Role of grazing by sea urchins *Strongylocentrotus droebachiensis* in regulating the invasive alga *Codium fragile* ssp. *tomentosoides* in Nova Scotia

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ABSTRACT: To assess the potential of herbivory in regulating the invasive green alga *Codium fragile* ssp. *tomentosoides*, field and laboratory experiments were conducted with the green sea urchin *Strongylocentrotus droebachiensis* in Nova Scotia, Canada. In the field, urchins at different densities (0, 50 and 100 urchins m^{-2}) were caged on boulders covered with a canopy of either the kelp *Laminaria longicruris*, *Codium*, or a mixture of both species for 13 wk. In the treatment with *Laminaria* only, ~90% of the canopy was removed within 34 and 75 d in cages with 100 and 50 urchins m^{-2}, respectively. In contrast, *Codium* cover decreased by ~20% at both levels of urchin density in the treatment with *Codium* only, and did not differ significantly from the control (no urchins) at the end of the experiment. In the mixed canopy treatment, urchins showed a preference for *Laminaria*, consuming 90% of kelp cover within 39 and 54 d (at 100 and 50 urchins m^{-2}, respectively), while *Codium* cover increased gradually. Urchins grazed turf-forming red algae in all treatments, although in treatments with *Laminaria*, intensive grazing of turf only occurred once kelp was completely consumed. In the laboratory, urchins fed single diets of *Laminaria* or *Codium* for 8 wk had similar grazing rates (~0.20 dry weight g urchin^{-1} d^{-1}), while urchins fed a mixed diet consumed 2 times more kelp (0.15 g urchin^{-1} d^{-1}) than *Codium* (0.08 g urchin^{-1} d^{-1}). These experimental results indicate that urchins prefer kelp but will consume *Codium* when other algal foods are not available. We predict that urchin aggregations encountering mixed stands of kelp and *Codium* will initially graze the kelp and turf algae, creating patches of *Codium* that ultimately will be consumed as well.

KEY WORDS: *Codium fragile* ssp. *tomentosoides* · Herbivory · Sea urchins · *Strongylocentrotus droebachiensis* · Kelp · *Laminaria longicruris* · Feeding behaviour · Invasion ecology

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INTRODUCTION

The accelerating rate of species invasions in marine coastal habitats has focused research on ecological factors that regulate the establishment and spread of invasive species (Carlton & Geller 1993, Ruiz et al. 1997, 2000). For introduced marine macroalgae, vulnerability to native herbivores may be an important determinant of invasion success. Sea urchins are generalist grazers that play a key role in regulating the distribution, abundance and diversity of native macroalgae in subtidal communities worldwide (Lawrence

1975, 2001). Consequently, urchins may also be expected to influence the establishment, spread and persistence of introduced algal species. However, few studies have addressed this possibility, and those that have, have yielded mixed results. In the Mediterranean, for example, grazing by *Paracentrotus lividus* reduced the abundance of the invasive brown alga *Sargassum muticum* (Ribera & Boudouresque 1995) but could not control the spread of another invasive species, the green alga *Caulerpa taxifolia* (Meinesz 2001). In Tasmania, extensive stands of the invasive kelp *Undaria pinnatifida* are associated with urchin

Heliocidaris erythrogramma barrens, but recruitment and growth rates of the alga can exceed the urchins' grazing capacity (Valentine & Johnson 2003).

Codium fragile ssp. *tomentosoides* (hereafter *Codium*) is a siphonaceous green alga, probably native to Japan (Silva 1955), which has invaded temperate rocky coasts in both hemispheres during the past century (Trowbridge 1998). It was first reported in eastern Canada in the late 1980s in Nova Scotia (Bird et al. 1993) and has since spread rapidly to form dense stands in shallow subtidal (Chapman et al. 2002, Theriault 2003) and intertidal (Bégin & Scheibling 2003) habitats along the Atlantic coast. One hypothesis to account for the invasiveness of *Codium* is that it escapes herbivory (Malinowski & Ramus 1973, Chapman 1999).

The green sea urchin *Strongylocentrotus droebachiensis* is the dominant grazer in the rocky subtidal zone of the NW Atlantic and plays a pivotal role in determining benthic community structure (Chapman & Johnson 1990, Vadas & Elner 1992, Scheibling 1996). Where urchins occur at low density, macroalgal assemblages are dominated by canopy-forming kelps, mainly *Laminaria longicruris* and *L. digitata*. As urchins increase in abundance, they form feeding aggregations (or fronts) that destructively graze kelps and other fleshy algae to create so-called urchin barrens (Scheibling et al. 1999). The barrens phase, dominated by encrusting coralline algae, persists unless urchin populations are eliminated by disease (Scheibling 1984). Mass mortality of urchins enables fleshy macroalgae to colonize the substratum and the successional climax, *Laminaria* beds, is re-established within 2 to 3 yr (Miller 1985, Scheibling 1986).

