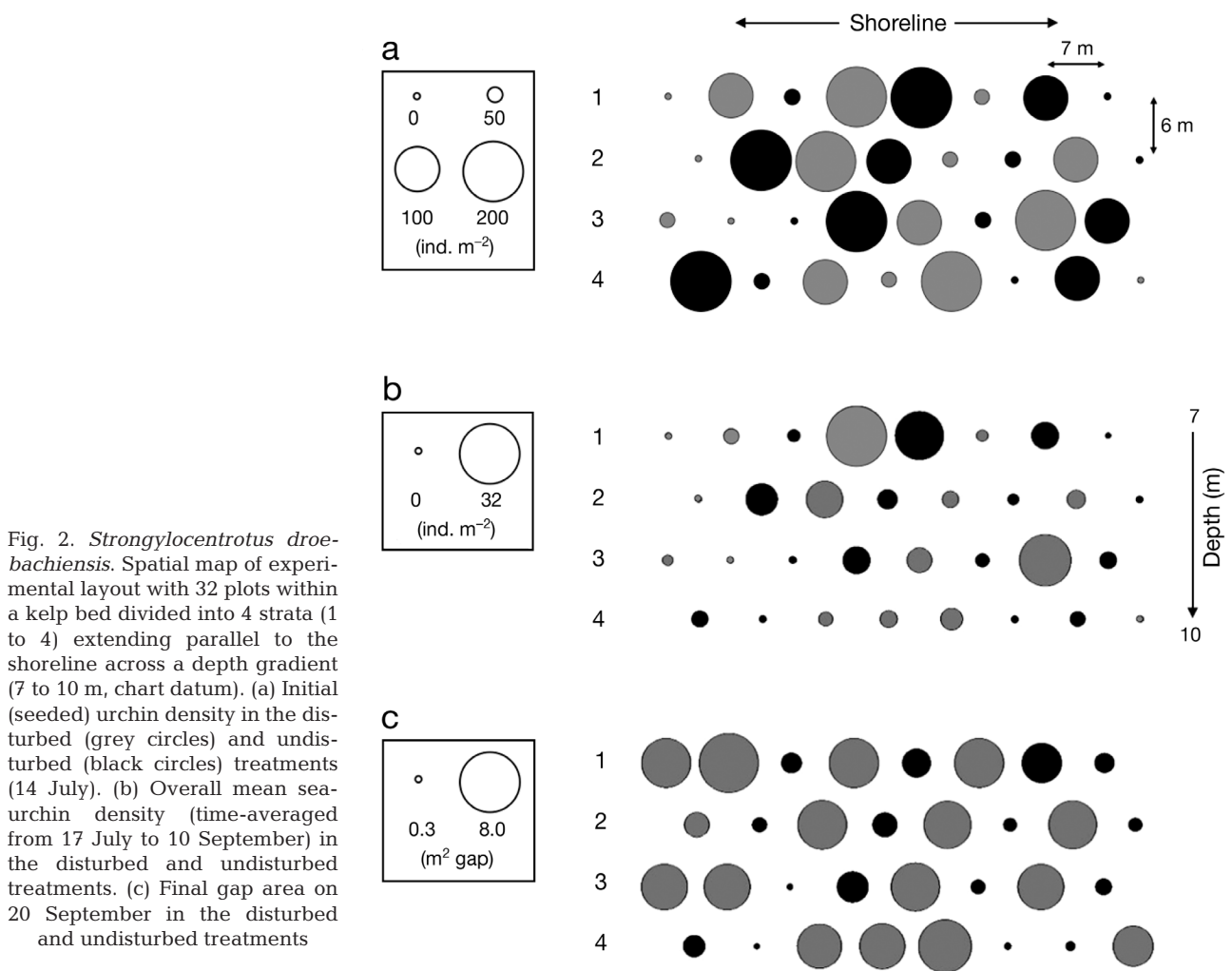


Fig. 2. *Strongylocentrotus droebachiensis*. Spatial map of experimental layout with 32 plots within a kelp bed divided into 4 strata (1 to 4) extending parallel to the shoreline across a depth gradient (7 to 10 m, chart datum). (a) Initial (seeded) urchin density in the disturbed (grey circles) and undisturbed (black circles) treatments (14 July). (b) Overall mean sea-urchin density (time-averaged from 17 July to 10 September) in the disturbed and undisturbed treatments. (c) Final gap area on 20 September in the disturbed and undisturbed treatments

at The Lodge throughout the experiment. Significant wave height (SWH; average height of the highest one-third of waves in a wave field) was recorded at a meteorological buoy ([www.meds-sdmm.dfo-mpo.gc.ca](http://www.meds-sdmm.dfo-mpo.gc.ca), buoy identification no. C44258) at the mouth of Halifax Harbour (44° 30' N, 63° 24' W).

#### Kelp and sea-urchin biomass

Kelp biomass at the experimental site was  $3.4 \pm 1.6$  kg m<sup>-2</sup> (mean  $\pm$  1 SD,  $n = 32$ ) based on pooled samples of kelps harvested from a 1 m<sup>2</sup> quadrat placed haphazardly 2 to 4 m from each end of the experimental array at each depth stratum on 14 July, 2 August, and 3 and 24 September 2009 (quadrat locations were staggered among sampling dates to preclude overlap), and weighed on shore with a spring scale. Wet weight of the experimental sea urchins was  $68 \pm 20$  g (mean  $\pm$  1 SD,  $n = 40$ ) based on haphazard collections of 20 sea urchins from the

experimental population on 24 July and 17 September 2009 weighed in the laboratory on an analytical scale (0.001 g precision) within 24 h of collection. Sea-urchin biomass (fresh weight) was calculated for each experimental plot as the mean sea-urchin wet weight multiplied by sea-urchin density.

#### Sea-urchin abundance

The abundance of sea urchins within experimental plots was monitored weekly for 9 wk beginning 17 July 2009. SCUBA divers counted all adult sea urchins in a 0.25 m<sup>2</sup> quadrat initially placed at the center of each plot and then flipped in 4 contiguous lines radiating at right angles from the center, stopping when sea urchins were no longer observed in the quadrat. The 4 quadrat counts taken equidistant from the center of a plot in each radial line were summed and extrapolated to the total area of a conceptualized concentric circular band (0.5 m wide). The total sea

