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PROCEEDINGS OF THE WORKSHOP ON THE RELATIONSHIP BETWEEN SEA URCHIN GRAZING AND COMMERCIAL PLANT/ANIMAL HARVESTING

July, 1980

By

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ABSTRACT

Pringle, J.D., G.J. Sharp, and J.F. Caddy (Ed.). 1980. Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can. Tech. Rept., Fish. Aquat. Sci. 954.

Workers in eastern Nova Scotia hypothesized that: 1) lobsters are the keystone predator of kelp bed ecosystems; 2) lobster populations have declined due to poor management; 3) this has permitted urchin populations to explode, causing destructive grazing of macroalgae; and 4) the resultant barren system is permanent. A workshop, sponsored by Fisheries Management, discussed these hypotheses in light of presented papers and recommended remedial action. It was concluded that kelp bed destruction in St. Margaret's Bay, Nova Scotia, was due to urchins; but the triggering process was unclear. Allochthonous sources, kelp disease, and release from predation were discussed. Lack of historical data east and west of St. Margaret's Bay and evidence the south and west coasts of Newfoundland have not had *Laminaria* beds for possibly centuries made it difficult to assess the cause of the urchin problem along Atlantic Nova Scotia and the Bay of fundy. Evidence was presented suggesting the urchin population increases off coastal, southern California was due to the overharvesting of at least three commercial carnivores (spiny lobster, California sheephead, and the sea otter) and one herbivore (abalone). Many natural predators of urchins were cited for the northwest Atlantic, some being of commercial importance (lobsters, cod, haddock, flounder, wolffish, etc.) while others (crab, ducks, etc.) have had population decreases due to man's activities. It appears, then, that the trophic pyramid has been simplified with the possible consequence that significant annual changes in carnivore densities permit the system to oscillate wildly. It was felt premature to claim the kelp bed ecosystem of St. Margaret's Bay had been permanently lost; however, it was recommended that a multispecies/ecosystem approach be employed in fisheries resource management.

Key Words: Lobster, sea urchin, kelp, crab, predator, prey, macroalgae, multispecies resource management, lobster fishing, marine plant harvesting, barren grounds, herbivore, carnivore.

RÉSUMÉ

Pringle, J.D., G.J. Sharp, and J.F. Caddy (Ed.). 1980. Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can. Tech. Rept., Fish. Aquat. Sci. 954.

Les chercheurs de la Nouvelle-Écosse one émis les hypothèses que 1) le homard est le prédateur dominant des écosystèmes de lits de varechs; 2) les populations de homards ont diminué par suite d'une mauvaise gestion; 3) ceci a entraîné une explosion des populations d'oursins de mer et, par voie de conséquence, un broutage destructeur des macroalgues; et 4) le système dénudé que en est résulté est permanent. Un atelier de travail, patronné par les gestionnaires de pêches, a examiné ces hypothèses à la lumière des communications présentées et recommandé une action en vue de rémédier à cet état de choses. On en est venu à la conclusion que la destruction de lits de varechs de la baie St. Margaret, en Nouvelle-Écosse, était l'oeuvre des oursins de mer; par contre, le mécanisme de déclenchement n'est pas clair. On a examiné tour à tour les sources allochthones, la maladie du varech et le dégagement de la prédation. Le manque de données historiques à l'est et à l'ouest de la baie St. Margaret et l'absence, depuis peut-être des siècles, de lits de Laminaria sure les côtes méridionale et occidentale de Terre-Neuve font qu'il est difficile d'évaleur l'ampleur de problème de l'oursin de mer le long de la côte atlantique de la Nouvelle-Écosse et dans la baie de Fundy. Des données furent présentées suggérant que les augmentations de populations d'oursins le long des côtes de la Californie méridionale résultent de la prédation excessive par au moins trois carnivores d'importance commerciale (langouste, labre de Californie et loutre de mer) et un herbivore (ormeau). La présence de plusieurs prédateurs naturels de l'oursin de mer en Atlantique nord-ouest fut mentionnée, certains ayant une importance commerciale (homard, morue, aiglefin, plies, loups, etc.). Par ailleurs, d'autres espèces (crabes, canards, etc.) ont vu leurs populations dimineur par suite des activités de l'homme. Il semble donc que la pyramide alimentaire ait été simplifiée et qu'une conséquence possible en ait été d'imporants changements annuels de densité des carnivores, avec, comme résultat, un système qui oscille de façon désordonnée. On est d'opinion qu'il est trop tôt pour sontenir que l'écosystème de la baie St. Margaret est à jamais détruit; cependant, on recommande d'utiliser une approche multiespèces/écosysteme à la gestion des ressources halieutiques.

INTRODUCTION TO THE WORKSHOP THEME

By

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A study was initiated in St. Margaret's Bay, Nova Scotia, to assess the trophic relationships in the food chain leading to lobsters. "The dominant algae are the kelps...and in these forests are found large numbers of herbivorous sea urchins... which in turn are preyed upon by...the lobster Homarus americanus." (Mann, 1972a). Studies on lobster ecology, with the view to resource management, are not new; but Mann felt that the ecosystem approach might be more profitable; "...we now know that you can get only so far by studying the interactions of a single species with its environment" (Mann, 1972c).

His study was begun in 1968 with the assessment of the benthic algal biomass of the Bay (Mann, 1972a). At this time, the diversity appeared normal; "At any given point on a transect several species of macrophytes could be found within a radius of 1 m"; but, "...over a considerable depth range, one species, or at most two, made up the greatest part of the biomass." The latter species belonged to the genus Laminaria. The annual primary productivity contributed to the Bay by the seaweeds was 608 g c/m^2 (Mann, 1972b); the phytoplankton contributed 190 g c/m^2 (Platt, 1971).