In the mid to late 1990s, the structure of the benthic community along the Atlantic coast of Nova Scotia was dramatically altered by the introduction of the epiphytic bryozoan *Membranipora membranacea* and the green alga *Codium* (Scheibling et al. 1999, Chapman et al. 2002). Outbreaks of *M. membranacea* caused extensive losses in kelp canopy in shallow nearshore areas, enabling *Codium* to replace kelp as the dominant canopy-forming macroalga. During the same period, mass mortality of urchins released *Codium* (and other macroalgae) from intensive grazing in offshore barrens (Scheibling & Hennigar 1997). In the succession that followed, recruitment and growth of *Codium* surpassed that of *Laminaria* (Scheibling 2000[1]). Currently, *Codium* meadows are widespread throughout the shallow

rocky subtidal zone (<8 m below chart datum) along more than 100 km (straight-line distance) of coast (Theriault 2003, R. E. Scheibling & T. Balch unpubl. data). Similar shifts in algal dominance associated with these invasive species have been documented in the Gulf of Maine (Harris & Tyrell 2001, Levin et al. 2002, Mathieson et al. 2003).

Laboratory studies have shown that *Strongylocentrotus droebachiensis* consumes *Codium* (Prince & LeBlanc 1992, Scheibling & Anthony 2001) and thus may be capable of limiting its abundance in nature. Although these studies found that urchins preferentially consume kelp, intensive grazing by high densities of urchins (as occurs at fronts) may destroy all erect algae, including *Codium*. Urchins have not as yet repopulated areas dominated by *Codium* after the mass mortality, and urchin grazing of *Codium* has not been recorded in the field. Our study examines feeding rates of *S. droebachiensis* on *Codium* and *Laminaria* in field and laboratory experiments to assess the potential of urchins in regulating *Codium* along the Atlantic coast of Nova Scotia.

MATERIALS AND METHODS

Field experiment. To compare *in situ* grazing rates of the sea urchin *Strongylocentrotus droebachiensis* on kelp *Laminaria longicruris* and *Codium*, we conducted a 13 wk experiment (11 June to 9 September 2002) at Cranberry Cove, a small, moderately exposed embayment on the Atlantic coast of Nova Scotia (44° 28′ N, 63° 56′ W) near Halifax. Depth in the experimental area ranges from 2 to 4 m (below chart datum) and the substratum is composed of granitic outcrops and boulders. The canopy-forming algae consist mainly of *L. longicruris* and *Codium*. Other canopy-forming species, including *L. digitata*, *Fucus evanescens* and *Desmarestia viridis*, occur sporadically as scattered plants or in small patches. The understory turf consists of the articulated coralline alga *Corallina officinalis* and various foliose and filamentous red algae, mainly *Chondrus crispus* and *Bonnemaisonia hamifera*.

The completely randomized design consisted of 2 fixed factors, algal canopy type and urchin density, each with 3 levels. Urchins at densities of 0, 50 and 100 m^{-2}, representing an autogenic control treatment and typical adult densities in barrens and grazing fronts, respectively (Meidel & Scheibling 1999), were placed in cages enclosing boulders with monospecific stands of either *Codium* or *Laminaria longicruris* (hereafter *Laminaria*), or mixed stands of both species. Boulders ranged from 1.5 to 3 m in circumference and were selected for high cover (>70%) of the respective canopy algae, although some gardening was done in a

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few cases to increase initial treatment homogeneity. Cages were placed on the selected boulders and replicates of each level of urchin density were randomly allocated to boulders in each level of algal canopy type. Each treatment combination had 3 replicates, with the exception of control treatments with monospecific stands of *Laminaria* or *Codium*, which had 4 replicates.

The cylindrical cages were constructed from aquaculture netting (mesh aperture: 4 cm^2) coated with an anti-foulant. They were ~2 m in height and 0.5 to 1.0 m in diameter (depending on the size of the boulder). Chain (link diameter: 12.7 mm) sewn to the bottom of the netting served as an anchor to seal the bottom of the cage to the irregular substratum. Small floats attached to a plastic hoop (Hula Hoop) sewn into the netting suspended the upper rim of the cage. The top of each cage was closed by a lid of netting sewn around a second hoop, and plastic cable ties were used to bind the lid and rim hoops together.

Adult urchins were collected using SCUBA from a site near the mouth of Halifax Harbour (Chebucto Head, at ~10 m depth). The urchins were transported in coolers directly to Cranberry Cove and immediately placed into the appropriate cages. Urchins ranged from 35 to 55 mm in horizontal test diameter.

Before the addition of urchins, the initial percentage cover of *Laminaria* and *Codium* on each boulder was video-recorded and then monitored at weekly intervals with a diver-held video camera (Sony CCD-V801 Hi 8 camera in an Amphibico housing). The percentage cover of turf algae (mainly *Chondrus crispus*, *Corallina officinalis* and *Bonnemaisonia hamifera*) in all treatments was recorded on 22 September (21 d after the end of the experiment), after we manually removed all remaining canopy algae. To record, the cage lid was temporarily removed and the camera was inserted until the boulder filled the screen. Unattached *Codium* thalli also were temporarily removed for the recording. The videotapes were analyzed with a videocassette recorder (Sony EV-S900VCR) and color monitor (Sony KV-20EXR2). The percentage cover of each algal species was measured by freeze-framing the video tape, projecting 100 regularly spaced points onto the screen, scoring each point for the underlying algal type, and dividing the number of points for each algal type by the total number of points overlying the boulder.

Routine observations were conducted twice weekly from the beginning of the experiment until mid-July and then at weekly intervals. These included noting the location and activity of urchins in cages (e.g. climbing the cage wall, holding kelp or *Codium*, or under the canopy algae); the occurrence of rock crabs (urchin predators) in cages (if found, they were removed); and

the occurrence of moribund urchins (if found, they were removed and replaced with healthy urchins from the same source to maintain treatment densities).

