Mar Biol (2007) 151:1175–1183
DOI 10.1007/s00227-006-0562-3

RESEARCH ARTICLE

Feeding aggregations of sea stars (*Asterias* spp. and *Henricia sanguinolenta*) associated with sea urchin (*Strongylocentrotus droebachiensis*) grazing fronts in Nova Scotia

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Received: 18 July 2006 / Accepted: 14 November 2006 / Published online: 14 December 2006

Abstract Migrating feeding aggregations (or fronts) of sea urchins can dramatically alter subtidal seascapes by destructively grazing macrophytes. While direct effects of urchin fronts on macrophytes (particularly kelps) are well documented, indirect effects on associated fauna are largely unknown. Secondary aggregations of predators and scavengers form around fronts of *Strongylocentrotus droebachiensis* in Nova Scotia. We recorded mean densities of the sea stars *Asterias* spp. (mainly *A. rubens*) and *Henricia sanguinolenta* of up to 11.6 and 1.7 individuals 0.25 m^{-2} along an urchin front over 1 year. For *Asterias*, mean density at the front was 7 and 15 times greater than in the kelp bed and adjacent barrens, respectively. There was strong concordance between locations of peak density of urchins and sea stars (*Asterias* $r = 0.98$; *H. sanguinolenta* $r = 0.97$) along transects across the kelp–barrens interface, indicating that sea star aggregations migrated along with the urchin front at rates of up to 2.5 m per month. Size–frequency distributions suggest that *Asterias* at the front were drawn from both the barrens (smaller individuals) and the kelp bed (larger individuals). These sea stars fed intensively on mussels on kelp holdfasts and in adjacent patches. Urchin grazing may precipitate aggregations of sea stars and other predators or scavengers by incidentally consuming or damaging mussels and other small invertebrates, and thereby releasing a strong odor cue. Consumption of protective holdfasts and turf algae by urchins could facilitate feeding by these consumers, which may obtain a substantial energy subsidy during destructive grazing events.

Introduction

Animal populations generally are aggregated at some spatial scale, and heterogeneity in food resources is a common cause of aggregation (Parrish and Edelstein-Keshet 1999). Many mobile species, for example, form dense feeding aggregations along the margins of food patches as their foraging movements decrease. Among benthic marine invertebrates, this phenomenon has been reported for various grazers [e.g., littorinid snails (Silliman et al. 2005)] and deposit feeders [e.g., queen conch (Stoner and Lally 1994), oreasterid sea stars (Scheibling 1980)], but is best known for sea urchins (Lawrence 1975; Lawrence and Sammarco 1982).

Migrating feeding aggregations (or fronts) of sea urchins can dramatically alter subtidal macrophyte communities by destructive grazing (Lawrence 1975). The behaviour of these fronts and their impact on macrophyte assemblages are particularly well documented for strongylocentrotid urchins that graze on kelp beds. Grazing fronts of the green sea urchin *Strongylocentrotus droebachiensis* have been reported throughout the circumpolar range of this species (Scheibling and Hatcher 2001). Dense fronts of *S. droebachiensis* (100s of urchins m^{-2}) form along the margins of kelp beds (mainly *Laminaria* spp.) and advance at rates of up to

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Communicated by R.J. Thompson, St. John's.

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4 m per month, consuming all fleshy seaweeds and leaving barrens dominated by encrusting coralline algae in their wake (Hagen 1995; Hjörleifsson et al. 1995; Sivertsen 1997; Scheibling et al. 1999; Gagnon et al. 2004; Lauzon-Guay and Scheibling 2007). While direct effects of intensive grazing by urchins on kelps and other macrophytes are well known, indirect effects on associated fauna are seldom reported (Himmelman et al. 1983).

During recent studies of urchin fronts in Nova Scotia (Brady and Scheibling 2005; Lauzon-Guay and Scheibling 2007), we observed secondary aggregations of predators and scavengers at the kelp-barrens interface, amid dense aggregations of *S. droebachiensis*. Asteriid sea stars *Asterias rubens* (*vulgaris*) and *A. forbesi* are particularly conspicuous in these areas, where they feed on clusters of small mussels in and around kelp holdfasts (Fig. 1a, b). In this study, we examine spatial and temporal patterns of abundance of *Asterias* spp., and of a smaller microphagous sea star *Henricia sanguinolenta*, in relation to an advancing front of *S. droebachiensis*. We show that these sea stars aggregate at the urchin front, at densities much greater than in the adjacent kelp bed and barrens habitats, and migrate along with the front as it advances through the kelp bed. We also measure the reduction in small invertebrate prey (bivalves) in kelp beds, which occurs with the passage of the urchin and sea star front. Finally, we discuss possible mechanisms of sea star aggregation and feeding facilitation, which may confer an important nutritional subsidy for sea stars and other scavengers associated with urchin fronts.

