

Destruction of kelp-beds by sea-urchins: A cyclical phenomenon or irreversible degradation?

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ABSTRACT: A stable kelp bed ecosystem in St. Margaret's Bay, Nova Scotia (Canada), had as its main producers *Laminaria longicruris* and *L. digita*. Most algal production was exported as detritus, but there was a moderate population of herbivores, mainly the sea urchins *Strongylocentrotus droebachiensis*. These were eaten by crabs, *Cancer irroratus* and by lobsters, *Homarus americanus*. Lobsters also preyed on crabs. Beginning in 1968, sea urchins became locally abundant and overgrazed the kelp beds, converting large areas to urchin-dominated barren grounds. Almost all kelp beds in St. Margaret's Bay (140 km²) have now been destroyed. During the same period, lobster biomass decreased, and the hypothesis was put forward that reduction in lobster predation led to increased urchin abundance and kelp bed destruction. Evidence is presented for the hypothesis that urchin-dominated barren grounds are a new, stable configuration of the ecosystem, and that a long-term decrease in primary and secondary productivity of these coastal waters can be expected.

INTRODUCTION

This paper deals with a problem related to the management of a valuable resource, the American lobster *Homarus americanus*. Traditionally, approaches to such a problem have been based on the discipline of population dynamics. However, it happens that after approaching the question from the ecosystem point of view I had the remarkable experience of witnessing a major perturbation of the system. The questions that arise from that experience are at the interface between population dynamics and ecosystem theory. Ecologists in those two areas have tended to develop their thinking along radically different lines, and it is proving difficult to find common ground. I hope that this paper will help draw attention to the need to build bridges between the two lines of advance.

DESCRIPTION OF INITIAL STATE OF THE SYSTEM

The system, which will be called a kelp-bed ecosystem, was first studied in St. Margaret's Bay, Nova Scotia, but subsequent investigations have shown that the area is representative of many hundreds of km of eastern North American coastline.

The kelps *Laminaria longicruris* and *L. digitata*, extended from near low water mark to a depth of about 20 m, on all shores having a hard, rocky surface for attachment of holdfasts. They were very productive, having a biomass of about 16 kg fresh weight per m² and an annual production estimated at 1750 gCm⁻² in St. Margaret's Bay (Mann, 1972a, b).

Newly metamorphosed young lobsters live about 8–10 years in these beds before reaching catchable size. They feed as predators on a variety of invertebrates. Breen (1974) showed that when offered a choice between pairs of prey species in spacious cages on the sea floor lobsters exhibited preferences in the following order: (1) crabs, (2) sea urchins, (3) starfish, (4) periwinkles, (5) mussels.

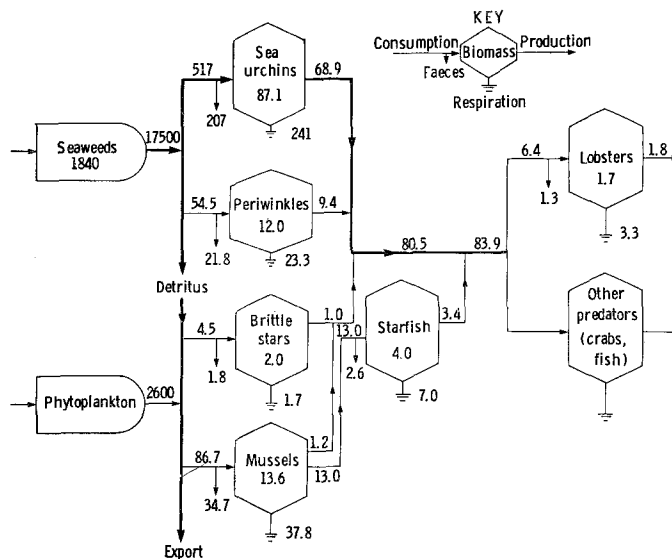


Fig. 1: Energy flow diagram for a kelp bed ecosystem in St. Margaret's Bay, Nova Scotia, as it was in 1968. Units are Kcal m⁻² per year, except biomass, which is Kcal m⁻². (From Miller et al., 1971)

The pathways of energy flow were charted by Miller et al. (1971) (Fig. 1). Most of the production of the kelp entered detritus pathways. The invertebrates consumed only a small proportion of it and a large amount was exported to nearby planktonic and benthic communities (Webster et al., 1975). The largest primary consumer was the sea urchin *Strongylocentrotus droebachiensis*. When a large number of quadrat samples was taken in 1968 the population averaged 37 animals per m² with a fresh weight of 150 g/m². It appeared that the sea urchin population was in equilibrium with the kelp. Wave-induced movement of the kelp prevented the urchins from climbing on the plants and devouring them. They remained for the most part on the rocks at the base and fed on fragments breaking off the plants. In a few places sea urchin biomass had built up to the point where they could climb on the plants, weigh them down, and hold them while devouring them completely. This led to "holes" in the

kelp canopy, a few tens of metres in diameter. In the 1968 survey, 6 such holes were found in the course of 26 transects. Miller & Mann (1973) developed an energy budget for the sea urchins at this time (Fig. 1). The results will be compared below with those obtained in the perturbed system.

