

# Lobster (*Homarus americanus*) population declines, sea urchins, and 'barren grounds': a space-mediated competition hypothesis

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**ABSTRACT:** Long-term declines in lobster landings on the Atlantic coast of Nova Scotia, Canada, have been correlated with decreased algal abundance, which is in turn associated with destructive grazing by sea urchins. Explanations for the lobster declines have focused on collapse of kelp-associated food webs and on loss of concealing kelp cover. However, such trophic- and predation-mediated linkages are not strongly supported by available evidence. This paper advances the hypothesis that competition between lobsters and sea urchins for shelter space is a major factor in these declines. Lobsters are strongly shelter-oriented, and shelter availability appears to be a locally limiting factor. Destructive grazing situations feature high densities of shelter-seeking urchins. Given the relative lobster and urchin densities involved, it is plausible that urchins could depress shelter availability and, consequently, lobster numbers. Although space for refuge is generally considered a critical resource in benthic marine systems, its importance is easily overlooked in the context of vagile benthic organisms. In light of the present argument, substrate-mediated competition involving such species deserves further attention.

## INTRODUCTION

Although landings of lobster *Homarus americanus* in eastern Canada have on the whole remained fairly stable since the 1920's, landings on the Atlantic coast of eastern Nova Scotia exhibited a marked depression between the late 1950's and the early 1980's (Robinson 1979, Harding et al. 1983), and a number of hypotheses have been advanced to explain this decline (Pringle et al. 1980). Robinson (1979) presented evidence of increased effort and attributed lobster stock declines to recruitment overfishing. Dadswell (1979) concluded that the physical closure of the Canso Strait in 1954 (due to the construction of the Canso Causeway) blocked the flow of larvae into Chedabucto Bay, and postulated that this may have subsequently affected lobster stocks along the entire eastern Nova Scotia coast. Harding et al. (1983) agreed that the causeway could have indeed led to decreased larval recruitment, at least in Chedabucto Bay, but concluded that the basic, underlying cause for these declines was a general climatic cooling trend inimical to larval survival. Pringle (1986), Sutcliffe (1973), and Sheldon et al.

(1982) all, either directly or indirectly, implicate terrestrial runoff patterns, ocean circulation, nutrient concentrations, and organic loads of the waters involved and the resulting influences of these factors upon overall ecosystem productivity. However, these hypotheses are based upon correlations of lobster landings with environmental data and are, as such, difficult or impossible to test experimentally. In summarizing the conclusions of a 1979 workshop on kelp-urchin-lobster interactions, Pringle et al. (1980, p. 245) state that overfishing appears to have been a major factor in lobster stock declines but that no 'overwhelming evidence' existed to substantiate an important role for environmental factors.

In their overall assessments, both Harding et al. (1983) and Pringle (1986) echo the assertions of a number of other authors (see Pringle et al. 1980, Wharton & Mann 1981) as to the importance to lobster stock dynamics of ecological interactions involving lobsters, sea urchins *Strongylocentrotus droebachiensis*, and macroalgae. In St. Margaret's Bay, Nova Scotia, for example, commercial landings of lobsters correlate positively with seaweed abundance for the period 1968

to 1983 – the only period and location for which a time series of more than a few years exists (Miller 1985b). Moreover, lobster catches and grazing damage by sea urchins have been found to be inversely correlated in county-level surveys (Wharton 1980) and in anecdotal reports of fishermen (Mann & Breen 1972).

This correlation is of particular significance because destructive grazing by *Strongylocentrotus droebachiensis* has led to large-scale replacement of algal beds in Nova Scotia by 'urchin-dominated barren grounds' (Bernstein et al. 1981, p.39). In St. Margaret's Bay during that same 1968 to 1983 period, sea urchins cleared and kept free of macroalgae most of the subtidal rocky habitat, and plant biomass and primary production in affected areas dropped by as much as 2 orders of magnitude (Pringle et al. 1982, Miller & Colodey 1983) – a phenomenon that appears to have occurred along much of Nova Scotia's Atlantic coast (Bernstein et al. 1981, Miller & Colodey 1983).