Materials and methods

Our study was conducted at Splitnose Point (44°28.609′N, 63°32.741′W), a wave exposed site at the mouth of Ketch Harbour on the Atlantic coast near Halifax, Nova Scotia, Canada. The seabed at this site consists of gently sloping granite bedrock with irregular ledges and crevices, which extends to ~35 m depth (below chart datum) before grading to sand. At the start of our study (5 August 2005), a kelp bed composed mainly of *Laminaria longicruris* and *L. digitata* extended from shore to 12 m depth over an offshore distance of ~150 m. A dense front of *Strongylocentrotus droebachiensis* was destructively grazing kelps and understory seaweeds along the lower margin of the kelp bed, creating barrens dominated by encrusting coralline algae. For a further description of the sea urchin front and kelp bed at this site see Lauzon-Guay and Scheibling (2007).

Our sampling area extended 100 m (linear distance) along the interface between the kelp bed and urchin barrens (i.e. along the urchin front), and was divided into four roughly equal blocks, each spanning 12–20 m. Each block was divided into six plots that were 2 m wide. These plots were delineated by a linear series of benchmarks: numbered stainless-steel eyebolts attached to the seabed with marine epoxy at 2 m intervals in the barrens ~1 m behind the leading edge of the urchin front. Additional series of benchmarks were deployed on 23 August 2005 and 17 March 2006 to maintain a spatial reference system as the urchin front advanced.

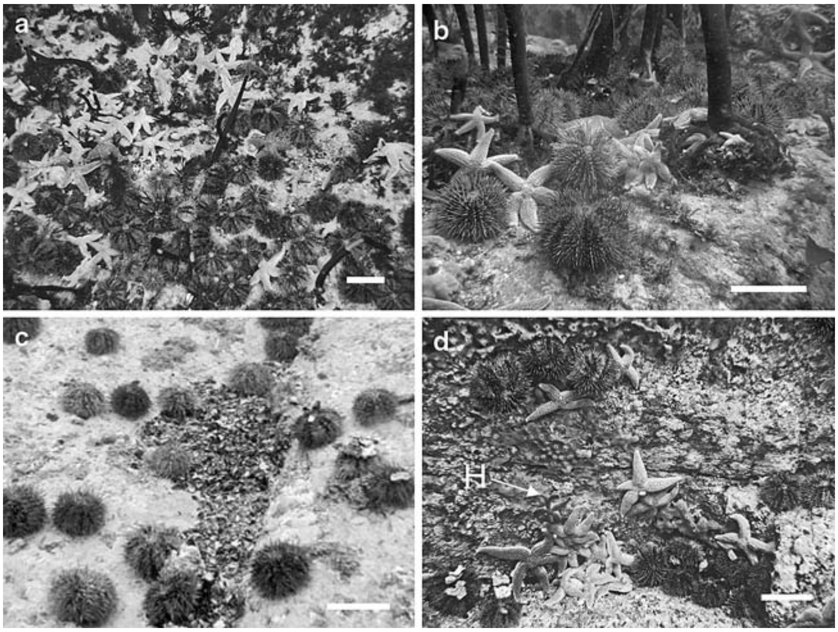


Fig. 1 A dense aggregation of *Asterias* spp. along a grazing front of *Strongylocentrotus droebachiensis* (**a**); *Asterias* spp. feeding on small mussels (*Mytilus* spp.) in and around the holdfasts of kelp (*Laminaria digitata*) along the front (**b**), accumulation of mussel shells in the barrens in the wake of the front (**c**), *Asterias* spp. and *Henricia sanguinolenta* (*H*) on a sponge (*Halichondria panicea*) in barrens (**d**). All photographs were taken at 10–12 m depth at Splitnose Point in 2005. *Scale bar* = 5 cm

Densities of urchins and the sea stars *Asterias* spp. (mainly *A. rubens*) and *Henricia sanguinolenta* were measured concurrently on 15 dates (at about 1–4 week intervals) between 5 August and 6 December 2005, and between 17 March and 12 July 2006. On each sampling date, we measured densities in a linear series of contiguous 0.25 m^2 quadrats along a 0.5-m wide belt transect centrally positioned in each plot and extending perpendicular to the kelp–barrens interface, from 1 m into the kelp bed to 3 m into the barrens. Urchins and sea stars in the barrens behind the leading edge of the front were counted in a video transect recorded by a diver swimming along the transect from the edge of the kelp bed into the barrens, with the camera positioned at 0.75-m above bottom. A quadrat at the leading edge of the front was included in each video for scale. Video sequences were transformed into still images using video stitching software (PanoraGen.DV V1.0, http://www.fml-home.de/panoragen). The dimension of the reference quadrat was measured using image processing software (ImageJ, http://www.rsb.info.nih.gov/ij/) and a series of five contiguous 0.25 m^2 quadrats was juxtaposed with the reference quadrat, forming a 0.5 × 2.5 m belt extending from the leading edge of the front into the barrens. Urchins and sea stars were counted in each of those digital quadrats using digital magnification and image enhancement software (Photoshop v.9.0, Adobe Systems Inc.) as required. Urchins and sea stars were counted by divers where their density could not be resolved using video: in the two quadrats in the kelp bed (where animals were obscured by the kelp canopy) and the one at the leading edge of the front (where high urchin density required manually dissembling the front to attain reliable counts).