The major herbivore found in this community was the sea urchin Strongylocentrotus droebachiensis Muller. Miller et al. (1971) claimed that "...the production of seaweeds (17 000 kcal/m^2/yr) far exceeds the ingestion by herbivores (663 kcal/m^2/yr)..." and "...it appears that food production greatly exceeds that needed to support the lobster population." However, at the time this information was published destructive grazing of the kelp by urchins must have begun. Mann and Breen (1972) had the foresight to speculate "...that heavy exploitation of lobsters may lead to the overgrazing of seaweed by urchins..." Breen in 1979 noted, "We published support for this hypothesis...and my thesis project (Breen, 1974) was to test it." Breen had resurveyed six of Mann's (1972a) transects and noted a 53% reduction in size of the kelp beds. By 1979 the beds had been reduced to 1% of its former size (A.R.O. Chapman, pers. comm.).

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Thus between 1968 and 1977 Mann had witnessed, in St. Margaret's Bay, a marked change in what appeared to be a stable ecosystem. The urchins had appeared to be in equilibrium with the macrophytes but apparently were not (Mann, 1977). The system went from one which had supported a luxuriant algal cover to urchin-dominated barren grounds (Mann, op. cit.).

Mann and Breen (1972) suggested that the lobster was the "keystone" species in the system and the major predator of the urchin. They suggested that the lobster, being an important commercial species, had been reduced to numbers insufficient to control urchin densities. This release from predation has allowed the urchins to overgraze the benthic algae (Mann and Breen, 1972). They go on to argue that this is likely a stable domain and not cyclic in spite of local anecdotes to the contrary and comparable observations elsewhere. Similar studies in California have demonstrated cyclicity between urchin densities and kelp biomass. Mann and Breen (1972) conclude, "It is possible we are witnessing a similar cycle in Laminaria abundance (similar to California). However, this seems improbable when extensive areas of urchin-dominated barren grounds are reported simultaneously from Newfoundland... from the Fundy shore...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 (sic) involving dense growths of kelp to another domain involving barren grounds." Evans and Mann (1977) go on to claim that "Sea urchins have destroyed kelp beds along many hundreds of miles of Canadian Atlantic coastline and in the same areas lobster stocks have declined." Wharton (1980; pers. comm.), in recent investigations, claims that both the eastern and southern shores of Nova Scotia's Atlantic coast have little benthic algal cover and that if there is a positive correlation between kelp beds and lobster abundance then, due to the presence of urchin-dominated barren grounds off eastern Shelburne Co. (Figure 1), the lobster catches are bound to decrease.

Most commercial fisheries in Canada are afflicted with large oscillations in annual landings. "The reasons for the fluctuations are many, and fisheries science has not been particularly successful either in isolating the critical factor or factors or finding ways of predicting future events..." (Ketchen, 1972). We are only now moving from a single species concept of resource management to a mutlispecies approach which will hopefully include "whole ecological units - units consisting of a number of species, including those which constitute several links in the food chain..." (Ketchen, op. cit.). Mann (1977) was more explicit when he felt resource managers should marry ecosystem theory