Despite the inverse correlation between lobster abundance and intensive sea urchin grazing, a proximate mechanism governing lobster declines has yet to be conclusively demonstrated, and the precise roles played by seaweed and sea urchins remain unclear. Mann & Breen (1972) were among the first to examine the relationship of lobster abundance to sea urchins and kelp beds, and they hypothesized that 'the lobster is a key [predator] species, controlling sea urchin populations in eastern Canada, and that reduction of lobster populations below a critical density ... led to overgrazing of seaweeds in many places (Mann & Breen 1972, p. 603).' By this reasoning, the importance of algal beds to lobster recruitment creates an exacerbating feedback loop (Wharton & Mann 1981). However, sea urchins do not appear to be sufficiently important lobster prey items to support the hypothesis (Miller 1985b, Elner & Campbell 1987).

In this paper, I develop the hypothesis that, at high sea urchin densities, space-mediated competition between lobsters and urchins may play an important role in the dynamics of lobster populations in Nova Scotia. Correlated declines in kelp and lobster abundance may, therefore, both be directly attributable to explosive sea urchin population increases rather than the result of some direct causative link between lobsters and kelp.

### Lobster biology and kelp

Urchin-caused kelp bed destruction has received considerable attention (Bernstein et al. 1981), including focus upon the relationship between kelp and lobster declines. As Wharton & Mann (1981, p. 1348) state, 'it seems to us highly improbable that the decline in

lobster stocks and the disappearance of kelps, in the same general time frame and moving down the coast in the same direction, are entirely coincidental'. In fact, the lobster decline is thought by some to have been a more or less direct result of the kelp loss (Breen 1980)

Disappearance of kelp was accompanied by the virtual disappearance of a number of species associated with kelp communities (Breen & Mann 1976, Breen 1980, Ennis 1986), and Wharton & Mann (1981) and Harding et al. (1983) note that the substantial reductions in primary production in the affected areas should translate to concomitantly reduced productivity by organisms comprising the food of lobsters. Thus, Wharton & Mann (1981) and Breen (1980) conclude that food supply is a mediator of the lobster-kelp relationship. In addition to its impact on lobster food supply, kelp is an important structural component of lobster habitat. In particular, kelp is thought to provide shelter (Breen & Mann 1976, Breen 1980, Wharton 1980, Wharton & Mann 1981, Ennis 1986), and, in laboratory studies, Johns & Mann (1987) reported that lobsters exposed to fish predation experienced smaller predation losses in habitats with seaweed. However, Miller (1985b, p. 2070) states 'seaweed may yet be shown to enhance the lobster population on Nova Scotia's south coast, but, to date, this relationship has only weak support from the data'.

Food is unlikely to be limiting because lobsters are known to have generalized food preferences, and their stomach contents usually reflect local prey abundances (Cooper & Uzmann 1980, Harding et al. 1983). Thus, Elner & Campbell (1987) found the mean stomach fullness and gross dietary composition of lobsters collected from 'urchin denuded barrens' to be similar to those of lobsters collected from a dense macroalgal stand. As many authors have noted, lobsters are shelter-seeking animals, and their basic substrate preference is for rocky bottoms, wherein they can tunnel or burrow in rock crevices or between boulders (Ennis 1984). Clearly, a burrow or tunnel will offer much safer refuge than a kelp frond. Lobsters only occasionally take up shelter under algal fronds (Cooper & Uzmann 1980), and, in the course of extensive field experimental work in an area of high lobster abundance on the coast of Maine, USA, I observed relatively few lobsters under kelp fronds during daylight hours – the vast majority were in rocky shelters or excavated sand tunnels.