On each sampling date, the distance of the leading edge of the urchin front (at the plot center) to each of the two benchmarks delimiting a plot was measured with a plastic tape (1 cm accuracy). These two measures were then converted, by triangulation, into a perpendicular distance between the front and the 2 m line connecting the benchmarks. We designated the position of the kelp–barrens interface (leading edge of the front) as 0; negative values indicate a distance into the barrens (offshore direction) and positive values a distance into the kelp bed (inshore).

We also sampled sea stars in 0.25 m^{-2} quadrats ($n = 11$–51) haphazardly placed in the kelp bed 3 m in advance of the front and in the barrens 3–5 m behind its trailing edge in Block 4 on four sampling dates 9 August, 5 October, 6 December 2005, and 12 July 2006. We counted individuals of each species per quadrat and measured their size (as radius of a normal arm) with a plastic tape (1 mm accuracy). We also measured sizes in an additional sample of sea stars haphazardly collected on encounter on 18 March 2006. We could not reliably differentiate between *Asterias rubens* and *A. forbesi* (hereafter pooled as *Asterias*) in these samples or in our field counts. The great majority of individuals exhibited characters of *Asterias vulgaris* (Clark and Downey 1992); few exhibited distinctive characters of *A. forbesi* and many (likely hybrids; Harper 2004) exhibited intermediate characters.

To estimate the amount of potential prey available to sea stars foraging at the front and the loss of these food items due to predation, we sampled a linear series of 0.1 m^{-2} quadrats placed in the kelp bed ~3 m in advance of the front and in the barrens ~3 m behind its trailing edge in October 2005. These quadrats were spaced at 2 m intervals and approximately aligned with the belt transects through each plot in all blocks. The benthos was scraped and picked from quadrats in barrens and collected in plastic bags. Material from quadrats in the kelp bed was collected using an air-lift suction sampler with a 1-mm mesh collection bag, and transferred to plastic bags. The quadrat samples were frozen until processed. Samples were then thawed at room temperature and sorted to the lowest taxonomic grouping based on external features (Gosner 1978). For this study, we focused mainly on bivalves, which are a preferred prey of *Asterias* spp. (Gaymer et al. 2001a). Small mussels (<20 mm shell length) were abundant but difficult to resolve to species. These likely were *Mytilus edulis* and/or *M. trossulus* (both species co-occur in Nova Scotia; Pedersen et al. 2000), as larger mussels (54–72 mm) clearly identified as *Modiolis modiolis* were rare in samples. Mussels, and small clams (*Hiatella arctica*) and saddle oysters (*Anomia* sp.) were counted in each quadrat and shell length was measured with vernier calipers (1 mm accuracy).

Results

The front of *Strongylocentrotus droebachiensis* advanced an average of 11 m (linear along-bottom distance) along the 100 m span that we monitored for 1 year (August 2005 to July 2006) (Fig. 2). Average urchin density along the front ranged from 66.0 (November 2005) to 30.1 (March 2006) individuals 0.25 m^{-2}. High densities of the sea stars *Asterias* (mainly *A. rubens*) and *Henricia sanguinolenta*, up to 11.6 and 1.7 individuals 0.25 m^{-2}, respectively, occurred along the urchin front during this period (Fig. 2). There was strong concordance (Pearson product moment correlation, $P < 0.001$) between locations of peak density of urchins