urchin count was calculated as the central quadrat ( $\sim 0.25$  m radius) plus the estimates from each concentric band (0.25 to 0.75 m, 0.75 to 1.25 m, etc.). The total radius surveyed within each plot was increased over the course of the experiment from 2.25 to 3.25 m (corresponding to 4 to 6 contiguous quadrat samples from the center of a plot) to account for urchins that had migrated toward the periphery of plots. Naturally occurring juvenile sea urchins ( $< 20$  mm test diameter), which were cryptic and at low density, and dead sea urchins and tests were recorded within the quadrat during urchin abundance surveys. Decapod predators of sea urchins (cancrid crabs *Cancer irroratus* and *C. borealis*, and lobster *Homarus americanus*) were also recorded when observed within plots. Sea-urchin densities decreased rapidly during the initial 2 wk of the experiment. Therefore, on 2 August each experimental plot was supplemented with sea urchins taken from a surplus supply (from the same experimental source population) maintained in a mesh corral on the sand bottom near the offshore margin of the kelp bed (18 m depth), and fed kelp. We added an additional 10% of the respective initial sea-urchin density to each plot. During the final survey of sea-urchin abundance on 17 September, divers exhaustively searched each experimental plot, up to a 3.5 m radius, and counted all dead and live sea urchins. At this time, an amoebic disease associated with the passage of Hurricane Bill on 23 August 2009 had caused 35% morbidity of the remaining urchins (Scheibling et al. 2010), and the experiment was terminated. For statistical analyses, mean sea-urchin density (urchins  $\text{m}^{-2}$ ) was calculated within each plot at weekly intervals as the total sea-urchin count per  $\text{m}^2$  within a 2.25 m radius of the center of the plot (96% of all sea urchins were found within this radius), to coincide with the radius used to monitor gap formation and expansion (see next section). Overall mean sea-urchin density (urchins  $\text{m}^{-2}$ ) was calculated as the time-averaged (grand mean) density for each plot from 17 July to 10 September. To maintain relevant mean values, only sea-urchin abundance data collected prior to the disease outbreak (up to 10 September, when moribund sea urchins were rare) were included in the statistical analyses.

### Gap formation and expansion

Kelp loss was monitored within experimental plots using 2 types of measures: gap area and patch area. For all plots, gap area is the planar surface area of bottom not covered by kelp blades when a plot is

viewed from a set height above bottom. Gap area increases as gaps form (in undisturbed plots) or expand (in all plots) because of grazing by sea urchins. Other biotic and abiotic factors can contribute to increases in gap area, as evidenced by increases in control plots without sea urchins. Patch area is the planar surface area of bottom devoid of attached kelps and was only measured in disturbed plots, where initial patches were created by clearing kelps within a 1.2 m radius ( $4.5 \text{ m}^2$ ). Patch area increases by removal of additional kelp thalli by sea-urchin grazing at the patch perimeter. Patch area is expected to be larger than gap area because patches, when viewed from above, may be partially occluded by kelp blades around the patch perimeter. Wave-driven movement of these blades can cause some variation in successive measurements of gap area, even when patch area remains constant. In undisturbed plots, small and irregular patches of bottom devoid of kelps were created as a result of sea-urchin grazing, but these were too difficult to measure as they increased in number and size and changed shape over time. Also, these small patches could not be referred to a known baseline, as in the disturbed plots. Thus, patch area was not measured in the undisturbed plots.

To determine gap area, all plots were photographed (Canon Powershot G10) from 4 to 6 m above bottom, approximately weekly for 5 to 6 wk, beginning at Week 3 (7 August) for the undisturbed plots (at the first appearance of gaps in these plots), and at Week 4 (14 August) for the disturbed plots. A  $0.25 \text{ m}^2$  quadrat, or 2 m long crossed plastic poles with 0.5 m graduations, was placed at the center of each plot as a scale reference for all photographs. During the final week of the experiment we observed small amounts of drift kelp within the plots where these were previously absent. Divers removed the drift kelp prior to taking the final set of photographs (20 September). Gap area was measured from photographs using ImageJ (National Institutes of Health, USA). Gaps were identified as areas devoid of kelp cover where underlying turf algae, granite rock, or sand was visible. The area of all gaps observed within a plot was summed to yield the total gap area ( $\text{m}^2$ ). For statistical analyses, gap area measurements up to 20 September (after the disease outbreak) were included, as sea urchins were present in the plots until this date (albeit in low numbers in the final week) and could potentially cause kelp loss.

Patch area was monitored in the disturbed plots approximately weekly for a 7 wk period from 23 July (1 wk after sea urchin introduction) to 10 September.



Divers used a plastic measuring tape to measure the radius from the plot center to the nearest kelp stipes at 8 equidistant locations along the circumference of the plot. The radial measurements ( $r$ ) were averaged within each plot to get an estimate of the patch area ( $\pi r^2$ ).

### Statistical analysis

To test the efficacy of our manipulation of sea-urchin density over the initial 8 wk of the experiment (prior to disease outbreak), we used repeated-measures ANOVA (RM-ANOVA) with initial sea-urchin density (3 levels) and disturbance (2 levels) as fixed factors, depth stratum (4 levels) as a random blocking factor, and time as the repeated factor. Sea-urchin density was square-root-transformed to meet the assumption of homoscedasticity, and control plots (0 sea urchins  $\text{m}^{-2}$ ) were not included in the analysis to eliminate zero counts. We also used RM-ANOVA to test for the effect of initial sea-urchin density (4 levels, fixed), depth stratum (4 levels, random), and time on: (1) gap area of undisturbed plots over a 6 wk period (7 August to 20 September), (2) gap area of disturbed plots over a 5 wk period (14 August to 20 September), and (3) patch area of disturbed plots over a 7 wk period (23 July to 10 September). Because sea-urchin density during the experiment

was variable both within and among the initial urchin-density treatments, we used linear regression with overall mean sea-urchin density (time-averaged from 17 July to 10 September for each plot) as the predictor variable to test for the effect of sea-urchin abundance throughout the experiment on: (1) final gap area of undisturbed plots (on 20 September), (2) final gap area of disturbed plots (on 20 September), and (3) final patch area of the disturbed plots (on 10 September, the last date patch area was measured).

Statistical tests were run with Statistica 8 (StatSoft). Assumptions of homoscedasticity were tested using Cochran's  $C$ -test ( $\alpha = 0.05$ ). For ANOVA, interactions with the random blocking factor (depth stratum) that were highly non-significant ( $p > 0.25$ ) were removed from the analysis and the interaction mean square was pooled with residual mean square (Underwood 1997). The assumption of sphericity in RM-ANOVA was non-significant using Mauchly's test ( $\alpha = 0.05$ ). Tukey's HSD test ( $\alpha = 0.05$ ) was used to compare levels of factors that were significant in ANOVA.

## RESULTS

### Environmental conditions

Daily temperature (average  $\pm 1$  SD) from 14 July to 20 September was  $12.7 \pm 1.8^\circ\text{C}$  within the experimental area at 8 m depth and  $10.5 \pm 2.7^\circ\text{C}$  at 12 m depth, i.e. 2 m below the deepest stratum (Fig. 3a). SWH generally ranged from 0.5 to 2 m throughout the experiment, except for 2 storm events: Hurricane Bill (maximum SWH: 9 m) on 23 August and Tropical Storm Danny (maximum SWH: 3.5 m) on 30 August (Fig. 3b).

