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Temporal variation in community interfaces: kelp-bed boundary dynamics adjacent to persistent urchin barrens

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Abstract We examined, over 2 years, factors affecting the temporal stability of the lower limit of kelp beds (*Alaria esculenta*) at five subtidal sites in the Mingan Islands, northern Gulf of St. Lawrence. The position of the lower limit of the beds varied markedly among sites and over time and was largely controlled by the green sea urchin, *Strongylocentrotus droebachiensis*, which formed dense (up to 500 individuals m^{-2}) feeding fronts at the lower edge of the beds. These aggregations advanced over the kelp most rapidly during the summer (at rates as high as 2.5 $m\ month^{-1}$), and there appeared to be a threshold urchin biomass of $\sim 5\ kg\ m^{-2}$ below which the fronts could not substantially reduce the limit of the beds. The fronts consisted mainly of large individuals, whereas smaller urchins predominated in the barrens zone below the kelp beds. At one site, we recorded large seasonal shifts in overall urchin densities, with large increases and decreases during the summer and winter, respectively. An urchin exclusion experiment indicated that algal recruitment in the barrens was two orders of magnitude greater in the absence than in the presence of urchins. The kelp *Agarum cribrosum* greatly restricted urchin movements, and the greater temporal stability of the kelp bed at one site appeared related to the gradual replacement of *Alaria esculenta* in the lower kelp bed by a large stand of *Agarum cribrosum*. We propose that perturbations by abiotic factors (e.g., ice scouring and water motion) trigger important but localized changes in urchin densities that, in turn, largely determine the limits of kelp bed distribution in this region of the Atlantic where urchin barrens are a persistent community state.

Introduction

Kelp beds are highly diverse shallow coastal communities found in temperate and polar zones worldwide. They are organized around the physical structure and primary productivity provided by large brown algae of the order Laminariales (Tegner and Dayton 2000). In addition to being among the most productive systems on earth (Mann 1973), kelp beds provide habitat to many species for recruitment, feeding, reproduction, and refuge from predators and from strong water motion (e.g., Bernstein et al. 1981; Himmelman et al. 1983; Himmelman and Lavergne 1985; Duggins et al. 1990; Vadas and Elnor 1992; Vasquez 1993; Balch and Scheibling 2000; Gagnon et al. 2003b). Although the light environment and substratum type are primary factors determining where kelp beds develop, many other factors, such as sedimentation, nutrients, salinity, water motion, and ice scour can modify local patterns of occurrence (see review in Dayton 1985b; but also Hooper 1981; Cowen et al. 1982; Ebeling et al. 1985; Keats et al. 1985; Seymour et al. 1989; Sivertsen 1997; Kawamata 2001). The most important factor in many regions is grazing by sea urchins (see review in Lawrence 1975; but also Paine and Vadas 1969; Pearse and Hines 1979; Hagen 1983; Dean et al. 1984; Himmelman 1984; Dayton 1985a; Witman 1987; Leinaas and Christie 1996; Sivertsen 1997; Vasquez and Buschmann 1997). Although urchins and kelp can co-occur at small spatial scales (i.e., within the foraging distance of urchins), high densities of urchins usually completely denude areas of fleshy macrophytes, including kelp. Such areas, referred to as urchin barrens (Lawrence 1975), have both low diversity (but see Bégin et al. 2003) and low productivity, although the abundance and diversity of coralline algae can be quite high (Steneck 1983, 1986; Chapman and Johnson 1990; Scheibling and Hatcher 2001). Urchin barrens can be both extensive and persistent (Breen and Mann 1976b; Chapman 1981; Hagen 1983; Himmelman et al. 1983; Miller 1985; Scheibling 1986; Leinaas and Christie 1996;

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Sivertsen 1997), and natural and experimental removals of urchins demonstrate that kelp can rapidly colonize barrens when urchins are absent (e.g., Pearse and Hines 1979; Himmelman et al. 1983; Scheibling 1986; Witman 1987; Keats et al. 1990; Scheibling et al. 1999).

In the northwestern North Atlantic, the green sea urchin, *Strongylocentrotus droebachiensis*, severely limits the distribution of kelp in rocky subtidal environments and often forms dense feeding aggregations at the lower edge of kelp beds. This phenomenon is reported in the Gulf of Maine (Sebens 1985; Witman 1985, 1987), Newfoundland (Himmelman 1984; Keats et al. 1985, 1990), and the St. Lawrence Estuary (Himmelman et al. 1983; Himmelman and Lavergne 1985). In Nova Scotia (the most extensively studied region), urchin fronts can destroy kelp beds (primarily *Laminaria longicruris*) at rates as high as 4 m month⁻¹, and as long as the urchins remain sufficiently abundant, fleshy macroalgae cannot recolonize (Breen and Mann 1976a, 1976b; Chapman 1981; Miller 1985; Scheibling 1986; Scheibling et al. 1999). As outlined by Scheibling et al. (Scheibling 1986; Scheibling et al. 1999), mass mortality of *S. droebachiensis* caused by a pathogenic amoeba (see review in Scheibling 1988) is the only known natural mechanism for the large-scale shift in community state from urchin barrens to kelp beds. Such mortalities have been reported a number of times over the last decades and have always been followed by rapid kelp colonization (Miller and Colodey 1983; Scheibling and Stephenson 1984; Miller 1985; Scheibling 1986; Scheibling and Hennigar 1997; Scheibling et al. 1999). Although lobsters, crabs, sea stars, wolffish, sea gulls, and eider ducks are all predators of *S. droebachiensis* in the northwestern North Atlantic (Himmelman and Steele 1971), they have never been shown to regulate urchin populations (see review in Scheibling 1996).

Two such community states are found on shallow bedrock platforms in wave-exposed areas in the Mingan Islands, northern Gulf of St. Lawrence: (1) kelp beds dominated by *Alaria esculenta* (but also including *Laminaria* spp., *Saccorhiza dermatodea*, and *Agarum cribrosum*) in shallow water, and (2) urchin barrens dominated by *Strongylocentrotus droebachiensis*. Within the kelp bed, urchin densities are low, and algal and invertebrate biomass is high (Bégin et al. 2003). In the barrens, urchins often attain densities of 300 individuals m⁻² (Himmelman and Nédélec 1990; Gagnon et al. 2003a), and the main algae are crustose coralline red algae (*Lithothamnion* sp. and *Clathromorphum* sp.). The only common fleshy macroalgae in the barrens are the brown algae *A. cribrosum* and *Desmarestia viridis* and the red alga *Ptilota serrata*. In most locations *A. cribrosum* is found near the lower limit of the kelp zone where it usually forms small patches (1–10 m²), but it occasionally covers larger areas (> 500 m²). *D. viridis*, a filamentous annual, also forms patches in urchin barrens, but the patches are typically small (1–5 m²) and are only present from winter to early fall (Gagnon et al. 2003a). Both *A. cribrosum* and *D. viridis* are thought to

be chemically defended from urchin grazing (Vadas 1977; Larson et al. 1980; Himmelman and Nédélec 1990; Lobban and Harrison 1994) although more recent work suggests that tactile contact induced by water movement is more important, particularly for the finely branched *D. viridis* (Gagnon et al. 2003a). *P. serrata* often grows under patches of *A. cribrosum* but can also form extensive turfs at greater depths.

