Destructive grazing, epiphytism, and disease: the dynamics of sea urchin – kelp interactions in Nova Scotia

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Abstract: We measured the rate of advance of urchin (Strongylocentrotus droebachiensis) feeding aggregations (fronts) as they destructively grazed kelp beds (Laminaria longicapsa) at both a wave-exposed site and a sheltered site in Nova Scotia over 3.5 years. The grazing fronts were composed of high densities of large adults (up to 98 and 70 per 0.25 m² at the exposed and sheltered sites, respectively). Urchins in the recently formed barrens, or in adjacent kelp beds, occurred at much lower densities and consisted mainly of juveniles. The fronts moved onshore into shallower water at each site, but their rate of advance varied markedly between sites and over time at each site, ranging from 0 to 4 m month⁻¹. The rate of advance of a front was related to the biomass of urchins; fronts did not advance below a threshold biomass of ~2 kg m⁻². Infestations of kelp by an epiphytic brown alga (Membranipora membranacea) caused marked reductions in kelp canopy cover and biomass during winter, but the canopy regenerates through recruitment of juvenile sporophytes in spring. A localized outbreak of disease decimated S. droebachiensis at the exposed site in 1993, which enabled kelp to recolonize the barrens. Surviving urchins gradually reaggregated and resumed destructive grazing after ~1.5 years. A recurrence of disease in 1995 eliminated urchins at both sites and terminated the transition from kelp beds to barrens on a coastal scale. Our findings have important implications for the management of the urchin fishery, which targets grazing fronts for harvesting.

Résumé : Nous avons mesuré la vitesse d’avancement de concentrations (fronts) d’alimentation de oursins (Strongylocentrotus droebachiensis) à mesure qu’ils broutaient de façon destructive les laminaires (Laminaria longicapsa) dans un site exposé et un site non exposé à la houle de la Nouvelle-Écosse, au cours d’une période de 3,5 années. Les fronts d’oursins brouteurs étaient composés de fortes concentrations de gros adultes (jusqu’à 98 et 70 par 0,25 m² dans, respectivement, les sites exposés et non exposés). Les oursins des zones récemment dévastées, ou se trouvant dans des concentrations de laminaires voisines, s’y trouvaient à des densités beaucoup plus faibles et étaient surtout des juvéniles. Les fronts se déplaçaient dans des eaux moins profondes en direction de la côte à chacun des sites, mais la vitesse d’avancement variait de façon marquée entre les sites et en fonction du temps, allant de 0 à 4 m mois⁻¹. La vitesse d’avancement d’un front était fonction de la biomasse des oursins : les fronts n’avançaient pas en deçà d’une biomasse seuil de 2 kg·m⁻² environ. Les infestations des laminaires par un épiphyte bruno (Membranipora membranacea) donnait lieu à de fortes réductions de la couverture et de la biomasse des laminaires en hiver, mais le couvert se regénéré par le recrutement des sporophytes juvéniles au printemps. Une épidémie localisée a décimé les S. droebachiensis du site exposé en 1993, ce qui a permis aux laminaires de recoloniser les zones dévastées. Les oursins survivants se sont graduellement regroupées et ont recommencé à brouter de façon destructive après 1,5 an environ. La réapparition de la maladie en 1995 a fait disparaître les oursins aux deux sites et mis fin à la transformation des zones à laminaires en zones dévastées à la grandeur de la côte. Nos résultats ont d’importantes incidences pour la gestion de la pêche des oursins, qui cible les fronts de broutage.

[Traduit par la Rédaction]

Introduction

Kelp beds (forests) are among the most productive communities of temperate coasts worldwide (Mann 1982). The high productivity and large standing biomass of kelps and associated macroalgae support large numbers of fish and invertebrates, which utilize the kelp as both a food resource and habitat (Dayton 1985). Among the numerous grazers that inhabit kelp beds, the pivotal role of urchins in determining community structure and stability is well recognized. Destructive grazing by urchins, which results in less productive, coralline algal-dominated assemblages termed "barrens," has been documented on a global scale in a variety of kelp habitats (Harrold and Pearse 1987). Because urchins can persist in barrens and prevent recolonization by kelps, destructive grazing can cause large-scale shifts in community state (Mann 1977).

Off the Atlantic coast of Nova Scotia, destructive grazing of kelp by the green sea urchin Strongylocentrotus droebachiensis is a recurrent phenomenon. The process is initiated when urchins form dense feeding aggregations that
move as "fronts" through a kelp bed, consuming all erect macroalgae in their path. This was first documented in St. Margaret's Bay in the early 1970s (Breen and Mann 1976a, 1976b), and surveys in 1979 reported urchin barrens, presumably the result of previous episodes of destructive grazing, along ~500 km (straight-line distance) of coast (Wharton and Mann 1981). In the early 1980s, recurrent outbreaks of disease caused mass mortalities of urchins in the shallow (<25 m) subtidal zone throughout this range (Miller 1985a; Scheibling 1986). Release from grazing pressure enabled the reestablishment of kelp beds by the mid-1980s (Scheibling 1986; Johnson and Mann 1988). However, increasing densities of S. droebachiensis in this zone precipitated another wave of destructive grazing and the system began to shift back to the barrens state in the early 1990s (Scheibling et al. 1994).

Because the loss of kelp is associated with major changes in habitat structure and productivity in the coastal zone, understanding the dynamics of urchin–kelp interactions, and the biotic and physical factors regulating these interactions, is particularly relevant to the management of the inshore fisheries. American lobster (Homarus americanus), the most valuable invertebrate species in eastern Canada and the Gulf of Maine, has been implicated as a controlling predator of urchins (Mann 1977; Hagen and Mann 1992; but see Miller 1985b; Elner and Vadas 1990), and urchins were viewed as pests because their grazing activity reduced kelp bed habitat utilized by lobster (Wharton and Mann 1981; Bologna and Steneck 1993). In recent years, however, the roe fishery for S. droebachiensis in this region has expanded rapidly, transforming urchins into a valuable resource (Hatcher and Hatcher 1997). Commercial fishing for urchins, and their crustacean and fish predators, can have important direct and indirect effects on the dynamics of the coastal ecosystem (Vadas and Steneck 1995; Scheibling 1996).