PERTURBATION OF THE SYSTEM

The changes observed between 1968 and 1974 have been described by Breen & Mann (1976). The holes in the kelp canopy grew larger and larger until they coalesced, and in 6 years it was estimated that 70 % of the kelp along a 15 km length of shore was destroyed. It was achieved by "wavefronts" of large sea urchins, at densities up to 15 kg m^{-2} fresh weight, devouring the kelp and thus advancing into the bed at rates up to 1.7 m per month.

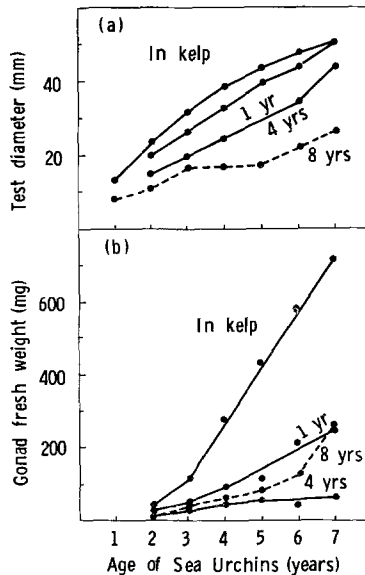


Fig. 2: (a) Change in test diameter with age, for sea urchins *Strongylocentrotus droebachiensis*, collected from healthy kelp-beds and from sites where kelp had been destroyed 1, 4 and 8 years earlier. (b) Mean gonad size in summer of urchins of different ages collected from the same locations as above. Solid lines from Lang & Mann (1976). Broken line from Wharton (unpublished manuscript)

It is difficult to reconcile this observation with Figure 1 in which it is shown that sea urchins consumed only a few percent of the production of the kelp in a healthy kelp bed, yet within a few years they had destroyed the beds. The explanation is that local concentrations of urchins, by destroying a whole kelp plant, not only consume the biomass of that plant but prevent it from completing its annual cycle of production. Since the ratio of production to biomass is high, a modest consumption of biomass can remove a large amount of potential production.

Our expectation was that once the kelp had been cleared from an area, sea urchins would starve to death or move away. Indeed, local fishermen provided anecdotal evidence of localized cycles of sea urchin abundance and such cycles were recorded as early as 1847 (Mortensen, 1943). However, we have found that the sea urchin populations have persisted over the 8 years since the destruction of kelp beds was first observed, and in the whole of St. Margaret's Bay (about 140 km^{-2}) we have not found evidence of natural kelp regeneration. Lang & Mann (1976) have shown that with each year after kelp disappearance the growth rate and gonad production of the urchins has declined, and this is supported by even more recent evidence of Wharton (unpublished) (Fig. 2a). In all but the most sheltered sites there is a refugium for marine algae close to low tide level, where the wave action prevents establishment of dense sea urchin populations. Sea urchins live nearby and feed on the fragments of algae washed into deeper water. Hence, there is a danger that the kelp refugia may provide enough food to maintain urchin populations indefinitely, and that the urchins, in their turn, will prevent regeneration of kelp by grazing down any newly germinated young plants. These urchin-dominated communities are known from other parts of the world and are referred to by Lawrence (1975) as "urchin-dominated barren grounds". The rock surface has coralline algae and encrusting diatoms, but apart from the urchins few invertebrates occur: the main components of the biomass appear to be mussels (*Modiolus demissus*, and *Mytilus edulis*) various brittle stars, with occasional starfishes.