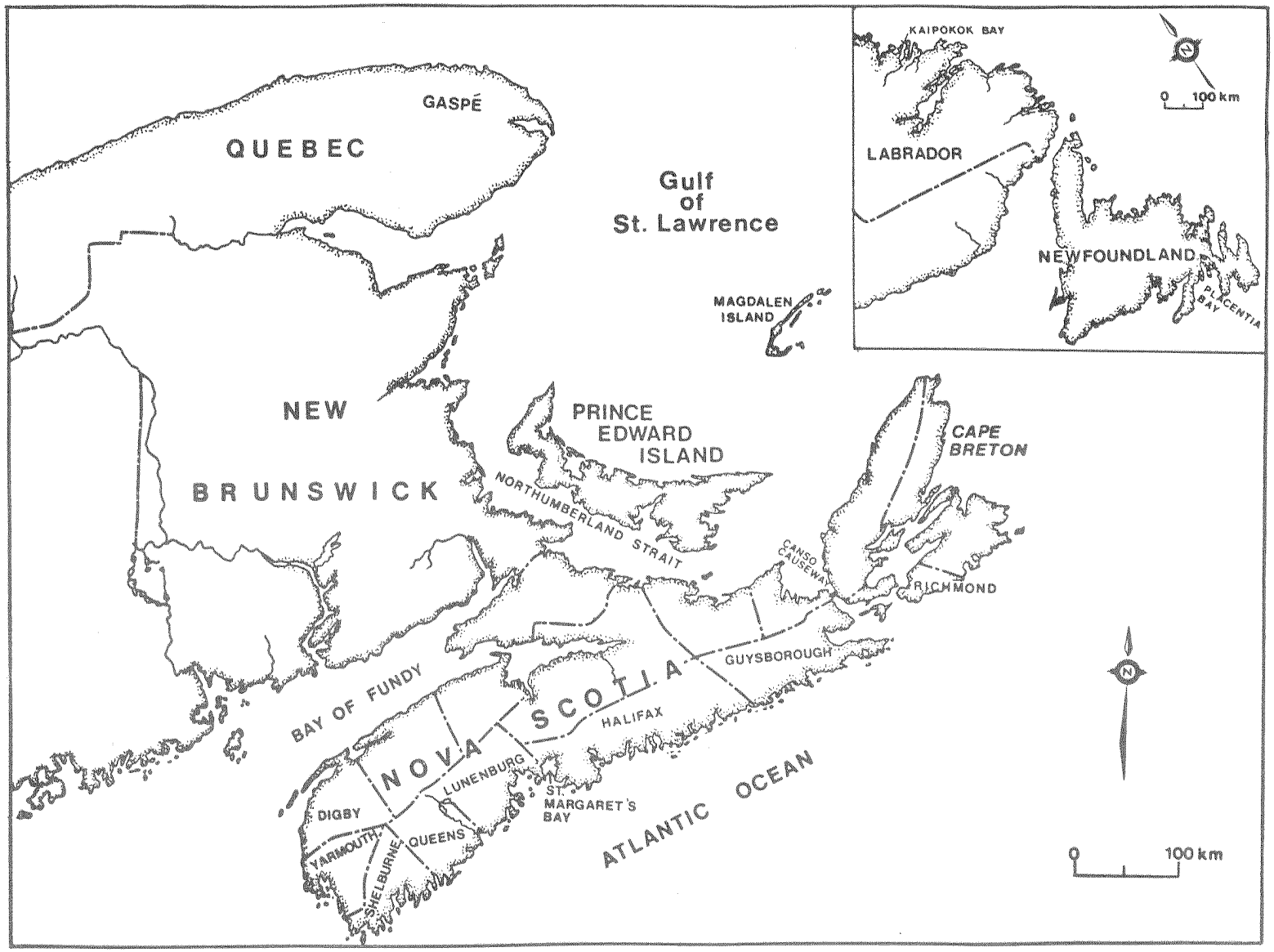

Figure 1. Atlantic Canada, showing selected counties of Nova Scotia.

and population dynamics: "Ecologists in those two areas have tended to develop their thinking along radically different lines." He suggested (Mann, 1977) that if this had been done there may yet have been a healthy kelp bed in St. Margaret's Bay; "...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 resistent to human exploitation."

The coastal waters off the counties of Shelburne and Yarmouth produce 30% of the lobsters in the Maritimes. Many other commercial species are also landed in large annual quantities including 20 000 MT of benthic algae (mainly Chondrus and Ascophyllum) (Pringle, 1980). The development of barren grounds could have a devastating effect on the total fishery through direct reduction in the plant resource, through change in habitat, and through reducing the primary production base of the food chain.

Consequently, fisheries management personnel sponsored a workshop in March, 1979, principally to assess Mann's hypothesis: "...the explosion of sea urchin populations was made possible by reduction of predation pressure. An obvious choice of key predator is the lobster." (Mann, 1977).

Approximately sixty delegates (see Appendix 1) attended the two-day session. Eighteen background papers were presented (see Appendix II) throughout three individual sessions. The fourth session consisted of a structured, round-table, taped discussion of topics relevant to the "Mann Hypothesis." The chairman, Dr. J. Caddy, presented "statements" (see Appendix III) pertinent to the central theme, and discussion followed each statement. The chairman then tabled conclusions based on each discussion session. They were debated and modified to satisfy the majority in attendance. The taped session was transposed to type. This, along with the fourteen submitted papers, was re-examined by the editors and a review paper prepared. A summary of the latter, with conclusions and recommendations, was submitted to CAFSAC [Canadian Atlantic Fisheries Scientific Advisory Committee (Appendix IV)] for fisheries management considerations.

It should be noted that four papers presented at the workshop are not published in this proceedings. Dr. Foreman's paper was published prior to the meeting (Foreman, 1977), Dr. McPeak, due to time restraints, was able to sumbit only one of two papers presented, and Drs. Bernstein and Vadas did not submit their papers.

A review paper of the workshop was written by the editors. The submitted papers and taped discussions were used as reference material. The above introduction forms a portion of this paper. The remainder of the latter is presented as the final chapter of this proceedings.

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WELCOMING ADDRESS

Dr. B.S. Muir*
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The Resource Branch of the Department of Fisheries and Oceans is pleased to welcome you to this workshop. As the head of the Resource Branch, I will familiarize you with the make up of the Fisheries Management group. This group consists of a Field Services Branch, made up of two divisions: Conservation and Protection, and Inspection. Both provide surveillance and enforcement of regulations. Our Branch, the Resource Branch, is the "biological arm" of Fisheries Management. In the Resource Branch we have three biological divisions based upon general species groupings, including the Invertebrates and Marine Plants Division which organized this workshop. A fourth division, Fisheries and Environmental Sciences, provides biochemical and population genetics research.

The Resource Branch formed CAFSAC (Canadian Atlantic Fisheries Scientific Advisory Committee) which fills the void left by ICNAF. This group provides scientific advice to both the Director General of Fisheries Management and industry on each commercial resource. The results of this workshop will be presented to this group for evaluation of management recommendations.

The Resource Branch has, in the past, only considered each species as a management unit. More recently, the need for a multispecies approach was identified; this workshop is a step in that direction. The purpose of the latter is to provide a sound basis for further research and development of management options with regard to interactions of commercial animals and plants.

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HISTORY OF THE LOBSTER FISHERY ON THE EASTERN SHORE OF NOVA SCOTIA

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INTRODUCTION

In recent years, attention has been drawn to those lobster-producing areas of the Canadian Maritime provinces which have experienced severe declines in landings. In particular, these included the central portion of Northumberland Strait in the southern Gulf of St. Lawrence, and the southeastern coast of Nova Scotia centered around Chedabucto Bay.

A multidisciplinary study was initiated in Northumberland Strait in 1975 (Caddy et al., 1977; Stasko et al., 1977) which failed to identify any environment-related event of sufficient magnitude to explain the decline, whereas fishery-related events were such as to suggest the possibility of recruitment overfishing (Robinson, 1976). Subsequent investigations have focused upon this latter hypothesis (Robinson, 1977; 1979).

In the meantime, public requests for an inquiry into events in the Chedabucto Bay area subsequent to the construction of the Canso Causeway in 1954 led to the Canso Marine Environment Workshop. The first session was held in November, 1977, and further sessions to focus on selected topics were held during 1978. No environmental event was identified sufficient to explain the scope and magnitude of the decline in lobster landings. Two hypotheses presented to explain the recruitment failure which had occurred are discussed later.