Natural or anthropogenic disturbances can facilitate invasion of a community by introduced species, which in turn may alter the disturbance regime of the disrupted community (Mack and Antonio 1998). An epiphytic brown alga (Membranipora membranacea) that infests kelps causing fragmentation and loss of fronds (Dixon et al. 1981) has recently invaded the Gulf of Maine (Berman et al. 1992) and Atlantic coast of Nova Scotia. Unlike destructive grazing, this loss of canopy cover is temporary, since recruitment by juvenile kelps can regenerate a kelp bed (Lambert et al. 1992). However, the coincidence of epizoan infestation and high urchin densities may have synergistic effects that accelerate the destruction of kelp beds.

In this study, we examine ecological interactions that regulate the mode and tempo of transition between alternative states of the rocky subtidal community through detailed monitoring of two contrasting sites in Nova Scotia. Over a 3.5-year period, we recorded massive losses of kelp biomass because of recent destructive grazing by S. droebachiensis and epiphytism by M. membranacea and recovery of kelp beds following mass mortalities of urchins from disease. In particular, we focus on the composition and behaviour of grazing fronts to provide new insights into their formation and the dynamics of urchin population outbreaks. We also examine the implications of our findings for the management of a sustainable urchin fishery.

### Materials and methods

#### Study sites

We selected two sites to represent contrasting types of kelp bed habitat with different hydrodynamic regimes: Little Duck Island (44°22′N, 64°11′W) and the northern end of Mahone Bay, adjacent to Mill Cove (44°35′N, 64°3′W). These sites were chosen for their different hydrodynamic regimes: Little Duck Island is characterized by the gentle tidal currents that are typical of the northern Gulf of Maine, while Mill Cove is characterized by the strong tidal currents that are typical of the southern Gulf of Maine.

#### Dynamics of urchin fronts

A sampling grid was established at each site in June 1992 with reference to four fixed position markers (steel eyebolts anchored in concrete blocks) placed in the barrens 10–12 m from the urchin front and spaced at 10-m intervals (Fig. 1). These were used as benchmarks to map the leading edge of the urchin front. We used a plastic measuring tape and a compass to record the polar coordinates (10-cm and 5° accuracy) of three positions along the front with reference to each of the four benchmarks: the perpendicular distance from the benchmark to the front and the distances at 20° to either side of the perpendicular. This gave a total of 12 positions along the leading edge of the front (or offshore border of the macroalgal bed) that were recorded at 1- to 3-month intervals between June 1992 and August 1995. In August 1993, we established a second series of benchmarks at Little Duck Island that was placed 20 m along the onshore bearing from the first series (Fig. 1) to reduce the distance between the front and the benchmark (which increased with destructive grazing of the kelp). In June 1994, we returned to the original benchmarks at Little Duck Island, as the macroalgal bed had expanded offshore by this time. In December 1994, we used a third set of benchmarks ~10 m along the onshore bearing from the second series, as the macroalgae receded again (Fig. 1). In April 1995, we extended the study area at Little Duck Island to encompass a second site (B) with an active grazing front that was ~50 m west of the original site (A) and 5 m deep. Two position markers were placed in the barrens ~10 m from the front and 10 m apart. The distribution of the front at site B was the same as at site A. At Mill Cove, we located a second set of benchmarks in July 1994 that were ~10 m along the onshore bearing from the first series and closer to the receding kelp bed (Fig. 1).

We estimated the rate of advance of the urchin front as the average distance between successive positions on the leading edge based on the three measurements taken from each benchmark. For the measurements at 20° to either side of the perpendicular, the perpendicular distance between successive positions was calculated trigonometrically. The three measurements were averaged for each

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Fig. 1. Sequential maps of the study grids at Little Duck Island and Mill Cove showing the changing boundary between the kelp bed (shaded) and barrens at selected sampling dates between June 1992 and August 1995. Numbered points show locations of different series of benchmarks within the grid at each site (see Materials and methods). Depth ranges from 5 to 8 m across the grid (from 60 to 0 m along the onshore axis) at Little Duck Island and from 6 to 10 m at Mill Cove.
Density and biomass of macroalgae and urchins

To compare interannually the abundance of macroalgae in the kelp bed and urchins in the barrens, we sampled 10 quadrats of 1 m² randomly positioned along a belt transect of 4 m by 50 m (200 m²) that extended along-shore (i.e., parallel to the series of benchmarks) in each habitat and at each site. The transects in the kelp bed were located 5–10 m into the bed from the offshore border. The initial kelp bed transect in June–July 1992 was 15 m along the onshore bearing from the original series of benchmarks (Fig. 1). In September–October 1993 and July–August 1994 and 1995, we located another kelp bed transect (because the kelp in the initial transect had been destructively grazed) 40 and 30 m onshore from the original series of benchmarks at Little Duck Island and Mill Cove, respectively (Fig. 1). The location of the second transect was staggered by 4 m each year to preclude overlap of sampling areas among years. We manually collected large, canopy-forming macroalgae (kelps and Desmarestia spp.) from each quadrat and placed them in separate net bags. All specimens from alternate quadrats were counted and the drained fresh weight of each species (all specimens pooled) was recorded for each quadrat using a spring balance (25-g accuracy for wet weight >500 g).

The initial transects in the barrens were located 5–10 m from the offshore border of the kelp bed in June–July 1992 (5 m along the onshore bearing from the original series of benchmarks; Fig. 1). The same general area was sampled in subsequent years, but transect locations were staggered as described above. In September–October 1993, we sampled an additional three transects in the barrens to establish vertical profiles of biomass that were 5, 15, and 25 m offshore from the border of the kelp bed at that time. Urchins were collected and counted in each quadrat in both the kelp bed and barrens transects, and horizontal test diameter of each specimen (in alternate quadrats when urchins were abundant) was measured with vernier calipers (0.1-mm accuracy). In spring (March–May) and autumn (September–November) each year, urchins along the front at each site were collected in 10–20 haphazardly positioned quadrats of 0.25 m² for measurement of test diameter.

We estimated the biomass (fresh weight) of urchins by converting the test diameter (D, millimetres) to wet weight (W grams) using the regression equation \( W = W.281 \times \frac{D}{7.0} \). This regression was based on a pooled sample of 424 urchins from both sites (211 from Little Duck Island, 213 from Mill Cove) ranging in diameter from 15 to 53 mm. Preliminary analyses showed no significant differences in regression parameters between habitats or sites. We estimated the biomass density of urchins by first determining the proportion of urchins in each 5-mm size-class in a sample and multiplying that by the mean density of urchins in that sample to estimate the numerical density of each size-class. We then multiplied the density of each size-class by the biomass of an individual at the midpoint of the respective size-class (estimated from the regression equation given above) to estimate the biomass density of each size-class. The average biomass density of the sample was then estimated by summing the biomass density over all size-classes.