### Sea-urchin abundance

Our initial measure of sea-urchin abundance after 3 d (17 July) showed that densities were already well below the levels seeded, and lowest in Stratum 4 (Fig. 4). Although sea-urchin density continued to decrease throughout the experiment (Table 1, Fig. 4), particularly in the high-initial-density (200 urchins  $\text{m}^{-2}$ ) plots (Fig. 5), significant differences in relative abundance among initial density lev-

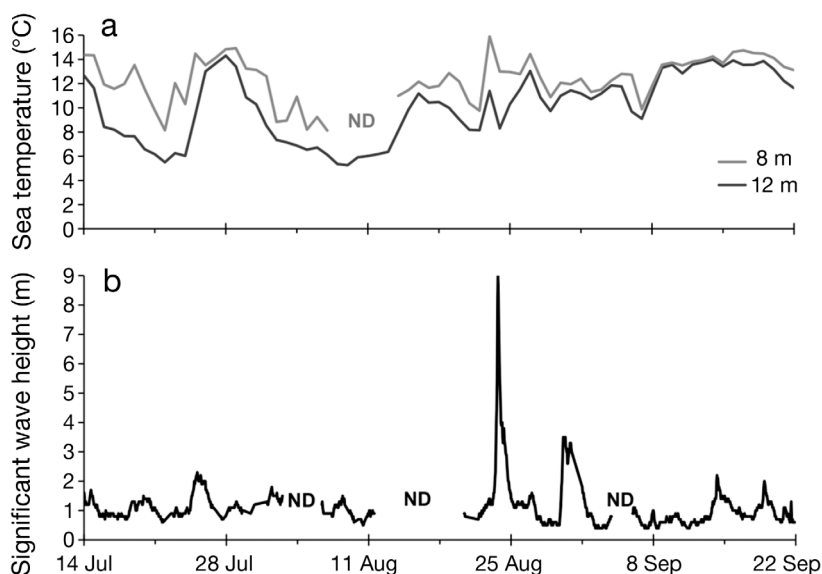


Fig. 3. (a) Temperature at 8 and 12 m depth at The Lodge and (b) significant wave height (measured off Halifax) during the experiment. Note abrupt fluctuations in temperature and significant wave height associated with the passage of Hurricane Bill on 23 August and Tropical Storm Danny on 30 August, 2009. ND: no data available

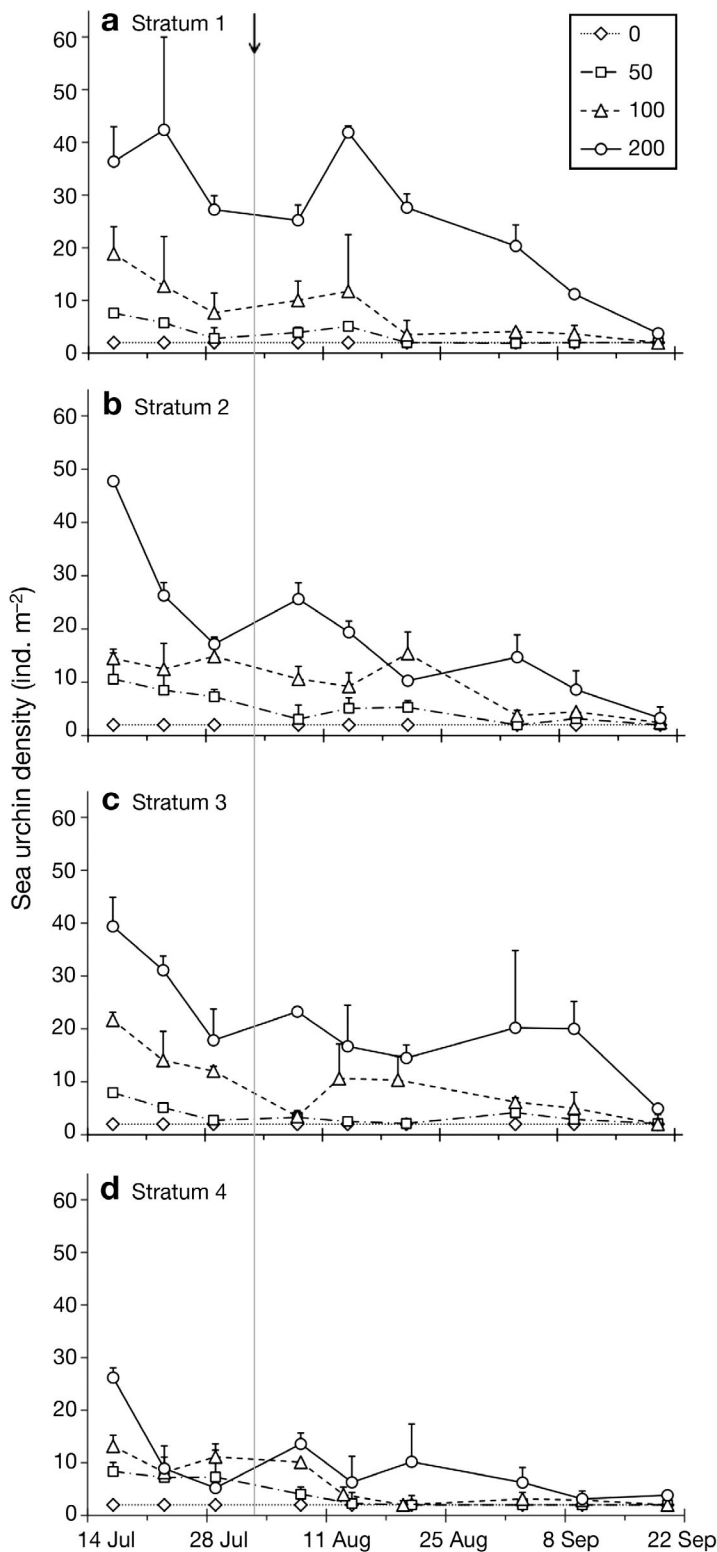


Fig. 4. *Strongylocentrotus droebachiensis*. Sea-urchin density (ind. m<sup>-2</sup>, mean  $\pm$  SE) at 4 levels of initial urchin density (see key) within depth strata 1 to 4 (a,b,c,d) over a 9 wk period. Means are pooled over 2 levels of disturbance. Vertical arrow: sea urchins replenished in the plots

Table 1. *Strongylocentrotus droebachiensis*. Repeated-measures ANOVA of effect of initial sea-urchin density (3 levels: 50, 100, 200 ind. m<sup>-2</sup>), disturbance (2 levels: disturbed, undisturbed), depth stratum (4 levels), and time on sea-urchin density (ind. m<sup>-2</sup>, square-root transformed) over 8 wk. **Bold** values are significant at  $p \leq 0.05$ . For within-subject effects, Time (T)  $\times$  Density (Dens), T  $\times$  Disturbance (Dist), T  $\times$  Dens  $\times$  Dist, and T  $\times$  Dens  $\times$  Stratum (Strat) are tested against pooled T  $\times$  Dist  $\times$  Strat MS and residual MS. For between-subject effects, Dist, Strat, Dens  $\times$  Dist, and Dens  $\times$  Strat are tested against pooled Dist  $\times$  Strat MS and residual MS