Mass mortality of urchins, as occurs in Nova Scotia, has never been reported in the northern Gulf. Thus, the urchin barrens appear to be a persistent community state. The transition between kelp beds and barrens is distinct as the kelp generally abruptly disappear where fronts of urchins begin (Fig. 1). The factors controlling the stability of this conspicuous interface are poorly understood. Qualitative observations over 20 years (Himmelman and coworkers) suggest that its position (i.e., its depth and distance from shore) varies over time from site to site (with wave exposure and slope). Although the kelp-barrens interface represents an equilibrium in an important herbivore-plant interaction, there are no long-term observations of how it fluctuates over time, or an understanding of how such changes are affected by other environmental factors (e.g., ice scour, dislodgment by waves and currents, competition). A necessary first step is a detailed examination of the spatial and temporal dynamics of this interface relative to the demographic changes in both the kelp bed and the urchin population.

Here, we examine factors affecting the temporal stability of the lower limit of kelp beds in the Mingan Islands. Specifically, we (1) record temporal variations in the position of the lower limit of kelp beds, (2) measure temporal changes in the structure (density and size distribution) of kelp beds and urchin fronts in the transition zone, (3) examine the relationship between urchin biomass in grazing fronts and the rate of change in the position of the lower limit of kelp beds, (4) determine the impact of



Fig. 1 A grazing front of the green sea urchin, *Strongylocentrotus droebachiensis* (two to three layers thick), at a depth of 3–4 m at the lower edge of a subtidal kelp (*Alaria esculenta*) bed in the Mingan Islands in June 2000. The urchins are actively consuming kelp blades and leaving only the bases of stipes in their path

urchins on the recruitment of kelp in the barrens zone, and (5) assess the effectiveness of *Agarum cribrosum* stands in limiting upward movements of urchins into the shallower kelp zone dominated by *Alaria esculenta*.

Materials and methods

Study sites

Our study was conducted during the summer and fall of 2000, 2001, and 2002 at five subtidal sites on four of the Mingan Islands, northern Gulf of St. Lawrence (Fig. 2). All sites were gently sloping bedrock platforms and had kelp beds in shallow water (to a maximal depth of 6 m) and urchin barrens in deeper water. At the beginning of the study, the kelp beds at the sites were composed primarily of *Alaria esculenta* and the transition from kelp beds to barrens was abrupt. The sites varied markedly in exposure to waves and tidal currents due to differences in orientation and topography. After initial qualitative surveys, two sites, Île à Firmin East and Île du Havre, were selected for intensive study due to striking differences in algal density within the kelp beds (kelp were more dense at the former site). The Île à Firmin East site was exposed to strong wave action and tidal currents, whereas the Île du Havre site had less exposure to waves and had moderate tidal currents. The three other sites, Île Niapiskau, Île à Firmin West, and Petite île au Marteau, were studied less intensively and served to provide information on the generality of the temporal patterns observed at the two intensively studied sites. We did not make measurements during other seasons due to the remote location of the field sites, unpredictable weather conditions, and ice cover in winter.

Temporal variability in *A. esculenta* beds and urchin populations

We evaluated community shifts by monitoring changes over 2 years in (1) the absolute position of the lower limit of the kelp bed, and (2) the density and size distribution of kelp and urchins in the kelp-barrens transition zone. For each of the two intensively studied sites, we delineated 12 permanent 16-m-long transects that ran perpendicular to the kelp-barrens transition and parallel to one another. The transects were spaced at 3-m intervals and thus covered 33 m of shoreline. The ends of each transect were tied to two 33-m-long benchmark lines (one located in the kelp bed and the other in the barrens) running parallel to the shoreline and anchored by bolts (three on each line) permanently set into holes drilled into the substratum. The transect lines were removed between sampling periods.

The absolute position of the kelp-barrens interface was determined by measuring the distance (to the nearest 1 cm) from the deep end of each transect up to the interface. To measure the abundance and size of urchins and kelp, we placed quadrats along each transect line in both seaward and landward directions from the kelp-barrens interface. Quadrats were positioned by placing the edge of a quadrat (25×25 cm) at distances of 0.0 (i.e., at the interface), 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 4.0, and 5.0 m in each direction (this arrangement placed the two quadrats at 0.0 m immediately adjacent to one another). In each quadrat we counted the number of urchins in three size classes (<2 cm, 2–4 cm, and >4 cm in test diameter). We also categorized each quadrat according to the density of kelp (0–10, 11–30, 31–50, and >50 individuals per quadrat) and their length (<50 cm, 50–100 cm, and >100 cm). Sampling was done six times over a 2-year period: June, August, and October 2000, June and August 2001, and June 2002. We could not, however, take all measurements each time. Bad weather precluded the measurement of the density and size distribution of kelp and urchins in October 2000, and time considerations limited the quadrat samplings in 2001 and 2002 to five distances (0.0, 0.5, 1.0, 3.0, and 5.0 m) in each direction from the kelp-barrens interface.

At the other three sites, we simply measured the absolute position of the kelp-barrens interface along 20 m of shoreline. At each site, a transect line was placed along the lower limit of the kelp bed

(two positions were permanently marked by bolts set into the substratum), and on each observation date (August 2000, June and August 2001, and June 2002), we recorded the perpendicular distance to the lower limit of the kelp bed at 5-m intervals along the transect line. The line was removed between sampling dates.

Should grazing by urchins cause the reduction of kelp beds, the rate of kelp-bed regression should be positively correlated with urchin biomass in the grazing fronts. To test this hypothesis, we examined the data on the position of the lower limit of kelp beds and urchin densities acquired from the 2-year monitoring at Île à Firmin East and Île du Havre sites. For each site, we first determined the monthly rate of change (advance or regression) in the mean position of the lower limit of the kelp bed (the average over the 12 transect lines) by comparing their position at the beginning and at the end of each of four time periods (between June and August 2000 and 2001, and between August and June 2000–2001 and 2001–2002). For each period, we then calculated the urchin biomass within the first meter of the edge of the barrens (i.e., the front). We used the average of the quadrats placed at 0.0, 0.5, and 1.0 m from the edge and converted densities to biomass using a regression (wet weight (grams) = 0.000908 × diameter^{2.804} (millimeters); $r^2 = 0.99$) obtained from a sample of 144 urchins (ranging in test diameter from 0.8 to 6.1 cm) collected at the Île du Havre site. Test diameters used for each size class (<2 cm, 2–4 cm, and >4 cm) were 1, 3, and 5 cm, respectively, and densities were the average of the urchins sampled at the beginning and end of each period. We then examined the relationship between urchin biomass in the grazing fronts and monthly rate of changes in the position of the lower limit of kelp beds at each site.