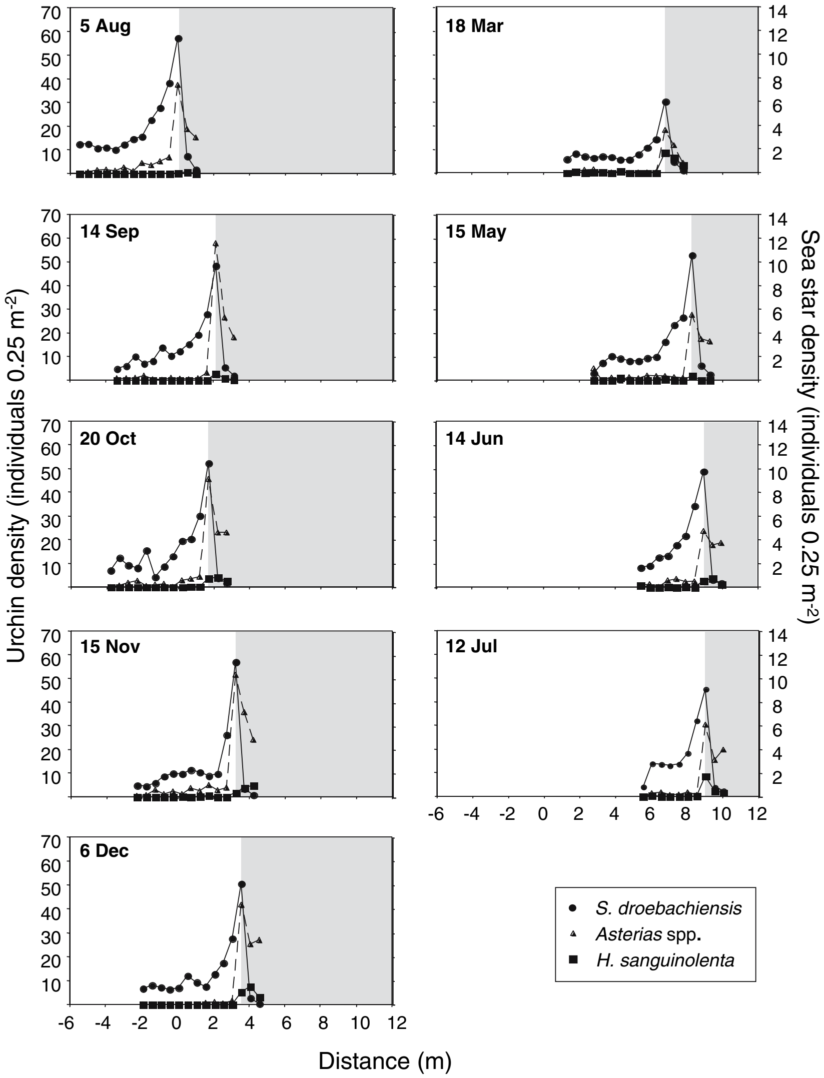


Fig. 2 Density of urchins (*Strongylocentrotus droebachiensis*) and sea stars (*Asterias* spp. and *Henricia sanguinolenta*) in transects across the kelp–barrens interface at Splitnose Point for nine dates between August 2005 and July 2006. Data are mean number of individuals 0.25 m^{-2} ($n = 24$). The *x*-axis is scaled relative to the position of the leading edge of the urchin front (0 m) at the start of the study (5 August 2005). The shaded area is kelp bed ahead of the front

and sea stars (*Asterias*: $n = 330$, $r = 0.98$; *H. sanguinolenta*: $n = 161$, $r = 0.97$) along transects across the kelp–barrens interface (Fig. 2), indicating that sea star aggregations migrated along with the urchin front at rates of up to 2.5 m per month (Lauzon-Guay and Scheibling, unpublished data).

Densities of *S. droebachiensis* (Fig. 3a) and *Asterias* (Fig. 3b) at the leading edge of the urchin front varied significantly among blocks in 2005, with the highest densities in Block 4 (repeated measures ANOVA with block as a random factor, log-transformed data: *S. droebachiensis*, $F_{3,20} = 4.15$, $P = 0.019$; *Asterias*, $F_{3,16} = 8.14$, $P = 0.002$). There was no difference among blocks for either group in 2006 ($P > 0.17$). In each year, there was no effect of sampling date [over three approximately 5–8 week intervals (5 August, 14 September, 1 November and 6 December 2005; 18 March, 24 April, 14 June, and 12 July 2006) or interaction between date and block. Density of *H. sanguinolenta* (Fig. 3c) at the front was much lower than that of *Asterias*, and did not vary consistently among blocks or over time throughout the study (many zero counts precluded statistical analysis). Density of *Asterias* at the urchin front was positively related to that of *S. droebachiensis* over all sampling dates (Fig. 4a). In contrast, density of *H. sanguinolenta* was negatively related to that of *S. droebachiensis* in the same samples (Fig. 4b).

Mean density of *Asterias* at the front (averaged over 4 sampling dates) was consistently greater, by about 7 or 15 times on average, than densities in the adjacent kelp bed or barrens, respectively (Fig. 5). Two-way ANOVA (log-transformed data), with habitat (front, kelp bed, barrens) as a fixed factor and sampling date as a random factor, showed a significant effect of both habitat ($F_{2,6} = 65.8$, $P < 0.001$) and date ($F_{3,136} = 17.3$, $P < 0.001$) but no interaction between these factors ($F_{6,136} = 1.17$, $P = 0.326$). A post hoc comparison showed that *Asterias* density differed significantly