Changes in percentage cover of *Laminaria* or *Codium* for each algal canopy type (*Laminaria*, *Codium*, mixed stands of both species) were compared among levels of urchin density (fixed factor: 0, 50, 100 urchins m^{-2}) by 2-factor analysis of variance (ANOVA) with repeated measures on date. In the treatments with kelp (alone or in mixed stands), the date when average canopy cover was reduced by ~90 % in a treatment (July 15) was used as an end point for statistical analysis. In the treatments with *Codium* (alone or in mixed stands), the analytical end point was the end of the experiment (9 September). Due to large differences in the rate of loss in canopy cover between treatments with *Laminaria* and those with *Codium*, different intervals were used in the analysis for each species (bi-weekly and monthly respectively). Due to the potential non-independence of time-series data, we used Greenhouse-Geisser adjusted probabilities when sphericity assumptions were not met ($\alpha = 0.05$). The cover of turf algae was compared between treatments at the end of the experiment by 2-factor ANOVA (Fixed Factor 1: algal canopy type [*Laminaria*, *Codium*, mixed]; Fixed Factor 2: urchin density [0, 50, 100 urchins m^{-2}]). All analyses were performed on untransformed data and satisfied the assumption of homogeneity of variance, as indicated by Levene's test ($\alpha = 0.05$). Post hoc comparisons among means were performed using Tukey's Honestly Significant Difference test.

Effects of urchin grazing in monospecific and mixed canopy treatments were also analyzed after the methods of Peterson & Renaud (1989), using control treatments to adjust for autogenic changes in the algae. For monospecific canopy treatments, proportional changes in percentage cover (the response variable) during the first 34 d (11 June to 15 July) were analyzed by 2-factor ANOVA (Fixed Factor 1: algal canopy type [*Laminaria*, *Codium*]] Fixed Factor 2: urchin density [0, 50 or 100 urchins m^{-2}]). Proportional rather than absolute difference in cover was used to adjust for small variations in the initial cover. A significant interaction indicates a difference in consumption rate between algal species because differences in the change in cover varied with the presence or absence of grazers. In the mixed canopy treatment, the difference in the change in cover of *Laminaria* and *Codium* was calculated for each level of urchin density. The difference in the control without urchins was compared to that in treatments with urchins (50 or 100 m^{-2}) by Student's *t*-test. The difference between *Laminaria* and *Codium* cover was used because changes in cover of the 2 species are not independent.

Laboratory experiment. Feeding rates of *Strongylocentrotus droebachiensis* on *Laminaria* and *Codium* were measured in an 8 wk laboratory experiment (26 June to 26 August 2002) with similar algal treatments as the field experiment: *Laminaria*, *Codium* or a mixture of both species. Aquaria with flowing seawater (L × W × H: 57.5 × 29.0 × 32.5 cm) were set up in a randomized block design, on 3 tiers with 6 aquaria per tier. Each diet treatment had 2 replicate aquaria per tier for a total of 6 replicates. Each aquarium contained 16 urchins, equivalent to the highest density in the field experiment (100 urchins m^{-2}). The urchins were from the same collection as for the field experiment, and of the same size range. They were transported in coolers to the laboratory and placed in large flowing seawater tanks and fed kelp ad libitum until a week before the experiment, when they were starved to standardize initial conditions. Each aquarium was supplied with an air stone to increase oxygenation and circulation. Northward facing windows provided a natural photoperiod. Average daily seawater temperature ranged from 8 to 11.5°C throughout the experiment.

Urchins were fed *Laminaria* and/or *Codium* at weekly intervals. The algae were freshly collected at Cranberry Cove when required during the experiment. To simulate the natural vertical aspect of algae on the seabed, sections of each species (20 to 30 cm in length) were inserted into 14 evenly spaced holes on a weighted plexiglass panel that covered the aquarium bottom, and held in position with small wedges of plastic tubing. The single diet treatments had 14 pieces of the respective 'plants' per aquarium (~1200 g fresh weight of kelp or *Codium*) and the mixed diet treatment had 7 'plants' of each species per aquarium (~700 g of each species) randomly placed in holes on the panel. The algae were air-dried on paper towels for 5 min before weighing rations on an electronic balance. To maintain equal numbers of plants of *Laminaria* and *Codium* available to urchins in the mixed treatment, grazed plants were replaced after 3 to 5 d. At weekly intervals, all remaining algae in each aquarium were removed and re-weighed to estimate the amount consumed, and each tank was vacuumed to remove urchin faeces. Since *Laminaria* and *Codium* have very different water contents, their fresh weight was converted into dry weight using the conversion coefficients of 0.063 for *Codium* and 0.199 for kelp (Scheibling & Anthony 2001).

Autogenic controls (without urchins), with 6 replicate aquaria for each algal treatment, were run during the last week of the experiment. The mean change in algal weight in autogenic control treatments was used to adjust changes in experimental treatments to estimate the mass of algae consumed by urchins throughout the experiment. Feeding rates, measured as the dry weight of algae consumed per urchin per day, were analyzed by 2-factor repeated-measures ANOVA, as in the field experiment. The design allowed us to include tier as an additional factor in the model. However, preliminary analysis indicated no significant effect (p > 0.05) of tier or its interaction with other factors (time or diet). Similarly, previous experiments using this system showed tier effects were not significant (Minor & Scheibling 1997, Scheibling & Anthony 2001). Therefore, we conducted our analyses without tier as a factor.