Source of variation	df	MS	F	p
<b>Within-subject effects</b>				
T	7	12.68	24.67	<b>&lt;0.0001</b>
T $\times$ Dens	14	0.53	1.04	0.428
T $\times$ Dist	7	0.42	0.82	0.571
T $\times$ Strat	21	0.65	1.26	0.240
T $\times$ Dens $\times$ Dist	14	0.55	1.07	0.397
T $\times$ Dens $\times$ Strat	42	0.56	1.08	0.383
T $\times$ Dist $\times$ Strat	21	0.43	0.77	0.733
Residual	63	0.51		
<b>Between-subject effects</b>				
Dens	2	97.52	22.47	<b>0.002</b>
Dist	1	3.65	1.70	0.224
Strat	3	9.76	4.57	<b>0.033</b>
Dens $\times$ Dist	2	2.77	1.29	0.321
Dens $\times$ Strat	6	4.34	2.03	0.164
Dist $\times$ Strat	3	2.50	1.28	0.365
Residual	9	2.14		

els were maintained throughout the experiment (Tukey's test,  $p < 0.05$ ) until the mass mortality on 17 September (Table 1, Figs. 2b & 4). The effect of the disturbance treatment on sea-urchin abundance was non-significant (Table 1). Sea-urchin density varied significantly among the 4 depth strata (Table 1), with the fewest sea urchins remaining in Stratum 4 (Fig. 4). This result is concordant with our observations of dead urchins in quadrat surveys, which were most abundant in Strata 2 and 4, with a total of 29, 76, 33, and 82 observations of dead urchins or tests in Strata 1 to 4, respectively, during the experiment. We observed crabs and lobsters preying on sea urchins within experimental plots, but their abundance within strata (6, 5, 1, and 2 crabs and 9, 17, 16, and 13 lobsters in total in Strata 1 to 4, respectively) did not correlate with the abundance of dead urchins. Cunnners *Tautogolabrus adspersus* preyed on moribund sea urchins during the disease outbreak.

Generally, sea urchins formed small actively grazing aggregations scattered throughout the plots (Fig. 6a,b). However, in 2 of the high-density (200 ind. m<sup>-2</sup>) disturbed plots, sea urchins formed a single large sedentary aggregation in the center of the plot that persisted throughout the experiment (Strata 1 and 3;

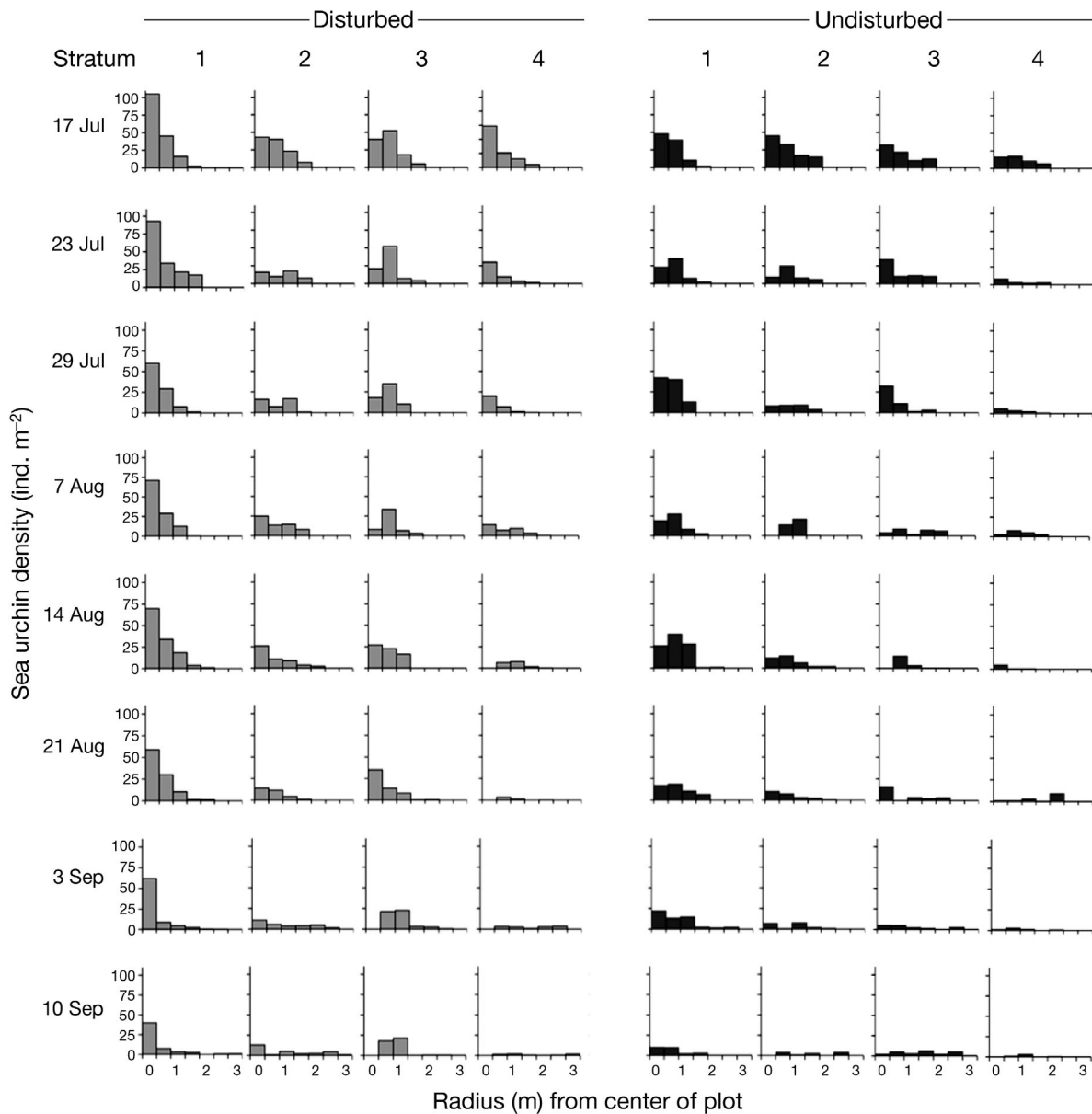


Fig. 5. *Strongylocentrotus droebachiensis*. Distribution of sea-urchin density over 8 wk measured in 0.5 m increments from the center of the plots to a 3 m radius for the 200 ind. m<sup>-2</sup> initial density treatment at 2 levels of disturbance within 4 depth strata

Figs. 5 & 6c,d). In both of the plots, the large aggregation formed on a boulder at the center of the plot, and divers periodically observed sea urchins feeding on drift kelp, or attached blades that fell into the plot from the edge of the cleared area (Fig. 6d).