Effect of urchins on algal recruitment in the barrens

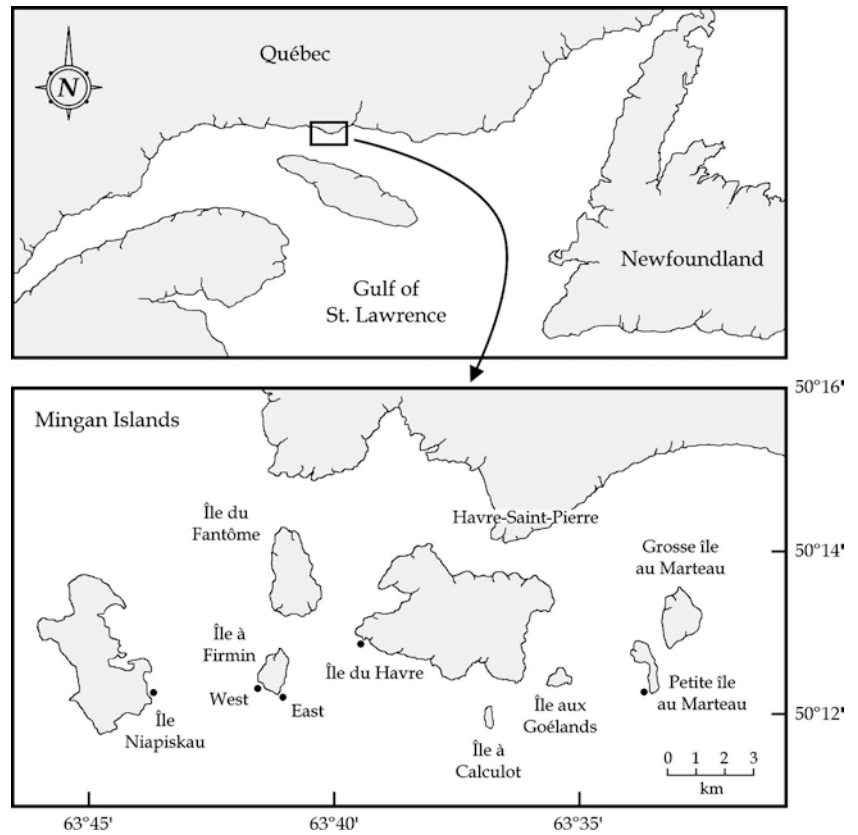
To quantify the impact of urchins on algal recruitment in the barrens, we experimentally manipulated urchins using exclosures. The experiment consisted of three treatments: (1) grazed (no manipulation), to quantify algal recruitment under natural urchin densities; (2) ungrazed (exclosure and urchins manually removed), to quantify algal recruitment in the absence of urchins; and (3) fence control (exclosure, but urchins not manually removed), to test for effects of the exclosure beyond those associated with the presence of grazers.

For the ungrazed and fence control treatments, we constructed exclosures that consisted of a 0.75×0.75-m fence of 60-cm-wide strips of hardware cloth (1-cm mesh size) supported by a PVC frame. The fences were anchored to the substratum with nylon ropes connecting the top of each corner to eyebolts set into the bedrock. Urchins were able to climb the fences but with visits every 2–3 days to hand remove them, we were able to limit greatly their penetration inside the fences. Fence controls were identical except that urchins were never removed after starting the experiment. We selected 12 experimental areas (each marked with a bolt in the center) in June 2000, spaced at 3.8-m intervals 3–4 m below the lower limit of the kelp bed at Île du Havre (near the transects at this location). The areas were grouped into four blocks of three adjacent areas that were then randomly assigned the three treatments. The experiment began on 3 July 2000, when we removed the urchins from all the areas (releasing them at least 3 m from the areas) and then wire-brushed the rock surface to remove any fleshy macroalgae present (e.g., rare recruits of *Laminaria* sp. and *Agarum cribrosum*), thereby increasing the homogeneity of the initial conditions of the experimental units. The experiment ended 44 days later at which time we quantified the density of kelp recruits in each area using two quadrats (25×25 cm) placed on the north and south sides of the center bolt in each area. We averaged the data from the two quadrats in each area before statistically comparing densities of kelp recruits among treatments.

Limitation of upward movements of urchins by *A. cribrosum*

During the first year of the study, changes were seen in the kelp-barrens transition that were related to an observed increase in the abundance of *A. cribrosum* at the Île du Havre site. To assess

Fig. 2 Location of study sites at Île Niapiskau, Île à Firmin (West and East), Île du Havre, and Petite île au Marteau, in the Mingan Islands, northern Gulf of St. Lawrence, eastern Canada



the effectiveness of mature stands of *A. cribrusum* in limiting the upward movement of urchin fronts into the kelp (*Alaria esculenta*) zone, we conducted an experiment to compare the rate of penetration of urchins in the absence and presence of adult *Agarum cribrusum*. The two treatments consisted of *A. cribrusum* removal (stipes cut off at the holdfasts) and a control (no manipulation). Experimental units consisted of eight 4-m² areas spaced at 3.8-m intervals along the lower edge of a large (over 500 m²) mature stand of *A. cribrusum* located near the transect lines at the Île du Havre site. Each area, 1 m wide and extending 4 m up into the *A. cribrusum* zone, was marked with bolts at the lower and upper edge. The areas were grouped into four blocks of two adjacent areas to which the two treatments were randomly assigned. The experiment began on 27 June 2001 with the removal of all adult and juvenile *A. cribrusum* for the removal treatment and the removal of all urchins (released >25 m away) from all experimental units. The movement of urchins into the experimental units was then recorded on six dates over the next 20 days (28, 29, and 30 June and 4, 10, and 17 July). On each date we counted the number of urchins in three size classes (<2 cm, 2–4 cm, and >4 cm) in quadrats (40×40 cm) placed at 0, 1, 2, and 3 m from the edge of the original *A. cribrusum* zone in each area. To provide an indication of the overall urchin densities, we then averaged the densities of urchins from the 1-, 2- and 3-m distances in each area on each date before comparing treatments.

Statistical analysis

Temporal changes in the density of sea urchins in the kelp-barrens transition zones of Île à Firmin East and Île du Havre were analyzed using a repeated measures analysis of variance (ANOVA) (Hand and Taylor 1987; Crowder and Hand 1990) with the factors Time (June 2000, July 2000, June 2001, July

2001, and June 2002) and Site (Île à Firmin East and Île du Havre) with one nested element (transect replicate within island). Since variances did not vary over time within the islands, and the correlation in the data over time was similar between the islands, we used a pooled covariance structure in the ANOVA (Proc Mixed, Type=CS, SAS Institute Inc. 1999). We applied the analysis to the raw data as the data for each time were normally distributed.

We examined the relationship between urchin biomass in grazing fronts and rate of change in the position of the lower limit of kelp beds at Île à Firmin East and Île du Havre using regression analysis (Draper and Smith 1981; Proc Reg, SAS Institute Inc. 1999). We applied the analysis to the raw data as the data for each site were homoscedastic and normally distributed. We evaluated the effect of urchins on algal recruitment in the barrens using a two-way ANOVA (Zar 1999) with the factors Block (four) and Treatment (grazed, ungrazed, enclosure control) applied to the raw data as they were homoscedastic and normally distributed. To test whether *A. cribrusum* impeded the upward movement of urchin fronts, we carried out a repeated measures ANOVA with the factors Block (four), Treatment (with/without canopy), and Time (after 1, 2, 3, 7, 13, and 20 days) with one nested element (treatment within block). Since we detected fluctuations in the variances over time, we modeled the covariance structure with a heterogeneous compound symmetry structure (Proc Mixed, Type=CSH, SAS Institute Inc. 1999). We analyzed the raw data as the data for each time were normally distributed.

In the above analyses, normality was verified using Shapiro-Wilk's statistic (SAS Institute Inc. 1999) and homoscedasticity by examining the graphical distribution of the residuals and by applying the Levene test (Snedecor and Cochran 1989). To detect differences among levels within a factor, we used least-square means multiple comparisons tests (LS means, SAS Institute Inc. 1999). A significance level of 0.05 was used for all statistical tests.

