

The role of predation in regulating sea urchin populations in eastern Canada

Sea urchin
Strongylocentrotus droebachiensis
Population dynamics
Predation
Eastern Canada

Oursin
Strongylocentrotus droebachiensis
Dynamique de population
Prédation
Côte est du Canada

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ABSTRACT

The green sea urchin *Strongylocentrotus droebachiensis* is the dominant grazer in the rocky subtidal zone in eastern Canada and its local abundance largely determines the structure and dynamics of the coastal ecosystem. Predation has been cited as an important factor controlling populations of this species, although the evidence for this assertion is equivocal. In this review, I examine the effects of predators on the distribution, abundance and behaviour of *S. droebachiensis* at each life history stage and evaluate the potential for predatory control. I conclude that our understanding of interactions between this species and its predators is insufficient to support any generalizations about the role of predation in regulating populations. Carefully designed field and laboratory experiments are required to rigorously test hypotheses about the effects of predators under realistic conditions, and to identify critical life history stages. Numerical modelling is a promising but underutilized approach in the study of sea urchin population dynamics and predator-prey interaction.

RÉSUMÉ

Le rôle de la prédation dans le contrôle des populations d'oursins dans l'est du Canada.

L'oursin commun (*Strongylocentrotus droebachiensis*) est un herbivore dominant de la zone rocailleuse et sous-littorale sur la côte est du Canada. Son abondance locale détermine en grande partie la structure et les dynamiques de l'écosystème côtier. La prédation a été mentionnée comme étant un facteur important contrôlant les populations d'oursins communs, mais l'évidence de cette affirmation est équivoque. Dans la présente revue, j'examine l'effet des prédateurs sur la distribution, l'abondance et le comportement de *S. droebachiensis* à chaque stade biologique, et évalue l'importance de la prédation comme élément contrôleur. Je conclus que notre compréhension des interactions entre l'oursin et ses prédateurs est insuffisante pour généraliser sur le rôle primaire de la prédation sur la taille des populations. Des expériences sur le terrain et en laboratoire, soigneusement planifiées, sont requises pour vérifier rigoureusement les hypothèses sur les effets de la prédation dans des conditions réalistes, et pour identifier les stades les plus vulnérables de l'oursin. De plus, la modélisation numérique est une approche prometteuse mais peu utilisée dans l'étude des dynamiques de population et des interactions prédateur-proie de l'oursin commun.

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INTRODUCTION

Sea urchins, through their grazing activities, play a pivotal role in determining the biomass, diversity and productivity of subtidal macrophyte communities (reviewed by Lawrence, 1975; Lawrence and Sammarco, 1982; Harrold and Pearse, 1987). Due to their ecological importance, there is considerable interest in understanding key factors, such as predation, which regulate sea urchin populations. Increased commercial exploitation of sea urchins in recent years has provided a further impetus for research in this area. Numerous studies indicate that interactions with predators influence the distribution and abundance of sea urchins, and a reduction in predation pressure has been implicated as a causal factor in sea urchin population outbreaks in some areas. However, except for the case of sea otters (*Enhydra lutris*) in the Northwest Pacific, evidence for predatory control of sea urchin populations is inconclusive (Harrold and Pearse, 1987).

In eastern Canada, the green sea urchin *Strongylocentrotus droebachiensis* is the only herbivorous sea urchin in shallow coastal waters and the dominant grazer. The abundance of this key species largely determines the structure and dynamics of the rocky subtidal ecosystem (Miller, 1985a; Scheibling, 1986). Where sea urchins occur at low densities, kelp beds (*Laminaria* spp.) flourish, providing a highly productive and structurally complex habitat for a variety of fish and invertebrates. However, sea urchins periodically undergo population outbreaks which result in widespread destructive grazing of kelp beds and the formation of "barren grounds" (Mann, 1977, 1982) with much lower primary productivity (Chapman, 1981). In areas off Newfoundland and in the Gulf of Saint Lawrence, sea urchin-dominated barren grounds persist for long periods (Himmelman *et al.*, 1983; Himmelman, 1986). Along the Atlantic coast of Nova Scotia, however, transitions between kelp beds and barren grounds occur on decadal time scales in association with large fluctuations in sea urchin abundance (Miller, 1985a; Scheibling 1984, 1986; Johnson and Mann, 1988).