Investigations and analysis of data from eastern Maritime lobster populations initiated in 1976 quickly revealed that they were being grossly "growth overfished". Central to this conclusion was the observation that the size limit in the current fisheries was at or around the size of first female maturity. The fishery was highly intensive, with rates of removal as high or higher than any other known fishery. Every analysis indicated the biological desirability of substantial increases in the minimum legal size, or drastic (in human terms) reductions in fishing

effort (Robinson, 1977). Coincidentally, the same general conclusions were independently being reached by American, Newfoundland, and European investigators (Morrisey, 1976; Ennis, 1978; Anonymous, 1977). The Maritime inshore lobster fishery is regarded as a largely juvenile fishery, with every potential for recruitment overfishing.

One of the analytical techniques of a fishery population ecologist is an estimation of the conditions which lend themselves to MSY (maximum sustainable yield). A classical technique is to plot time-series of catch and effort. An attempt to do this, combined with literature reviews, led to the conclusion that, on the whole, this was a futile endeavor. Over-exploitation on the part of the fishery appeared to predate the scientific literature and to have a significant effect on the interpretation of production studies conducted over the last half century.

Within the concept of the "theory of ecological limits," if the lobster fishery is seen as a highly effective predator whose impact upon the prey species plays a significant role in limiting production, and if this role is suspected to have been operative for most of the history of the fishery, then an investigation into that history may shed some perspective on recent events in the fishery.

The following is a brief review of that history, with special reference to the southeastern coast of Nova Scotia. In many instances, references are made on the basis of the perspectives of current population dynamics studies. To facilitate discussion, Maritimes counties and lobster districts are illustrated in Figure 1.

HISTORY OF THE FISHERY

The origins of the Canadian lobster fishery can be traced to 1851, when five small canneries were operating in western Nova Scotia (White, F.M. in Wakeham, 1909; p. 440). Modern fishery development commenced in 1869, when the first large cannery was constructed in the same area by American entrepreneurs seeking new sources of supply in light of declining catches in the U.S. fishery. In that year 61,100 1-lb cans were preserved (Prince, 1899). Subsequent growth of the industry was rapid. By 1873, 67 canneries (Table 1) recorded 4,865,000 1-lb cans preserved. Of the Nova Scotia canneries, 40 (93%) were located along the southeast coast from Shelburne County to Cape Breton County inclusive. The first live shipment of 543 tons was recorded in 1881; as well, 17,491,000 1-lb cans were preserved. The development of the live trade was controlled by the proximity of the fishery to the Boston market.

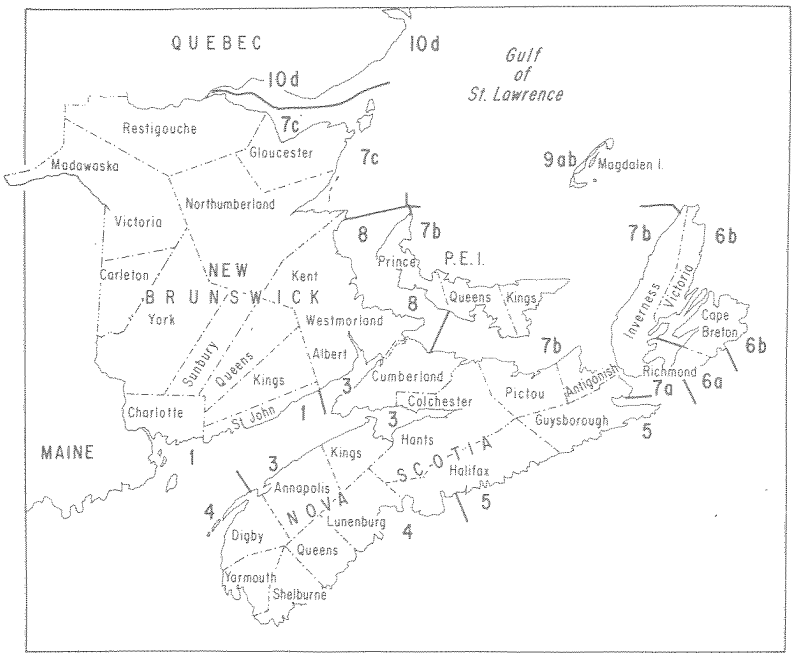


Figure 1. Canadian Maritime Provinces lobster districts as of 1977.

TABLE 1. Numbers of Maritimes canneries.

Year	N.S.	N.B.	P.E.I.	Total
1873	43	24	-	67
1890	133	100+	98	331+
1892	182	185	212	579
1900	277	237	246	760
1910	214	185	187	586
1925	139	144	148	431
1939	-	-	-	191
1944	39	49	49	137
1978	2	11	10	23

By 1890 there were more than 331 canneries in the Maritimes; 24 were in Nova Scotia west of Halifax County and 74 were in mainland Nova Scotia from Halifax County east (Anonymous, 1890). In that year, about one-third of the western Nova Scotia catch was sold alive in the United States (Inspector Kinney, in above), whereas in eastern Nova Scotia "a very small trade (in live exports) due from west division of Halifax County; none from other divisions" (Inspector Hockin, in above).

Material production peaked in the mid 1880's, but a number of events led to further industry development during the 1890's. American fishery production continued to decline; but demand increased, causing the landed price in Canada to increase tenfold from "1 or 2 cents" per lobster to "10 or 20 cents" (Prince, 1899). In just one year "a case (48 lbs) of canned lobster which sold in 1897 for $4 or $5 can now readily be sold for $8 or $9, or even more". The demand for canned Canadian lobster was further spurred by the 1897 closing of canneries in Maine, resulting from a decision to restrict the fishery in that state to lobsters large enough for the live market trade. The number of canneries more than doubled during this decade to 760 in 1900, the year of the greatest number ever in all provinces (Table 1). Improved rail facilities rendered live shipments from the eastern shore (east of Halifax) more feasible so that by 1900 about 20% of the catch was exported alive. The price jump of 1898 was also a key factor.