Results

Temporal variability in the lower limit of kelp beds

During the 2-year study, the lower limit of kelp beds showed greater temporal variability at Île à Firmin East than at Île du Havre (Fig. 3). At Île à Firmin East, the kelp bed retreated steadily during the first year and by August 2001 had been pushed back by 11.9 ± 5.0 (SD) m (equivalent to a loss of 0.9 m month^{-1}). Nearly 40% of this loss occurred between June and August 2001 (2.5 m month^{-1}). There was a strong recruitment event during the winter of 2001–2002, and the kelp bed reinvaded a distance of 13.7 ± 4.8 m, exceeding by 1.8 ± 2.0 m the initial lower limit. In contrast, the kelp-barrens interface at Île du Havre was relatively stable over the 2-year period: the greatest regression was just 3.5 ± 1.3 m, with a maximal rate of loss (1.3 m month^{-1}) between August and October 2000. Some recolonization occurred during the first winter so that the lower limit in June 2001 was only 0.9 ± 1.7 m above the lower limit of the bed in the previous June. The bed extended deeper during the second year and, as for the Île à Firmin East site, slightly exceeded the initial lower limit by the end of the study. Thus, although monthly changes in the position of the lower limit of the kelp bed were much greater at Île à Firmin East than at Île du Havre, the net displacement of the lower limit of the kelp bed over 2 years was similar at the two sites.

Measurements of the lower limit of the kelp beds at the three less intensely studied sites also showed a high degree of variability among sites and over time. At two sites, Île Niapiskau and Petite île au Marteau, there was a substantial regression of the kelp bed (over a distance of 3.8 ± 1.1 m and 5.9 ± 1.4 m, respectively) during the first 12 months, as observed at Île à Firmin East. In the second year, there was little change at Petite île au Marteau as the lower limit of the bed in June 2002 was only 1.0 ± 1.3 m below the lower limit in August 2001. However, as seen at Île à Firmin East, substantial recolonization appeared to occur at Île Niapiskau during the winter of 2001–2002. We were unable to locate reference points at this site in June 2002 due to the kelp cover but noted that the lower limit of the kelp bed was well below that of the previous summer. In contrast to all other sites, the third site, Île à Firmin West, showed a major extension of the kelp bed during the first winter (7.1 ± 1.2 m) and then retreated during the summer season (4.4 ± 1.9 m). We were also unable to find the reference points at this site in 2002 but again observed another major extension of the kelp bed during the second winter. There appeared to have been a major disturbance over the winter 2001–2002 as cobbles and boulders covered with small kelp were scattered over the bottom. Also, there were denuded areas at shallower depths in the kelp bed that were likely due to ice scour. None of these sites showed the stability in the kelp-barrens interface seen at the Île du Havre site.

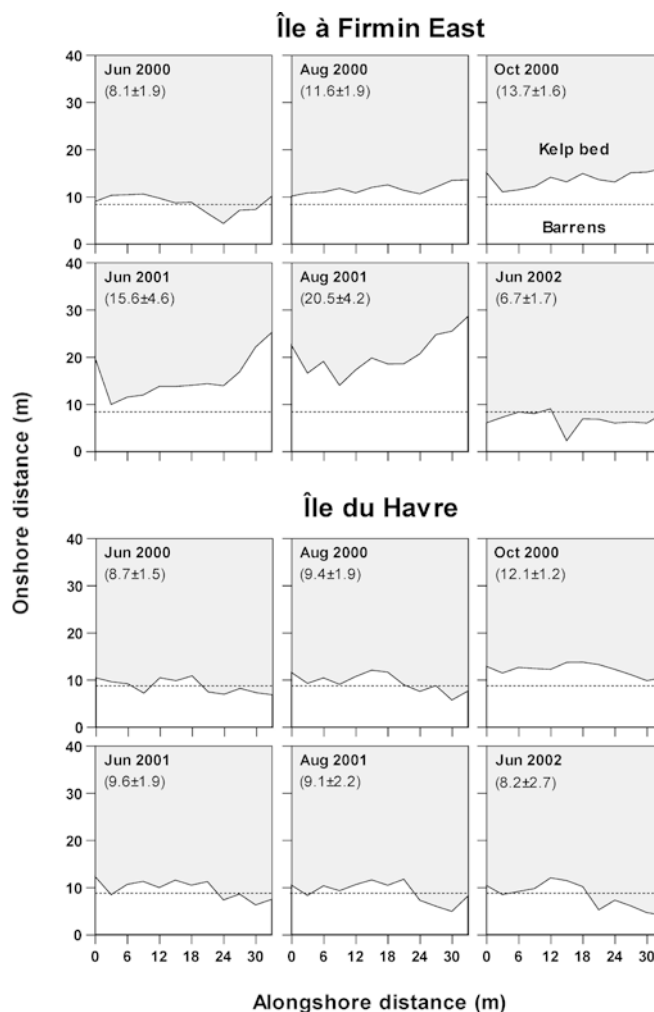


Fig. 3 Changes in the position of the kelp-barrens interface at Île à Firmin East and Île du Havre between June 2000 and June 2002. The depth across the grid (from 40 to 0 m along the y-axis) was from 3 to 5 m at Île à Firmin East, and from 4 to 6 m at Île du Havre. Values in parenthesis represent the mean distance (\pm SD) of the kelp interface relative to the benchmark transect in the urchin barrens (0 m). Horizontal dashed lines indicate the mean distance of the kelp bed on the first sampling date (June 2000)

Structure of kelp beds

The 2-year monitoring of the density and size of kelp in the transition zone indicated that kelp in the lower 5 m of the bed were always more abundant (Table 1) and larger (Table 2) at Île à Firmin East than at Île du Havre. At Île à Firmin East, there were >50 kelp plants in almost half of the quadrats at the beginning of the study. However, densities decreased sharply during the summers of 2000 and 2001 as the kelp bed retreated to a shallower depth (Fig. 3). The major increase in June 2002 relative to August 2001 was due to the newly recruited kelp that caused a major extension of the kelp bed (Fig. 3). The occurrence of >100 -cm plants was relatively high at all times (13–32%). *Alaria esculenta* always dominated, but *Laminaria digitata* and *Saccorhiza dermatodea* were also common and patches of the green

Table 1 Proportion of quadrats (out of 48) containing different density classes of kelp (0–10, 11–30, 31–50, and > 50 individuals per 25×25-cm quadrat) on different dates from June 2000 to June 2002 for the lower 5 m of the kelp-bed zone (quadrats placed at 0.0, 1.0, 3.0, and 5.0 m) at Île à Firmin East and Île du Havre

	Île à Firmin East				Île du Havre			
	0–10	11–30	31–50	> 50	0–10	11–30	31–50	> 50
June 2000	27	12	15	46	61	35	0	4
August 2000	54	27	8	11	90	10	0	0
June 2001	50	17	21	12	92	4	2	2
August 2001	94	6	0	0	98	2	0	0
June 2002	21	19	27	33	100	0	0	0

Table 2 Proportion of quadrats (out of 48 25×25-cm quadrats) containing different size classes of kelp (< 50, 50–100, and > 100 cm in length) on different dates from June 2000 to June 2002 for the lower 5 m of the kelp-bed zone (quadrats placed at 0.0, 1.0, 3.0, and 5.0 m) at Île à Firmin East and Île du Havre

	Île à Firmin East			Île du Havre		
	< 50 cm	50–100 cm	> 100 cm	< 50 cm	50–100 cm	> 100 cm
June 2000	73	13	14	71	21	8
August 2000	73	12	15	82	10	8
June 2001	74	4	22	97	1	2
August 2001	58	10	32	91	5	4
June 2002	51	36	13	95	5	0

alga *Spongomorpha arcta*, ulvoid algae, and the brown alga *Scytosiphon lomentaria* were present on surfaces between kelp holdfasts, especially in June of each year.