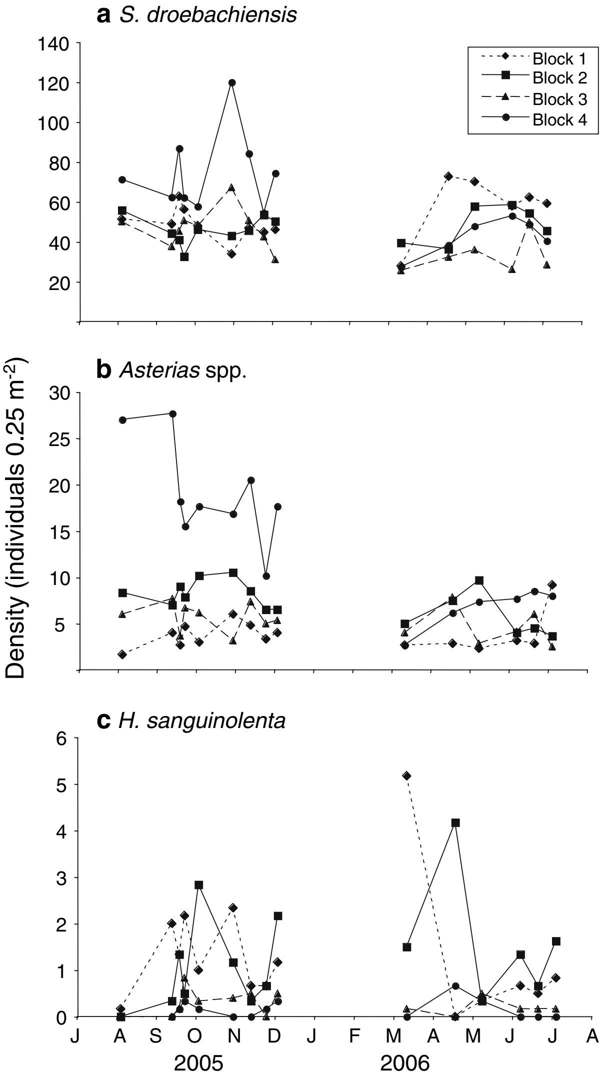


Fig. 3 Density of urchins *Strongylocentrotus droebachiensis* (**a**), and sea stars *Asterias* spp. (**b**) and *Henricia sanguinolenta* (**c**), at the leading of the urchin front in each of four sampling blocks at Splitnose Point at 15 sampling dates between August 2005 and July 2006. Data are mean number of individuals 0.25 m^{-2} ($n = 6$)

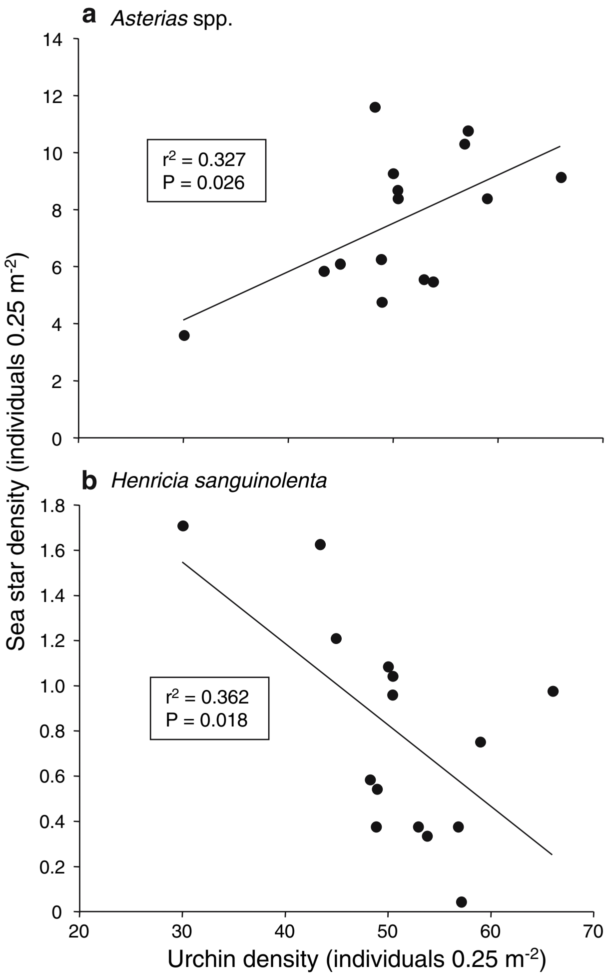


Fig. 4 Relationship between density of sea stars *Asterias* spp. (**a**) and *Henricia sanguinolenta* (**b**) and density of urchins *Strongylocentrotus droebachiensis.* Data are mean number of individuals 0.25 m^{-2} at the leading edge of the urchin front at each sampling date ($n = 15$). Trendline, r^2, and P indicate fit to linear regression model

between each habitat type (Tukey's test, $P < 0.05$). The same pattern in mean density of *H. sanguinolenta* was evident for quadrat samples ($n = 6$–24) from the urchin front (0.15 individuals 0.25 m^{-2}), kelp bed (0.04 individuals 0.25 m^{-2}), and barrens (0) in August 2005.

