NAFO Sci. Coun. Studies, 5: 101-105

Changes in the Nearshore Ecosystem of the Atlantic Coast of Nova Scotia, 1968-81

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Abstract

Beginning in the early 1970's, grazing by aggregations of sea urchins, *Strongylocentrotus droebachiensis*, completely destroyed subtidal kelp beds in St. Margaret's Bay, Nova Scotia, leaving barrens devoid of macroalgae. Similar destructive grazing appears to have occurred along the entire Atlantic coast of Nova Scotia. In thriving kelp beds, predation pressure by lobsters, crabs, starfish and fish keeps sea urchins at low density and in hiding. Sea urchin density increased in the late 1960's, perhaps as a result of environmental change and reduction of predators, and, upon reaching a threshold level of abundance, they changed their behavior and aggregated as a defence against predation.

The barrens that result from destructive grazing are characterized by very low productivity, in contrast with thriving kelp beds, and represent a stable configuration of the ecosystem, because the surviving sea urchins are abundant enough to prevent resettlement of macroalgae. Because of their low productivity, these barrens can support only very low abundance of predators. Also, without macroalgae for shelter, the small lobsters are more vulnerable to predation by fish and large crabs. Increased knowledge of the kelp-bed ecosystem has shown that there are complex relationships among its constituent inhabitants, and that only a multispecies approach to management will be effective.

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, *Strongylocentrotus droebachiensis*, has transformed these areas into barrens devoid of macroalgae. This paper reviews data on the development and progress of this destructive grazing and on current awareness of how sea urchin aggregations form. It also shows how man's impacts, such as overfishing, contributed to this situation and how ecological interactions in this system constrain management responses, especially for the important lobster fishery.

Sea Urchin Grazing in St. Margaret's Bay

The large kelps, *Laminaria longicruris* and *L. digitata*, are the most abundant subtidal macrophytes in the rocky coastal zone of eastern Canada (Mann, 1972a). The rate of primary production in these beds is very high (Mann, 1972b), 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, Nova Scotia, in 1968, Mann (1972a) reported that kelp beds were nearly continuous along the western shore to a depth of 12 m. The subtidal habitats in St. Margaret's Bay are typical of most of those along the Atlantic coast of Nova Scotia.

Although kelp cover was nearly continuous in 1968, there existed areas within the *Laminaria* zone that were completely devoid of macrophytes except for encrusted coralline algae. Such barren areas were also characterized by large numbers of sea urchins, which were less numerous in the *Laminaria* beds. During 1971 and 1972, casual observations and reports from amateur divers indicated that the barren areas with sea urchins were becoming more common near Halifax, Nova Scotia, and that the kelp beds were decreasing in size and number. In 1973, Breen and Mann (1976a) resurveyed the western shore of St. Margaret's Bay 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 large numbers of sea urchins. They observed dense aggregations of large sea urchins actively grazing on kelp 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 sea urchins from an area and observing the reestablishment of kelp, whereas a control area with sea urchins remained unchanged.

Sea-urchin grazing continued after 1973, and by 1980 only a few relict beds remained, apparently unsuitable for sea urchins.

Breen and Mann (1976a) showed that only the largest sea urchins in the population formed aggregations and grazed actively on kelp. After the disappearance of kelp, the sea urchin populations underwent a series of changes over a period of several years (Lang and Mann, 1976). During the first 2 years after kelp-bed destruction, high recruitment resulted in increased population size, with a consequent decrease in growth and reduction in gonad size. The population gradually decreased over several years, the average density on established barren areas remaining at about 15–30 sea urchins per m^2. Such densities are sufficient to prevent the successful resettlement of kelp. Chapman (1981) has demonstrated this experimentally and also has shown that productivity of a barren area, while much lower than in the kelp beds, is sufficient to support the population of sea urchins which feed on benthic diatoms and on encrusting coralline and ephemeral algae.

Formation of Sea Urchin Aggregations

The mechanism by which sea urchins destroy kelp beds is the formation of dense, widespread aggregations, which can quickly destroy the kelp over large areas by chewing through the *Laminaria* stipes, sometimes without consuming the plants. The formation of these dense feeding aggregations thus determines whether the ecosystem will contain healthy kelp beds or sea-urchin dominated barren areas.