In contrast, at Île du Havre, there were < 10 kelp plants in most quadrats at the beginning of the study. Densities decreased further over time and were extremely low by June 2002. This decrease in kelp density was accompanied by a general decrease in kelp size. For example, the occurrence of plants > 50 cm in length was initially only 29% but decreased to 5% by the end of the study. The decline in both kelp density and length was due to a shift from *A. esculenta* to *Agarum cribrosum* in the lower kelp bed (in mature stands, *A. cribrosum* rarely exceeds 1 m in length, and individuals are more dispersed than in a bed of *A. esculenta*; P. Gagnon, personal observation). By June 2002, the lowest portion of the bed was a mature stand of *Agarum cribrosum* that extended up to 8 m from the lower limit of the *Alaria esculenta* zone. Above the *Agarum cribrosum* stand, a luxuriant kelp bed of large *Alaria esculenta* still flourished. There were also a few large *L. longicuris* (often > 2 m in length), but *L. digitata* and *Saccorhiza dermatodea* were virtually absent, and *Spongomorpha arcta*, ulvoid algae, and *Scytosiphon lomentaria* were scarce. We never observed any major recruitment events at this site.

Structure of urchin populations

The 2-year monitoring of the density and size structure of urchin populations in the transition zone showed substantial changes at each site as well as major differences between sites. There was an overall decline in urchin abundance by approximately 50% during the

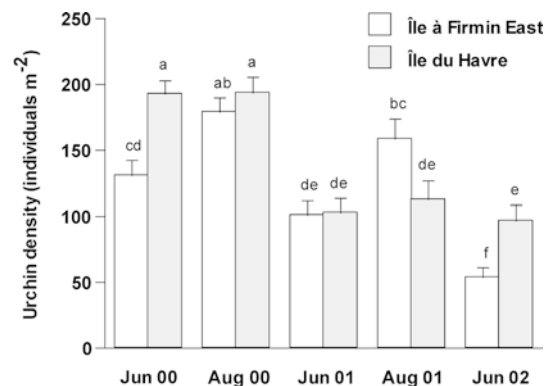
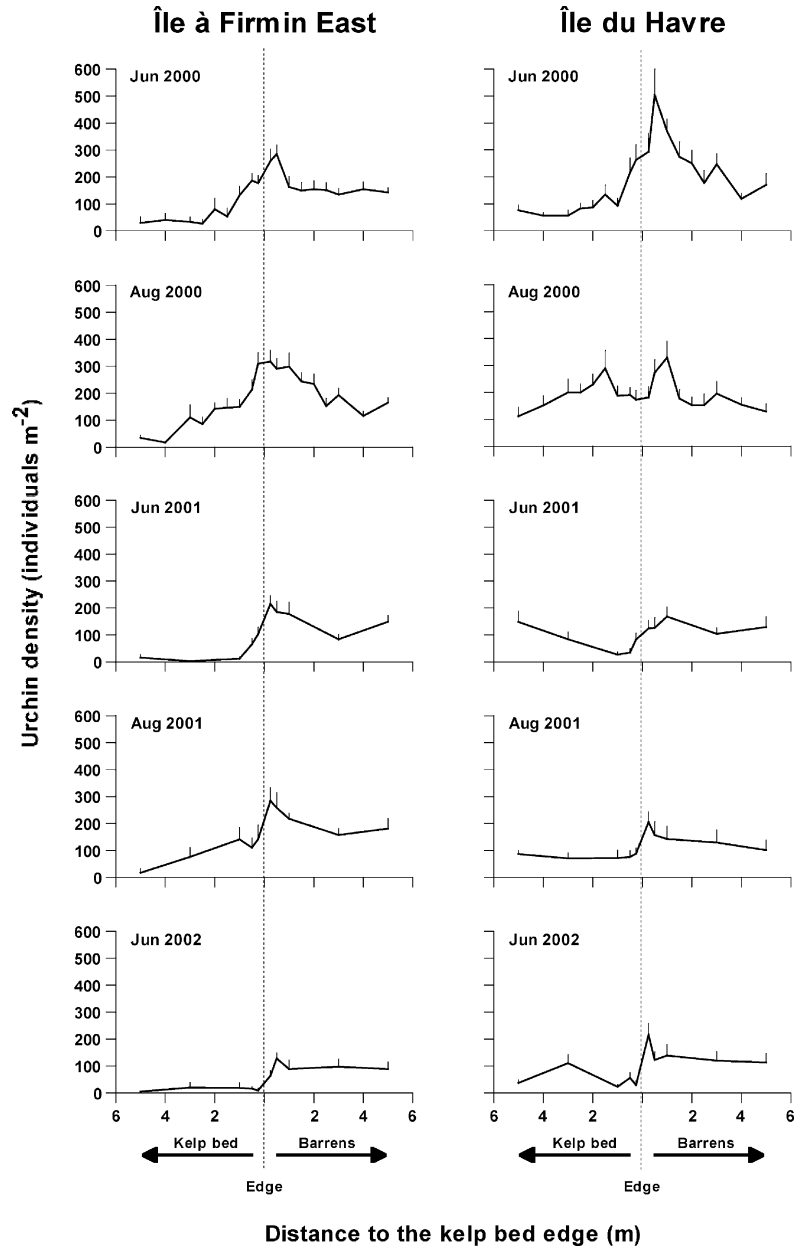


Fig. 4 Changes in the mean density (+ SE) of the green sea urchin, *S. droebachiensis*, within 5 m of the lower limit of kelp beds at Île à Firmin East and Île du Havre between June 2000 and June 2002. Values not sharing the same letter are different (LS means, $P < 0.05$)

course of the study at both sites (Fig. 4). At Île à Firmin East, this trend was seasonally reversed with dramatic increases during the summer. In contrast, no seasonal variation was seen at Île du Havre, and a massive decline in densities (47%) between August 2000 and June 2001 accounted for most of the change during the study.

The sampling at different distances from the kelp-barrens interface (into the barrens and into the kelp bed) showed that urchin densities consistently peaked in the first meter below the edge of the bed at both sites (Fig. 5). There was almost always a distinct front of urchins, often two to three layers thick. Urchin abundance fell off much more rapidly within the kelp bed than in the urchin barrens although at times, there were substantial densities (> 100 m⁻²) within the first 2 m, and occasionally even far into the kelp bed (e.g., Île du

Fig. 5 Changes in the densities of the green sea urchin, *S. droebachiensis*, within 5 m of the lower limit of kelp beds at Île à Firmin East and Île du Havre between June 2000 and June 2002. Data are means (+SE) for quadrats ($n=12$) placed at different distances inside and outside the kelp-barrens interface (at 0.0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 4.0, and 5.0 m in June and August 2000, and at 0.0, 0.5, 1.0, 3.0, and 5.0 m in June and August 2001 and June 2002)