More generally, 'the presence or absence of a dense algal cover does not seem to affect *Homarus americanus* distribution' (Cobb 1977, p. 147). Botero & Atema (1982) conclude, on the basis of laboratory studies, that rocky substrate is a key factor in the benthic settlement of post-larval lobsters. Although such lobsters, when offered a choice, exhibited a preference for algal-

covered rock over rock alone, Botero & Atema concluded that algae do not seem to be essential for substrate choice. Miller (1985b) even suggests that any preferences of lobsters for kelp beds may simply be artifacts of concentration at prominent ecotones.

The apparent association of lobsters with kelp may largely be a reflection of the strong preference of lobsters for rocky substrates, which also afford attachment opportunities for the kelp: 'within the *Laminaria* forest you may well find increase in the availability of suitably sized crevices which small lobsters might exploit' (D. J. Scarratt, as quoted by Pringle et al. 1980, p. 245).

### The lobster-substrate interaction

As mentioned above, lobsters have been clearly demonstrated to be strongly adapted and tied to shelter use (Cobb 1971, O'Neill & Cobb 1979, Ennis 1984, Lawton 1987). Juvenile lobsters in particular are exposed to considerable predation risk (Lawton 1987), and, in laboratory experiments, lobsters exposed to fish predators experienced substantially smaller predation losses in treatments that included shelter (Cobb et al. 1986). In addition, shelters offer refugia from conspecifics and such adverse physical factors as surge and high current velocities (Cobb 1971, O'Neill & Cobb 1979). The retention of shelter has also been shown to be a clear index of dominance in both laboratory and field studies (O'Neill & Cobb 1979), and the fitness of subdominants may be reduced because their growth rates and survivorship are lower than those of lobsters living in optimal shelters (Lawton 1987). The ability to gain and hold shelter of suitable size, then, is clearly central to a lobster's survival (O'Neill & Cobb 1979, Fogarty & Idoine 1986).

Moreover, shelter space appears to be a locally limiting factor in lobster population dynamics. Surveys of natural lobster populations and habitat types show lobsters to be most abundant in areas of sand overlain by rocks and boulders (Cobb 1977, Cooper & Uzmann 1977). These substrates afford cracks and crevices that can be readily utilized as shelters (Scarratt 1968), and direct competition among lobsters for shelter seems to exist under natural conditions (O'Neill & Cobb 1979, Ennis 1983). Hudon (1987, p. 1859), for example, found only small lobsters on a bottom type featuring 'only small crevices and little surface cover', whereas he found adults as well as postlarvae and juveniles co-existing in areas in which 'crevices of all sizes and shapes were abundant'. (It should be added that these latter areas also featured additional macroalgal surface cover.) Similarly, Howard (1980) correlated bottom topography and rock outcrop sizes with size-frequency distributions of European lobster *Homarus*

*gammarus* populations in 3 locations. These observations from natural habitats are strongly substantiated by consistent reports of increased local carrying capacities with the addition of artificial shelters (Scarratt 1968, Sheehy 1976, Atema & Cobb 1980, Aiken & Waddy 1986). Therefore, the availability of appropriate shelter or the suitability of the substrate for modification into shelter will in turn strongly influence the suitability and carrying capacity of a given habitat for lobsters (Cobb 1977).

### Kelp, sea urchins, and substrate

Although the most prominent characteristic of 'barren grounds' may be the absence of kelp, they also feature high densities of *Strongylocentrotus droebachiensis*. In healthy, persistent kelp beds, urchin densities are reported to be 'extremely low' (Bernstein et al. 1981, p. 41), with estimates ranging from 0.4 to 4.0 m<sup>-2</sup> (Wharton & Mann 1981) to 'less than 10' m<sup>-2</sup> (Bernstein et al. 1981). In contrast, urchin density estimates for barren grounds range from 20 m<sup>-2</sup> to over 100 m<sup>-2</sup> (Bernstein et al. 1981, Wharton & Mann 1981). Urchin biomass is also higher in barrens: estimates of urchin biomass from apparently persistent Nova Scotia kelp beds range from 0 to 150 g m<sup>-2</sup>, whereas urchin biomass estimates from barren grounds range from 250 to 1200 g m<sup>-2</sup> (Mann & Breen 1972, Miller 1985b).