#### Gap formation and expansion

Gaps first appeared in the undisturbed treatment after 3 wk (7 August; Fig. 6a) and increased signifi-

cantly over time during the next 6 wk (Table 2, Fig. 7a). Although the effect of initial sea-urchin density on gap area was marginally non-significant ( $p = 0.067$ ) among undisturbed plots (low replication and high variability in density treatments limited the power of the analysis), the mean increase in gap area was greatest in the high-initial-density treatments (100 and 200 urchins m<sup>-2</sup>) (Table 2, Fig. 7a). The effect of stratum on gap area varied across time in the undisturbed treatment (Table 2), with the rate of gap expansion decreasing from Stratum 1 to Stratum 4.



This significant interaction of time and stratum is likely the result of differences in sea-urchin density among strata (at all initial density levels, excluding the control), with density decreasing from Stratum 1 to Stratum 4 (Fig. 4).

In the disturbed treatment, gap area measured over a 5 wk period from 14 August to 20 September did not depend on initial sea-urchin density or depth stratum but increased significantly with time (Table 2, Fig. 7b). However, initial sea-urchin density, depth stratum, and time all had significant effects on patch area over a 7 wk period from 23 July to 10 September (Table 2). Patch area in the control treatment (initial density: 0 urchins  $\text{m}^{-2}$ ) was significantly lower than at all other levels of initial sea-urchin density over this period (Tukey's test,  $p < 0.03$ ; Fig. 7c). Patch area in the control treatment on 23 July ( $5.5 \text{ m}^2$ ; Fig. 7c)

approximates initial patch area in disturbed plots at the start of the experiment (14 July). Initial patch area exceeded the cleared area ( $4.5 \text{ m}^2$ ) because some kelps along the patch perimeter were outside the 1.2 m radius that was experimentally cleared. Overall, patches were significantly smaller on 23 July than during any of the succeeding weeks, which did not differ significantly (Tukey's test,  $p > 0.50$ ; Fig. 7c). This result suggests that patches expanded at initial density levels of 50, 100, and 200 urchins  $\text{m}^{-2}$  (as compared to the control with 0 urchins  $\text{m}^{-2}$ ) within the first 1 to 2 wk of the experiment, when mean sea-urchin densities were the highest (Fig. 4).

Overall, sea-urchin density was highly variable both within and among treatments during the experiment. When final gap area is analyzed in relation to the overall time-averaged density during the ex-

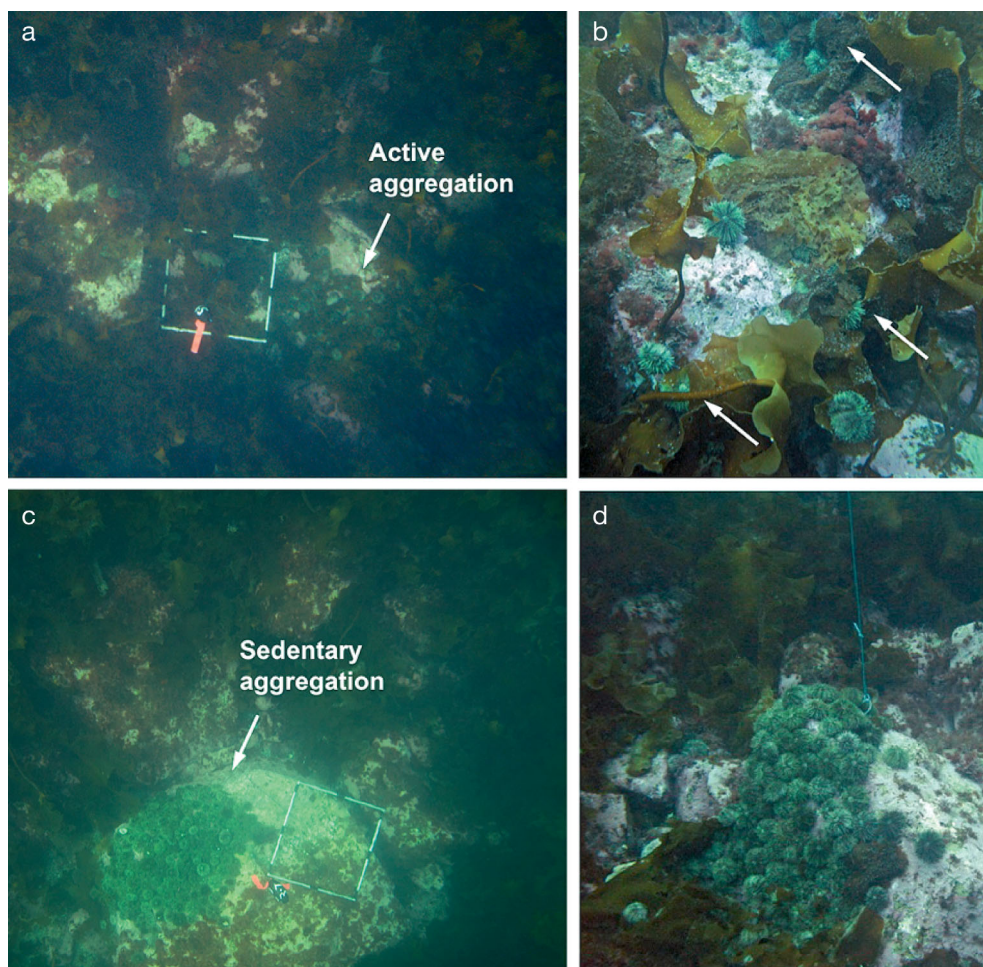


Fig. 6. *Strongylocentrotus droebachiensis*. (a,b) Small active grazing aggregations of sea urchins (indicated by arrows in b) initiate small gaps in the kelp canopy of undisturbed plots. (c,d) Large sedentary (non-grazing) aggregations in disturbed plots passively feed on drift algae or prostrate kelp blades. Scale: sea urchins are ~5 cm diameter and the quadrat in (a,c) is  $50 \times 50 \text{ cm}$ . (Photographs by R. E. Scheibling)

Table 2. *Strongylocentrotus droebachiensis*. Repeated-measures ANOVA of effect of initial sea-urchin density (4 levels: 0, 50, 100, 200 ind. m<sup>-2</sup>), depth stratum (4 levels), and time on: gap area of undisturbed plots over 6 wk from 7 August to 20 September; gap area of disturbed plots over 5 wk from 14 August to 20 September; and patch area of the disturbed plots over 7 wk from 23 July to 10 September.