Population outbreaks of *Strongylocentrotus droebachiensis* in Nova Scotia in the late 1960s were attributed to a release from predation by lobsters (reviewed by Mann 1977, 1982; Wharton and Mann, 1981). This hypothesis sparked considerable interest in the role of predators in regulating sea urchin populations, but after more than two decades of research the issue of predatory control of *S. droebachiensis* remains controversial (Miller, 1985b; Pringle *et al.*, 1982; Pringle 1986; Chapman and Johnson, 1990; Elner and Vadas, 1990; Hagen and Mann, 1992). In this review, I summarize what is known about the effects of predators on the distribution, abundance and behaviour of this species at each stage of its life history. In so doing, I evaluate the potential for predatory control and identify gaps in our understanding of predator-prey interactions which may serve to direct future research.

Predation and sea urchin population outbreaks

To account for a population outbreak of *Strongylocentrotus droebachiensis* in the late 1960s in St. Margaret's Bay,

Nova Scotia, K.H. Mann and P.A. Breen hypothesized that the lobster *Homarus americanus* was the keystone predator in this system, and that overfishing of lobsters, as evidenced by declining commercial catches during the previous decade, enabled the sea urchin population to expand (Mann and Breen, 1972; Breen and Mann, 1976a). Breen and Mann (1976b) tested this hypothesis with a simulation model based on estimates of sea urchin and lobster population density and size structure; urchin recruitment, growth and natural mortality; and size-selective feeding rates of lobsters on sea urchins. The model predicted that lobsters could control sea urchin density in kelp beds below the level at which destructive grazing occurs (but *see* also Miller, 1985b). When the model was expanded to include two other sea urchin predators, rock crabs (*Cancer irroratus*) and wolffish (*Anarhichus lupus*), the critical density of lobsters required to control sea urchin populations was reduced, but this effect was almost entirely due to crabs. Wharton and Mann (1981) proposed that destruction of kelp beds by sea urchins led to further declines in lobster abundance, due to loss of habitat and productivity, resulting in a positive feedback that maintains the system in the barren ground state.

The predation hypothesis, particularly as it relates to lobsters as keystone species, has been widely criticized (Pringle *et al.*, 1982; Pringle, 1986; Miller, 1985b; Vadas *et al.*, 1986; Elner and Vadas, 1990). The fundamental assumption that lobsters are important predators of *Strongylocentrotus droebachiensis* has not been substantiated by field and laboratory studies (reviewed by Miller, 1985b). Analyses of the stomach contents of lobsters from kelp beds and barrens indicate that sea urchins are not an important component of the diet (Scarratt, 1980; Carter and Steele, 1982; Elner and Campbell, 1987; but *see* also Breen, 1987) and laboratory feeding experiments have shown that sea urchins are not a preferred prey of lobsters (Evans and Mann, 1977; Hirtle and Mann, 1978; Elner, 1980). Miller (1985b) calculated predation rates of sea urchins by lobsters based on feeding studies and estimates of lobster biomass and concluded that lobsters were unimportant predators of *S. droebachiensis* in Nova Scotia. Keats (1986) and Hagen and Mann (1992) argue that these calculations do not take into consideration a functional response of lobsters to increased sea urchin density. However, another sea urchin outbreak off Nova Scotia in the early 1990s was preceded by a period of record high lobster landings (Scheibling, 1994). This undermines even the correlational basis of the initial hypothesis, that outbreaks in the early 1970s were preceded by a decline in lobster abundance.

Mann and Breen's (1972) keystone predator hypothesis was later modified to include crabs and fish as well as lobsters (Breen and Mann, 1976 b; Wharton and Mann, 1981; Bernstein *et al.*, 1981, 1983). Miller (1985b) examined the evidence for crab and fish predation on *Strongylocentrotus droebachiensis* and concluded that these predators, like lobsters, can not control sea urchin populations. Keats *et al.* (1986) argued that there are insufficient data to assess the potential of Atlantic wolffish in limiting sea urchin abundance in Newfoundland (*see* also Hagen and Mann, 1992). As pointed out by Pringle *et al.* (1982), com-

mercial overexploitation has markedly reduced the density of a number of fish species as well as lobsters in eastern Canada. Sea urchin outbreaks, if they are related to a relaxation in predation pressure, are more likely to be due to the removal of a complex of predators rather than just one or a few.

Mohn and Miller (1987) developed a simulation model of the dynamics of the rocky subtidal community in Nova Scotia based on interactions between kelp, sea urchins and their predators, and a pathogen which causes mass mortality of sea urchins. Predators were aggregated as a class comprised of lobsters, rock crabs, and a fish (the cunner *Tautoglabrus adsperses*). Parameters describing the dynamics of the predator class included rates of ingestion (of sea urchins), growth and natural mortality, and a control variable representing fishing pressure. Sensitivity analyses of the model showed that predators had little effect on sea urchin abundance, relative to the effects of kelp abundance and catastrophic mortality due to the pathogen.