As is the case with lobsters, concealment is an important component of sea urchin behaviour: field and laboratory studies have demonstrated in *Strongylocentrotus droebachiensis* a tendency to seek shelter in crevices or under rocks (Garnick 1978, Bernstein et al. 1981, Miller 1985a). These cryptic tendencies are particularly strong for relatively small urchins (Bernstein et al. 1981, Miller 1985a), which size classes exist at disproportionately high densities on 'barrens' (Bernstein et al. 1981, Wharton & Mann 1981). Once sheltered in cracks and crevices, urchins lodge themselves tenaciously and are as such extremely difficult to dislodge (Garnick 1978).

### HYPOTHESIS

The shared cryptic tendencies of lobsters and sea urchins, then, is potentially a basis for interspecific competition. Because sea urchin densities in kelp beds are ordinarily relatively low (Bernstein et al. 1981, Wharton & Mann 1981, Miller 1985b) and lobsters do not exist in particularly high local abundance, spatial competition between these 2 species within kelp beds would seem to be unlikely. However, such competition could occur on 'barren grounds', where sea urchins

attain extremely high densities of size classes strongly disposed towards crack and crevice occupation.

Cooper & Uzmann (1977) reported lobster densities on 'prime fishing grounds' to average  $1.2\text{ m}^{-2}$ , and Hudon (1987) reported densities of up to  $3.80\text{ m}^{-2}$  (including adults, juveniles, and postlarvae). If, as the evidence from bottom-type surveys of natural populations and from installations of artificial shelters suggests, shelter availability plays a role in limiting local lobster abundance, then the density of suitable shelters may also be on this order of magnitude (or, in light of fishing pressures upon lobsters, perhaps somewhat higher). Therefore, urchin densities of 20 to over  $100\text{ m}^{-2}$  could readily exert a depressing influence on shelter availability and, by implication, on lobster numbers. To the extent that kelp affords some shelter to lobsters, lobster-urchin competition would be further exacerbated on barren grounds.

Clearly, new data are needed, and the present hypothesis posits a simple, direct, eminently testable mechanism as underlying the lobster-sea urchin relationship. As an initial approach, relative abilities of lobsters and urchins to compete for shelter space could be assessed in laboratory experiments by measuring lobsters' shelter occupancy in relation to manipulations or urchin densities on the one hand and shelter size and numbers on the other. In the field, locally increased lobster biomass with (controlled) removal of urchins (and removal of any establishing kelp) in an area of high urchin density on barren grounds would constitute strong evidence for the proposed mechanism. This could be complemented by decreasing the availability of shelter in an area of otherwise abundant lobsters and kelp, which could be accomplished by filling lobster lairs with underwater cement or perhaps even 'artificial' sea urchins. If shelter availability is indeed a limiting factor (as opposed to trophic limitations), then there should be a decrease in lobster numbers and/or a change in their size frequency distributions.

Even if the hypothesized mechanism were operating, the question would remain as to its relative importance. Kelp-related limitations are certainly plausible, and lobsters, as previously discussed, are subject to substantial exploitation pressure. As Harding et al. (1983, p. 180) have noted, 'there is no reason to expect that the same factors would be limiting in all places and times, given the variety of habitats frequented by the lobster and the multiform interactions between the lobster and its surroundings'. The relative importance of kelp and shelter limitations could be assessed through combinations of controlled shelter removal and kelp exclusion in an area otherwise abundant in lobsters and kelp.