SUGGESTED EXPLANATION

Our suggested explanation of these events (Mann & Breen, 1972; Breen & Mann, 1976a) is that the explosion of sea urchin populations was made possible by reduction of predation pressure. An obvious choice of key predator is the lobster. The best areas



Fig. 3: *Homarus americanus*. Annual catch per unit effort, as an index of lobster biomass in St. Margaret's Bay, Nova Scotia from 1959 onwards. Crosses indicate values based on estimated numbers of men fishing. (From Breen & Mann, 1976)

for lobster fishing on this coast are approximately those areas normally inhabited by kelp. Breen & Mann (1976b) showed that destruction of sea urchins led to regeneration of kelp beds, and that lobsters eat sea urchins in amounts which would enable them to hold sea urchin biomasses below critical levels for maintenance of healthy kelp beds. Moreover, the catch per unit effort and presumably the population density of lobsters in St. Margaret's Bay has declined by over 50 % in the last 15 years (Fig. 3). There are fishes which prey on sea urchins, but there is no evidence of a decline in abundance of these fishes during recent years. Destruction of the kelp beds leads to destruction of the habitat for young lobsters, and there appears to be a positive feedback leading to loss of productivity at both primary and secondary levels.

CYCLICAL PHENOMENON OR IRREVERSIBLE TREND?

It is of crucial importance to the future management of these coastal waters and the valuable lobster fishery to know whether the kelp system will return to something like its original state. In other words, we need to know whether the system is sufficiently stable to persist after the severe perturbation that we have witnessed. From the plethora of terms on ecosystem stability I have chosen to follow Margalef (1969) and distinguish *persistence stability* and *adjustment stability*. Persistence stability is the capacity of the system to persist in a recognizable state even when subject to internal perturbation or change in environmental parameters. The term is roughly synonymous with resilience of Holling (1973), and includes aspects of both persistence and inertia of Orians (1975). Adjustment stability is the relative ability of a disturbed system to return to some pre-disturbance state, and is roughly equivalent to stability in Holling (1973) and elasticity in Orians (1975).

Holling (1973) gave illuminating examples of the two kinds of property. Many lake systems have been found to exhibit high adjustment stability until subjected to an abnormal stress such as over-fishing or eutrophication. They then show wide amplitude fluctuations in their constituent populations until, rather abruptly, a point of no return is reached and the whole system changes character. This is an example of low persistence stability.

By contrast, temperate forest systems subject to recurring severe outbreaks of spruce budworm infestation have been shown to undergo, as a normal course of events, wide fluctuations in the numbers of trees and of budworms, but a remarkable ability to persist through time. Such a system has high persistence stability but low adjustment stability. Holling (1973) further suggested that low adjustment stability itself confers high persistence stability in situations in which large, random fluctuations of environmental conditions occur. As in human conflict, the ability to "roll with the punches" may confer an ability to survive!

May (1975) developed convergent ideas when he suggested that as a system becomes more complex, with more species and more interactions, it becomes "dynamically more fragile", whereas a relatively simple community will be "dynamically more robust". Since complex systems are often found in environments of low random fluctuation and simple systems in harsh environments with a high level of random

fluctuation, it appears that dynamic robustness may be the equivalent of high persistence stability with, perhaps, low adjustment stability, and vice versa.

How can we describe what happens when a system changes suddenly from one form to another, as in the rapid eutrophication of a lake? Figure 4, after Holling (1973) shows the derivation of a phase diagram to illustrate the relationship between two populations, which might be a predator and its prey. Phase diagrams may show unstable equilibrium (increasing oscillations leading to extinction of one species), stable

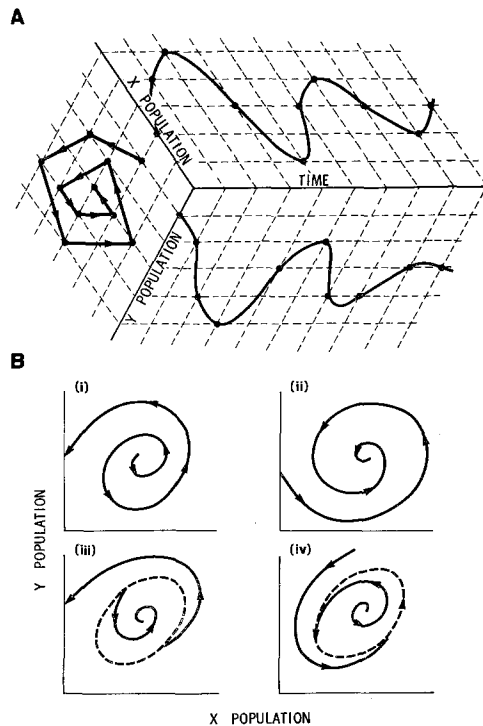


Fig. 4: *A* Derivation of a phase diagram showing the changes in numbers of two populations with time. *B* Four examples of possible behaviours of systems in a phase plane: (i) unstable equilibrium (ii) stable equilibrium (iii) domain of attraction, (iv) stable limit cycle. (Modified from Holling, 1973)

equilibrium (damped oscillations), stable limit cycles (on which trajectories tend to converge), or domains of attraction (regions within which stability occurs, but outside which the system is unstable). From work with simulation models (Holling & Ewing, 1971) it was concluded that many systems have stable domains of attraction, within which persistence stability is high, but when the system is pushed beyond its stable domain it becomes unstable and either goes to extinction or takes up a new domain of attraction.