Feeding rates and preferences in the single and mixed algal treatments were analyzed as for the field experiment. For the single algal treatments, the changes in the mass of algae in treatments with urchins (during Week 8) and in the autogenic control were analyzed by 2-factor ANOVA. In the mixed algal treatment, the differences in the autogenic control treatment were compared to those in treatments with urchins present using Student's *t*-test.

RESULTS

Field experiment

Laminaria cover in both the monospecific and mixed canopy treatments decreased exponentially to 0 in cages with urchins (Fig. 1). In the monospecific treatment, ~90% of *Laminaria* cover was removed within 34 and 75 d in cages with 100 and 50 urchins m^{-2}, respectively (Fig. 1). Two-factor repeated-measures ANOVA of *Laminaria* cover during the first 34 d (11 June to 15 July) showed a significant effect of date and urchin density, and no interaction between these factors (Table 1). Tukey's test indicated that kelp cover in both the 50 and 100 urchins m^{-2} treatments was significantly lower than in the control without urchins (Table 1). In the treatment with *Codium* only, cover decreased by ~20% at both levels of urchin density and increased slightly in the control. However, ANOVA did not detect any significant effect of date, urchin density, or interaction between these factors (Table 1).

In the mixed canopy treatment, urchins consumed 90% of the cover of *Laminaria* within 39 and 54 d in cages with 100 and 50 urchins m^{-2}, respectively, while the cover of *Codium* increased gradually at both levels of urchin density and in the control (Fig. 1). ANOVA detected a significant decrease in *Laminaria* cover during the first 34 d (Table 2). Although the rate of decrease was greater in treatments with urchins, the effect of urchin density was not significant and there was no interaction between date and density. *Codium* cover in the mixed canopy treatment did not differ
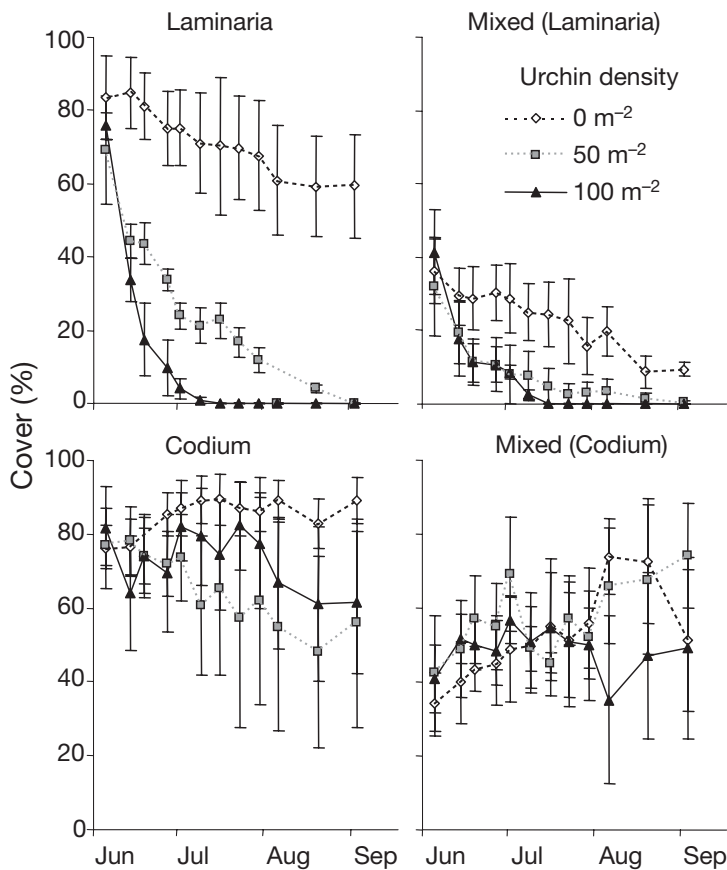
Fig. 1. Change in canopy cover (mean ± SE, %) of *Codium* and/or *Laminaria* in cages with monospecific stands (*Codium*, *Laminaria*) or an equal mixture (Mixed) of the 2 species, and 3 levels of sea urchin *Strongylocentrotus droebachiensis* density (0, 50, or 100 urchins m^{-2}), from 11 June and 9 September 2002

significantly with date or urchin density, and there was no interaction between these factors (Table 2).

Urchins typically consumed *Laminaria* by climbing upon the fronds and weighing them down, as observed in natural grazing fronts (Scheibling et al. 1999). Occasionally, urchins held down thalli of *Codium* with their aboral tube feet, or clustered on top of the plants. In the mixed canopy and *Codium* treatments, drifting fragments of *Codium* were first observed in late July in cages with urchins, and a month later in the controls. In contrast, drifting *Laminaria* was rare in cages with urchins and never observed in control cages.