Massive, disease-induced sea urchin mortalities, which were accompanied by recovery of macroalgae, occurred in 1981 to 1984 (Miller 1985a, Scheibling 1986,

Pringle pers. comm.\*). In addition, Robinson (pers. comm.\*\*\*) noted a strong pulse of pre-recruit lobsters in 1979 along Nova Scotia's eastern shore, and landings of lobsters in the entire region, with the exception of the Bay of Fundy, increased synchronously and sharply between 1982 and 1987 (Miller et al. 1987). Miller et al. presume the increase to have been caused by some as yet unidentified but widespread environmental factor. Clearly, the coincidence of lobster population rebound and precipitous urchin population declines is consistent with the present hypothesis (as well as others), whereas a strong dependency of lobsters upon kelp would dictate a time lag between the demise of urchins (and concomitant recovery of macroalgae) and increases in lobster densities. Although initial recruitment for the lobster recovery appears to have actually *preceded* most of the mass urchin mortalities (Pringle pers. comm.), the small individuals comprising initial benthic recruitment would be unlikely to experience significant space-mediated competition from sea urchins until they were older and larger. In any case, the present hypothesis concerns a local, proximate mechanism, and kelp shelter manipulations would therefore be of particular interest in areas of lobster stock increases and reestablishing macroalgal beds.

## CONCLUSIONS

Direct competitive interactions have received little consideration in the context of lobster stock declines. However, Pringle et al. (1982) suggest that species interactions, while traditionally overlooked, may prove to play important roles in lobster population dynamics.

Substrate interactions have also received little attention in this context despite the general concession that space for attachment or refuge is 'the most important limiting resource in benthic marine systems' (Roughgarden 1986, p. 505) and is, as such, a major axis of interspecific competition in such systems (Lewin 1987). However, this principle is usually considered in relation to sessile organisms (Roughgarden 1986, Steger 1987), and is easily overlooked in a system involving vagile subtidal organisms such as lobsters and sea urchins. Nevertheless, Steger (1987) reported that gonodactylid stomatopods were size-specific in their occupation of cavities in coral rubble and that the numbers of such cavities limited local stomatopod densities. In rocky intertidal studies in Panama, Menge

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& Lubchenco (1981, p. 436) found that 'most individuals of most invertebrate species occur in cracks, depressions, crevices, and holes', and they concluded that holes and crevices seemed to be of 'unusually great importance to patterns of community structure' in that system (Menge & Lubchenco 1981, p. 447). In central California, USA, Hines & Pearse (1982) noted that, in areas of intensive sea otter predation, abalones were largely confined to crevices and larger abalones suffered disproportionately heavier predation than smaller ones – presumably because of crevice size limitations. In contrast, in comparable areas out of the range of sea otters, Hines & Pearse found abalone to be numerous outside of crevices and over twice as large as their counterparts in otter-inhabited areas. Finally, this phenomenon does not appear to be limited to marine invertebrates. Caddy (1986) notes that crevice-limited recruitment and mortality appear to exist for coral reef fish, and a study by Morse et al. (1985) demonstrates that an analogous process may act, in terrestrial systems, upon insects with respect to vegetation structure.

Attention to such factors is strongly warranted in the context of lobster biology because, as the foregoing arguments suggest, an interaction of shelter requirements and interspecific competition may be responsible for stock declines in Nova Scotia. Moreover, destructive grazing of kelp and seagrasses has been reported for a number of temperate and tropical sea urchin species (Mann & Breen 1972, Breen & Mann 1976, Pearse & Hines 1979, Lawrence & Sammarco 1982, Pringle et al. 1982) [see also Lawrence (1975) for a thorough, detailed review], and the present hypothesis might apply in other situations. Significantly, in their studies in Panama, Menge et al. (1983) found the assemblages of organisms occurring in rocky intertidal holes to vary with the presence of sea urchins. The studies of Howard (1980), Menge & Lubchenco (1981), Hines & Pearse (1982), Caddy (1986), Hudon (1987), and Steger (1987) all demonstrate that refuge availability can limit local densities, and more generally, space availability could readily limit population densities and even size-frequency distributions of crevice- or hole-dwelling species with a high degree of shelter size specificity (such as lobsters). Such species could, therefore, experience substantial competition for space in the face of even moderate increases in numbers of a tenacious species with some propensity for cryptic behaviour – particularly if the competing species were relatively large and vagile (as is the case with many sea urchins).

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