The Great Lakes were cited by Holling (1973) to illustrate this phenomenon. Fish populations were heavily exploited over a prolonged period, and suddenly there was a precipitous drop in population density. "It is as if the population had been

shifted by fishing pressure from a domain with a high equilibrium to a domain with a lower one." – "The fishing activity, however, progressively reduced the resilience of the system so that when the inevitable unexpected event occurred, the populations collapsed."

We may now, in the light of these considerations, rephrase the question about the kelp-bed ecosystem in Eastern Canada. Has the fishing pressure on the lobster population progressively reduced the persistence stability of the system to the point where it has abruptly changed to a new stable domain, namely urchin-dominated barren-ground, or is the system one of high persistence stability and low adjustment stability which can be expected to swing slowly back to its original state?

To explore this question, each trophic level will be considered in turn.

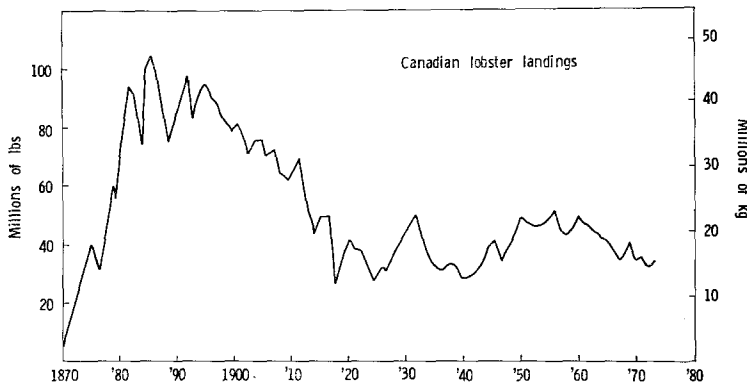


Fig. 5: Total Canadian catch of lobsters, plotted annually from 1870. (Data from Statistics Canada)

Factors influencing the abundance of lobsters

The history of the Canadian lobster fishery is summarized in Figure 5. Early writings indicate that when Europeans first arrived lobsters were much more abundant than at present. They could be caught even in the intertidal zone, and were not particularly prized as food. Beginning in the later part of the last century, a growing fishery passed through a period of very high catches, then settled down to a lower level of catch, and presumably of lobster biomass. In the last 50 years catches have fluctuated between 14 and 24 million kg (the market value after processing was \$ 64 million in 1973). Fishing pressure is very intense; in some places 90 % of a size class is caught in the year in which it reaches catchable size. The catch for 1971–1973 was below the long-term average, not only in St. Margaret's Bay but also along some 500 km of Nova Scotia coast extending north and east from St. Margaret's Bay, in Newfoundland and St. John's county, New Brunswick (Statistics Canada). These are all areas where extensive destruction of kelp has been noted (see below). Hence, there are grounds for noting parallels with the declining fisheries of the Great Lakes.

There is also evidence that environmental variables may have influenced lobster catches and probably also the densities of lobster populations. Dow (1969) showed

that high catches in the USA and in Canada were associated with above-average water temperatures. One possible explanation is that high temperatures are associated with high levels of lobster activity and hence high vulnerability to traps. The correlations noted by Sutcliffe (1973) can not be explained in this way. He showed (Fig. 6) that lobster catches in the Gulf of St. Lawrence were well correlated ($r = 0.831$, $p < .001$) with the runoff of the St. Lawrence River in April, 9 years earlier. Since the lobsters take about 9 years to grow from larvae to catchable size, he concluded that high river runoff was associated with good larval survival. A possible mechanism is that the river runoff in association with winds and tides produces upwelling of nutrient-rich water, hence good phytoplankton growth and abundant food for the larvae. Sutcliffe predicted that because the river runoff began to increase in 1964 there would be an increase in lobster landings after 1973. This prediction has been fulfilled (Fig. 6).