Predation on early life history stages: the regulation of recruitment

Strongylocentrotus droebachiensis, like other sea urchins with widely dispersing planktonic larvae (reviewed by Ebert, 1983), exhibits large interannual and regional fluctuations in recruitment (Himmelman, 1986; Himmelman *et al.*, 1983; Raymond and Scheibling, 1987; Scheibling, 1986; Scheibling and Raymond, 1990). Although predation on the planktonic larvae and recently settled juveniles may be an important determinant of recruitment rate, few studies have examined the effect of predators on the early life history stages of sea urchins (reviewed by Ebert, 1983; Young and Chia, 1987).

Sea urchin larvae are prey to various zooplanktonic predators, including copepods, euphausiids, amphipods, brachyuran zoea, hydro- and scyphomedusae, chaetognaths, and ctenophores (Hooper, 1980; Pennington *et al.*, 1986). Predation intensity in the plankton will be influenced by stage-specific probabilities of encounter and capture at each embryonic and larval stage. Laboratory experiments with embryos and larvae of *Strongylocentrotus purpuratus*, *S. franciscanus* and the sand dollar *Dendraster excentricus* indicate that predation by invertebrate zooplankton may be most intense at the early larval stages because non-motile embryos 1) probably occur at high densities, 2) are small and unprotected by spicules, and 3) do not have the behavioural capability to escape predators (Rumrill and Chia,

1985; Rumrill *et al.*, 1985; Pennington *et al.*, 1986). Small planktivorous fish, however, are capable of consuming plutei at high rates (Pennington *et al.*, 1986).

Thorson (1950) proposed that environmental factors such as temperature, which affect the developmental rate of invertebrate larvae, influence larval survivorship by reducing or extending the period of exposure to planktonic predators. In laboratory experiments, Hart and Scheibling (1988) demonstrated a strong effect of temperature on larval development of *Strongylocentrotus droebachiensis*, much greater than the effect of food availability. By examining long-term temperature records, they showed that the urchin outbreak off Nova Scotia in the late 1960s was preceded by anomalously warm sea temperatures in the spring (when the larvae are in the plankton) of 1960. Extension of this analysis shows that another outbreak, first observed in the early 1990s (Scheibling *et al.*, 1994), was preceded by a warm temperature anomaly in the spring of 1983 (Fig. 1). Given the post-metamorphic growth rate of this species (Raymond and Scheibling, 1987), it seems reasonable to propose that large settlement pulses, associated with accelerated larval development in warm years, may presage sea urchin population outbreaks in Nova Scotia. In contrast, Foreman (1977) concluded that low spring temperatures favoured larval survival and high settlement rates of *S. droebachiensis* in British Columbia, Canada. Ebert (1983) reviewed evidence for a correlation between temperature and sea urchin recruitment and found no consistent relationship. An inherent problem with Thorson's hypothesis is that temperature, or some environmental covariate of temperature, is likely to influence rates of survival and activity of predators as well as their prey. Until more is known about predator-prey interactions in the plankton and how they are influenced by environmental factors such as temperature, we can only speculate about causal mechanisms regulating larval availability.

As larvae approach the bottom to settle, they are exposed to a variety of predators. Benthic suspension feeders, such as anemones, mussels and ascidians, can capture settling sea urchin larvae or entangle them in mucus (Hooper, 1980; Cowden *et al.*, 1984). Planktivorous fish associated with kelp beds and small invertebrates encrusting kelp fronds, such as bryozoans, hydroids and serpulid polychaetes, may remove larvae from the plankton (Bernstein and Jung, 1979; Tegner and Dayton, 1981). This may account for reduced rates of sea urchin recruitment within kelp beds compared to urchin-dominated barren grounds outside of kelp beds, a pattern observed both in Nova Scotia (Scheibling, 1986) and California, USA (Pearse *et al.*,