Asterias along the urchin front ranged in size from 3 to 80 mm radius. In August 2005, the size distribution was bimodal, with modes at 15–20 and 55–60 mm that were comparable to the dominant modal classes in the barrens and kelp bed, respectively (Fig. 6). In subsequent samples, the smaller mode dominated the size distribution at the front, and large seas stars became progressively less abundant. The population in the barrens habitat was comprised of primarily small individuals (<30 mm) throughout the year. In March 2006, large sea stars were not recorded in our samples in the kelp bed and barrens, although a few remained along the front. By July, however, large *Asterias* had reappeared in each habitat. *H. sanguinolenta* generally were much smaller than *Asterias* (mean ± SD for all samples pooled: 24 ± 14 mm radius, $n = 22$)

Asterias fed intensively on small mussels (*Mytilus* spp.) on kelp holdfasts and in adjacent patches along the urchin front. Individual sea stars frequently were observed with the cardiac stomach everted on mussels, or with mussel shells adhering to their oral tube feet. Large numbers of empty mussel shells, many with valves attached at the hinge, accumulated in depressions on the seabed (Fig. 1c). This was particularly evident in summer and fall 2005 in Block 4, where *Asterias* were most abundant. *Asterias* also were observed

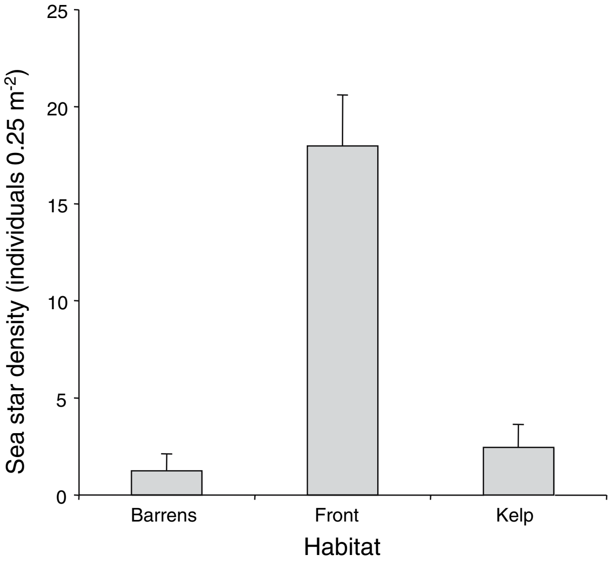


Fig. 5 Density of *Asterias* spp. along the urchin front (at the leading edge) and in the adjacent kelp bed and barrens (3–5 m from the front) at Splitnose Point. Data are grand mean ± SD of the mean number of individuals 0.25 m^{-2} for each of four sampling dates between August 2005 and July 2006 (9 August, 5 October, 6 December 2005, and 12 July 2006)

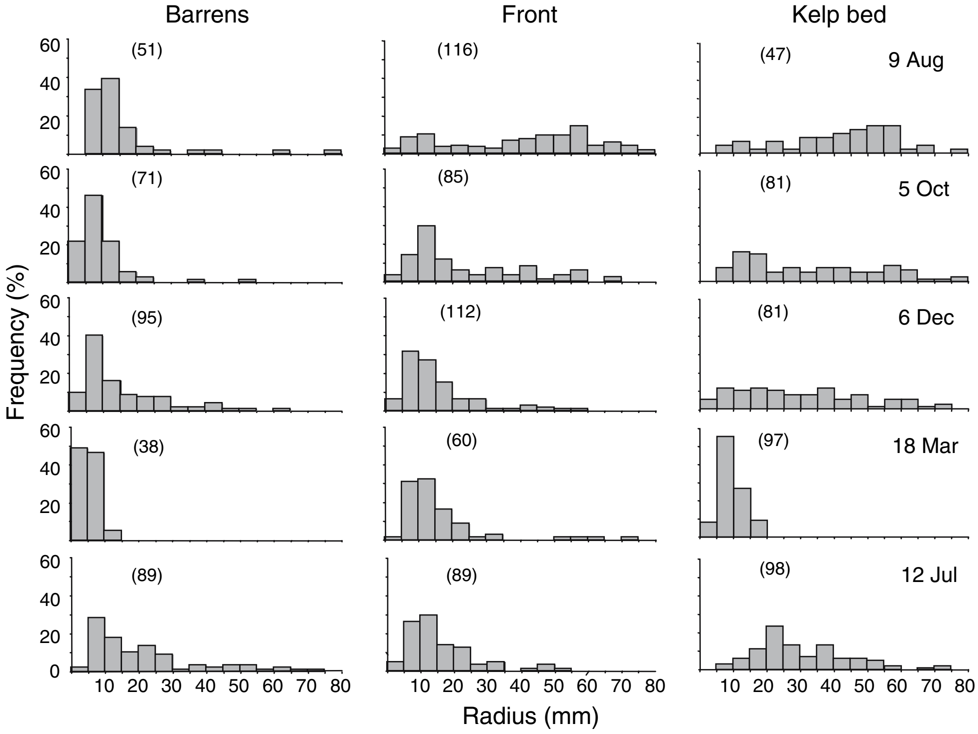
consuming mussels in the kelp bed. In a random sample of *Asterias* ($n = 31$) in the kelp bed (3 m ahead of the front) on 5 August 2005, 11 out of 18 feeding individuals (61%) were consuming mussels; the remainder had their stomach everted on the substratum, presumably digesting a surface film or detritus. However, in a concurrent sample ($n = 64$) in the barrens (~5 m behind the front), only 1 out 11 feeding individuals was observed digesting a mussel and the rest were feeding on surface film. Mussel density in the kelp bed varied significantly among blocks in October 2005 (one-way ANOVA, log-transformed data: $F_{3,20} = 18.67$, $P < 0.001$). Mean density ranged from 15 (Block 1) to 729 individuals 0.25 m^{-2} (Block 2) and averaged 310 individuals 0.25 m^{-2} over all blocks (Fig. 7). Other bivalves were much less abundant in the kelp bed (mean density: *Hiatella arctica*, 57.2; *Anomia* sp., 12.1 individuals 0.25 m^{-2}; Fig. 7) and showed no differences in density between blocks ($P > 0.16$). Mean shell length (±SD) for individuals pooled over all quadrats was 9.1 ± 3.1 mm ($n = 204$) for *Mytilus* spp., 8.5 ± 2.8 mm ($n = 182$) for *H. arctica*, and 7.1 ± 1.7 mm ($n = 50$) for *Anomia* sp.