Algal recolonization after urchin mass mortality

To monitor the recolonization of the barrens by macroalgae after a mass mortality of urchins in October 1993, and the subsequent reformation of grazing fronts, we measured macroalgal cover and urchin density along four transects of 50 m length in June, September, and November 1994 and April 1995 at Little Duck Island. The transects extended from each of the original benchmarks along the onshore bearing towards and into the kelp bed (except in November 1994 when only one transect was sampled due to inclement weather). Because the position of the offshore border of the kelp bed during this period differed markedly between the eastern and western halves of the sampling grid (Fig. 1), data were averaged for the two easternmost transects and the two westernmost transects, respectively, after aligning each pair of transects with reference to the kelp bed border. A similar series of transects was run at Mill Cove in November 1994 and March and June 1995. Data were averaged for all four transects (after alignment with reference to the kelp bed border) for the first two sampling dates. We videorecorded macroalgal cover along a 1 × 50 m belt transect, delineated by a weighted line graduated in metres, with a diver-held video camera (Sony CCD-V801 Hi-8 video camera recorder in an Amphibico housing). A 1-m-wide frame attached to the camera housing was used to keep the camera 0.6 m above the seabed and centred on the transect line. The videotapes were analyzed with a videocassette recorder (Sony EV-9000 VCR) and colour monitor (Sony KV-20EXR2). We measured the percentage cover of kelps (L. longicirratis, L. digitata, A. esculenta, Saccorhiza submollis), large plumose brown algae (Desmarestia spp.), branching and filamentous understory algae, and articulated coralline algae (Corallina officinalis) by freezing frames of contiguous 1-m² quadrats on videotape, projecting 100 regularly spaced points onto the screen, and counting the number of points overlying each algal type. We hand-counted urchins in 0.25-m² quadrats placed at 1-m intervals along the entire transect (or for 10 m around the barrens–kelp bed border in November 1994 and March 1995 at Mill Cove only).

Results

Density and size structure of urchin fronts

At the start of our study in June 1992, S. droebachiensis at Little Duck Island were aggregated in an extremely dense grazing front along the offshore border of the kelp bed. Peak densities within 1–2 m of the bed (averaged over four transects) ranged from 52 to 98±0.25 m² between June 1992 and September 1993 (Fig. 2). The urchins were piled on top of one another in three-dimensional aggregations that were typically three or four animals deep. These aggregations were 1–2 m wide and continuous over more than 200 m of seabed (which we surveyed by diving). Densities at the front were lowest in August 1992 and July 1993 when urchins shifted from three-dimensional aggregations to closely packed two-dimensional clusters that carpeted the bottom. This resulted in a broadening of the front in summer (e.g., July 1993) (Fig. 2), but dense three-dimensional aggregations were reestablished within 1 or 2 months. Urchins along the leading edge of the front climbed up the stipes and blades of kelp, weighing down the plants, which were rapidly consumed by the aggregation. Partially eaten kelp stipes and understory turf left in the wake of the front were consumed by trailing urchins.

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Fig. 2. Density of urchins in successive quadrats along 2- to 10-m transects extending from the kelp bed (shaded) into the barrens and perpendicular to the interface between habitats at selected sampling dates between June 1992 and August 1995 at Little Duck Island and Mill Cove. Data are means ± SE for quadrats (n = 4) at each 0.5-m interval relative to the edge of the kelp bed (shaded).

**Little Duck Island**

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**Distance from Edge of Kelp Bed (m)**

The front at Little Duck Island was composed almost exclusively of large adults with an approximately normal size distribution about a mean test diameter ranging from 38 to 51 mm (Fig. 3). Urchins at the front were consistently larger than those in either the barrens or the kelp bed within 5–10 m of the front, where size distributions were skewed by a preponderance of juveniles with modal sizes of 10–15 (1992-1994) or 5–10 mm (1995) (Fig. 3).

The front at Mill Cove was much less dense than that at Little Duck Island, consisting of clusters of urchins (rather than a continuous three-dimensional aggregation) along the offshore border of the kelp bed. Urchin density at the front was high at the start of our study (up to 70-0.25 m⁻² in June 1992) but subsequently decreased to between 10 and 40-0.25 m⁻². Aside from temporary increases in urchin density in December 1992 and June 1993, a distinct front was not evident during the rest of our study at Mill Cove (Fig. 2). Because of low currents at Mill Cove, the kelp fronds were prostrate on the sea bed. Urchins along the border of the kelp bed often formed two-dimensional feeding aggregations on these fronds; in June 1992, they also were observed climbing up the stipes to graze. As at Little Duck Island,
urchins in the front at Mill Cove were consistently larger (mean test diameter 24–32 mm) than those in the barrens or the kelp bed within 5–10 m of the front, where the modal diameter was generally 5–10 mm (Fig. 3). The mean diameter of urchins in each habitat was consistently smaller at Mill Cove than at Little Duck Island (Fig. 3).

**Destructive grazing of kelp beds**

At both sites, the urchin front advanced as a relatively linear feature, with small convolutions of the leading edge arising as the animals encountered topographical irregularities (e.g., boulders, ridges, sandy depressions) that altered their rate of advance (Fig. 1). Few urchins infiltrated the kelp bed in advance of the main aggregation, resulting in a discrete boundary at the leading edge of the front between the kelp bed and newly formed barrens (Fig. 2). At Little Duck Island, the rate of advance of the front varied markedly between June 1992 and September 1993; it peaked at 3–4 m/month$^{-1}$ in June of each year, declined to ~1 m/month$^{-1}$ by August, and remained low throughout the autumn and winter (Fig. 4a). At Mill Cove, the advance of the front was much slower, usually <1 m/month$^{-1}$ and negligible (or not detectable over measurement error) in late summer each year (Fig. 4a). Regression analysis showed no significant relationship between the rate of advance of the front and urchin density (Fig. 4b) at Little Duck Island between June 1992 and September 1993 ($F_{[1,13]} = 2.41$, $P = 0.165$), although decreases in the rate of advance in August 1992 and July 1993 were associated with a shift from three- to two-dimensional aggregation and concomitant decreases in urchin density. There was also no significant relationship between front advance and urchin density at Mill Cove throughout the study period ($F_{[1,10]} = 0.425$, $P = 0.52$).

