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Changes in the Near-Shore Ecosystem of the Atlantic Coast of Nova Scotia, 1968-1981.

by

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INTRODUCTION

Nearshore subtidal kelp beds in St. Margaret's Bay, and most probably along the entire Atlantic coast of Nova Scotia, have undergone a radical change of state over the last decade. Widespread destructive grazing by aggregations of herbivorous sea urchins has transformed these areas into barrens devoid of macroalgae. This paper reviews data on the development and progress of this destructive grazing, and current awareness of how urchin aggregations form. It also shows how human impacts such as overfishing contributed to this situation, and how ecological interactions in this system constrain management responses, especially for the important lobster fishery.

DESTRUCTIVE SEA URCHIN GRAZING IN ST. MARGARET'S BAY, N.S.

The large kelps Laminaria longicuris and L. digitata are the most abundant subtidal macrophytes in the rocky coastal zone of Eastern Canada (Mann 1972). The rate of primary production in these beds is very high (Mann 1973), and these plants make an important contribution through detritus food chains to the nearshore food web. During an extensive survey of St. Margaret's Bay in 1968, Mann (1972) reported that kelp beds were nearly continuous along the western shore to a depth of 12 metres.

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SYMPOSIUM ON ENVIRONMENTAL CONDITIONS, 1970-79

St. Margaret's Bay is a large bay on the southern, Atlantic coast of Nova Scotia, Canada. It's subtidal habitats are typical of most of those on Nova Scotia's Atlantic coast.

Although kelp cover was nearly continuous in 1968, there existed areas within the Laminaria zone completely devoid of macrophytes except for encrusting coralline algae. Such barren areas were also characterized by large numbers of sea urchins (Strongylocentrotus droebachiensis) which are much less numerous in Laminaria beds. During 1971 and 1972, casual observations and reports from amateur divers suggested that barren areas with sea urchins were becoming more common near Halifax, Nova Scotia, and that kelp beds were decreasing in size and number. In 1973, Breen and Mann (1976) resurveyed the western shore of St. Margaret's Bay, N.S., and found that kelp beds were either missing or greatly reduced. The transition zone between kelp and barren rock was narrow and sharp in most cases and was often accompanied by a dense band of sea urchins.

They observed dense aggregations of large sea urchins actively grazing on kelp plants, and documented destruction of kelp beds under sea urchin attack. They also showed experimentally that sea urchins were the cause of kelp disappearance by removing urchins from an area and observing the reestablishment of kelp. A control plot with urchins remained unchanged. Sea urchin grazing continued after 1973, and by 1980 only a few relict beds remained in habitats apparently unsuitable for sea urchins.

Breen and Mann (1976) showed that only the largest sea urchins in the population formed aggregations and grazed actively on kelp. After kelp disappearance, urchin populations underwent a series of changes lasting several years (Lang and Mann (1976) . With increase of time since kelp disappearance, sea urchins showed decreased growth rate and reduced gonad size, but an increase in numbers resulting from high recruitment rates in the first two years after kelp bed destruction. Further studies have shown that these high densities gradually decrease over a period of years. Long term average sea urchin density on established barrens remains at about 15-30 m⁻².

These urchin populations are sufficient to prevent the successful resettlement of kelp. Chapman (in press) has demonstrated this experimentally, and has also shown that productivity on the barrens, while much lower than in kelp beds, is sufficient to support the urchin population. These barrens urchins feed on encrusting coralline and summer ephemeral algae, and on benthic diatoms.

FORMATION OF SEA URCHIN AGGREGATIONS

The mechanism by which sea urchins destroy kelp beds is the formation of dense and widespread feeding aggregations. Once these form, they can quickly graze large areas, because urchins may chew through Laminaria spp. stipes and destroy plants without having consumed them. The formation of these dense feeding aggregations is thus a critical point in determining which of two states this ecosystem will enter: healthy kelp beds or sea urchin dominated barrens.

While we do not know the precise stimulus for the formation of these aggregations, it obviously represents a behavioural change in sea urchin foraging tactics. Sea urchins (Strongylocentrotus droebachiensis) usually spend most of their time hidden, and only leave these refuges to feed (Garnick 1978). Destructive grazing differs in that all or most of the large urchins remain exposed all the time.

Bernstein et al. (1981) used field observations and laboratory experiments to demonstrate that several factors interact to influence urchin aggregating behaviour. They found that large urchins are much more likely than small ones to form aggregations as a defence against predation by crabs, an important sea urchin predator. The presence of crabs enhanced this aggregating behaviour. This is an effective defence, since large urchins in an aggregation are almost immune to crab attacks. Small urchins, in contrast, hide individually in and under rocks as a defensive behaviour.