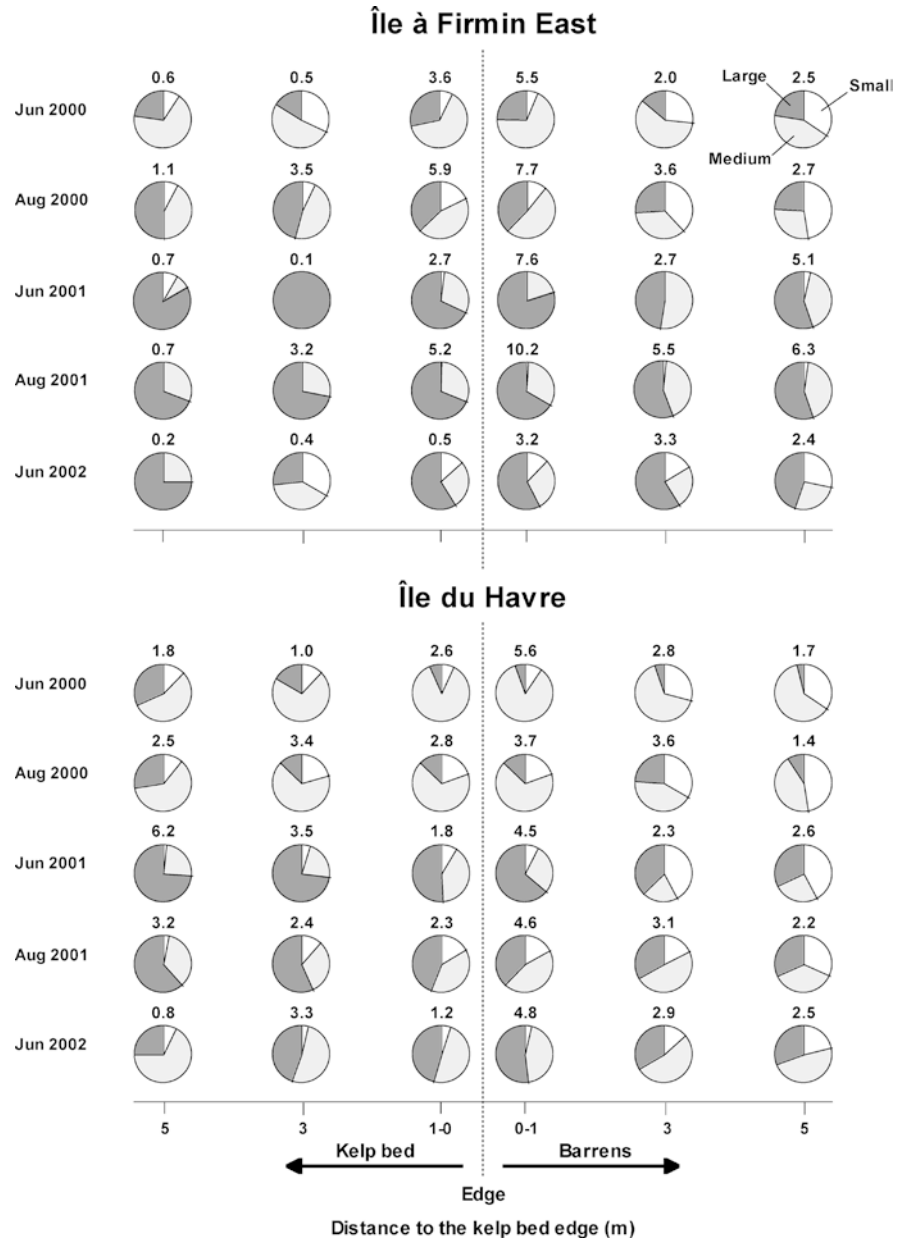
Havre in June 2001). The bell-shaped distribution around the kelp-barrens interface flattened with time, particularly at Île à Firmin East, associated with the overall decrease in urchin numbers (see above).

The analysis of the size structure of urchins in the transition zone showed that mean size generally increased over time at both sites, but urchins were always larger at Île à Firmin East (Fig. 6). In the kelp bed above the interface, urchins were generally larger with the largest size class often comprising more than 50% of the sample and the smallest size class usually accounting for <25%. Most urchins in the front and in the kelp bed were medium (2–4 cm) to large (>4 cm) in size (Fig. 6) whereas small urchins (<2 cm) were far more common in the urchin barrens, particularly at Île du Havre. At Île à Firmin East, the proportion of small urchins in the

overall area decreased during the first year (to nearly nil in the summer of 2001) and then increased by June 2002. Urchin biomass in the grazing front (in the first meter below the kelp edge) was initially similar ($\sim 5.5 \text{ kg m}^{-2}$) at the two sites (Fig. 6). Although the biomass increased almost twofold over the following 14 months at Île à Firmin East (to August 2001), it always remained less than the initial value at Île du Havre. Thus, during most of the study, the grazing potential was higher at Île à Firmin East than at Île du Havre.

Our data did not support the hypothesis that the rate of kelp-bed regression is positively correlated with urchin biomass in the grazing fronts. We found no significant relationship between the biomass of urchins in the grazing fronts and the rate of change in the position of the lower limit of kelp beds at the two intensively studied

Fig. 6 Changes in the proportions of small (< 2 cm test diameter), medium-sized (2–4 cm), and large (> 4 cm) urchins, *S. droebachiensis*, within 5 m of the lower limit of kelp beds at Île à Firmin East and Île du Havre between June 2000 and June 2002. Data are means for quadrats ($n=12$) placed at 0.0, 0.5, and 1.0 m (averaged and designated as 0- to 1-m intervals), and at 3.0 and 5.0 m inside and outside of the kelp-barrens interface. Values above the circle plots represent urchin biomass (kilograms per square meter) estimated from a regression equation relating fresh weight to test diameter ($n=144$) collected at Île du Havre



sites, either when averaged for the entire site (Fig. 7) or when examined within a site using transects as replicates (data not shown). Nevertheless, we noted a tendency toward increased kelp regression with increased urchin biomass at Île à Firmin East ($r^2=0.33$, $P=0.42$). There appeared to be a threshold biomass of urchins of $\sim 5 \text{ kg m}^{-2}$ [estimated from a regression equation of the pooled data from both sites; that is, when kelp edge displacement (meters) = $0 = 1.79 - 0.37 \times$ urchin biomass (kilograms per square meter), $r^2=0.29$, $P=0.17$] above which the beds receded. As urchin biomass was usually just below 5 kg m^{-2} (June 2000 being the only exception) at Île du Havre, this might explain why changes in the position of the kelp-bed interface varied little during the study (but see below). Overall, these results indicate that the variability in the position of the kelp-barrens interface is a more complex function than simply being related

to the urchin biomass in the grazing front (e.g., related to kelp density, wave exposure, tendency of urchins to feed).

Effect of urchins on algal recruitment in the barrens

The 44-day exclusion of urchins from experimental areas in the urchin barrens demonstrated that urchins strongly limited kelp recruitment as recruitment was more than 100 times greater in the ungrazed treatment [232.0 ± 66.5 (SE) recruits m^{-2}] than in the grazed treatment (2.0 ± 2.0 ; LS means, $P=0.0053$). Early colonists, such as diatoms, ulvoid algae, and *Spongomorpha arcta*, also flourished in the absence of urchins. The similarity between the fence control (4.0 ± 2.3) and grazed treatments (LS means, $P=0.97$) demonstrated that the manipulation did not affect recruitment beyond the effect of grazing by urchins.