The kelp bed at Little Duck Island consisted primarily of a dense canopy of *L. longicuris* (Fig. 5b). Large plume brown algae (*Desmarestia viridis* and *Desmarestia aculeata*)
Fig. 4. (a) Rate of advance of urchin fronts in successive sampling intervals between June 1992 and August 1995 at Little Duck Island and Mill Cove. Data are means ± SE (n = 4, except from April to August 1995 when n = 2 at site A (western half of the study grid) and site B, Little Duck Island). (b) Density of urchins in the front and barrens between June 1992 and October 1995 at Little Duck Island and Mill Cove. Data are means ± SE for grand means based on averages of three or four quadrats of 0.25 m² in the front and 68–72 quadrats in the barrens, averaged over four transects, except for the front at Little Duck Island (sites A and B) in 1995, where grand means are based on two transects.

Fig. 5. (a) Biomass of total canopy macroalgae (total bar) as the dominant species *L. longicurris* (light shading) and other macroalgae (mainly *Desmarestia viridis* and *D. aculeata*) (open) at Little Duck Island, and *L. longicurris* (dark shading) at Mill Cove, and (b) density of *L. longicurris* at Little Duck Island (light shading) and Mill Cove (dark shading) between 1992 and 1995. Data are means ± SD based on 10 randomly positioned 1-m² quadrats sampled in kelp beds in July–August (1992, 1994, 1995) or September–October (1993).

and an annual kelp (*S. dermatodea*) occurred sporadically in the bed, particularly in metre-scale gaps in the kelp canopy. The understory comprised turfs of articulated coralline algae (*Corallina officinalis*) and various fleshy and filamentous red algae (e.g., *Ceramium rubrum*, *Ptilota serrata*, *Phymenia plumosa*, *Chondrus crispus*, *Palmaria palmata*). The grazing rate per metre along the urchin front at Little Duck Island, estimated by multiplying the rate of advance of the front over a sampling interval (Fig. 4a) by the average biomass (fresh weight) of macroalgae in the kelp bed (4.1 kg m⁻²), based on pooled samples from transects in 1992 and 1993, n = 20; Fig. 5a), ranged from 2.7 (August–September 1992) to 17.1 kg m⁻¹ month⁻¹ (June–July 1993). During the first year of our study (June 1992 to June 1993), the front advanced 16.5 m (Figs. 2 and 5a), giving an annual grazing rate of 67.7 kg m⁻². Individual grazing rates, estimated by dividing monthly grazing rate of the front by the average density of urchins at the front in the corresponding sampling interval (Fig. 4b), ranged from 13.5 to 67.9 g m⁻¹.

The kelp bed at Mill Cove was almost exclusively *L. longicurris* with lower densities of larger plants than those at Little Duck Island (Fig. 5b). The understory turf was similar to that at Little Duck Island but less luxuriant. The estimated grazing rate per metre of urchin front at Mill Cove in 1992–1993, based on the macroalgal biomass measured in 1992 (5.2 kg m⁻², n = 10; Fig. 5a) because the kelp bed had begun to erode by October 1993 (see Defoliation and recolonization of kelp beds), ranged from 0 (November 1992) to 4.9 kg m⁻¹ month⁻¹ (June 1993) and was 24.4 kg m⁻¹ (corresponding to an advance of 4.7 m) during the first year of study. Estimated individual grazing rates ranged from ~0 to 61.3 g m⁻¹ during this period.

The uniformly low rate of advance at Mill Cove was related to both the smaller size and the lower density of ur-
Fig. 6. Relationship between rate of advance of the urchin front (see Fig. 4a) relative to urchin biomass at the front for pooled data from Little Duck Island (sites A and B) and Mill Cove, 1992–1995. Biomass is estimated from mean density of urchins at the front (see Fig. 4b) based on the size frequency distribution of urchins (see Fig. 3) and a regression equation relating fresh weight to test diameter (see Materials and methods).

![Graph showing the relationship between urchin front advance and sea urchin biomass](image)

Fig. 7. Urchin density and biomass at 5- to 10-m intervals in an offshore direction from the kelp bed (shaded), across the front, and into the barrens at Little Duck Island and Mill Cove in September–October 1993. Data are means ± SD for urchin density based on 10 quadrats of 1 m² randomly sampled along 50-m transects running alongshore in the kelp bed and barrens and 12–16 quadrats of 0.25 m² along the front. Biomass is estimated from mean density of urchins at the front (see Fig. 4b) based on the size frequency distribution of urchins (see Fig. 3) and a regression equation relating fresh weight to test diameter (see Materials and methods).

![Graph showing urchin density and biomass](image)

urchins at Mill Cove compared with Little Duck Island, which resulted in a lower biomass density at the former site. A linear regression based on pooled samples from both sites (excluding the period between October 1993 and May 1995 after the mass mortality of urchins at Little Duck Island) showed a significant positive relationship ($F_{1,32} = 26.01$, $P < 0.001$) between the rate of advance of the front (R, metres per month) and estimates of urchin biomass density ($W$, kilograms wet weight) given by the equation ($r^2 = 0.431$, $R = 0.775 \times W + 0.325$) (Fig. 6).

At Little Duck Island, destructive grazing was arrested in autumn 1993 when urchin density was reduced to <10-0.25 m⁻² along the front and <5-0.25 m⁻² in the adjacent barrens by an outbreak of disease (Figs. 3 and 5b). Most urchins exhibited characteristic symptoms of an amoebic infection (paramoebiasis, Jones et al. 1985) in early September, and by mid-October, there were masses of dead and moribund urchins on the seabed. Urchin densities at Little Duck Island remained low over the next year and grazing of the kelp bed effectively ceased. Although a few urchins at Mill Cove exhibited symptoms of disease in September 1993, there was no evidence of significant mortality, nor did we observe a decline in density in October 1993 (Figs. 2 and 4b).