Bernstein et al. (1981) also found that sea urchin aggregating

behaviour is markedly seasonal. During the summer, almost all urchins remain sheltered among the rocks, and form exposed feeding aggregations mostly in the fall and winter. Summer is the season when predatory fish such as the wolffish (Anarhichas lupus) are abundant in the nearshore. There are extremely strong correlations between the number of predatory fish present and the weight of broken sea urchin tests in quantitative samples (positive), the number of urchin aggregations (negative), and the number of individually exposed urchins (negative).

This evidence led Bernstein et al. (1981) to develop the following scenario for the formation of dense sea urchin feeding aggregations. This scenario is based in part on numerous observations (Bernstein et al. 1981, Wharton and Mann 1981) that healthy kelp beds have extremely low densities of urchins.

In a healthy Laminaria spp. bed, very low densities of urchins hide in refuges because of predation pressure. Aggregation is a more effective defence against crab attack than hiding, but aggregation is not a feasible strategy at very low densities, probably because widely separated urchins would be exposed to predation as they sought each other out. It is therefore the combination of very low densities and urchin hiding that constitutes an equilibrium condition with respect to kelp bed predators.

Urchins begin to increase in density (presumably on account of reduced predator pressure, though direct evidence for this is not yet available) and eventually become so abundant that predators find them easily. At high densities, urchins switch strategy, forming exposed aggregations and feeding openly on kelp. Such aggregations are an effective anti-predator strategy, but require high urchin population densities. This scenario requires that there be some critical threshold density, depending on the size of the urchins and the density of their predators, above which urchins will aggregate and begin forming holes in the kelp bed. Experiments have shown that the presence of predators (crabs) facilitates the formation of urchin aggregations. Predation thus contributes to kelp bed persistence at low urchin

densities but triggers destructive grazing at high urchin densities through a behavioural mechanism.

THE ROLE OF PREDATORS

Predators play several roles in this system. They keep urchins in healthy kelp beds at very low densities and in hiding. They modify urchins' aggregating behaviour. They may be involved in positive feedback cycles which result from the disappearance of kelp. Each of these is discussed in more detail below.

In nearly two and one-half years of sampling, Bernstein *et al.* (1981) found sea urchins inside a healthy kelp bed in St. Margaret's Bay only once, and these were deep in cracks in the rocks. Miller and Mann (1973) stated that in St. Margaret's Bay in 1968, just before the onset of widespread kelp bed destruction by urchins, their average density was 36.8 m^{-2} . A reexamination of the data showed that the dense kelp beds contained less than 10 m^{-2} , and the partially grazed areas were characterized by much higher densities. Wharton (1980) has also found that an extensive healthy kelp community in Yarmouth County, Nova Scotia contains very few urchins, and that destructive grazing is preceded by a sharp rise in population density.

Breen and Mann (1976) attempted to artificially increase sea urchin density inside a kelp bed by transplanting as many as 400 urchins to its center. These failed to form a feeding aggregation. One month after the addition, there were no signs of the transplanted urchins except for empty tests revealing signs of predation by starfish, crabs, and lobster. These observations, along with others that show the densities of starfish, crabs, lobsters, and predatory fish to be higher in and around kelp beds than in barrens, strongly suggest that predation pressure is responsible for the virtual absence of urchins from healthy kelp beds.

As mentioned above, the seasonal abundance of predatory fish during the summer modifies urchins' aggregation behaviour. These fish, however, are active only during the daytime, and at night urchins leave their refugia and forage actively. They

return to their hiding places when the fish become active again in the morning. Thus, the presence of predators has a marked effect on urchins' behaviour. Barb Welsford has shown in laboratory experiments that individual urchins actively avoid water containing the scent of crabs or lobsters. It is likely that such chemoreception plays an important role in urchins' flexible responses to predators (fish, crabs, lobsters, starfish) in the field.

These interactions provide ideas about how destructive sea urchin feeding aggregations form, once urchin density rises above a critical threshold. We do not, however, have clear evidence about what factors permit urchin densities to begin rising in the first place. Since it appears that predation pressure keeps urchin densities low in a healthy kelp bed, it is reasonable to assume that a reduction in this pressure was responsible for increased urchin density. Mann and Breen (1972) and Breen and Mann (1976) hypothesized that reduced lobster stocks were responsible. They based this on laboratory observations of lobster feeding and on the documented reduction in lobster stocks over the recent past. They argued that abundant lobsters would normally break up urchin feeding aggregations whenever they formed. In the absence of lobsters, urchin survival increased and the feeding aggregations enlarged to begin the destructive grazing observed in the 1970's.

In Breen and Mann's view, the lobster is a keystone predator in this system, and a change in its density had disproportionate effects on the rest of the ecosystem. We now know that this is an oversimplification. There is, in fact, a suite of sea urchin predators. Some, like the wolffish, are abundant and voracious enough to perhaps be more important than lobsters. In any event, virtually all of these predators, but especially the lobster and the larger predatory fishes, have suffered severe stock declines in the last 10-15 years due to heavy fishing pressure. This has resulted in a much reduced predation pressure on sea urchins.