Proportional changes in the cover of *Laminaria* and *Codium*, measured during the first 34 d, show a progressive reduction in cover of *Laminaria*, and little change in cover of *Codium*, with increasing urchin density in both monospecific and mixed canopy treatments (Fig. 2). Two-factor ANOVA of proportional change in cover in monospecific treatments did not detect a significant interaction ($F_{1,10} = 0.221$, p = 0.649)

Table 1. Two-factor repeated-measures ANOVA of the change in cover (%) of *Laminaria* and *Codium* in monospecific canopy treatments with date (20 June, 3 and 15 July for *Laminaria*; 3 July, 5 August, and 9 September for *Codium*) and sea urchin *Strongylocentrotus droebachiensis* density (0, 50 and 100 urchins m^{-2}). Degrees of freedom (df) are Greenhouse-Geisser-adjusted when sphericity assumptions are not met ($\alpha = 0.05$). Also shown are pairwise comparisons among means (Tukey's test) for the *Laminaria* treatment, where the effect of urchin density is significant

	Source	df	MS	*F*	p
Laminaria					
Between plots	Urchin density	2	11319	10.9	0.007
	Error	7	1037		
Within plots	Date	1.2	2248	12.0	0.007
	Date × Density	2.4	173.1	0.93	0.450
	Error	8.3	187.0		
Codium					
Between plots	Urchin density	2	1461	0.72	0.519
	Error	7	2025		
Within plots	Date	2	11.2	0.07	0.935
	Date × Density	4	132.1	0.79	0.550
	Error	14	167.0		
Tukey's test (*Laminaria*)					
Density levels	Effect size			p	
0, 50	44.9			0.037	
0, 100	63.4			0.007	
50, 100	18.4			0.483	

Table 2. Two-factor repeated-measures ANOVA of the change in cover (%) of *Laminaria* and *Codium* in the mixed-canopy treatment with date (20 June, 3 and 15 July for *Laminaria*; 3 July, 5 August, and 9 September for *Codium*) and sea urchin *Strongylocentrotus droebachiensis* density (0, 50 and 100 urchins m^{-2}). Degrees of freedom (df) are Greenhouse-Geisser-adjusted when sphericity assumptions are not met ($\alpha = 0.05$)

	Source	df	MS	*F*	p
Laminaria					
Between plots	Urchin density	2	846.4	1.98	0.219
	Error	6	427.7		
Within plots	Date	1.1	440.3	11.05	0.012
	Date × Density	2.3	59.7	1.50	0.293
	Error	6.8	39.9		
Codium					
Between plots	Urchin density	2	339.0	0.19	0.823
	Error	6	1744.4		
Within plots	Date	2	177.1	1.17	0.344
	Date × Density	4	176.4	1.18	0.367
	Error	12	149.4		

of algal species (*Laminaria* vs *Codium*) and urchin presence at the lower density (0 vs 50 urchins m^{-2}). However, a significant interaction at the higher density ($F_{1,10} = 6.02$, p = 0.034) indicated urchins consumed kelp at a greater rate than *Codium*.
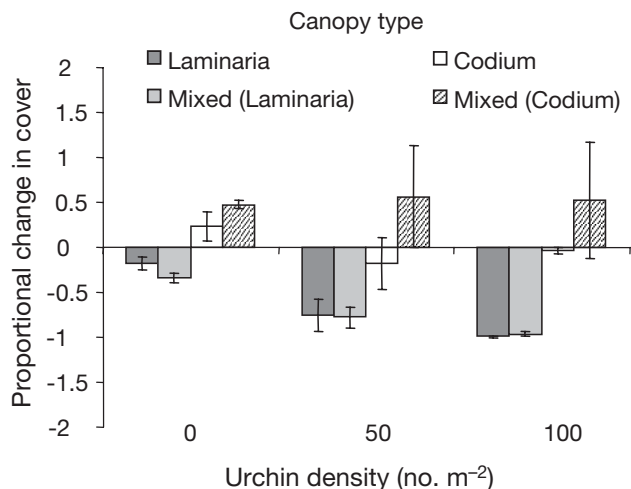
Fig. 2. Proportional changes in canopy cover (mean ± SE, %) of *Codium* and/or *Laminaria* in cages with monospecific stands (*Codium*, *Laminaria*) or an equal mixture (Mixed) of the 2 species, and 3 levels of sea urchin *Strongylocentrotus droebachiensis* density (0, 50, or 100 urchins m^{-2}), from 11 June and 15 July 2002 (when >90% of kelp was consumed)
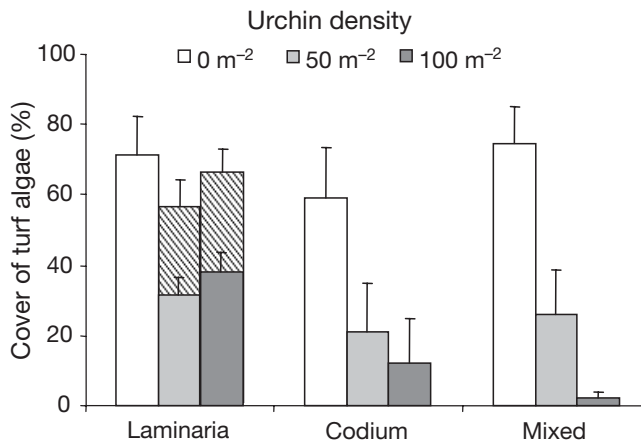

Fig. 3. Cover (mean ± SE, %) of turf-forming algae (mainly *Chondrus crispus*, *Corallina officinalis* and *Bonnemaisonia hamifera*) in treatments with monospecific stands of *Codium* or *Laminaria* or an equal mixture (Mixed) of the 2 species, and 3 levels of sea urchin *Strongylocentrotus droebachiensis* density (0, 50, or 100 urchins m^{-2}), on 22 September. Also shown for the *Laminaria* treatment is cover at the dates (between 25 June and 29 August) once all kelp had been consumed in treatments with urchins (hatched bars)