Densities of *Mytilus* spp. and *Anomia* sp. in the barrens in the wake of the urchin front were negligible (0.2 and 0.3 individuals 0.25 m^{-2}, respectively) in October 2005. The density of *H. arctica* (13.7 individuals 0.25 m^{-2}) was about one quarter of that in the kelp bed at this time.

Discussion

Sea stars are highly mobile, opportunistic predators that readily exploit increases in prey abundance (Sloan 1980; Menge 1982; Witman et al. 2003). Asteriid sea

Fig. 6 Size–frequency (radius, mm) distributions of *Asterias* spp. along the urchin front (at the leading edge) and in the adjacent kelp bed and barrens (3–5 m from the front) at Splitnose Point at five sampling dates between August 2005 and July 2006. Sample size is in *parentheses*



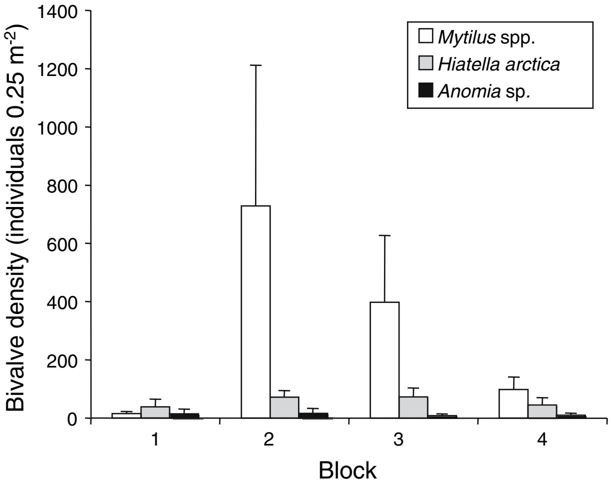


Fig. 7 Densities of bivalves (*Mytilus* spp., *Hiatella arctica*, *Anomia* sp.) in the kelp bed 3 m from the urchin front in each of four sampling blocks at Splitnose Point on 22 October 2005. Data are mean number of individuals 0.25 m^{-2} ± SD ($n = 6$)

stars can locate prey patches by distance chemoreception (Sloan and Campbell 1982; Moore and Lepper 1997; Gagnon et al. 2003; Drolet and Himmelman 2004) and form dense feeding aggregations that rapidly decimate prey populations (Dare 1982; Gaymer et al. 2001a; Gaymer and Himmelman 2002). In our study, *Asterias* were highly aggregated along the urchin front, where they preyed intensively on small mussels (mainly *Mytilus* spp.) on kelp holdfasts and in dense patches on the sea bed. Densities of *Asterias* were much greater along the front than in the adjacent undisturbed kelp bed (where mussels were abundant), suggesting that the aggregation of sea stars was a consequence of urchin grazing activity. *Strongylocentrotus droebachiensis* consumes small mussels in subtidal beds and in the laboratory (Briscoe and Sebens 1988; Meidel and Scheibling 1999), and we observed damaged mussels amid heavily chewed kelp holdfasts along the grazing front. The release of body fluids from these and other damaged invertebrates likely provides a strong odor cue that attracts sea stars from surrounding barrens and kelp habitats (Sloan and Campbell 1982; Moore and Lepper 1997). As *Asterias* accumulates along a grazing front, increased predation of mussels may enhance the odor plume and accelerate the process of aggregation.