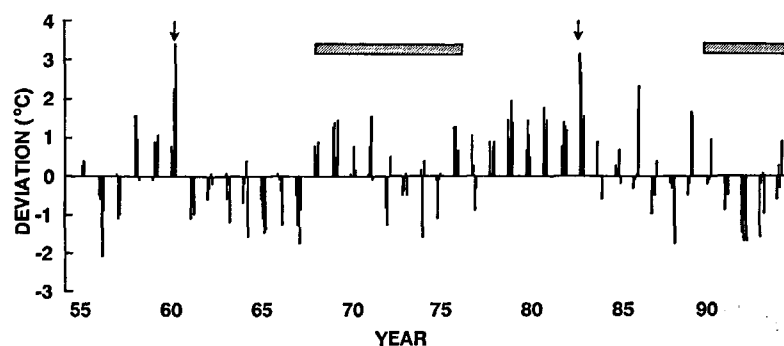


Figure 1

Annual deviations from long-term (1926-1967, Lauzier and Hull, 1969) mean spring (March-June) sea surface temperatures in Halifax Harbour, 1955 to 1994. Data are from Bedford Institute of Oceanography, Department of Fisheries and Oceans Canada (Gregory *et al.*, 1993, 1994, and unpublished data). Shaded bars indicate periods of sea urchin population outbreaks. Arrows indicate large positive deviations from long-term means in 1960 and 1983.

1970; Bernstein and Jung, 1979; Tegner and Dayton, 1981). Balch and Scheibling (1994 and unpub. data) found that settlement rates of *Strongylocentrotus droebachiensis* (and other echinoderms) on artificial collectors were lower in kelp beds than in barren grounds in Nova Scotia. However, Rowley (1989) recorded similar densities of recently settled *S. purpuratus* and *S. franciscanus* on the dominant substrata of kelp beds (red algal turf) and barren grounds (crustose coralline algae) in California. He observed rapid declines in the abundance of new cohorts over a period of weeks and concluded that differential juvenile mortality is the most likely mechanism accounting for the greater recruitment of sea urchins in barren grounds (Rowley, 1990). Laboratory experiments show that larvae of *Strongylocentrotus droebachiensis* (Pearse and Scheibling, 1991) and other strongylocentrotids (Cameron and Schroeter, 1980; Rowley, 1989) settle and metamorphose in response to a variety of natural substrata, suggesting that settlement preferences are less important in determining patterns of sea urchin recruitment than post-settlement predation or migration.

Recently settled *Strongylocentrotus droebachiensis* live cryptically under rocks and in small crevices, or in biogenic microhabitats such as undercut crustose coralline algae, macroalgal turfs, and patches of sessile macroinvertebrates (Keats *et al.*, 1985; Witman, 1985; Scheibling and Raymond, 1990). These microhabitats presumably provide a refuge from fish and macroinvertebrate predators, although few studies have identified predators of the early juvenile stages (Hooper, 1980; Ojeda and Dearborn, 1991). Scheibling and Hamm (1991) introduced various predators into experimental cages containing young juveniles (3–6 mm test diameter) of *S. droebachiensis* in a subtidal cobble bed in Nova Scotia. They found that rock crabs (*Cancer irroratus*), juvenile lobsters (*Homarus americanus*) and juvenile sculpins (*Myoxocephalus octodecemspinosus*) significantly reduced the abundance of the small recruits, whereas green crabs (*Carcinus maenas*), and whelks (*Buccinum undatum*) had no effect. Although cryptic microhabitats provide a refuge from larger predators, they also harbour a suite of small predators (*e.g.* polychaetes, nemertean, crustaceans, juvenile sea stars) which may prey upon young urchins.

Size-selective predation and the importance of refuges

Larger juveniles and small adults of *Strongylocentrotus droebachiensis* are vulnerable to a broad range of predators, including small-mouthed fish, decapod crustaceans, and sea stars (Himmelman and Steele, 1971; Bernstein *et al.*, 1981; Green *et al.*, 1984; Keats *et al.*, 1985, 1987; Keats, 1990; Ojeda and Dearborn, 1991; Scheibling and Hamm, 1991; Hagen and Mann, 1992). Not surprisingly, small sea urchins tend to occupy cryptic microhabitats and only come out to forage on exposed rock surfaces as they grow larger (Keats *et al.*, 1985; Himmelman, 1986; Scheibling and Raymond, 1990). In urchin-dominated habitats in Newfoundland, Canada, Keats *et al.* (1985) found that juveniles of *S. droebachiensis* were largely restricted to branched and undercut coralline algal crusts (*Lithothamnion glaciale*), and proposed that intense predation by fish, particularly cunner, accounts for this pattern. Scheibling

and Raymond (1990) monitored a cohort of *S. droebachiensis* which settled in a cobble bed off Nova Scotia soon after a mass mortality of conspecifics due to disease. They found recently settled urchins in the interstices of coralline-encrusted cobbles. As the juveniles eventually outgrew these spatial refuges, they decreased in abundance in the cobble bed, presumably due to predation. Larger juveniles persisted on an adjacent boulder ridge and beneath boulders experimentally transplanted to the bed. In a series of caging experiments at this site, Scheibling and Hamm (1991) showed that sheltering beneath cobbles reduced predation on small juveniles of *S. droebachiensis* by crabs and lobsters, but as these juveniles approached adult size they required larger spatial refuges, such as boulders, to escape predation.