**Urchins in the barrens**

At Little Duck Island, the density of urchins in the barrens directly in the wake of the front (within 10 m of the kelp bed border) was markedly lower than that in the front (Fig. 2) and relatively constant between June 1992 and September 1993, with mean density ranging from 14 to 27-0.25 m⁻² (Fig. 4b). In a series of alongshore transects in September 1993, urchin density did not vary significantly between 5 and 25 m from the edge of the kelp bed (6–7 m depth) but decreased significantly in the cobble bed at the offshore boundary of the site (35 m from the edge, 8 m depth) (one-way ANOVA, log-transformed data: $F_{13,36} = 6.53$, $P = 0.001$; Student–Neuman–Keuls test: $P < 0.05$). Urchins in the front at that time were about three times more abundant than those in the barrens and about six times more abundant than those in the cobble bed (Fig. 7). The mean size of urchins was similar between transects in the rocky barrens (test diameter 17.6 mm) but decreased in the cobble bed (16.6 mm), where few individuals exceeded 25 mm (Fig. 3). The distribution of urchin biomass paralleled that of density across the sampling gradient (Fig. 7), although the variation in biomass was even more pronounced (ranging from one to two orders of magnitude) because of the large size of urchins at the front (Fig. 3). Urchins were relatively rare (<5-0.25 m⁻³) and generally small in the kelp bed (Figs. 3 and 7).

Urchins exhibited a similar pattern of distribution at Mill Cove as at Little Duck Island, although densities were generally much lower (Figs. 2 and 7). Densities in the wake of the front and within 10 m of the kelp bed were usually <15-0.25 m⁻² (Fig. 2). Transects in October 1993 showed that urchin density in the barrens at Mill Cove did not vary significantly between 5 and 35 m from the edge of the kelp bed (7–10 m depth) (one-way ANOVA, log-transformed data: $F_{13,36} = 1.41$, $P = 0.256$). As at Little Duck Island, the size distribution of urchins across most of the barrens at Mill Cove was fairly constant (mean diameter ~13 mm), although the proportion of small juveniles (<10 mm) was lower in the deepest transect (mean diameter 21 mm) (Fig. 3). The larger average size of urchins in the deeper region resulted in an

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Fig. 8. Density of urchins and cover of the canopy-forming and other (understorey and ephemeral species) macroalgae in successive quadrats of 0.25 m² (urchin density) and 1 m² (algae cover) along 50-m transects running offshore from the kelp bed and into the barrens at selected sampling dates at Little Duck Island. Data are means (±SE for density) for quadrats (n = 2) at 1-m intervals relative to the edge of the kelp bed based on two transects in each half of the study grid (one transect in November in the eastern half).

Little Duck Island

(a) June 1994
(b) September 1994
(c) November 1994
(d) April 1995

Distance from Edge of Kelp Bed (m)

- Desmarestia
- Laminaria
- Saccorhiza
- other algae
- sea urchins

Sea Urchin Density (0.25 m²)

increase in biomass relative to the shallower barrens (Fig. 7). On a diving survey to 22 m depth in July 1994, we observed very few urchins on the gravel and silt bottom deeper than 15 m.

The size distribution of urchins in the barrens at both Little Duck Island and Mill Cove was relatively stable between 1992 and 1994, but a large increase in the abundance of small juveniles resulted in a marked drop in mean size by August 1995 (Fig. 3). The increase in mean size of urchins in the barrens at both sites between June and August 1995 (Figs. 2 and 4b) reflected our increased detection of these recruits from a major settlement pulse in July 1994 (T. Balch and R.E. Scheibling, unpublished data).

Defoliation and recolonization of kelp beds

In September 1993, colonies of *M. membranaceae*, an epiphytic bryozoa, expanded rapidly on kelp fronds at Little Duck Island and Mill Cove. Fronds heavily encrusted with bryozoa became brittle and friable and were fragmented by strong wave action during late autumn and winter. By mid-November 1993, the once luxuriant kelp beds at both sites were reduced to stands of stipes (which eventually died and rotted), resulting in a major loss of kelp biomass and canopy cover.

The loss of the kelp canopy at Little Duck Island over the winter in 1993–1994 facilitated recruitment, during the following spring, of juvenile sporophytes of *L. longicruris*, which are normally light limited under a healthy canopy. By June 1994, the mean density of kelp recruits was ~80 m⁻² in the kelp bed (R.E. Scheibling and A. Shaw, unpublished data). The cover of two other canopy-forming species (that usually are restricted to gaps in the *Laminaria* canopy), *D. viridis* and *S. dermatodea*, also expanded rapidly in summer 1994. By June 1994, *D. viridis* covered 60–100% of the previously barren area within 30 m of the border of the kelp bed (Fig. 8a). *Desmarestia viridis* and *S. dermatodea* are both annuals and began to die back in autumn (Fig. 8b). By November 1994, the cover of both species was generally <5% (Fig. 8c).

The rapid growth of the young kelp plants resulted in the offshore expansion of the kelp bed at Little Duck Island in 1994. By June, a large patch of *L. longicruris* and *S. dermatodea* had become established in the former barrens in the western half of the study grid (Fig. 8a), which by De-
Fig. 9. Density of urchins and cover of the canopy-forming and other (understorey and ephemeral species) macroalgae in successive quadrats of 0.25 m² (urchin density) and 1 m² (agal cover) along 35- to 50-m transects running offshore from the kelp bed and into the barrens at selected sampling dates at Mill Cove. Data are means (±SE for density) for quadrats (n = 2) at 1-m intervals relative to the edge of the kelp bed based on four transects for November 1994 and March and June 1995. Data for individual transects are given for June 1995.

Mill Cove

Distance from Edge of Kelp Bed (m)

November 1994

(c) June 1995

Algal Cover (%)

Desmarestia
Laminaria
Saccharina
other algae
sea urchins

Sea Urchin Density (0.25 m⁻²)

Transect 1

Transect 2

Transect 3

Transect 4

December extended the lower boundary of the bed close to its location at the start of the study in June 1992 (Figs. 1 and 8b). In the eastern half of the grid, however, the boundary of the kelp bed expanded only a few metres offshore during 1994 (Fig. 1). A recurrent outbreak of *M. membranacea* in October–November 1994 further reduced the canopy cover during that winter, but to a lesser extent than the previous year. By April 1995, a luxuriant kelp canopy had regenerated at Little Duck Island (Figs. 5 and 8d).