This nearshore ecosystem is now in a state of drastically lower productivity, and there are positive feedbacks among

its components that appear to be operating to maintain it there. One of the more obvious of these is the fact that this lower productivity can support only a few predators, compared to a healthy kelp bed. This means there is unlikely to be an increase in predation pressure on urchins sufficient to allow the return of kelp. Another potential feedback cycle has been identified by Wharton and Mann (1981). They argue that juvenile lobsters require macroalgal cover as protection from predators while foraging. This increased susceptibility to predation results in a population bottleneck that prevents lobsters from maturing and reproducing.

We at the Welsford Research Group have made collections of juvenile lobsters for the Gillian MacNab Marine Biology Research Fund and for Fisheries and Oceans Canada. We have collected samples in several barren areas in Nova Scotia and have found evidence that supports Wharton and Mann's hypothesis. We found abundant juveniles, to about 30mm carapace length, all in sheltered habitats. Abundance dropped sharply between 30 and 35mm carapace length. This is about the size at which spiny lobsters in Australia begin to forage actively and become susceptible to trapping and predation (Chittleborough 1970, 1974).

It thus appears that, as Mann (1977) suggested, these urchin-dominated barrens are a new stable configuration of the nearshore ecosystem, with feedback cycles operating to maintain it.

THE ATLANTIC COAST OF NOVA SCOTIA

The detailed ecological information reviewed above comes mainly from work performed in St. Margaret's Bay, Nova Scotia. In 1978 and 1979, Wharton and Mann (1981) attempted to expand this scenario to include the entire Atlantic coast of Nova Scotia. They documented that, east of Cape Sable Island in southwest Nova Scotia, the nearshore subtidal is almost completely made up of urchin dominated barrens. Kelp exists only in refugia inaccessible to sea urchins. They review evidence that shows kelp was abundant along this coast as recently as the late

1960's, and contend that the disappearance of kelp in St. Margaret's Bay was part of a much larger pattern of destructive sea urchin grazing along the entire Atlantic coast of Nova Scotia.

Using sea urchin growth rates and size frequency distributions at several sites along the coast, they attempt to date the disappearance of kelp. They then place these sites in a temporal progression based on kelp disappearance and find that kelp disappeared first along the eastern shore of Nova Scotia, and most recently along the southwestern shore. They argue that, in each case, kelp was destroyed by destructive sea urchin grazing.

Wharton and Mann (1981) thus use data from several sites along a spatial gradient to construct a temporal gradient of events occurring at various times in the past. This assumes that all sites are replicates of each other, and that events followed the same course at each site. There are several subsidiary assumptions, too detailed to review here, that must be tested before Wharton and Mann's scenario can be completely accepted. It does, however, fit most of the available evidence.

Using records of lobster landings, Wharton and Mann show that declines in lobster catches along the Atlantic coast follow the same temporal progression as the disappearance of kelp. They contend that the two are related, and that healthy kelp beds are necessary for abundant lobster stocks for two reasons: 1) macroalgae shelters young lobsters from predators, and 2) the higher productivity of kelp beds provides food for lobsters. In this scenario (Figure), the decline in lobster stocks, resulting from overfishing and possible environmental changes, is one of the causes of kelp bed destruction; it then becomes a continuing result of kelp bed destruction.

IMPLICATIONS FOR FISHERIES MANAGEMENT

The extensive disappearance of kelp beds in Nova Scotia, and its complex suite of causes and effects, have serious implications for fisheries management. Perhaps most striking is the evidence that this ecosystem is characterized by a complex set of relationships

among many species, and that, as a result, human impacts such as overfishing can cascade through the system. This means that only a multispecies approach to management, based on sound ecological understanding, will be effective. For example, should limits be placed on groundfish catches in the nearshore? This decision can only be made with a knowledge of the abundances of other urchin predators, and some measure of how near urchin density in kelp beds is to the critical threshold that will transform the system. The positive feedback cycles also mean that merely lessening the human impacts that induced the change will not necessarily restore productivity. Recruitment overfishing of lobsters contributed to urchin increases, but reducing fishing pressure on lobsters will probably not increase lobster stocks much if indeed there is a population bottleneck as described above. Transformations in ecosystem state are not necessarily reversible reactions, because the different states are characterized by different ecological interactions. Effective management must be aware of and allow for these interactions.

The transformation of Nova Scotia's subtidal kelp beds to barrens represents a tremendous loss of productivity. This loss alone will result in the degradation of coastal resources utilized by man. In addition, ecological interactions in the barrens may act to continue to degrade the lobster fishery, and others, as human impacts cascade through the system.

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