Witman (1985) showed that beds of the horse mussel *Modiolis modiolis* are an important spatial refuge for small *Strongylocentrotus droebachiensis* and other invertebrates in the Gulf of Maine, USA. In experiments with tethered prey, he demonstrated that predation by fish, crabs and lobsters is greatly reduced within the structurally complex mussel beds compared to exposed substrata outside of the beds. Small-scale patterns in the distribution and abundance of *S. droebachiensis* and other small invertebrates have been linked to the distribution of mussel beds in rocky subtidal habitats in the Gulf of Maine, USA (Witman, 1985; Ojeda and Dearborn, 1989) and Newfoundland, Canada (Keats, 1990).

Juveniles of *Strongylocentrotus franciscanus* commonly shelter under the spine canopies of conspecific adults (Tegner and Dayton, 1977; Breen *et al.*, 1985; Sloan *et al.*, 1987). The primary function of this association appears to be protection from predation (Tegner and Dayton, 1977, 1981; Tegner and Levin, 1983). To a lesser extent, juveniles of *S. droebachiensis* and *S. purpuratus* also appear to utilize the spine canopy of *S. franciscanus* for protection (Duggins, 1981; Breen *et al.*, 1985). Although, juveniles of *S. droebachiensis* do not appear to actively seek shelter under conspecific adults, adult aggregations in urchin-dominated areas may enhance the survival of associated juveniles.

A bimodal size distribution, with prominent juvenile and adult modes and fewer intermediate-sized individuals, is a common feature of the population structure of *Strongylocentrotus droebachiensis* (Scheibling and Stephenson, 1984; Scheibling, 1986; Ojeda and Dearborn, 1991) and other temperate sea urchins (*e.g.* *Strongylocentrotus franciscanus*, Tegner and Dayton, 1981; Sloan *et al.*, 1987; *Evechinus chloroticus*, Choat and Scheil, 1982; Andrew and Choat, 1982; Andrew and MacDiarmid, 1991; and *Tetrapygus niger*, Rodriguez and Ojeda, 1993). Low rates of predation on cryptic juveniles (with a spatial refuge) and exposed large adults (with a size refuge), and more intensive predation on intermediate-sized animals in transition between these two stages, may account for these size distributions (Tegner and Dayton, 1981; Tegner and Levin, 1983; Andrew and MacDiarmid, 1991; Scheibling and Hamm, 1991; Rodriguez and Ojeda, 1993; but *see* also Himmelman, 1986). In support of this hypothesis, Tegner and Dayton (1981) found that the modal size of test remains of *S. franciscanus* in a kelp forest in California

conformed to the node between the two peaks of the size distribution. Furthermore, Tegner and Levin (1983) showed that sea urchins in this intermediate size range were the most vulnerable to predation by spiny lobsters in laboratory studies.

Predation intensity on intermediate-sized sea urchins (large juveniles, small adults) may be a key factor regulating population growth (Scheibling and Hamm, 1991). The rate at which individuals pass through this bottleneck will depend on several factors, including 1) the supply of juveniles (which depends on settlement rate and early juvenile mortality), 2) the types and abundance of predators, 3) the availability and size of spatial refuges, 4) the growth rate of sea urchins, and 5) the abundance of adults (if they affect juvenile survival). Spatial and temporal variations in these factors will dictate local population structure and dynamics, the rate of repopulation after commercial fishing or mass mortality, and the potential for population outbreaks.

Mortality due to predation generally decreases with increasing sea urchin size, presumably because there are fewer predators that can handle large prey. However, large sea urchins do not necessarily escape in size from predation. Elnor (1980) fed a broad size range of *Strongylocentrotus droebachiensis* to three size classes of lobsters or rock crabs in laboratory experiments. The size of the preferred prey increased with predator size and the largest lobsters and crabs were capable of consuming the largest sea urchins. Keats *et al.* (1986) measured the size of *S. droebachiensis* in the guts of wolffish from urchin-dominated barren grounds in eastern Newfoundland, and found that wolffish selected the largest individuals (which were also the least abundant) from the population. Hagen and Mann (1992) confirmed that feeding rates of wolffish were higher on large (> 20 mm test diam.) than small (\leq 20 mm) sea urchins in laboratory tank experiments.