**Bold** values are significant at  $p \leq 0.05$

Source of variation	df	MS	F	p
<b>Gap area, undisturbed</b>				
Within-subject effects				
Time	6	8.53	44.55	<b>&lt;0.0001</b>
Time × Density	18	0.33	1.75	0.059
Time × Stratum	18	0.45	2.33	<b>0.009</b>
Residual	54	0.19		
Between-subject effects				
Density	3	7.70	3.40	0.067
Stratum	3	7.51	3.32	0.071
Residual	9	2.26		
<b>Gap area, disturbed</b>				
Within-subject effects				
Time	5	10.83	23.50	<b>&lt;0.0001</b>
Time × Density	15	0.44	0.95	0.521
Time × Stratum	15	0.87	1.89	0.051
Residual	45	0.46		
Between-subject effects				
Density	3	9.32	2.15	0.164
Stratum	3	6.12	1.41	0.301
Residual	9	4.34		
<b>Patch area, disturbed</b>				
Within-subject effects				
Time	6	1.31	5.54	<b>&lt;0.001</b>
Time × Density	18	0.30	1.27	0.242
Time × Stratum	18	0.16	0.67	0.826
Residual	54	0.24		
Between-subject effects				
Density	3	22.06	9.88	<b>0.003</b>
Stratum	3	9.94	4.45	<b>0.035</b>
Residual	9	2.23		

periment (Fig. 2b,c), there is a significant positive linear relationship in the undisturbed treatment (Table 3, Fig. 7d). This relationship was not significant in the disturbed treatment (Table 3) in terms of both gap (Fig. 7e) and patch area (Fig. 7f), although there was a slight positive trend in patch area (Table 3).

## DISCUSSION

Our study is the first to demonstrate that localized increases in sea-urchin density can lead to the formation of destructive grazing aggregations and creation of gaps in a kelp bed in the NW Atlantic. We showed that gaps in the kelp canopy in undisturbed plots

increased in size with increasing mean sea-urchin density from 0 to 26 urchins m<sup>-2</sup> (0 to 1.8 kg urchins m<sup>-2</sup>) in a linear manner. The absence of a density threshold for destructive grazing is inconsistent with previous field observations (Breen & Mann 1976a,b, Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007a) and mathematical models (Lauzon-Guay et al. 2008, 2009). Given the biomass of kelp at our experimental site (3.4 kg m<sup>-2</sup>) and average individual weight of transplanted sea urchins (68 g), we would predict a threshold density of 25 urchins m<sup>-2</sup> (biomass of 1.7 kg urchins m<sup>-2</sup>) for destructive grazing, based on a 1:2 threshold ratio of sea urchin to kelp biomass (Lauzon-Guay et al. 2008).

Differences in wave exposure between our study site, within a semi-protected embayment, and studies conducted at more exposed sites, where extensive fronts of sea urchins form along the offshore margins of kelp beds (Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007b), may in part explain this discrepancy. Strong wave action can prevent sea urchins from climbing kelp stipes or anchoring kelp blades to feed (Velimirov & Griffiths 1979, Lauzon-Guay & Scheibling 2007b), and can inhibit sea-urchin aggregative behavior (Lauzon-Guay & Scheibling 2007b), thus increasing the threshold biomass of sea urchins required to pin-down and consume kelp. In contrast, at more wave-protected sites, kelp blades lie prostrate on the seabed, allowing smaller groups or individual sea urchins to consume them.

Differences in hydrodynamic conditions inside a kelp bed, compared to the kelp bed–barrens interface, also may account for the lack of a grazing threshold in our study. Breen & Mann (1976a,b) reported a grazing threshold of 2 kg urchins m<sup>-2</sup> at our experimental site and adjacent areas within St. Margarets Bay in the 1970s. However, they observed grazing by a sea-urchin front at the offshore kelp-bed margin, whereas in our study grazing occurred within the kelp bed. Similarly, Konar & Estes (2003) found that sea urchins *Strongylocentrotus polyacanthus* transplanted into a kelp bed in the Aleutian Islands destructively grazed kelps and decreased canopy cover, while sea urchins at a nearby kelp bed–barrens interface did not. They concluded that wave-induced kelp movement prevented sea urchins from breaching the kelp bed–barrens boundary. Water movement and pummeling of sea urchins can be dampened by drag on adjacent kelp blades (Friedland & Denny 1995), and this may allow sea urchins to feed more easily within a kelp bed.

Seasonal variation in the rate of destructive grazing of kelp beds by *Strongylocentrotus droebachiensis*