The basic character of the industry remained unchanged for the next three decades. As late as 1925 about 44% of the catch from southwestern Nova Scotia was being canned (Found, 1927) which probably did not change until the "application" of market size limits throughout western Nova Scotia (west of Halifax) in 1933 (Sutherland, 1937). In 1925, about 70% of the catch from the eastern shore was canned. Unfortunately, this was the last year for which such resolution of the catch is possible.

A shift occurred, spurred by declining prices for canned lobster meat during the 1920's (chiefly a function of competition on the European market from canned Japanese crab meat - 80% of pre-World War II cannery production was sold overseas) and increasing demand for live lobsters, which in part reflected declining catches everywhere. A subsidized collection service by vessel was inaugurated in 1930 along the eastern shore (including Richmond County) to facilitate live shipments, handling about one and one-half million pounds of lobster in 1934.

In 1940 a small section of the Richmond County coast (Lobster District 6A) was identified as observing a "market"

size limit. This district was expanded to its present boundaries in 1947; District 7A was also formed (as distinct from 7B) as a "market" fishery. In the latter 1950's fishermen in Districts 5 and 6B started to phase out the "cannery" portion of their fisheries. This process was completed in District 5 with the attainment of a market size limit in 1961, but was halted part way in District 6B after 1957. Thus, only the 6B portion of the southeast coast is today fishing at less than a market size.

Whereas the character of the Nova Scotia lobster industry was established by the turn of the century, the fishery itself continued developing. The introduction of gasoline engines into the fishery, and decreasing catches inshore led western Nova Scotia fishermen to tend to "relinquish the inshore and harbour fishing and carry on lobstering in deeper water...to 20 or 30 fathoms" (Prince, 1899). One power-driven boat would tow a number of others out to the grounds and back again at the end of the day. Southwestern Nova Scotia fishermen appear to have consistently led in fishery development, for in 1916 it was observed that "around the shores of the counties of Shelburne and Yarmouth...they go out some 18 or 20 miles off the coast of the mainland. This has necessitated the best equipment of motor boats and fishing gear, and there was nothing to be seen elsewhere to match their mechanically worked trap-hoists, the general efficiency of their boats, or their methods of fishing" (Halkett, 1916). By contrast, fishermen interviewed by the author stated that trap-haulers were not generally introduced into the Guysborough County fishery until after World War II.

Two other significant developments were the introduction of the parlour trap early in the century and the echo sounder in the post-war era. Superficially, the fishery appears unchanged (men go out in boats and catch lobsters in traps); in fact, the fisherman of today is a far more efficient predator of lobsters than any of his predessors. The interaction of the demands of the industry and the capability of the men in the fishery would appear to have had an impact on the capability of the ecosystem to produce raw material - the lobster itself.

TRENDS IN RESOURCE PRODUCTION

The fishery of 1873 landed about 25 million lb of lobster (Figure 2). This value, and others in whole or in part for the next 60 years, is derived from estimates of meat extraction efficiencies of 17-22% (Wakeham, 1909; Venning,

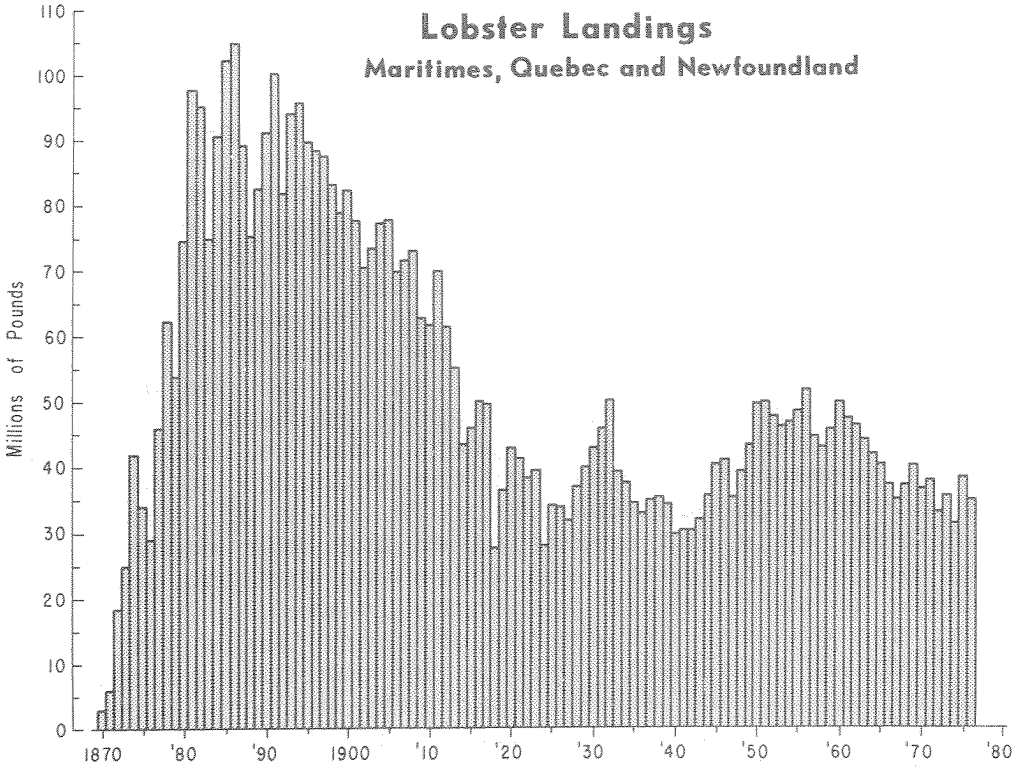


Figure 2. Canadian lobster landings, 1870-1977.