Effects of predators on sea urchin behaviour and distribution

Sea urchins have well-developed chemosensory capabilities (reviewed by Sloan and Campbell, 1982), and many species exhibit flight (or alarm) responses upon contact or exposure to predators (Parker and Shulman, 1986; reviewed by Harrold and Pearse, 1987). In laboratory chemotaxis experiments, Mann *et al.* (1984) and Scheibling and Hamm (1991) showed that *Strongylocentrotus droebachiensis* is repelled by waterborne odors emanating from potential predators (lobsters, rock crabs and cunners) and crushed conspecifics (which presumably signal the presence of nearby predators). In field experiments, Vadas *et al.* (1986) demonstrated flight responses of *S. droebachiensis* to tethered or caged lobsters and crabs, as well as crushed conspecifics. Scheibling and Hamm (1991) found that *S. droebachiensis* do not respond to waterborne stimuli from green crabs *Carcinus maenus* (which are not important predators of sea urchins) but exhibit a strong flight response to rock crabs *Cancer irroratus*, suggesting that the urchins are able to distinguish between crab species on the basis of potential threat. Similarly, *S. droebachiensis* shows no response to the sea star *Asterias vulgaris* (Mann

et al., 1984), which rarely consumes healthy sea urchins (pers. obs.), but flees from the presence of another sea star *Pycnopodia helianthoides*, an active predator (Duggins, 1983).

The adaptive significance of flight responses to highly mobile predators such as lobsters, crabs and fish remains to be established (Scheibling and Hamm, 1991). Tegner and Dayton (1983) point out that movement may increase the susceptibility of urchins to predators such as lobsters, since a moving sea urchin has a weak hold on the substratum (*see also* Snyder and Snyder, 1970). Mechanistic links between chemically-mediated responses in controlled laboratory experiments and the behaviour of sea urchins in nature should be viewed with caution.

Some species of sea urchins have adopted a nocturnal foraging pattern, presumably to avoid predation by diurnally-active fish (*e.g.* *Diadema antillarum*, Ogden *et al.*, 1973; *Centrostephanus coronatus*, Nelson and Vance, 1979; *Strongylocentrotus franciscanus* and *S. purpuratus*, Tegner and Dayton, 1983). Bernstein *et al.* (1981) found that *S. droebachiensis* in a barren ground in Nova Scotia tended to remain hidden during the day and forage more at night in summer than in winter. They related this seasonal change in sea urchin behaviour to an increase in the abundance and diurnal activity of predatory fish in summer (but *see also* Miller, 1985 *b*).

Aggregation has been interpreted as a form of defensive behaviour in *Strongylocentrotus droebachiensis* (Garnick, 1978; Bernstein *et al.*, 1981, 1983) and other strongylocentrotids (Tegner and Levin, 1983; Breen *et al.*, 1985), although this interpretation remains equivocal (Vadas *et al.*, 1986). Garnick (1978) proposed that sea urchins in aggregations are more difficult for a predator like a lobster to handle, since the aggregation is effectively like a single large animal. Bernstein *et al.* (1983) reported that rock crabs did not prey on *S. droebachiensis* in aggregations, although Vadas *et al.* (1986) observed both rock crabs and lobsters feeding on aggregated individuals in laboratory tanks.

Bernstein *et al.* (1981, 1983) proposed that defensive aggregation of *Strongylocentrotus droebachiensis* is the behavioural trigger that precipitates widespread destructive grazing and the transformation of kelp beds to barren grounds. In their scenario, predators such as crabs and lobsters keep sea urchins in kelp beds at low density and in hiding, which contributes to the persistence of kelp beds. As sea urchins increase in density, presumably due to a reduction in predation pressure, they form exposed feeding aggregations as a defensive response. These aggregations destructively graze the kelp, but are seasonally dispersed by intensive fish predation. Thus, depending on sea urchin density, season, and type and abundance of predators, predation can have either stabilizing or destabilizing effects on the community, through its influence on both the abundance and behaviour of sea urchins.