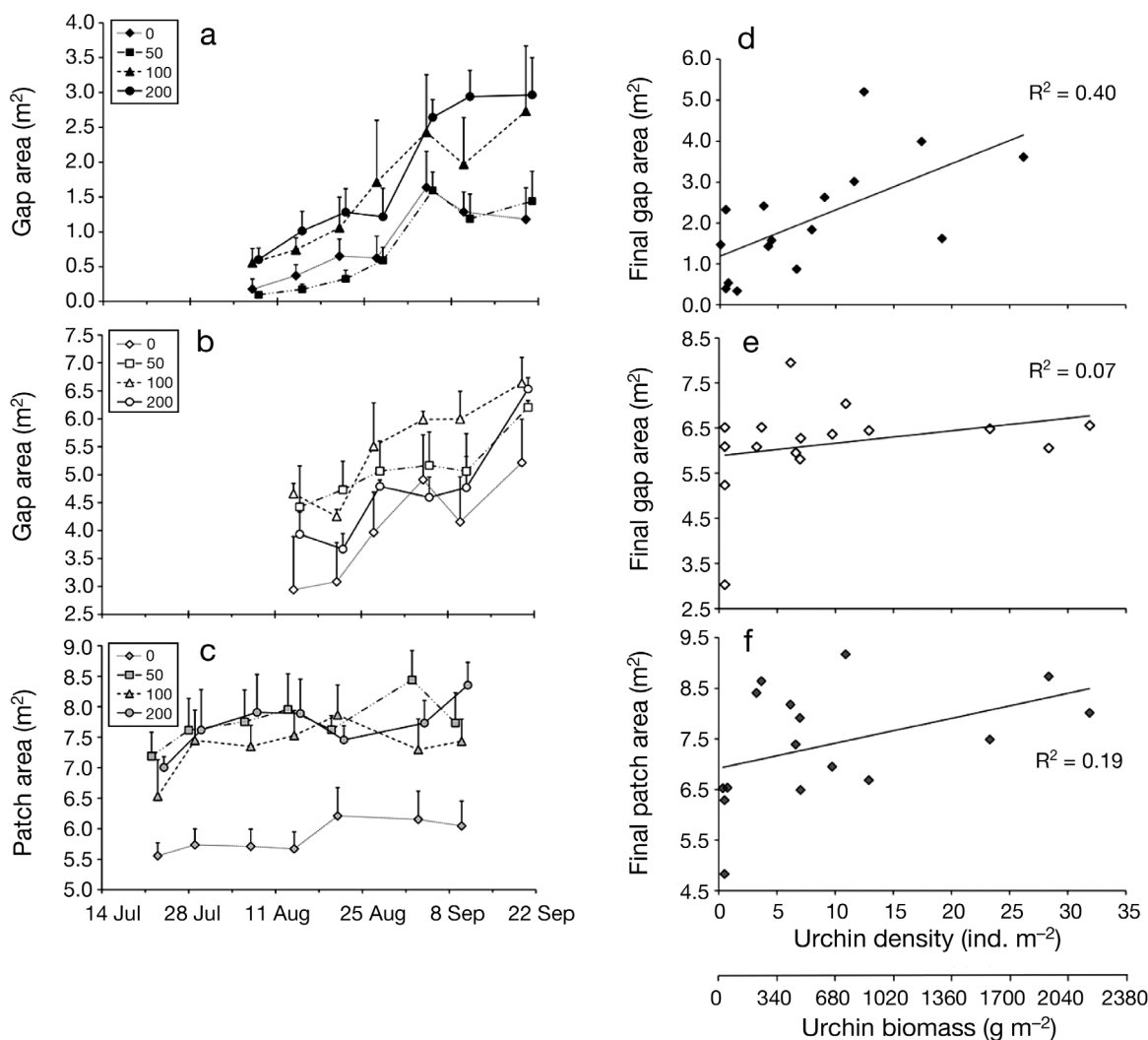


Fig. 7. *Strongylocentrotus droebachiensis*. Gap area (+1 SE;  $n = 4$ ) at 4 levels of initial sea-urchin density (ind. m<sup>-2</sup>; see keys) in the (a) undisturbed treatment over 6 wk and (b) disturbed treatment over 5 wk. (c) Patch area (+1 SE;  $n = 4$ ) in the disturbed treatment at 4 levels of initial sea-urchin density over 6 wk. Final gap area in the (d) undisturbed treatment and (e) disturbed treatment, and (f) final patch area in the disturbed treatment as a function of time-averaged overall sea-urchin density and biomass

has been attributed to increased wave action during late fall and winter (Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007b). Strong wave forces caused by Hurricane Bill, and to a lesser extent by Tropical Storm Danny, likely interrupted or slowed sea-urchin grazing for 1 or 2 d, although this had no apparent effect on change in gap area measured at weekly intervals (Fig. 7a,b). Water temperature appears to have little effect on the rate of destructive grazing below a threshold of ~17°C (Lauzon-Guay & Scheibling 2007b), when

Table 3. *Strongylocentrotus droebachiensis*. Linear regression of effect of overall mean sea-urchin density (ind. m<sup>-2</sup>) time-averaged from 17 July to 10 September on: final gap area of undisturbed plots on 20 September; final gap area of disturbed plots on 20 September; and final patch area of disturbed plots on 10 September. **Bold** values are significant at  $p \leq 0.05$

Source of variation		df	MS	<i>F</i>	p
<b>Gap area</b>					
Undisturbed	Density	1	11.44	9.55	<b>0.008</b>
	Residual	14	1.20		
Disturbed	Density	1	1.17	1.15	0.301
	Residual	14	1.02		
<b>Patch area</b>					
Disturbed	Density	1	3.77	3.32	0.090
	Residual	14	1.13		

sea-urchin foraging activity is arrested because of thermal stress (Percy 1973, Lyons & Scheibling 2007). Since temperatures at 8 m depth generally ranged between 10 and 14°C (average: 12.7°C), it is unlikely that small fluctuations in bottom temperature influenced sea-urchin grazing rate in our experiment.

In the northeast Pacific, destructive grazing of kelp can be mediated by changes in sea-urchin behavior, even without increases in sea-urchin abundance. Behavioral shifts from passive detritivory of drift kelp to active herbivory of attached sporophytes are strongly dependent on availability of kelp detritus (Ebeling et al. 1985, Harrold & Reed 1985, Tegner & Dayton 1991). Tegner & Dayton (1991) attribute the loss of kelp forests in Southern California in the late 1950s to dramatic reductions in the subsidy of kelp detritus to sea urchins (*Strongylocentrotus purpuratus*, *S. franciscanus*) within the forests, which caused a shift to destructive grazing. In some regions along the coast of California, patchiness in the availability of kelp detritus to *S. franciscanus* within the kelp forest can result in grazed patches (Harrold & Reed 1985). However, in contrast to the patches observed by Mann (1972) in St. Margarets Bay, these patches were ephemeral (due to seasonal changes in the abundance of detritus) and were re-colonized by kelps in the course of a 2 yr study (Harrold & Reed 1985).

Interestingly, we observed both passive and active feeding behavior within the high initial urchin density (200 ind. m<sup>-2</sup>) and disturbed treatment combination in our experimental array. Passive detritivory in *Strongylocentrotus droebachiensis* is only observed when detrital food is available; when macroalgae are scarce, adult sea urchins actively forage in search of drift algae on which to feed (Dumont et al. 2004). We detected no effect of sea-urchin density on final gap area or patch area in the disturbed treatment, which likely was due, at least in some plots, to passive feeding behavior by sea urchins on drift or prostrate kelp blades from the surrounding kelp bed that were trapped by sea urchins in the plot. This suggests a paradoxical effect of low wave exposure on sea-urchin feeding behavior in the kelp bed: reduced water motion may lower the threshold for destructive grazing while increasing the availability of prostrate kelp blades to sea urchins in sedentary aggregations and thereby inhibit foraging movements that would lead to active grazing at the patch edge. Low water motion also can increase the amount of drift kelp that is retained in kelp beds or forests (Harrold & Reed 1985), although drift kelp was rarely observed in our experimental plots (aside from fragments trapped by sea urchins).

A decrease in sea-urchin density at the kelp-barrens interface of cleared patches, which resulted from individuals migrating to the patch perimeter, also limited patch or gap expansion in the disturbed treatment. Lauzon-Guay & Scheibling (2010) predicted that sea urchins in a kelp bed will form a feeding aggregation around the perimeter of a patch, and that urchin density within the aggregation will decrease as the patch size (and specifically perimeter) increases. For a destructive grazing threshold to be maintained, according to their model, a background density of sea urchins within the kelp bed is required to supplement the declining density at the patch perimeter. Since a background population of adult sea urchins was effectively absent at our site, density decreased as the experimental animals moved outwards from the central seeded area of the plot, diminishing their capacity to destructively graze kelp as a front. However, we did detect a significant effect of initial sea-urchin density on patch area after the first 2 wk of the experiment, when each of the sea-urchin-seeded treatments (50, 100, and 200 ind. m<sup>-2</sup>) had a larger patch area than the control treatment with no added sea urchins. We propose that sea-urchin density at the edge of experimental patches was sufficiently high early in the experiment to cause destructive grazing and patch expansion. These observations also suggest that gaps in the undisturbed plots would likely have stopped expanding once they reached a critical size at which sea-urchin density along the edge of the patch decreased below the level required for sea urchins to graze cooperatively. An effect of initial sea-urchin density in the disturbed treatment was not detected as a change in gap area in our analysis because this was not measured until Week 4 of the experiment, when sea-urchin densities had already decreased markedly.