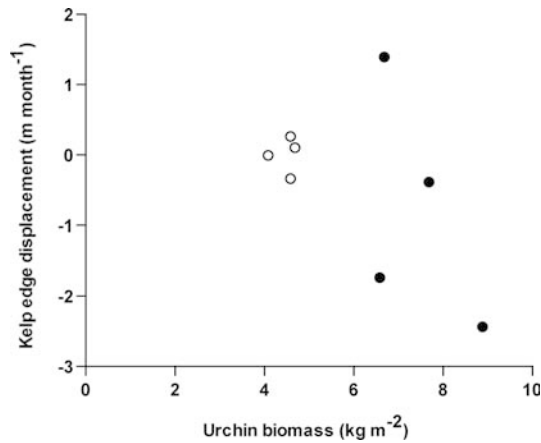


Fig. 7 Relationship between the rate of change in the position of the lower limit of kelp beds and urchin biomass in the grazing fronts at Île à Firmin East (filled circles) and Île du Havre (open circles) between June 2000 and June 2002. Positive rates indicate kelp-bed expansion and negative rates kelp-bed regression

Limitation of upward movements of urchins by *A. cribrosum*

The experimental removal of mature *Agarum cribrosum* showed that dense stands of kelp can greatly reduce shoreward movement of urchins. In the areas where *A. cribrosum* was not removed, the density of urchins in the lower *A. cribrosum* zone increased gradually over the first 3 days of the experiment but then remained low for the duration of the experiment ($< 34 \text{ m}^{-2}$, Fig. 8). In contrast, in the areas where the *A. cribrosum* canopy was removed, the density of urchins increased (particularly between 3 and 7 days), and after 20 days was more than four times greater than the first day. The final urchin density (after 20 days) was three times greater in the removal than in the non-removal areas. During the experiment, we observed dense urchin aggregations at the outer edge of the intact *A. cribrosum* areas (up to $356.3 \text{ urchins m}^{-2}$, $\text{SE} = 177.1$) during periods of calm wave conditions. Conditions were especially calm during the last 3 days of the study, and we observed groups of urchins at the edge of the bed anchoring the blades of *A. cribrosum* to the bottom. These aggregations likely accounted for the large increase in the density of urchins in the intact *A. cribrosum* areas as recorded on day 20.

Discussion

Although large seaweeds generally dominate shallow rocky subtidal communities on northwestern North Atlantic coasts (Chapman and Johnson 1990), grazing by the green sea urchin, *Strongylocentrotus droebachiensis*, nevertheless severely limits the distribution of kelp (Himmelman and Steele 1971; Breen and Mann 1976a, 1976b; Chapman 1981; Himmelman et al. 1983; Himmelman 1984; Miller 1985; Scheibling 1986; Witman 1987;

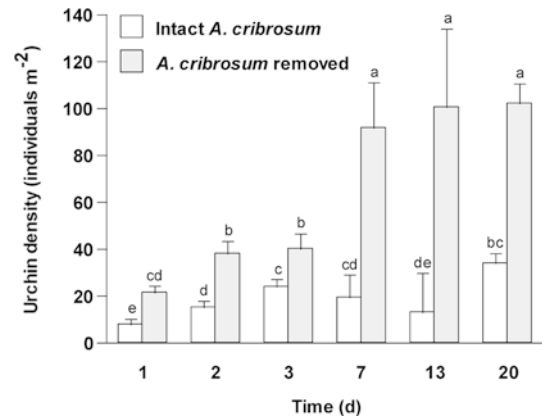


Fig. 8 Changes, over a 20-day period, in the mean density (+SE) of the green sea urchin, *S. droebachiensis*, in $1 \times 4\text{-m}$ areas along the lower edge of a mature stand of the kelp *Agarum cribrosum* where the kelp was removed and in $1 \times 4\text{-m}$ areas where *A. cribrosum* was left intact. Values not sharing the same letter are different (LS means, $P < 0.05$)

Keats et al. 1990; Scheibling et al. 1999). Our urchin exclusion experiment showing that urchins dramatically limited the recruitment of both kelp and ephemeral algae in the barrens is consistent with this body of knowledge. Thus, as seen elsewhere, urchin grazing is a primary factor controlling algal distribution in the shallow rocky subtidal zone of the Mingan Islands.

Most previous studies have focused on the negative impact of the green sea urchin on primary productivity, but these one-time observations have only provided limited information about interactions controlling changes in kelp-bed boundaries (but see Scheibling et al. 1999). Here we have shown that the kelp-barrens interface is dynamic and can shift over weeks to months. Moreover, we have demonstrated that these changes in the lower limit of kelp beds are site specific. For example, between August 2000 and June 2001, three sites experienced a regression in the kelp-barrens interface of 4–7 m, one site experienced no change, and one site showed an advance of 7 m. This variation was not clinal as the two most extreme sites (Île à Firmin East and West) were the closest together. Substantial temporal variation was also seen, especially at Île à Firmin East where there was a continuous regression of the kelp bed from 2000 to 2001, followed by massive kelp recolonization in 2002.

We had hypothesized that changes in the interface would be related to changes in the urchin population. Whereas the massive recruitment at Île à Firmin East occurred when urchin densities were at their lowest (August 2001 to June 2002), the movement of the interface did not track variations in urchin densities. For example, in spite of a 44% decrease in urchin density during the winter of 2000–2001, the kelp bed continued to regress. However, rates of regression were always highest during the summer (up to 2.5 m month^{-1}), when urchin numbers were increasing. Because urchin feeding

rates typically peak in summer (Vadas 1977; Larson et al. 1980; Himmelman 1984; Himmelman and Nédélec 1990; Meidel and Scheibling 1998), their increased voraciousness likely enhanced the effect of their increased density. The rates of kelp-bed regression that we observed were similar to those seen along the coast of Nova Scotia (up to 4.0 m month^{-1} , Breen and Mann 1976b; Mann 1977; Scheibling et al. 1999). Overall, our data suggest that the effect of urchins was nonlinear at Île à Firmin East and that kelp could only colonize when the urchin density was below $\sim 100 \text{ urchins m}^{-2}$. Possibly, the low number of urchins reduced their ability to weigh down and graze on the kelp. Biomass offers another measure of grazing pressure, and Breen and Mann (1976a, 1976b; and later supported by Scheibling et al. 1999) postulated that a threshold urchin biomass of $\sim 2 \text{ kg m}^{-2}$ causes kelp regression in Nova Scotia, a value less than half the threshold that we estimated for the Mingan Islands ($\sim 5 \text{ kg m}^{-2}$). The difference might be attributable to the higher kelp density in the Mingan Islands, or to the morphology or chemistry of the dominant kelps in the two systems, *Laminaria longicuris* in Nova Scotia and *Alaria esculenta* in the Mingan Islands. Another possibility is that our sites were more exposed to wave action or tidal currents than the sites in Nova Scotia, as increased wave action decreases the rate at which urchins move and attack algae (Kawamata 1998; Gagnon et al. unpublished manuscript). The greater exposure of the site at Île à Firmin East to waves and currents, compared to the site at Île du Havre, could have contributed to the increased variability in the lower limit of the kelp bed at this site. If urchins at Île à Firmin East experienced less predictable flow forces, they may have been able to move rapidly upward during periods of low wave action. Likewise, unexpected periods of high wave action could have dislodged urchins and permitted a massive expansion of the kelp bed. Finally, perhaps neither density nor biomass are individually the best measure of grazing pressure, and the best may be some combination of the two.

The large decrease in urchin density at Île à Firmin East during the winter of 2001–2002 was accompanied by an increased proportion of small urchins. Because of the much lower ingestion rate of small compared to large urchins (the rate for $< 15\text{-mm}$ urchins is tenfold less than for 50-mm urchins, Larson et al. 1980; Himmelman 1984; Minor and Scheibling 1997; Meidel and Scheibling 1999; Scheibling and Hatcher 2001), the overall grazing pressure may have been too low to prevent colonization by kelp. Several observations from Île du Havre support this idea. First, urchin densities were always > 100 individuals m^{-2} yet no massive colonization was observed (nevertheless, the greatest extension of the kelp bed did occur when urchin densities declined by 47% in the winter of 2000–2001). On the other hand, in spite of the constant high urchin densities, there was never a substantial regression of the kelp bed, even though kelp density was always lower and the plants smaller in the lower kelp bed compared to Île à Firmin East, which

should have facilitated the advance of the front (Scheibling et al. 1999). Our data support the hypothesis of a threshold urchin biomass as the grazing front at Île du Havre remained below 5 kg m^{-2} throughout most of the study and was apparently insufficient to cause a substantial regression of the interface there.