1910) assuming a mean value of 20%. Average weight of lobsters in the catch in the developing areas was given as 1-1/2 to 3 lb (eg. S.E. Nova Scotia, S.E. New Brunswick; [Venning, op. cit.]), whereas areas with little development yielded average weights of 4 to 5 lb (eg. Pictou and Antigonish Counties). It appears that the 1873 landings consisted of approximately 10 million lobsters.

The fishery appears to have become fully developed during the 1890's. By 1890 the average weight in the canner fisheries was about 1 lb per lobster, whereas market lobsters were about 1.25 lb (Anonymous, 1890). This suggests that the Canadian catch of just over 90 million lb comprised almost an equivalent number of lobsters. It also suggests that the fishery was no longer based upon a standing stock of old lobsters. By 1898, even with a catch of about 82 million lb, it was observed (Prince, 1899, p. 8) that "the signs of exhaustion are unmistakable. Small immature lobsters, 5 to 8 or 9 inches long (0.2-1.0 lb), which a few years ago were rejected with contempt, are now eagerly taken and form in some districts the staple article upon which the lobster canners depend. Instead of two or three lobsters sufficing to fill a 1-lb can, not less than five, six, seven, and even ten lobsters are now required". At 20% extraction efficiency, average canner weight would range from 0.5-1.0 lb. This suggests that the decline in landings to this date reflected a decreased average weight of lobsters rather than a decrease in numbers landed.

Landings are resolvable by county since the early 1890's, and these have been summarized in Figure 3. For the lobster fishery of 1898, clearly the worst was yet to be. The fishery of the eastern coast was to decline from about 13 million to less than 4 million lb landed per year in the early 1920's. The western Maritimes, for which the main area of production has always been the western Shore of Nova Scotia, declined from about 20 million to about 5 million lb landed per year in the mid 1930's.

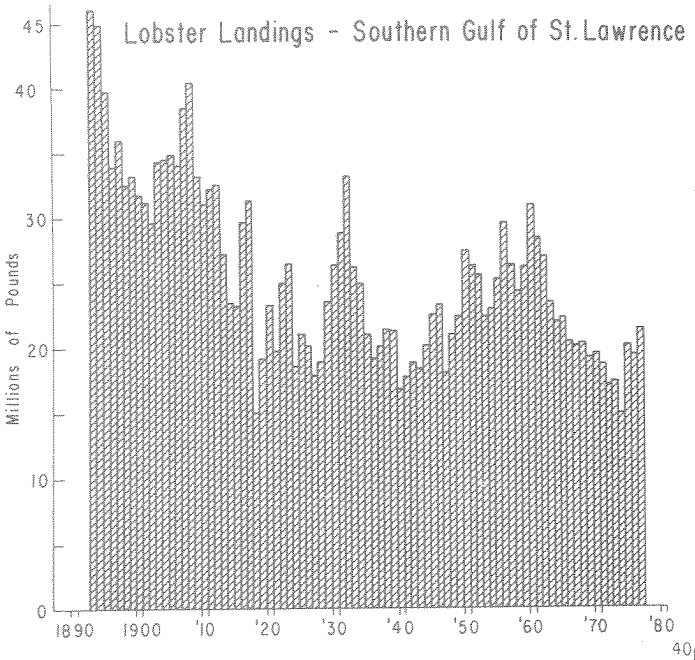
By 1898, many references clearly indicate that there were few lobsters being caught which had weights greater than 1-3 lb, the size acceptable for the live market trade. It was acknowledged by Professor Prince that the strict enforcement of the then universal 9 inch T.L. (ca. 1 lb) legal minimum size limit would put the canneries out of business, as much of their raw material was from lobsters of less than this size. In recognition of this, an 8 inch T.L. minimum size limit was instituted for the "canning" divisions east of Halifax, but the 9 inch T.L. limit was retained west of Halifax "in which waters the live lobster industry has attained some importance".

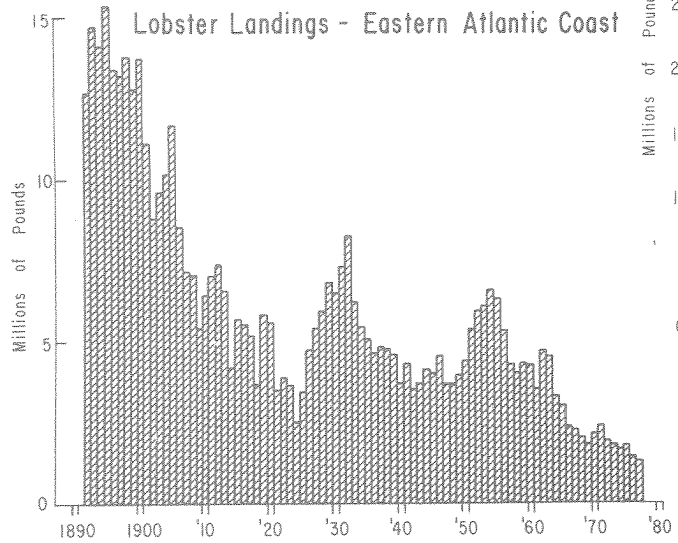
Figure 3. Lobster landings in the three fishery areas of the Maritimes:

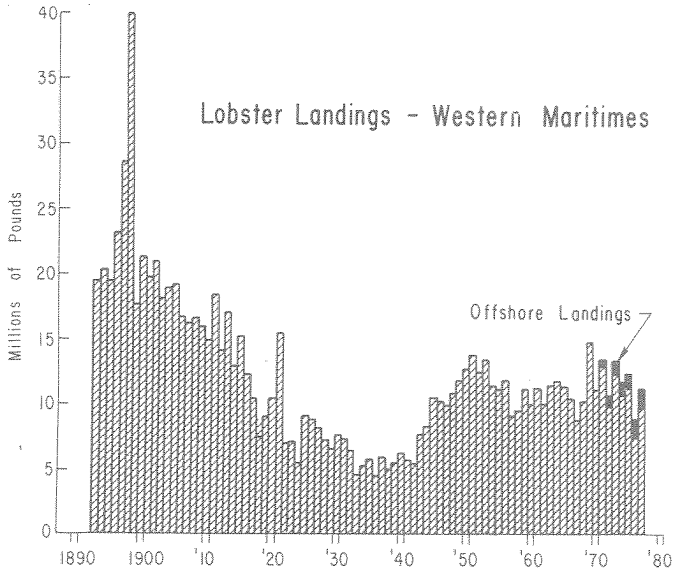
3a: Canner fisheries of the southern Gulf of St. Lawrence regime, including Magdalen Is. and Victoria Co., N.S.