Sea-urchin densities in kelp beds in Nova Scotia are typically well below levels required for destructive grazing, and lower than densities in adjacent barrens (mean  $\pm$  1 SD = 14  $\pm$  12 ind. m<sup>-2</sup> in healthy kelp beds vs. 71  $\pm$  28 ind. m<sup>-2</sup> in post-transitional barrens; Meidel & Scheibling 2001). This difference can be explained in part by lower recruitment of sea urchins in kelp beds than in barrens (Balch & Scheibling 2000). Although a high prevalence of predators and low cover of coralline algae (that induce larval settlement; Pearce & Scheibling 1990) may limit overall rates of recruitment in kelp beds (Raymond & Scheibling 1987, Balch & Scheibling 2000), localized high-density aggregations of sea urchins could arise as a result of spatial or temporal variability in recruitment (Scheibling 1996, Lauzon-Guay & Scheibling



2010). Stochastic processes such as temperature anomalies that affect larval survival may trigger major settlement events (Hart & Scheibling 1988).

We observed large reductions in the seeded sea-urchin population, particularly in the first 2 wk of the experiment and within the deepest stratum, that likely were caused by predation. Sea urchins remained rare in control plots (0 urchins  $\text{m}^{-2}$ ), even those adjacent to high-initial-density plots, indicating limited migration from seeded plots. We often observed cancer crabs and lobsters directly preying on experimental sea urchins throughout the experiment. Evidence from the Gulf of Maine indicates that *Cancer borealis* has become a voracious predator of juvenile and adult *Strongylocentrotus droebachiensis* in the NW Atlantic, due to the removal by overfishing of higher-level predators of crabs, such as cod *Gadus morhua* (Steneck et al. 2002). Leland (2002) found that *S. droebachiensis* transplanted into a kelp bed in the Gulf of Maine were heavily preyed on by *C. borealis* during August and September. Crabs and lobsters are particularly active in late summer and early fall when sea temperatures are the warmest. Accumulations of cracked and punctured tests in our experimental plots provided ample evidence of predation.

There was no consistent pattern among strata in predator abundance or sea-urchin remains that explains the progressive decline in sea-urchin abundance with depth. However, our surveys took place only during daylight hours, and nocturnal predation may account for depth-related differences in sea-urchin mortality. Also, the quality of spatial refuges for sea urchins may have differed among strata. Increased sedimentation associated with low wave action may have limited refuge space in the deep stratum by infilling crevices and spaces between boulders. The availability of spatial refuges has been shown to be an important factor mediating predation rates of small sea urchins by crabs and lobsters (Scheibling & Hamm 1991).

Disturbed plots with large sedentary aggregations of sea urchins showed the smallest decrease in urchin density. Previous research suggests that large, 2-dimensional aggregations can provide a 'size refuge' from predators such as crabs and lobsters by decreasing the vulnerability of individual sea urchins to handling and detachment (Garnick 1978, Bernstein et al. 1981, Scheibling 1996). The persistence of these aggregations in our experimental plots following extreme wave conditions associated with Hurricane Bill suggests that this behavior also may be adaptive in limiting dislodgment during storm events.

In a few cases, increases in gap area occurred in undisturbed plots without sea urchins or at the low initial urchin-density level (Fig. 7a). During our experiment, canopy loss that was not attributed to destructive grazing was most likely related to seasonal increases in erosion or fragmentation of kelp blades encrusted with *Membranipora membranacea* that are exposed to heavy wave action during storms (Krumhansl & Scheibling 2011). Following Hurricane Bill, we observed piles of drift kelp on the shore adjacent to our site. The cover of *M. membranacea* on kelps increased in September, and a concurrent study at the same site (but outside of our experimental array) showed that kelp erosion was significantly related to cover of the bryozoan during our experiment (Krumhansl & Scheibling 2011). Apart from direct effects on the kelp canopy cover, seasonal kelp erosion could accelerate destructive grazing by sea urchins by decreasing the kelp biomass (Lauzon-Guay & Scheibling 2007b).

Sea-urchin mortality in the final weeks of the experiment was caused by a disease outbreak (paramoebiasis) associated with the passage of Hurricane Bill (Scheibling et al. 2010). Historically, disease outbreaks have decimated sea-urchin populations in Nova Scotia, releasing kelp beds from grazing pressure and causing the shift from barrens to kelp beds (Scheibling 1984, Scheibling & Hennigar 1997). These outbreaks have increased in frequency over the past 3 decades, a pattern that appears to be linked to the frequency of severe storm events (Scheibling & Lauzon-Guay 2010). Interestingly, we found low-density populations of sea urchins in kelp beds elsewhere in St. Margarets Bay in June 2010 (C. Feehan et al. unpubl. data), indicating that sea urchins were not eliminated throughout the bay in fall 2009. This likely reflects the density-dependence of host-pathogen dynamics (Anderson & May 1986), which has been observed in previous outbreaks of sea-urchin disease in Nova Scotia (Scheibling & Stephenson 1984) and in California (Lafferty 2004). The increased likelihood of a disease outbreak occurring among dense aggregations of sea urchins (as observed during our experiment) suggests an important feedback mechanism that limits the resilience of sea-urchin populations in kelp beds, particularly given the predicted increase in hurricane intensity in the North Atlantic with global climate change (Bender et al. 2010, Scheibling et al. 2010).

We have demonstrated experimentally that localized increases in sea-urchin density can lead to the formation of grazing aggregations and expansion of gaps in a kelp bed. We did not find evidence for a



threshold density of sea urchins for destructive grazing, which suggests that kelp beds are less resilient to destructive grazing from within the bed than predicted by grazing dynamics at the deep margin of beds. Future research should compare the feeding behavior of high-density aggregations of sea urchins within kelp beds and at the kelp bed–barrens interface, together with relevant biotic and abiotic variables such as kelp biomass and wave action, to elucidate the mechanisms that determine grazing thresholds. The importance of predation and disease in controlling an experimental sea-urchin population in our study suggests a paradigm shift for the Nova Scotian system. With projected increases in the intensity of these top-down controls on sea urchins in the NW Atlantic (Steneck et al. 2002, Scheibling & Lauzon-Guay 2010), we may be observing an increase in the stability of the kelp-bed state. Increased understanding of aggregation and feeding behavior of sea-urchin populations within kelp beds, and of the roles of predation and disease in limiting these populations, will aid in predicting the dynamics of this alternative-state ecosystem.

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