At Mill Cove, the death of large but less dense kelp plants created expansive gaps in the canopy that were subsequently colonized by *D. viridis* and its perennial congener *D. aculeata* (Fig. 9c). urchins infiltrating the kelp bed had created large barren patches by June 1995 (Fig. 9c). In spring and summer 1994–1995, a film of diatoms and filamentous algae covered much of barrens (particularly in the shallower parts), but this disappeared over winter (Figs. 9a and 9b).

Reaggregation of urchins and resumption of destructive grazing

After the mass mortality of *S. droebachiensis* at Little Duck Island in 1993, the distribution of remaining urchins shifted offshore. By June 1994, densities were low (generally <20–0.25 m⁻²) in the area blanketed by *D. viridis* but increased towards the deeper barrens where algal cover was lower (Fig. 8a). By April 1995, urchins began to reaggregate at the border of the kelp bed, particularly along the arm of recently recruited kelp in the western half of the study grid, where a front had reformed (Fig. 8d). This front advanced at a rate of -0.5 m-month⁻¹ between April and August 1995 (Fig. 4a), reducing the arm of new kelp (Fig. 1). In April 1995, we located another grazing front (site B) that advanced at a faster rate than the front in our study grid (site A) ~50 m away: 3.8 m-month⁻¹ between April and June and 2.1 m-month⁻¹ between June and August 1995 (Fig. 4a). Although the mean density of urchins in the front at site B (22–28·0.25 m⁻²) was generally lower than that at site A (up to 82·0·25 m⁻²) (Fig. 4b), urchins were larger (Fig. 3), and the density of kelp plants was lower (personal observations) at site B, which may account for the greater rate of advance of the front there.

At Mill Cove, small aggregations of urchins formed along the border of the kelp bed in March 1994 and 1995, but in both years, these weak fronts dispersed within 1 or 2 months (Fig. 2). Although the highest rates of advance of the front were recorded in spring 1994 and 1995 (1.4 m-month⁻¹; Fig. 4a), algal consumption rates per metre of front were actually lower at these times (2.1 and 4.1 kg m⁻² month⁻¹, respectively) than in the first year of our study (up to
4.9 kg·m⁻¹·month⁻¹) because of the lower biomass of *L. longicurris* after the bryozoan outbreak in 1993 (Fig. 5a).

In September 1995, a recurrence of disease virtually eliminated *S. droebachiensis* at both of our sites (Fig. 4b). Analysis of tissue samples from urchins collected at Little Duck Island confirmed the cause of the epizootic as paramoebiiasis (Scheibling and Hennigar 1997).

**Discussion**

**Formation of urchin fronts**

Large-scale destructive grazing of *Laminaria* beds by *S. droebachiensis* was previously documented off Nova Scotia in the 1970s by K.H. Mann and co-workers (reviewed by Mann 1977). In a pioneering study of the kelp beds in St. Margaret's Bay in 1968, Mann (1972) observed that urchins generally occurred at low densities and fed on drift algae at the base of the canopy. However, in a few areas (including Mill Cove), he described “holes” in the kelp canopy, tens of metres in diameter, where urchins were abundant and grazed the kelp. These gaps expanded and coalesced. and by 1973, an estimated 70% of the kelp along 15 km of coast had been destroyed. Breen and Mann (1976a, 1976b) described high-density fronts of large urchins advancing through the kelp beds, similar to those that we observed in the early 1990s.

Bernstein et al. (1981, 1983) proposed that an increase in urchin density within kelp beds, presumably because of a reduction in predation pressure, results in the formation of aggregations that trigger destructive grazing. However, the grazing fronts that we observed did not originate within kelp beds, as suggested by these and other authors (Mann 1977; Hagen 1983). Rather, the beds were attacked along their offshore bounds as urchins moved onshore from deeper regions. We also observed the onshore migration of grazing fronts in other areas along the Atlantic coast of Nova Scotia, and this pattern has been corroborated by a number of commercial urchin harvesters. Hjorliefsson et al. (1995) described a similar pattern of aggregation of *S. droebachiensis* along the lower edge of a kelp forest (*Laminaria hyperborea*) and onshore advance of a dense grazing front in a fjord in northern Iceland.

Based on these observations, we propose an alternative explanation for the formation of destructive grazing aggregations in Nova Scotia. After mass mortalities of *S. droebachiensis* by disease, urchins that survive in deeper, colder waters (Scheibling 1984) begin to migrate into the shallower, recently established kelp beds. These migrations may be driven by chemical cues emanating from the plants: chemoreception experiments have shown that *S. droebachiensis* is strongly attracted to kelp (Mann et al. 1984). As urchins encounter a kelp bed, their movement decreases as they begin feeding on the plants. This results in increasing urchin densities along the edge of the bed and a grazing front forms. Time-lapse video records at Little Duck Island showed that urchins at the front moved little and spent most of their time grazing on kelp, whereas those in the barrens undertook more extensive, random movements (R.E. Scheibling and A.W. Hennigar, unpublished data). Similarly, studies with tagged urchins (*Strongylocentrotus franciscanus*) in California have shown that individuals at the edge of a kelp forest move much less than those in the barrens (Mattison et al. 1977).

**Density and size thresholds for destructive grazing**

Breen and Mann (1976a, 1976b) postulated that a threshold biomass of *S. droebachiensis* was required for destructive grazing. This threshold is related to the ability of urchins to weigh down kelp fronds so that they can be entirely consumed. (Normally, wave-induced movement of the kelp limits the ability of individual urchins to climb onto fronds and effectively graze.) They found a positive relationship between urchin biomass at the edge of the kelp bed (ranging from 0.5 to 15 kg·m⁻²) and the rate of kelp bed recession (0–1.75 m·month⁻¹) and a threshold biomass for destructive grazing of ~2 kg·m⁻². We found a similar relationship at Little Duck Island where urchin biomass at the front was generally well above the postulated threshold level (Fig. 6), ranging from 6.6 to 12.1 kg·m⁻² before the mass mortality in 1993 (site A) and from 2.5 to 8.5 kg·m⁻² after fronts had reformed in spring–summer 1995 (sites A and B). At Mill Cove, urchin biomass was consistently below the threshold proposed by Breen and Mann (1976a, 1976b), ranging from 0.4 to 1.5 kg·m⁻² throughout our study (Fig. 6). Nevertheless, a slow recession of the kelp bed occurred, although there was little or no advance of the front in autumn each year when densities of adult urchins usually were low.