Experimental studies have shown that the tendency of *Strongylocentrotus droebachiensis* to aggregate in laboratory tanks and field cages is enhanced in the presence of predatory crabs and lobsters (Bernstein *et al.*, 1981, 1983; Vadas *et al.*, 1986; Scheibling and Hamm, 1991; but *see*

also Hagen and Mann, 1994). However, Vadas *et al.* (1986) interpret these results as an artifact of containment which arises when the natural dispersal or flight response of sea urchins is impeded by artificial boundaries. These "artificial" aggregations may be related to the lack of topographical structure, other than the walls, in experimental tanks or cages (Scheibling and Hamm, 1991). When cobbles, small boulders or other structures are available in tanks or cages, sea urchins will aggregate around and beneath them (Bernstein *et al.*, 1981; Scheibling and Hamm, 1991). Whether aggregation of sea urchins, when enclosed with predators in tanks or cages, reflects an active defensive response or arises passively due to increased movement (*i.e.* a flight response) remains unclear. The general conclusion that emerges, however, is that sea urchins behave differently when predators are present.

Behavioural responses to predators can vary with sea urchin size (age) and the availability of food and spatial refuges. In kelp beds, where drift algae are readily available, even large adult strongylocentrotids may remain in hiding (Cowen, 1983; Mann, 1985). However, when the abundance of drift algae is decreased, or when increased population density results in competition for food or spatial refuges, sea urchins begin to actively forage in the open (Ebling *et al.*, 1985; Harrold and Reed, 1985; Mann, 1985). Laboratory tank experiments indicate that juvenile and adult *Strongylocentrotus droebachiensis*, collected from barren grounds, form feeding aggregations on kelp irrespective of the presence or absence of decapod predators (Vadas *et al.*, 1986; Scheibling and Hamm, 1991; Hagen and Mann, 1994). In tanks without kelp, however, juvenile and adult sea urchins respond differently to the presence of a predator: juveniles tend to become more cryptic, whereas adults tend to aggregate (Bernstein *et al.*, 1981; Scheibling and Hamm, 1991; Hagen and Mann, 1994). In barren grounds, small juveniles tend to remain cryptic, whereas larger individuals will aggregate on drift algae (Scheibling and Stephenson, 1984) or algae experimentally transplanted to these areas (Himmelman and Nedelec, 1990). In a multifactorial experiment, Hagen and Mann (1994) showed that aggregation of *S. droebachiensis* in laboratory tanks was a complex function of several interacting factors, including: sea urchin size, density and nutritional condition; the presence of kelp; the presence of a predator and the type of predator; and the availability of spatial refuges. Consequently, sea urchins may exhibit different aggregation patterns and defensive behaviours simultaneously in the same habitat. For example, in a barren ground in St. Margarets Bay, Nova Scotia, I have observed dense aggregations of *S. droebachiensis* on the tops of a few boulders, while the majority of the population was sheltering beneath other boulders, at a time when predators were abundant.

Conclusions and Directions for Future Research

At present there are insufficient data to support any general conclusions about the role of predation in regulating populations of *Strongylocentrotus droebachiensis* or to indicate the critical life history stage in this context. Given the enormous reproductive potential of sea urchins, mortality

in the plankton is undoubtedly important in limiting sea urchin abundance. However, the importance of predation at the larval stage in regulating recruitment of sea urchins remains speculative in the absence of more definitive experimental and observational studies. Due to the logistical difficulties of monitoring or manipulating small larvae in the hydrodynamic complexity of the oceans, it is unlikely that field studies will be effective in addressing this issue without major technological advances in larval tagging, real-time oceanographic tracking, and optical sampling. In the meanwhile, further laboratory experiments are needed to identify predators of planktonic larvae and measure predation rates under controlled conditions. An inherent problem with these sorts of studies, however, is that predator and prey behaviour may be influenced by the size of the experimental container and the static water conditions (Cowden *et al.*, 1986). Mesocosm experiments in large volume tanks or *in situ* enclosures, in which a known number of urchin larvae are introduced to a natural assemblage of predators, may provide more realistic estimates of predation rates in nature.

The effect of benthic predators on settling larvae and young juvenile sea urchins is more amenable to laboratory and field experimentation, although we know virtually nothing about the types of predators involved. Competent larvae could be released in laboratory flumes or field enclosures with different types and numbers of potential predators to measure predation rates. Settlement collectors placed in habitats with different predator fields (*e.g.* kelp beds and barren grounds) could be used to test for differences in larval abundance which may be due to predation (Balch and Scheibling, 1994). Studies of settlement and early post-metamorphic mortality will require frequent sampling to measure rates (Minchinton and Scheibling, 1994) and careful manipulation of invertebrate or fish predators to resolve their effects on sea urchin settlement.