In the mixed canopy treatment, the average difference in the change in cover between *Laminaria* and *Codium* during the first 34 d was similar at low and high urchin densities (112.1 and 114.8% respectively), and more than twice that in the control (49.5%) (Table 3). A *t*-test comparing this difference between treatments with urchins present (both density levels were pooled for analysis) and the control gave a marginally nonsignificant result ($t_7 = 1.60$, p = 0.077), indicating no preference. However, excluding replicate 3 in the highest density treatment, in which the cover of *Codium* decreased in contrast to all other replicates, yielded a significant result ($t_6 = 2.41$, p = 0.030). The difference in the change of cover between algal species was greater in the treatments with urchins than in the control, indicating that urchins preferentially consumed *Laminaria*.

By late June, it was evident that urchins were grazing the understory turf in the *Codium* treatment, since large patches of bare rock were forming. This also occurred in the mixed-canopy treatment and in the *Laminaria* treatment once all kelp was consumed. Urchins grazed the algal turf immediately around holdfasts of *Codium*, leaving the thalli undisturbed. After the experiment (on 22 September), the mean cover of turf algae in control treatments was 2 to 10 times higher than in treatments with urchins (Fig. 3). Two-factor ANOVA of turf cover at this time showed a significant effect of urchin density but no effect of canopy type and no interaction between these factors (Table 4). Tukey's test showed there was significantly less turf when urchins were present at both the low and high density than when they were absent (Table 4).

To determine whether urchins were grazing on turf algae in the *Laminaria* treatment while kelp was still present, the percentage cover of turf was measured on the sampling date, for each replicate, when all of the kelp had been consumed (between 25 June and 29 August for all replicates at both levels of urchin density) (Fig. 3). Single-factor ANOVA comparing turf cover in these treatments at this point and that in the control treatment on 22 September showed no significant difference between treatments ($F_{2,7} = 0.689$, p = 0.533). Assuming no change in turf

Table 3. Changes in cover (%) of *Codium* (C) and *Laminaria* (L) at 3 levels of urchin density (0, 50 and 100 urchins m^{-2}) within the mixed canopy treatment between 11 June and 15 July 2002. Positive values indicate an increase in cover; negative values indicate a loss in cover. Also shown are differences in the change in cover between algal species (C – L: *Codium* minus *Laminaria*) for each of 3 replicate cages, and the mean and SE of these differences for each level of urchin density

| Density (no. m^{-2}): | 0 | | | 50 | | | 100 | | |
Canopy:	C	L	C – L	C	L	C – L	C	L	C – L
Cage 1	42.70	−21.7	64.4	86.4	−53.6	140.0	45.7	−62.5	108.2
Cage 2	33.28	−27.1	60.5	6.5	−55.8	62.3	125.7	−86.4	212.2
Cage 3	22.20	−1.5	23.7	44.2	−89.9	134.1	−48.6	−72.7	24.2
Mean			49.5			112.1			114.8
SE			13.0			25.0			54.4

Table 4. Two-factor ANOVA of cover (%) of turf algae in orthogonal treatments of canopy type (*Laminaria*, *Codium* and mixed) and sea urchin *Strongylocentrotus droebachiensis* density (0, 50 and 100 urchins m^{-2}) on 22 September. Also shown are pairwise comparisons of means between levels of urchin density (Tukey's test)

Source	df	MS	*F*	p	Tukey's test		
					Density level	Effect size	p
Canopy type	2	7745.5	16.90	0.226	0, 50	41.5	0.001
Urchin density	2	705.2	1.06	<0.001	0, 100	50.3	<0.001
Canopy × Density	4	337.8	0.77	0.559	50, 100	8.8	0.653
Error	20	440.1					

cover over time in the control, this result indicates that urchins did not substantially graze turf algae until all kelp was consumed. A direct comparison with the control on these sampling dates was not possible because of the overlying kelp canopy, which was not removed until after the experiment was terminated.

Laboratory feeding rates

In autogenic controls without urchins, slight increases in the dry weight of *Laminaria* in the monospecific (0.2%) and mixed (0.8%) algal treatments, and of *Codium* in the monospecific treatment (2.9%), were non-significant (*t*-test, p > 0.37). Only *Codium* in the mixed treatment control increased significantly in weight (5.5%) (t_{10} = 2.23, p = 0.023). Feeding rates of *Strongylocentrotus droebachiensis*, adjusted for these changes in autogenic controls, were relatively constant throughout the 8 wk experiment (Fig. 4).