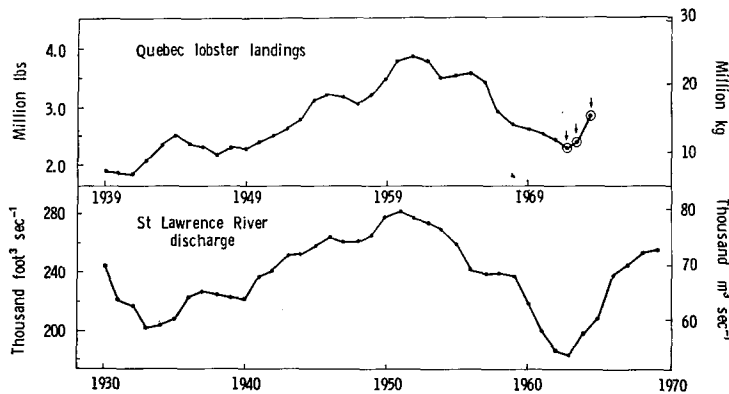


Fig. 6: Annual lobster catch for the Province of Quebec, and discharge of the St. Lawrence River during the month of April. Both are plotted as 3-year running means. The time scale of the catches is lagged 9 years behind the river discharge. Correlation coefficient $r = 0.831$. Data from Sutcliffe (1973) and Statistics Canada. Note the upward trend (marked with arrows) predicted by Sutcliffe and subsequently verified

In subsequent work, Sutcliffe et al. (1976) showed that the discharge of the St. Lawrence river affects oceanographic conditions and probably influences fish productivity along the whole Atlantic coast of Nova Scotia. Hence, environmental variables may have combined with fishing pressure to produce the declining lobster biomass observed at the time of the sea urchin population explosion.

Factors influencing the abundance of sea urchins

On land, cycles in the abundance of herbivores are well known. Caughley (in press) has discussed the occurrence of peaks of abundance followed by crashes and oscillations in numbers. As shown in Figure 4, such oscillations may take the form of a damped series, leading to stable equilibrium, stable limit cycles, or unstable, increasing oscillations which lead to extinction. From the literature he deduced that

damped oscillations were the most common, and argued that organisms responding in this way to perturbations of their relationship with their food supply would have a selective advantage.

In the sea, there are numerous records of sea urchins overgrazing their food supply (see Laurence, 1975, for review). Two questions remain unanswered: (1) What causes the sea urchin populations to become sufficiently abundant to graze their food supply close to extinction? (2) How do the urchins manage to persist for long periods after the algae have been almost completely devoured?

The most common and widely accepted explanation of urchin population explosions is decrease of predation. Release from predation by sea otters, *Enhydra lutris* has been shown to lead to high abundances of *Strongylocentrotus* spp. on the Pacific coast of North America, with consequent destruction of kelp beds (Leighton et al., 1966; Estes & Palmisano, 1974; Dayton, 1975). Predation by crabs, *Carcinus maenas*, has been shown to control the numbers of the urchin *Paracentrotus lividus* in Lough Ine, Ireland (Muntz et al., 1965). In our own study area sea urchins have many predators including several species of fish, starfish, and crabs. Crabs are also a preferred prey of lobsters (Evans, 1976; Mann & Breen, 1976) and Breen (1974) constructed a model to investigate the relative importance of lobsters, crabs and wolf-fish as predators of sea urchins. He concluded that lobsters alone could control sea urchin populations in about half of the conditions encountered in nature, and that crabs and lobsters combined could control sea urchin populations under almost all conditions occurring naturally. Note that the density of lobsters and crabs needed to keep a sea urchin population under control in a stable kelp ecosystem is much smaller than the number needed to reduce the population once it has expanded and begun to destroy a kelp bed.

The second question: how do sea urchins manage to persist after destruction of their main food source, has also been considered on the west coast of North America. One explanation is that drifting algal material may be carried from adjacent areas (such as the surf zone, where urchins cannot live in numbers) and provide a meagre diet for the animals on the barren-grounds (North, 1964). Others have suggested that allochthonous sources of particulate and dissolved organic matter, such as sewer outfalls, may serve to maintain persistent urchin populations in the absence of algal food (Pearse et al., 1970). Perhaps the most important factor is the ability of the urchins to survive with greatly reduced growth rates and gonad production (Fig. 2). We had expected a continuing and progressive decrease in gonad size with time, but at the site where kelp was destroyed 8 years ago the urchin gonads are somewhat larger than at the site where kelp disappeared 4 years ago. However, the 8-year site has a lower population density than the others. This may mean that more food per urchin is available.