The precise stimulus for formation of these aggregations is unknown, but it obviously involves a behavioral change in sea urchin foraging tactics. According to Garnick (1978), sea urchins (*S. droebachiensis*) usually spend most of their time hidden and only leave their refuges to feed. Destructive grazing differs from this, in that all or most of the large sea urchins remain exposed at all times.

Bernstien *et al.* (1981), using field observations and laboratory experiments, demonstrated that several factors interact to influence the aggregating behavior of sea urchins. Large sea urchins are much more likely than small ones to aggregate as a defense against predation by crabs, a major predator. The presence of crabs enhanced the formation of aggregations of large sea urchins as an effective defence, whereas small sea urchins hid individually under rocks as a defensive behavior. Bernstein *et al.* (1981) also found that the aggregating behavior is markedly seasonal. Almost all sea urchins remain sheltered among rocks in summer and form grazing aggregations mostly in autumn and winter. Summer is the season when predatory fish, such as the wolffish (*Anarhichas lupus*), are abundant in nearshore areas. Quantitative observations and sampling indicated a high positive correlation between the number of predatory fish and the weight of broken sea urchins tests, and high negative correlations between the number of predatory fish and both the number of sea urchin aggregations and the number of individually exposed sea urchins. These observations led Bernstein *et al.* (1981) to develop the following hypothesis for the formation of dense sea urchin aggregations.

In a thriving kelp bed, the density of sea urchins is low and they hide in refuges due to predation pressure. Although aggregation is a more effective defence against crab predation than hiding, it is not a feasible strategy at very low densities, probably because the sea urchins would be exposed to predation as they attempted to aggregate. Therefore, the hiding behavior of sea urchins at low density constitutes an equilibrium condition with respect to kelp-bed predators. As sea urchins increase in density (presumably due to reduced predator pressure, although direct evidence of this is not yet available), the lack of refuges makes them more susceptible to predation. At high density, therefore, the sea urchins change strategy, forming exposed aggregations which graze openly on kelp. The formation of such aggregations constitutes an effective anti-predation strategy. The threshold density, above which sea urchins begin to aggregate and form holes in kelp beds by grazing, depends on both the density of sea urchins and the density of their predators. Experiments have shown that the presence of predators (crabs) initiates the formation of sea urchin aggregations. Predation thus contributes to the persistence of kelp beds at low densities of sea urchins but triggers destructive grazing at high densities.

The Role of Predators

Predators play important roles in the nearshore ecosystem. They may prevent extensive grazing of kelp beds when the density of sea urchins is very low, but they may also initiate the aggregating behavior of sea urchins when abundance of the latter increases beyond some threshold level. In addition, they may be involved in positive feedback cycles that maintain the barrens after the disappearance of kelp. During nearly 2½ years of sampling in St. Margaret's Bay, Bernstein *et al.* (1981) found sea urchins in a healthy kelp bed only once, and these were deep in the crevices of rocks. Miller and Mann (1973) reported that, just before the onset of widespread kelp-bed destruction by sea urchins in St. Margaret's Bay in 1968, the average density of sea urchins was 36.8 per m^2. Reexamination of the data indicated that dense kelp beds contained less than 10 sea urchins per m^2, whereas partially grazed areas were characterized by much higher densities. Wharton (1980) noted that an extensive kelp bed near Yarmouth, Nova Scotia, contained very few sea urchins, and that destructive grazing was preceded by a rapid increase in population density.

Breen and Mann (1976a) attempted to artificially increase sea urchin density within a kelp bed by transplanting 400 urchins to its center. These failed to form a grazing aggregation, and there was no sign of the transplanted sea urchins one month later except for empty shells which indicated predation by starfish, crabs and lobsters. Such observations and others, which show that densities of starfish, crabs, lobsters and predatory fish are higher in and around kelp beds than in barren areas, strongly indicate that predation pressure is responsible for the scarcity of sea urchins in thriving kelp beds.