Another major difference between the two sites was the difference in kelps that formed the beds. *Alaria esculenta* was the dominant kelp present at Île à Firmin East, whereas we observed a shift from *A. esculenta* to *Agarum cribrosum* at the lower edge of the bed at Île du Havre during the study as reflected by the gradual decline in mean density and height of the kelp. *A. cribrosum* is probably more resistant to grazing than *Alaria esculenta* given the low preference of the urchin for this alga in both field and laboratory feeding studies (Himmelman and Steele 1971; Vadas 1977; Larson et al. 1980; Himmelman 1984; Himmelman and Nédélec 1990). This low preference may be partially due to chemical defenses, such as phenolics (Vadas 1977; Larson et al. 1980; Himmelman and Nédélec 1990). The tough stipe of *Agarum cribrosum*, which is fairly rigid and holds the blade above the bottom, may also contribute to its resistance to grazing. The greater resistance of *A. cribrosum* compared to *Alaria esculenta* is further shown by its ability to form patches within the barrens (Vadas 1968, 1977; Keats et al. 1982; Himmelman 1984). Moreover, as shown by our *Agarum cribrosum* removal trials, the presence of *A. cribrosum* can greatly reduce the upward movement of urchins. Thus, in certain situations, *A. cribrosum* appears to form a border at the lower edge of the kelp zone that limits incursions by urchins and in turn protects the more vulnerable *Alaria esculenta* growing at shallower depths from urchins. This effect on urchins may be unique to *Agarum cribrosum* because of its distinct grazing-resistant characteristics but could also be a general characteristic of any alga capable of forming a dense stand.

The mechanism by which *A. cribrosum* reduces movements of urchins remains to be determined. The alga might “block” the movement of urchins, by forming a barrier or repulsing the urchins, as seen for some other macroalgae (Velimirov and Griffiths 1979; Himmelman 1984; Dayton 1985a; Vasquez and McPeak 1998; Konar 2000; Gagnon et al. 2003a), or urchins might simply stop once they encounter a potential food source. A slowing of the advance of urchins by *A. cribrosum* was suggested by our observations at Île du Havre. Although the urchin front was clearly defined in June 2000 (high numbers at the lower edge of the kelp bed), the front became less pronounced over time as *A. cribrosum* gradually replaced *Alaria esculenta*. Because most of the urchins aggregated at the lower edge of the *Agarum cribrosum*, fewer urchins penetrated to the *Alaria esculenta* in shallower water. The greater temporal variability in the position of the lower limit of the kelp bed at Île à Firmin East, compared to Île du Havre, may thus have been related to the absence of *Agarum cribrosum* at this site.

We observed substantial declines in urchin abundance over time at both Île du Havre and Île à Firmin East, but events varied between sites. At Île du Havre, densities declined abruptly between August 2000 and June 2001, coincident with an increase in the average size, suggesting a demographic change (such as mortality or emigration). In contrast, at Île à Firmin East, we observed a more gradual temporal decline along with a seasonal pattern. The seasonal pattern was likely due to the migration of urchins into deeper water during the winter, perhaps to avoid ice scour (see below) or increased wave action as suggested for urchin populations in the St. Lawrence Estuary (Himmelman and Lavergne 1985), and their return the following spring. The gradual decline in density by > 50% between June 2000 and June 2002 is more difficult to explain. The decrease in the first year coincided with an increase in average size, as also seen at Île du Havre. A number of studies show that the growth rate of *S. droebachiensis* increases with size (Swan 1961; Thompson 1984; Raymond and Scheibling 1987; Russell et al. 1998). Possibly, the small urchins at Île à Firmin East benefited from the drop in large urchins that were either killed or moved away due to ice scour. The reduced intraspecific competition and increased food availability (with the new growth of kelp in the barrens) should have favored increased growth and thus increases in the average size. However, the change during the second year did not suggest a density-dependent response to resources as a shift to smaller urchins accompanied the decrease in numbers.

We documented striking differences between the two intensively studied sites, the most striking being the dynamics of the kelp-barrens interface and the general decline in urchin abundance. Unfortunately, we did not expect such extreme variation (e.g., the establishment of *A. cribrorum* at the Île du Havre site) and thus did not sufficiently replicate sampling for making definitive statements regarding the causes of these differences. Still, we postulate that *A. cribrorum* can play a pivotal role in determining the dynamics of the kelp-barrens interface by providing an herbivore-resistant fringe at the lower edge of the kelp bed. The distribution of *A. cribrorum* in shallow waters may, in turn, be controlled by ice scour, which occurs frequently during winter and early spring along rocky shores in the St. Lawrence Estuary and the Gulf of St. Lawrence (Archambault and Bourget 1983; Bergeron and Bourget 1984; Bourget et al. 1985), and along the coast of Newfoundland (Hooper 1981; Keats et al. 1985). We saw evidence of ice scour at Île à Firmin East during the winter of 2000–2001, as five of the six 10-cm steel bolts set into the bedrock as markers for the benchmark transects were found bent in June 2001. There was also evidence of ice scour (although less severe) in the winter of 2001–2002, as two out of six bolts were bent (the damaged bolts found in June 2001 had been replaced). These observations are consistent with those of Parks Canada personnel (Benoît Roberge and Nancy Dénomée, personal communications) who recorded a

solid ice sheet between the islands for only 2 weeks in 2001 (20 February to 6 March), whereas there was a solid cover for 2 months in 2002 (18 January to 17 March; there is less ice scouring when the cover is solid). In contrast, ice scour appeared to have been less at Île du Havre, as only three out of six bolts were bent during the winter of 2000–2001 (all three in the shallower part of the kelp bed) and only a single bolt during the 2001–2002 winter. If the condition of the bolts did reflect less ice scouring at Île du Havre, decreased disturbance may explain the greater survival of *A. cribrorum* at this site. The drop in urchin density observed at Île à Firmin East during winter of 2000–2001 is harder to explain but may reflect migration to greater depths due to winter conditions. Severe ice scouring appears to have occurred at the Île à Firmin West site during the winter of 2001–2002 as there were numerous denuded areas in the kelp community at shallower depths. More detailed observations are needed, however, to relate ice conditions to urchin aggregation and dispersion below the kelp bed.

Our study is the first to examine factors affecting the temporal stability in the lower limit of kelp beds in the northern Gulf of St. Lawrence. We provide evidence that sea urchin grazing plays a pivotal role in determining the lower limit of kelp. However, our results also show that the intensity of urchin-kelp interactions is both site and time specific. For example, the tendency of an increased rate of kelp-bed regression with increased urchin biomass was only seen at one of the intensively studied site (Île à Firmin East). We propose that perturbations by abiotic factors (e.g., ice scouring and water motion) triggering important but localized changes in urchin abundance are of primary importance for controlling kelp beds in the northern Gulf, rather than the large-scale effects of biotic factors as observed in other regions (e.g., predation and disease, Estes et al. 1978; Simenstad et al. 1978; Pearse and Hines 1979; Duggins 1980; Miller 1985; Scheibling 1986; Scheibling and Hennigar 1997; Scheibling et al. 1999). These perturbations would allow kelp beds to re-establish over the barrens during periods of reduced grazing. To increase our global understanding of the dynamics of such subtidal macroalgal communities, additional long-term studies are needed to examine the temporal stability of algal assemblages in the barrens zone, as well as to investigate the mechanisms by which a few fleshy macroalgae (e.g., *A. cribrorum* and *Desmarestia viridis*) withstand intensive grazing by urchins.

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