3b: Landings of the eastern Atlantic coast of Nova Scotia. Originally cannery fisheries (to 1940); are now market fisheries almost exclusively (since 1961). Includes Cape Breton, Richmond, Guysborough and Halifax Counties.

3c: Market fisheries (since 1933) of the western Maritimes. Includes areas west of Halifax Co., N.S., and the waters of the Bay of Fundy including southern New Brunswick.







There was not, however, any concerted attempt to enforce the new limits. The canneries required raw material, and the capability of the fishery to exploit the stocks continued to increase. Landings for the next decade can be seen to have held up in the southern Gulf but to be declining in other areas. In 1909, the newly formed select committee on Marine and Fisheries appointed "Commander William Wakeham, officer in charge of the Gulf Fisheries Division, commissioner to investigate the lobster fishery in Quebec and the Maritime Provinces". The 1,227 pages of evidence taken in sworn testimony by this commission (Wakeham, 1909) afford an intimate view of the fishery at that time. The one clear picture which emerges with respect to the resource was that catches were being sustained by much increased effort landing much smaller lobsters.

It was noted (page 1,218) "we have found them taking them so small that it required 14 to fill a pound tin" (average live weight about one-third of a pound). This is supported by data submitted to the commission which document the size-frequency distribution of the P.E.I. catch of 1909 (Table 2) and indicate 80% of the catch to be less than 8 inches T.L. Perhaps this was an extreme, as measurements at Forchu, Richmond County (Figure 4, data from Halkett, 1910) indicate a larger size range. This latter area may be at the opposite extreme, as "around the southeast coast of Cape Breton and along the shores of Gaspe...the average size, it is claimed, still continues fairly large" (Prince, 1899). Fishermen along the southeastern shore of Nova Scotia testified that about 50% of the catch was from below the 8 inch T.L. legal size limit. The suggestion is that the two sets of size-frequency data represent opposite extremes, with the rest of the Maritimes somewhere in between.

The special report on the lobster industry by Superintendent R.N. Venning (1910) submitted to the above select committee, besides containing an excellent review of fisheries regulations to that date, contains many of the same observations, but arrived at an amazing conclusion - that the size limit be abandoned altogether!

This conclusion was based on a number of "facts", some of which by now have a familiar ring to them. The "market" fisheries were well developed, especially in western Nova Scotia. The canneries thus depended upon lobsters of less than this size (9 inch T.L. or 1 lb) for their raw material. The closed seasons and "berried" female laws were fairly well observed, whereas the size limit was not, nor was it considered enforceable. A closed season in the summer was thought to protect the female during the "spawning season" - a concept we now know to be meaningless with respect to

TABLE 2. Summarized length-frequencies of lobsters landed at eight Prince Edward Island canneries owned by Portland Packing Co., May 14-July 10, 1909. (Data from W.F. Tidmarsh *in* Wakeham, 1909.)

Equivalent carapace length (mm) ♂	♀	Size group total length (inches)	Frequency	%	Σ%
< 42.9	42.8	Under 5	467	2.8	2.8
42.9	42.8	5 - 5½	1016	6.1	9.0
47.6	47.2	5½ - 6	2368	14.3	23.3
52.4	51.7	6 - 6½	2522	15.2	38.5
57.1	56.1	6½ - 7	3366	20.3	58.9
61.9	60.5	7 - 7½	1695	10.2	69.1
66.6	64.9	7½ - 8	1765	10.7	79.8
71.4	69.3	8 - 8½	1602	9.7	89.5
76.1	73.8	8½ - 9	718	4.3	93.8
80.9	78.2	9 - 9½	402	2.4	96.3
85.6	82.6	9½ - 10	335	2.0	98.3
> 90.3	87.0	Over 10	285	1.7	100.0
			16541	100.0	

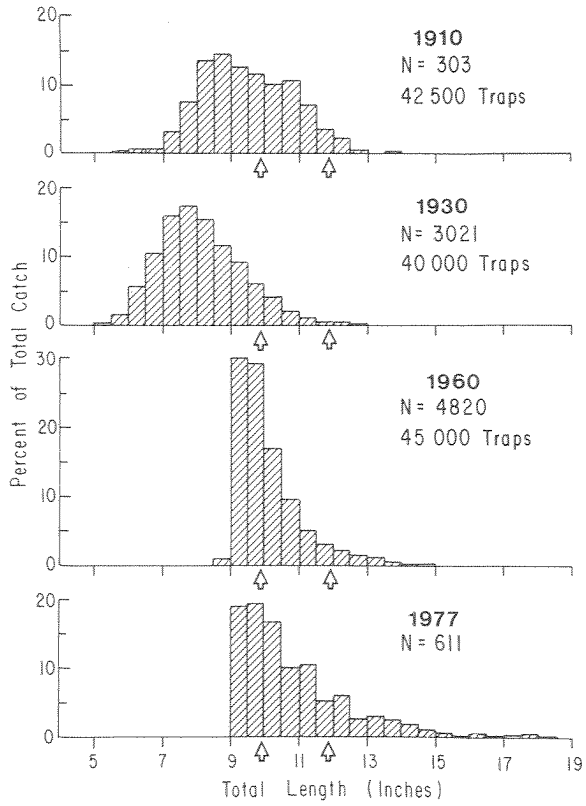


Figure 4. Size-frequency data from southern Cape Breton Island for some years. Trap numbers are for Richmond County only. Arrows indicate approximate sizes at which 50% and 100% of lobsters are mature.

lobster. Finally, from statistics of the last 12 years, "looking broadly over the whole lobster fishing areas, the fishery has been and continues to be a comparatively steady one". Although he did note that there had "been considerable reduction in the shipments of live lobsters", the significance was lost to him. Curiously, he makes no reference to the evidence collected by the Wakeham Commission, and we do not know if it were available to him. We must assume it was not, else how could he have had such faith in, for instance, berried female laws? The evidence clearly indicated few females to be mature at less than 9 inches T.L., whereas increasing percentages of the catch were of lobsters below this size.