The cryptic behaviour of juvenile sea urchins suggests strong selection pressure for predator avoidance. However, until there is more information about predation at the juvenile stage, we can only speculate about its importance in regulating recruitment to sea urchin populations. Studies of predation on juvenile and adult sea urchins under controlled conditions in laboratory aquaria, or in small-scale predator inclusion cages in the field, can identify potential predators and elucidate mechanisms underlying predator-prey interactions (Scheibling and Hamm, 1991). These studies should not in themselves be used to infer the importance of predation as a regulatory agent without information on the abundance, distribution, and behaviour of predators in their natural setting (Miller, 1985b; Andrew and MacDiarmid, 1991). Ideally, field experiments which manipulate predator density should be used to test the effect of predators on sea urchin abundance, although conducting these experiments with proper replication and at appropriate temporal and spatial scales is logistically difficult, especially for large and widely ranging predators such as fish and lobsters.

Manipulative field experiments also require careful assessment of artifactual effects of experimental procedures (*e.g.* caging, fencing, tethering) and the influence of spatial heterogeneity and environmental covariates on prey den-

sity. For example, cages or fences provide an artificial surface upon which sea urchins aggregate (Vadas *et al.*, 1986) or climb to escape predators (Scheibling and Hamm, 1991). The use of natural mesocosms, such as isolated boulders (Tegner and Dayton, 1977) or large tidepools (Paine and Vadas, 1969), may circumvent some of the confounding effects of artificial barriers. Tethering of predators may be effective in examining their effect on sea urchin behaviour and distribution in localized areas (Vadas *et al.*, 1987), but has limited applicability for assessing predation rates at realistic scales, especially for highly mobile predators. Tethering of sea urchins may be more profitably used to examine the importance of spatial refugia (Witman, 1985) and size-selective predation (McClanahan and Muthiga, 1989). For example, tethering sea urchins of different sizes in cryptic and exposed microhabitats would enable testing the hypothesis that increased vulnerability to predation, during an ontogenetic shift from crypsis to open foraging, is a bottleneck to population growth. However, tethering in itself is not without artifacts (Barbeau and Scheibling, 1994; Peterson and Black, 1994), and attachment of a tether to sea urchins without significant injury remains a challenge. An important advantage of tethering is that individuals can be monitored and different causes of mortality can be inferred by the remains left on the tethers. For example, intact tests are characteristic of sea star predation, whereas punctured, chipped or cracked tests are indicative of crab, lobster or fish predation (Tegner and Dayton, 1981; McClanahan and Muthiga, 1989). Survival times of tethered prey can be compared statistically for different agents of mortality, and the importance of environmental covariates can be assessed using Survival Analysis (Barbeau *et al.*, 1994).

Although conceptual models of community dynamics have been based on interactions between *Strongylocentrotus droebachiensis* and its predators (Bernstein *et al.*, 1981, 1983; Wharton and Mann, 1981), there have been few attempts to investigate these interactions using quantitative models (Breen and Mann, 1976b; Mohn and Miller, 1987). This is surprising, in view of the extensive use of numerical modelling in population ecology and the development of increasingly more sophisticated and robust models for the study of predator-prey systems (Hassel, 1978; De Angelis and Gross, 1992). The development of numerical

predator-prey models for sea urchin populations may serve to guide future research by indicating deficiencies in our understanding of dynamic interactions and nonlinear relationships influencing sea urchin abundance. Furthermore, such models are critical in formulating intelligent management strategies for sea urchin fisheries, not only in regulating human fishing pressure but also in assessing the effects of other predators (including commercially important species) on the resource. Modelling is clearly an approach that deserves further consideration in studies of sea urchin population dynamics.

While predators may limit recruitment of *Strongylocentrotus droebachiensis*, in most instances enough survive to maintain populations (Keats *et al.*, 1985; Himmelman, 1986). With the exception of the sea otter in the northwest Pacific, there is little definitive evidence that predators can control sea urchin abundance to the point of enabling the colonization of large macroalgae such as kelps. For this to occur, requires a mass mortality of sea urchins, like that resulting from disease (Scheibling, 1984, 1986; Miller, 1985a), adverse changes in the physical environment (Hooper, 1980), or artificial population control measures (Bernstein and Welsford, 1982; Scheibling, 1989). Considering the impact of fishing and other human activities on coastal ecosystems over the past decades or even centuries, predators such as lobsters and large fish which regulated sea urchin populations in the past, may now be insufficiently abundant to exert a controlling influence (Pringle *et al.*, 1982). Indeed, the sea otter was nearly hunted to extinction in the late 1880s (Estes *et al.*, 1989). With the recent expansion of sea urchin fisheries in eastern Canada and other parts of the world, the direct effects of human exploitation may ultimately have even greater and more far-reaching consequences for sea urchin abundance and the structure of benthic communities than any other predator, past or present.

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