Two-factor repeated-measures ANOVA of feeding rates on *Codium* between the single and mixed diets
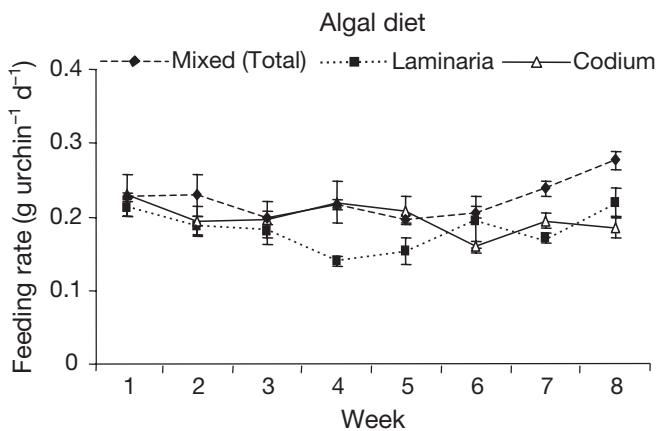
(Figs. 4 & 5) showed a significant difference between diets, but no change over time and no interaction between diet and time (Table 5). Averaging over time shows that the adjusted feeding rates on *Codium* in the single diet (0.20 g urchin^{-1} d^{-1}) was 2.5 times greater than in the mixed diet (0.08 g urchin^{-1} d^{-1}). A similar comparison of feeding rates on *Laminaria* (Figs. 4 & 5) also detected a significant difference between single and mixed diets (Table 6), but the time averaged difference was much smaller (0.19 and 0.15 g urchin^{-1} d^{-1}, respectively).

Two-factor ANOVA comparing the change in weight of *Laminaria* and *Codium* in single-diet treatments with that in the respective autogenic controls did not detect a significant interaction between algal species and urchin presence ($F_{1,20}$ = 1.56, p = 0.226), indicating no difference in consumption rate when urchins were

Table 5. Two-factor repeated-measures ANOVA of sea urchin *Strongylocentrotus droebachiensis* grazing rate (g urchin^{-1} d^{-1}) on *Codium* in monospecific and mixed diet (*Codium* and *Laminaria*) treatments over time (8 weekly intervals) in laboratory aquaria. Degrees of freedom (df) are Greenhouse-Geisser-adjusted where sphericity assumptions are not met (α = 0.05)

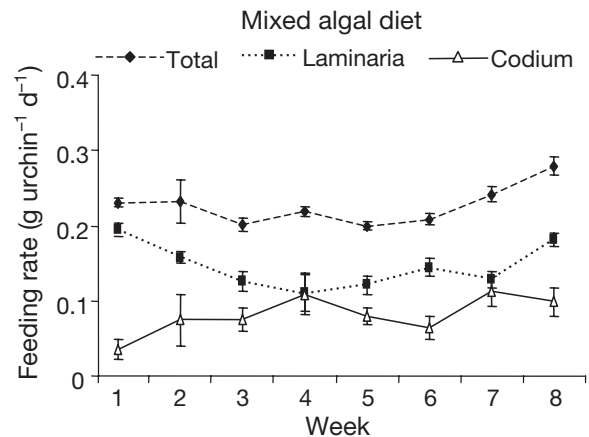|	Source	df	MS	*F*	p
Between plots	Diet	1	0.308	86.3	<0.001
	Error	9	0.004		
Within plots	Time	3.1	0.006	2.00	0.136
	Time × Diet	3.1	0.008	2.34	0.093
	Error	27.5	0.003		

Fig. 4. Feeding rate of sea urchins *Strongylocentrotus droebachiensis* on *Codium* and/or *Laminaria* (mean ± SE, g urchin^{-1} d^{-1}; adjusted for autogenic changes in algal weight) on single diets of *Codium* or *Laminaria*, or a mixed diet of both species, in laboratory aquaria from 26 June to 26 August 2002

Fig. 5. Feeding rate of sea urchins *Strongylocentrotus droebachiensis* on *Codium* and *Laminaria* (mean ± SE, g urchin^{-1} d^{-1}; adjusted for autogenic changes in algal weight) in a mixed diet in laboratory aquaria from 26 June to 26 August 2002

Table 6. Two-factor repeated-measures ANOVA of sea urchin *Strongylocentrotus droebachiensis* grazing rate (g urchin^{-1} d^{-1}) on *Laminaria* in monospecific and mixed diet (*Codium* and *Laminaria*) treatments over time (8 weekly intervals) in laboratory aquaria. Degrees of freedom (df) are Greenhouse-Geisser-adjusted where sphericity assumptions are not met ($\alpha = 0.05$)

	Source	df	MS	*F*	p
Between plots	Diet	1	0.032	26.9	0.001
	Error	9	0.001		
Within plots	Time	3.2	0.019	5.31	0.004
	Time × Diet	3.2	0.001	0.24	0.87
	Error	28.8	0.004		

offered one or the other algal species. In the mixed-diet treatment, however, urchins consumed 2 times more kelp (0.15 g urchin^{-1} d^{-1}) than *Codium* (0.08 g urchin^{-1} d^{-1}). The difference in the change in mass between *Laminaria* and *Codium* in the mixed-diet treatment compared to that in the mixed autogenic control was highly significant ($t_5 = 7.14$, p < 0.001), indicating that urchins preferred *Laminaria* when given a choice.

DISCUSSION

In the field experiment, a preference of *Strongylocentrotus droebachiensis* for *Laminaria longicruris* over *Codium fragile* ssp*. tomentosoides* was indicated by a rapid loss of kelp cover, compared to a gradual and non-significant decline in *Codium* cover, in both monospecific and mixed-canopy treatments. Once the kelp was consumed, urchins grazed turf algae, while mainly avoiding *Codium*. Sequential grazing of these different algal species is consistent with previous laboratory studies of feeding preferences of *S. droebachiensis* (Larsen et al. 1980, Prince & LeBlanc 1992).