It was noted above that predatory fish are abundant in nearshore areas during the summer. These fish, however, are active only during the daytime, thus enabling the sea urchins to leave their refuges at night to forage actively. Hence, the presence of predators has a marked effect on the behavior of sea urchins. Barbara Welsford (Halifax, Nova Scotia, pers. comm.) has shown in laboratory experiments that individual sea urchins avoid water containing the scent of crabs and lobsters. It is likely that such chemoreception plays an important role in the behavioral response of sea urchins to predators under natural conditions.

Although there are observations on the formation of grazing aggregations of sea urchins once their density rises above a critical threshold, there is no clear evidence about what factors permit their density to begin rising in the first place. Since predation pressure seems to have kept sea urchin densities low in thriving kelp beds, it is reasonable to assume that a reduction in predation pressure was responsible for increased sea-urchin density. Mann and Breen (1972) and Breen and Mann (1976b) hypothesized that the reduced abundance of lobsters was responsible. They based this conclusion on laboratory observations of lobster feeding and on the documented reduction in abundance of lobsters. They noted that an abundance of lobsters would normally disrupt the sea urchin aggregations whenever they formed. In the absence of lobsters, sea urchin survival increased and the feeding aggregations enlarged to begin the destructive grazing of kelp beds observed in the 1970's. In the view of Breen and Mann (1976b), lobsters represent the principal predator in the system and a change in their density has disproportionate effects on the rest of the system. This may be an oversimplification of the problem, as there are several sea urchin predators, and some, like wolffish, are abundant and voracious enough to be just as important as lobsters. In any event, most of the predators, especially lobsters and large fish, have declined significantly in abundance during the past 10–15 years due to heavy fishing pressure, and this has resulted in reduced predation pressure on sea urchins.

The nearshore ecosystem is now in a state of drastically lower productivity than previously, and positive feedbacks among its various components appear to be operating to maintain it there (Mann, 1977). It is obvious that the low productivity can support only a few predators, in contrast to the much higher predator density in thriving kelp beds. Predation pressure on sea urchins is consequently reduced. Another potential feedback cycle has been identified by Wharton and Mann (1981), who argued that juvenile lobsters require macroalgal cover as protection from predators while foraging. This increased susceptibility of juvenile lobster to predation may have a significant effect on preventing the lobster stocks from increasing.

State of Kelp Beds Along the Atlantic Coast of Nova Scotia

The ecological information reviewed above was derived mainly from studies in St. Margaret's Bay. In 1978 and 1979, Wharton and Mann (1981) expanded their studies to include the entire Atlantic coast of Nova Scotia. They found that the nearshore subtidal areas east of Cape Sable in southwestern Nova Scotia were almost completely barren and dominated by sea urchins. Kelp existed only in places inaccessible to sea urchins. They reviewed evidence that indicated an abundance of kelp along this part of the coast during the late 1960's, and they contended that the disappearance of kelp in St. Margaret's Bay was part of a much larger destructive pattern of sea urchin grazing along the entire Atlantic coast of Nova Scotia. Using growth rates and size distribution of sea urchins at several sites along the coast, they attempted to date the disappearance of kelp. They then placed these sites in a temporal progression, based on the disappearance of kelp, and found that kelp disappeared first along the eastern shore of Nova Scotia and more recently along the southwestern shore. Wharton and Mann (1981) also analyzed the records of lobster catches and showed that the decline in catches along the Atlantic coast of Nova Scotia followed the same temporal progression as the disapearance of kelp. They contended that healthy kelp beds are necessary for an abundance of lobsters for two reasons: (i) macroalgae shelter young lobsters from predators, and (ii) the high productivity of healthy kelp beds provides food for lobsters. In their model (Fig. 1), the initial decline in lobster abundance, due possibly to overfishing and environmental changes, is one of the causes of kelp-bed destruction, which in turn adversely affects lobster recruitment and contributes to further decline in lobster abundance.