The difference in threshold levels for destructive grazing between Little Duck Island and Mill Cove probably reflects differences in wave action, which can limit urchin feeding rate (Lissner 1983; Kawamata 1998). At Little Duck Island, where wave action is generally strong, fronds of *L. longicurris* are tossed back and forth in the surge. In contrast, because wave action is lower at Mill Cove, kelp fronds often lie along the bottom and are accessible to individuals or small clusters of urchins. Under calm conditions, urchins also can climb the kelp stipes with little risk of dislodgment. Therefore, the decrease in wave action with depth may enable the formation of fronts by a gradual accumulation of individuals, even in wave-exposed areas such as Little Duck Island.

Urchins in fronts are almost exclusively large adults, generally >30 mm in test diameter (also see Breen and Mann 1976a; Bernstein et al. 1981). At these sizes, *S. droebachiensis* typically forages in the open on attached plants if they are available. Smaller urchins (which comprise most of the population in the barrens) usually are cryptic, sheltering in crevices and on the undersides of rocks to avoid predators (Himmelman 1986; Scheibling and Hann 1991). The characteristic size structure of the front probably develops as large, actively foraging urchins encounter the kelp bed. Large size is also advantageous in weighing down the kelp fronds and facilitating consumption of whole plants (Kawamata 1998). Thus, there probably is a body size threshold below which destructive grazing will not occur, such that a population consisting mainly of juveniles (<20 mm) may be unable to consume kelp. Meidel and Scheibling (1998a) showed that the difference in size distribution of urchins between the front and the barrens was related to differences in both age structure and growth rate. At both Little Duck Island and Mill Cove, urchins in fronts were older.
(median age 6 and 5 years, respectively) than those in barrens (3 and 2 years, respectively); urchins also grew faster in fronts and kelp beds than in barrens (Meidel and Scheibling 1998a).

urchins within the kelp bed, like those in the barrens, were small and cryptic. They typically occurred at low densities and in small aggregations under bladders. There was no evidence of destructive grazing of *L. longicurris* within the kelp bed throughout most of our study. However, following a major reduction in the kelp at Mill Cove, due to repeated outbreaks of *M. membranacea*, adult urchins began to infiltrate the kelp bed in 1995, creating barren patches similar to those observed by Mann (1972).

**Rate of advance of urchin fronts**

The rate of advance of the front at Little Duck Island peaked around midsummer but declined sharply in late summer and remained low over autumn and winter. Seasonal changes in feeding rates, possibly related to the reproductive cycle, may account for seasonal variation in the rate of advance of the front. In a concurrent study at Little Duck Island, Meidel and Scheibling (1998b) found that the feeding rate of urchins decreased in late summer and increased in spring (directly after spawning). A similar pattern has been observed in other studies of *S. droebachiensis* (Keats et al. 1983; Himmelman and Nédélec 1990). Individual feeding rates on macroalgae, estimated for periods of greatest advance of the fronts at Little Duck Island and Mill Cove (2 g·day⁻¹), were consistent with those measured in laboratory studies where adult *S. droebachiensis* were fed kelp ad libitum (Minor and Scheibling 1997; Meidel and Scheibling 1999).

Strong wave surge also can influence the rate of destructive grazing when it inhibits the foraging activity of urchins. In oscillating-flow-tank experiments, Kawamata (1998) showed that the feeding rate (on kelp) of *Strongylocentrotus nudus* virtually ceased at water velocities of 0.3–0.4 m·s⁻¹ and that the urchins could hardly move at 0.7 m·s⁻¹. Peak velocities during storms readily exceed these limits in the barrens at Little Duck Island (>1 m·s⁻¹, T. Balch and R.E. Scheibling, unpublished data). Wave surge also has a "whiplash" effect on kelp that can prevent urchins from climbing up kelp fronds to feed (Velimirov and Griffiths 1979). Wave action is strongest in winter, particularly at Little Duck Island, which may partly account for the low rate of advance of the front at that time. In August 1995, during a period of heavy swell generated by Hurricane Felix in the North Atlantic, we observed urchins in two-dimensional clusters along the front at Little Duck Island (sites A and B). These urchins were previously in three-dimensional aggregations during a calmer period in June 1995, suggesting that they deaggregated in response to increased wave surge. This behavioural change was associated with a broadening of the front (particularly at site B, which was shallower) and a reduction in its rate of advance. Since urchins in two-dimensional clusters can attach firmly to the rock substratum, probably even more so than isolated individuals (Garnick 1978), this may be a behavioural adaptation against wave dislodgment. urchins also avoid dislodgment by taking refuge in sheltered microhabitats (Harrold and Reed 1985), and we observed many individuals packed into crevices during periods of strong wave action.

The rate of advance of a grazing front is directly related to the density and body size of urchins (which together determine biomass) and inversely related to the density or biomass of plants in the kelp bed. Thus, the larger size of urchins and smaller biomass of kelp at Little Duck Island, compared with Mill Cove, at the start of our study in June 1992 (when urchin densities were comparable between sites) likely account for the higher rate of advance of the front at Little Duck Island. Similarly, differences between locations (sites A and B) at Little Duck Island were related to differences in both the size and biomass of urchins and the density of kelp plants.

The maximum rates of advance of urchin fronts measured during our study (4.2 and 1.4 m·month⁻¹ at Little Duck Island and Mill Cove, respectively) are consistent with those recorded previously in St. Margaret’s Bay (1.8 m·month⁻¹, Breen and Mann 1976a, 1976b) and more recently in an Icelandic fjord (2 m·month⁻¹, Hjörleifsson et al. 1995). Given these grazing rates and a rough estimate of the average width of rocky subtidal habitat suitable for kelp (366 m, Moore and Miller 1983), we estimate that destructive grazing of the rocky subtidal zone, in the absence of urchin fishing or natural disturbances such as disease or byzoozoan outbreaks, would take place between 7 and 22 years. In St. Margaret’s Bay, urchins took at least 6 years (1968–1973) to destroy kelp throughout the bay (Breen and Mann 1976b). Thus, it seems reasonable to propose that the transition from kelp beds to barrens on a coastal scale would take about a decade.