Henricia sanguinolenta also aggregated along the urchin front but to a lesser degree than *Asterias*. In part this may reflect the lower density of *H. sanguinolenta* in surrounding habitats. *H. sanguinolenta* is a microphagous sea star that also preys on sponges (Jangoux 1982; Sheild and Witman 1993). Encrusting sponges (*Halichondria panicea*, *H. bowerbanki* and *Isodyctya palmata*) were common both within the kelp bed and in the barrens. Some sponges were superficially grazed by the urchin front, and this may have provided a chemical stimulus for aggregation of *H. sanguinolenta*. Although densities of this sea star were relatively low in the barrens, we often observed individuals on sponges in this habitat (Fig. 1d).

Aggregations of both *Asterias* and *H. sanguinolenta* migrated at the same rate as the urchin front. The rate of advance of the urchin front was positively related to urchin density at the front and negatively related to the biomass of kelp that it encountered and to wave action (Lauzon-Guay and Scheibling 2007, unpublished data). The greatest density of sea stars generally occurred along the leading edge of the urchin front. Sea star density also tended to be high immediately ahead of the leading edge, but dropped rapidly in the wake of the front. For *Asterias*, this probably reflects variation in prey availability across the urchin front. Mussel density, for example, decreased by three orders of magnitude between the kelp bed and the barrens. Density of *Asterias* was directly related to the density of urchins, and variation in sea star abundance among blocks (highest in Block 4 in 2005) did not correspond with variation in mussel abundance in the kelp bed ahead of the front (highest in Block 2). This suggests that the intensity of destructive grazing (and attendant damage to mussels and other small bivalves) is a stronger cue to aggregation of *Asterias* than areas of high abundance of intact mussels within the kelp bed.

Size–frequency distributions suggest that *Asterias* at the front were drawn from both the barrens (smaller individuals, <30 mm radius) and the kelp bed (larger individuals) in summer and fall 2005. By March 2006, few large individuals remained at the front, and none were recorded in the adjacent kelp bed and barrens. The decrease in large sea stars may be related to cold winter sea temperatures, ranging from 0.8 to 5.1°C between January and March 2006 (Lauzon-Guay and Scheibling, unpublished data), which decrease foraging activity in *Asterias* spp. (Harris et al. 1998; Gaymer et al. 2002) and may cause sea stars to migrate to deeper waters (Gaymer et al. 2001b). As temperatures increased to 9°C in June, larger sea stars were once again observed throughout the study area.

The preponderance of intact and undrilled mussel shell remains in the wake of the front suggests that asteriid sea stars contribute greatly to the reduction in bivalve populations between the kelp bed and the barrens, although urchins and other predators and scavengers also play a role (see below). The greater proportional survival of the clam *Hiatella arctica* reflects its crevice-dwelling habit, which provides some protection from sea star predation (Gaymer et al. 2001a). These clams often were found beneath heavy encrustations of coralline algae (*Lithothamnium* sp. and *Phymatolithon* sp.), which were broken apart in our destructive sampling of kelp bed and barrens habitats.

The high density of actively grazing urchins may increase the risk of damage to co-occurring seas stars. We occasionally observed individuals of *Asterias* with a scarred aboral body wall, which appeared to have been the result of urchin bites. On rare occasions we also observed cannibalism in *Asterias* with a larger individual preying upon a smaller one. Small juveniles of *Asterias* may be particularly prone to incidental damage or consumption by grazing urchins, although healthy juveniles (<5 mm radius) frequently were observed beneath 3-D aggregations of *S. droebachiensis*. The negative relationship between density of *H. sanguinolenta* and that of *S. droebachiensis* over the study period may reflect active avoidance or increased mortality around dense urchin aggregations, where these small sea stars may be attacked by urchins or larger asteroids.

Urchin grazing, together with intensive predation by sea stars, may precipitate aggregations of other predators or scavengers at urchin fronts, including the whelks (*Nucella lapillus*, *Buccinum undatum*), crabs (*Cancer irroratus* and *C. borealis*), and demersal fish, such as rock gunnel (*Pholis gunnellus*), shorthorn sculpin (*Myoxocephalus scorpius*), winter flounder (*Pseudopleuronectes americanus*), and cunner (*Tautogolabrus adspersus*). These species commonly were observed along the front, particularly in summer and fall. The aggregation of predators and scavengers at urchin fronts can be considered as an example of mass kleptoparasitism (Morissette and Himmelman 2000), where a variety of consumers exploit damaged prey resulting from intensive grazing by *S. droebachiensis*. Urchin grazing may facilitate consumption of mussels by sea stars and other predators by breaking the shell and/or by exposing small mussels that normally have a refuge within the holdfast or beneath an algal turf. Thus, sea stars and other consumers may obtain a substantial energy subsidy during destructive grazing events.

Acknowledgments We thank J. Lindley, D. Lyons, M. Saunders, P. Gagnon, and A. Pinder for assistance with diving, and especially D. Knip for help processing samples and data in the laboratory. The research was funded by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to RES. J-SL-G was supported by scholarships from Fonds Québécois de la Recherche sur la Nature et les Technologies and NSERC.

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