Factors influencing the abundance of kelp

The life history of *Macrocystis pyrifera* in California is such that plants of 3 to 4 years of age tend to break off and drift away, while young plants germinate in areas

where there are breaks in the canopy of large plants (North, 1971; Rosenthal et al., 1974). This leads to cycles with a periodicity of about 4 years in the biomass of *Macrocystis* in a given area. In addition there are cycles in which areas are denuded by sea urchin grazing. North (1971) records that the cycle may be completed when urchin concentrations are reduced by starvation or migration, and massive algal development occurs. Such natural cycles may take up to 12 years. In other cases, kelp regeneration has been induced by killing the urchins with quicklime.

It is possible that we are witnessing a similar cycle in *Laminaria* abundance. However, this seems improbable when extensive areas of urchin-dominated barren grounds are reported simultaneously from Newfoundland (Himmelman, 1969; Himmelman & Steele, 1971) from the Fundy Shore of New Brunswick (Neish, 1973) and from our own samples over about 200 km of coastline in Nova Scotia. The evidence strongly suggests that in these areas the system has moved from a stable domain of attraction involving dense growths of kelp to another domain involving barren-grounds.

DISCUSSION

There is no doubt that widespread destruction of kelp ecosystems has occurred along the Atlantic coast of Canada, and that this implies a serious loss of productivity at primary and secondary levels. It also represents a deterioration of habitat for lobsters and other invertebrates, so that repercussions on the lobster fishery are inevitable. It will be noticed that the total Canadian catch (Fig. 5) is not as depressed as the catches in Halifax and Lunenburg counties, adjacent to St. Margaret's Bay (Fig. 7). This may be explained by the existence of two types of coastal system with characteristics different from the one we have studied.

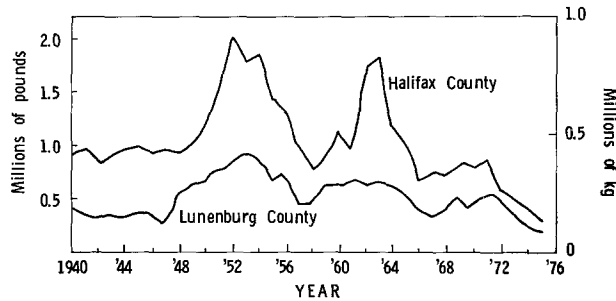


Fig. 7: Annual catches of lobsters in Halifax county and Lunenburg county, Nova Scotia, from 1940. (Data from Statistics Canada)

At the southwestern end of Nova Scotia there is a major area of upwelling of deep, nutrient-rich water (Lauzier, 1967). This is associated with vigorous, healthy kelp beds and extremely large catches of lobsters. The three counties adjacent to this upwelling together account for about 30% of the total Canadian catch (Statistics Canada). There is, as yet, no evidence that major kelp bed destruction has occurred in this area.

Secondly there are, in the Gulf of St. Lawrence, large lobster fishing areas which have a predominantly soft bottom and in which the ecosystem characteristics appear to be quite different from the rocky areas of the Atlantic coast. Many of these areas still have high catches of lobsters. Nevertheless, the fate of the kelp ecosystem in St. Margaret's Bay should serve to remind fishery managers that while the coastal zone is capable of sustaining high productivity over long periods it is not infinitely resistant to human exploitation.

There are two hypotheses which are not fully substantiated, although both seem likely to be true. These are (1) that the basic cause of kelp bed destruction is removal of lobsters from the system and (2) that urchin-dominated barren grounds represent a stable system rather than a short interlude between two peaks of kelp biomass. The model constructed by Breen (1974) and reported briefly by Breen & Mann (1976a) provides support for the hypothesis that lobsters are the key predators. Recent work by Evans (1976) has shown that lobsters have a higher dietary preference for crabs than Breen had realized. The effect of this change would be to increase the importance of crabs in the ecosystem dynamics. Perhaps in the end, the strongest argument is that lobsters were the only urchin predators that were being intensively exploited by man. In a system managed for maximum productivity the biomass of lobsters would be monitored and fishing would be stopped before the lobster biomass reached a critically low level.

The question of whether sea urchin dominated barren grounds constitute a stable system will be settled only after more years of observation. However, the evidence for oscillations in kelp abundance leading to a more severe and prolonged depletion than ever before is recurrent in the accounts given by lobster fishermen. In the only part of the system for which we have long-term data, namely the lobster populations, the occurrences of large amplitude fluctuations followed by a steady decline (Fig. 7) is in accordance with expectations.

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