**Defoliation and recolonization of kelp beds**

In the Northwest Atlantic, the byzoozan *M. membranacea* was first recorded in the Gulf of Maine in 1987, where it became the dominant epiphyte on laminarian kelps within 2 years (Berman et al. 1992). We observed small colonies of *M. membranacea* on kelp at the start of our study in 1992, but it was not until the following year that a heavy growth of byzoozoa resulted in a major loss of canopy at both of our sites (this study; R.E. Scheibling and A. Shaw, unpublished data). Similar defoliation events have been reported in the Gulf of Maine (Lambert et al. 1992) and the Northeast Pacific (Dixon et al. 1981). Byzoozoan-mediated defoliation of kelp beds could augment or accelerate destructive grazing by urchins. This did not occur at Little Duck Island because of a coincident mass mortality of urchins in autumn 1993. Rather, recruitment of *Laminaria* sporophores regenerated and extended the kelp bed by summer 1994. At Mill Cove, where there was little mortality of urchins in autumn 1993, the pronounced reduction in kelp density probably facilitated a gradual infiltration of the kelp bed by urchins, thereby increasing the rate of kelp destruction. Byzoozoan infestations also could hasten the demise of kelp beds by promoting population growth of urchins. urchins incidentally consume *M. membranacea* while grazing on kelp, and this protein supplement results in increased rates of growth and reproduction (Nestler and Harris 1994). Fragmentation of heavily encrusted fronds by wave action also may enhance the nutrition of urchins in the barrens through increased production of kelp detritus.

Disease is the only known mechanism for the large-scale shift in community state from urchin-dominated barrens to...
kelp beds (Scheibling 1986), although the occurrence of this transition depends on the severity of an epizootic, which, in turn, is directly related to sea temperature (Scheibling and Henning 1997). Thus, the lower incidence of urchin mortality at Mill Cove than at Little Duck Island in September 1993 was probably related to lower bottom temperatures at Mill Cove, which limited transmission and progression of the disease (Scheibling and Henning 1997). In 1995, both sites experienced a protracted period of high temperatures, which culminated in nearly complete mortality of urchins. Partial or localized mortalities of urchins may not reduce numbers below a threshold that enables extensive re-colonization of kelp. Threshold densities of urchins required to maintain a urchin front appear to be much lower than those required for destructive grazing of kelp (this study; Bernstein et al. 1981; Leinaas and Christie 1996). As we observed at Little Duck Island, even when populations are decimated by disease, urchins can reaggregate to form fronts and resume destructive grazing.

The epizootic that decimated the urchin population at Little Duck Island in 1993 arrested destructive grazing and enabled recolonization of recently formed barrens by macroalgae. The succession that we observed in 1994 was similar to that previously reported after urchin mass mortalities in Nova Scotia (Scheibling 1986; Johnson and Mann 1988) and Norway (Leinaas and Christie 1996). Opportunistic annuals, mainly D. viridis and S. derocheticum, were the first canopy-forming species to appear, but these were replaced within a year by L. longicribros, the competitive dominant (Johnson and Mann 1988). Interestingly, the surviving urchins at Little Duck Island appeared to migrate away from the edge of the kelp bed, where a dense cover of D. viridis had developed by summer 1994, into deeper regions with less macroalgae. Although S. derocheticum can feed on D. viridis, it is a nonpreferred species (Lemire and Himmelman 1996) containing chemical compounds that render it unpalatable to urchins (Anderson and Velimirov 1982). As D. viridis eventually died back in winter, urchins re-aggregated along the border of the kelp bed to form a front by spring 1995, but this second wave of destructive grazing was terminated by a recurrence of disease in September that eliminated urchins at both of our study sites and over -130 km of coast (Scheibling and Henning 1997). This widespread demise of urchins led to the reestablishment of kelp beds at both sites by summer 1998 (R.E. Scheibling and T. Balch, unpublished data) and presumably throughout the disease-affected area.

Implications for the management of coastal resources

Previous consideration of the economic implications of community dynamics in the rocky subtidal zone off Nova Scotia has focussed primarily on the losses of primary productivity and habitat structure that result from destructive grazing of kelp beds by urchins (Mann 1977; Pringle et al. 1982). Wharton and Mann (1981) argued that the shift in the subtidal ecosystem from luxuriant kelp beds to urchin barrens contributes to declining yields of commercially important species such as lobsters (but see also Elner and Campbell 1987). Concern about the stability of barrens has prompted research into urchin eradication procedures designed to promote the reestablishment of kelp beds, including the use of quicklime and pathogenic agents (reviewed by Scheibling 1988). In the early 1990s, however, the urchin roe fishery in eastern Canada expanded rapidly (Hatcher and Hatcher 1997), dramatically altering the economic importance of S. derocheticum from a pest species to a valuable commodity. The challenge facing fisheries managers today is conservation of urchin stocks, not their destruction.

Our empirical observations are relevant to understanding the impact of the urchin fishery on community dynamics because fishing mortality has a similar effect on urchin populations, and hence on community structure, as natural occurrences of disease. The fishery targets areas of high urchin density, primarily grazing fronts, in the shallow subtidal zone where urchins are harvested by scuba diving. Intensive harvesting of fronts can remove enough large urchins to enable the regrowth of kelp along the margins of a bed (personal observations). Thus, like disease, fishing can arrest the destruction of kelp beds and allow regeneration of macroalgae that are important food resources for urchins. Judicious harvesting procedures that leave sufficient numbers of urchins to allow fronts to reform after the fishing season, or rotate harvested areas on an annual basis, may enable stocks to be fished at a sustainable level and maintain the system in a transitional state. This underscores the key difference between fishing and disease: fishing pressure can be regulated to limit the intensity or frequency of urchin mortality, whereas outbreaks of disease appear to be related to uncontrollable stochastic events (Scheibling and Henning 1997).

Future studies that address the urchin density dependence of destructive grazing and kelp recolonization could provide important insights for development of sustainable harvesting and ranching procedures for an urchin fishery. Experimental fishing of grazing fronts, designed to reduce densities to specified levels and monitor responses of both urchins and algae, would be a particularly effective approach. As the roe fishery expands, human predation will become increasingly more important in regulating urchin numbers and the dynamics of kelp beds. However, given the history of recurrent outbreaks of disease in this system, the fishery along the Atlantic coast of Nova Scotia is destined to periodically crash, making it a "boom or bust" venture.

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References


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