Urchin grazing on *Codium* in the field experiment was probably overestimated because large drifting fragments of the alga, which may have become detached by the natural process of fragmentation, were removed when recording canopy cover. This confounding source of loss for *Codium* also biased the feeding preference analysis in favour of *Codium*. Removal of floating fragments of *Codium* could also explain some of the variability in *Codium* cover over time, as fragments that were temporarily removed for cover measurements at one sampling interval may have been pinned down by urchins in the next interval, resulting in an apparent increase in cover. *Codium* fragmentation in subtidal populations usually occurs in winter and spring (Fralick & Mathieson 1972, Trowbridge 1993); however, extensive fragmentation has

been recorded in low tide pools at Cranberry Cove during summer (Bégin & Scheibling 2003). Grazing by urchins on the surrounding turf algae may have contributed to the detachment of *Codium* thalli.

Results of the laboratory experiment also showed a preference by urchins for kelp over *Codium* when the 2 algal species were offered together in a mixed diet. In single-diet treatments, however, the mean grazing rate on *Codium* was similar to that on kelp (~0.2 g urchin^{-1} d^{-1}). This is in contrast to other laboratory experiments that have shown that urchins graze more rapidly on kelp than *Codium* in single-diet treatments (Prince & LeBlanc 1992, Scheibling & Anthony 2001, Levin et al. 2002). In our experiment, grazing on *Codium* may have been facilitated by anchoring the plants in aquaria, since urchins feed more efficiently on attached algae than on drift (Himmelman 1984). We often observed urchins in the laboratory eating through the thallus near the attachment point, and then consuming the plant from the bottom up. Scheibling & Anthony (2001) found that grazing rates of urchins on both *Laminaria* and *Codium* were lowest in late summer, and that grazing on kelp sharply increased in fall and winter (to 0.4 to 0.6 g urchin^{-1}), while *Codium* consumption remained low (~0.1 g urchin^{-1}). Had our experiment been conducted during winter, we may have found a larger difference between grazing rates on *Laminaria* and *Codium*.

Prince & LeBlanc (1992) suggested that *Codium* neither repulses nor attracts *Strongylocentrotus droebachiensis*, but urchins consume the alga upon contact. The relatively high grazing rate on *Codium* in the laboratory experiment supports this hypothesis. In the field experiment, however, urchins appeared to avoid *Codium* as they consumed turf algae. Individual thalli of *Codium* remained attached, while urchins completely consumed other algal species around the *Codium* holdfasts. Even *Bonnemaisonia hamifera*, which may be chemically defended against herbivory (Fenical 1975), was grazed before *Codium*. While little is known about chemical defences in *Codium* (Trowbridge 1998), chemical deterrents in many green algae are not evenly distributed throughout the plant (Hay & Fenical 1988). *Codium* used in the laboratory experiment consisted mainly of upper branches of large plants; the holdfast and lower parts of the thallus were rarely used. If a feeding deterrent is more concentrated in the basal areas, it could explain the avoidance of *Codium* in the field.

Algal shape and handling time are other factors that affect grazing rates of urchins (Lawrence 1975, Klinger 1982). The bushy, branched morphology of *Codium* may be more difficult for urchins to manipulate than the flat fronds of kelp, particularly in the field where wave action further complicates feeding (Himmelman

& Steele 1971). At high densities, however, urchins are able to pin down thalli of *Codium*, as observed in single replicates of both the *Codium* and the mixed algal treatments, in which there were appreciable decreases in *Codium* cover.

Our findings with *Strongylocentrotus droebachiensis* are consistent with previous studies that have found that *Codium* is not an attractive food to generalist grazers (Trowbridge 1998). In intertidal pools in Nova Scotia, the gastropod *Littorina littorea* grazes small recruits of *Codium*, residual holdfasts of dislodged plants, and damaged tissues, but appears to have little effect on healthy thalli longer than a few centimeters (Bégin & Scheibling 2003, Sumi 2003). In New Zealand, Trowbridge (1995) showed that several species of gastropods and echinoids consume *Codium* in the laboratory, although there is little grazing pressure on the alga in intertidal habitats. In contrast, specialist grazers such as the sacoglossan nudibranchs *Elysia viridis* and *Placida dendritica* may play an important role in regulating *Codium* in the NE Atlantic (Trowbridge & Todd 1999, Trowbridge 2002).

Following the mass mortality of *Strongylocentrotus droebachiensis* in the mid and late 1990s, *Codium* has replaced kelp as the dominant canopy-forming species over large areas of the Atlantic coast of Nova Scotia (Chapman et al. 2002). Our experimental results suggest that as urchins re-populate the shallow subtidal zone inhabited by *Codium*, they will not substantially reduce the alga's abundance. Given the clear preference of *S. droebachiensis* for kelp over *Codium*, an urchin front encountering a mixed stand of kelp and *Codium* will likely first consume the kelp, leaving patches of *Codium* in its wake. Once kelps and turf-forming understory species have been consumed, urchins may graze *Codium*, as suggested by our laboratory study and others (Prince & LeBlanc 1992, Scheibling & Anthony 2001, Levin et al. 2002). However, the minor loss of *Codium* cover attributable to urchin grazing in our field experiment, even at urchin densities of 100 m^{-2} and over 13 wk, supports the prediction of Scheibling & Anthony (2001) that urchins would consume monospecific stands of *Codium* at a much slower rate than kelp beds. Moreover, prolonged feeding on a sole diet of *Codium* may be deleterious to urchin reproduction and survival (Scheibling & Anthony 2001), which would further limit the ability of *S. droebachiensis* to regulate this invasive alga.

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