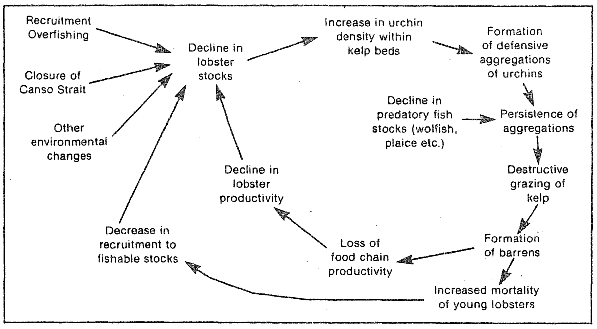

Fig. 1. Possible feedback relationships in the kelp-bed barrens ecosystem. (From Wharton and Mann, 1981.)

Relationship to the Physical Environment

The physical environment is an integral part of ecological systems, and changes in physical parameters can often initiate or influence biological changes. The association of changes in physical parameters (currents, temperature, etc.) with the documented ecological trends is presently unknown, but there are several ways in which the nearshore kelp ecosystem may be vulnerable to such oceanographic variations.

The reproductive cycles of all animals in the nearshore ecosystem are highly attuned to seasonal fluctuations in temperature, day length, and nutrients. Sea urchins begin spawning in the spring, and juvenile lobsters settle to the bottom during the summer. A change in the temperature regime could affect the viability or behavioral response of larvae and thereby affect settlement success. Currents also affect settlement success by controlling the distribution of larvae, which require particular habitats in order to complete their metamorphosis to adults. The distribution and activity patterns of animals (fish, crabs, starfish) which prey on juvenile sea urchins and lobsters are also influenced by the temperature regime. The survival of newly-settled sea urchins may also be in part controlled by predation from small crabs. Colder water would reduce the metabolism and activity of crabs, and reduced predation would increase the survival rate of sea urchins. Even seemingly small variation in settlement success and subsequent survival of the components of the ecosystem may have extensive long-term effects.

The growth rates of algae in the ecosystem are controlled by the seasonal cycle of nutrients. Several species exhibit sophisticated adaptations that enable them to store nutrients and thus continue growing during periods when the nutrient content of the water is very low (Kain, 1979; Gagne *et al.*, 1982). A change in the seasonal nutrient cycle or in the nearshore upwelling regime may decrease the growth rates of kelp and thus make them more susceptible to sea urchin grazing. Such changes may also lead to lower productivity in barren areas and consequently reduce the food supply of sea urchins, which continue to maintain the barren areas in their present state. A reduced food supply may reduce the viability of sea urchins and make them more susceptible to the type of disease which recently decimated sea urchin populations along the Atlantic coast of Nova Scotia (Robert Miller, Dept. of Fisheries and Oceans, Halifax, pers. comm.).

It is obvious, therefore, that changes in the nearshore ecosystem may be induced by variations in the physical environment. The actual understanding of the potential mechanisms which drive the system must await further understanding of the physical-biological interactions.

Implications for Fisheries Management

The extensive disappearance of kelp beds in Nova Scotian waters and the 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 speices, and, consequently, human impacts, such as overfishing, can influence the system in unexpected ways. This implies that only a multispecies approach to management, based on sound ecological understanding, will be effective. For example, a decision to limit the nearshore catches of fish which prey on sea urchins should only be made with a knowledge of the abundance of other sea urchin predators and with some indication of how near sea urchin density in kelp beds is to the critical threshold that will transform the system. Merely lessening man's impacts that induced the changes will not necessarily restore productivity. Overfishing of lobsters appears to have contributed to the increase in sea urchin abundance, but a reduction in fishing pressure on lobsters may not significantly increase lobster abundance if indeed the young depend on the protection provided by kelp beds for survival. Transformations in the state of an ecosystem are not necessarily reversible, because the different states are characterized by different ecological interactions. Effective management must be aware of and allow for these relationships.

The recent transformation of Nova Scotia's subtidal kelp beds to barren areas represents a tremendous loss of productivity, which alone results in the degradation of the coastal resources utilized by man. Also, ecological interactions in the barren areas may act to continue the degradation in the fishery for lobsters and other species, as man's impacts cascade through the system.

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