The size limit was abandoned, and no further reference to the Wakeham Commission has yet been found by this author. Data available from the southeastern coast of Nova Scotia are illustrated in Figure 4 and appear typical of the area. In the 1914 Annual Report (p. 8), the inspector for western Nova Scotia noted that "the large proportion of the catch for packing purposes is of lobsters less than 7 inches in length." There does not appear to have been any reversal of this trend until the combined poor catches and poor canner prices of the 1920's encouraged fishermen to opt for "market" fisheries.

The landings in western Nova Scotia (Figure 3c) rebounded in the early 1940's, about a generation length after the application of market size limits. Prior to 1933 they document a fairly steady decline since the turn of the century. The 1921 peak reflects effort (a six-week season extension), the impact of which may be seen in the years immediately following. The landings have held up rather well since the mid 1940's, in spite of generally increasing fishing pressure, until fairly recently. The causes are open to question. Some of the initial decline reflects reduced average size, but this is clearly not sufficient for a total explanation. To a larger degree it must reflect reduced recruitment. The onset was partially masked by the ability of the fleet to exploit grounds further and further offshore as inshore grounds became depleted, a feature unique to this area. In this regard, history appears to be repeating itself. The suggestion is that a "stock-recruitment" event caused most of the 75% decline in landings, the partial amelioration of which permitted the partial rebound. If this hypothesis is supportable, it does not explain the likely effect of the current fishery: size limit low relative to maturity, highly efficient fleet, effort moving offshore as nearshore stocks become depleted.

Landings from along the eastern shore (Figure 3b) have recently come under intensive scrutiny by the Canso Marine Environmental Impact Workshop (McCracken, Ed., 1979). In the light of no likely environmental impact associated with the Canso Causeway being of sufficient scope to explain events subsequent to its construction in 1954, two major hypotheses were presented.

One of these hypotheses (Robinson, 1979) viewed the initial decline as recruitment overfishing, with subsequent events reflecting antagonistic interactions of population dynamics and the fishery. The second hypothesis (Dadswell, 1979) viewed events subsequent to 1956 from the assumption that a major proportion of eastern shore lobsters originated as southern Gulf of St. Lawrence larvae, the supply of which was blocked by the causeway. The former implies that the system will recover given sufficient removal of fishing effort; the latter implies either juvenile inputs (eg., hatcheries) or behavioral adaptation on the part of the lobsters before recovery is possible. Various options are under investigation, and a management program is in preparation.

The following is a summary of the argument for the first hypothesis. The long-term downward trend in the eastern shore landings is a result of increasingly effective fishing effort. Short-term cycles imposed upon this trend reflect to some degree a relaxing of that effort, but may also reflect atypically good year-class survival of larvae. Southern Gulf landings (Figure 3a) have held up due to the summer temperature regime allowing significant numbers of newly mature females to extrude eggs before the application of fishing effort the next spring. Central Northumberland Strait recruitment is under the influence of the fall (August 10 to October 10) fishery of District 8 and accounts for most of the variation in southern Gulf landings. The eastern shore, like Northumberland Strait, does not have the "refuge-in-time" afforded the remainder of the southern Gulf, and when fishing effort decreases survival enough, suffers a recruitment failure. By analogy, southwestern Nova Scotia has had a "refuge-in-space" in the offshore areas, which have harboured sufficient brood stock to replenish the inshore grounds. The proportion of this stock currently subject to increased effort needs to be assessed.

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RELATIONS AMONG LOBSTER, SEA URCHINS, AND KELP IN NOVA SCOTIA

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INTRODUCTION

Since the work that I will be discussing has all been previously published, I will give a brief summary of the work I did, letting the reader refer to the original papers for data if he wishes. I will be more colloquial and more speculative were this story not published.

The basic framework for the project that I began in 1971 was developed by K.H. Mann and R.J. Miller. Mann had carried out a survey of seaweed populations in St. Margaret's Bay, as part of a larger IBP program to study production processes in the Bay (Mann, 1972a). The survey showed a simple seaweed community structure, stratified with depth: an intertidal fucoid zone, a shallow subtidal zone dominated by Chondrus and Chorda, then a broad zone dominated by two species of Laminaria, and finally a deep Agarum zone. The Laminaria zone accounted for most of the algal biomass per unit of shoreline.

The productivity of the benthic algae was shown to be extremely high (Mann, 1972b), equalling the annual planktonic productivity of 3.4 km of adjacent shelf. However, within the Laminaria zone were barren patches with relatively high densities of sea urchins. These were the most important direct consumers of kelp (Miller et al., 1971), although they took only a small part of the annual algal production. The existence of barren patches within the Laminaria zone was puzzling; and the much higher density of sea urchins in these patches, rather than in the kelp, seemed at first a paradox. If sea urchins were consumers of kelp, why were they most abundant outside the kelp beds? Why were there no algae growing on patches of seemingly suitable habitat that was surrounded by dense kelp?

It was suggested that sea urchins were grazing away the kelp and had caused the patches. Miller observed a barren patch within his study site that was increasing in size. Mann talked with fishermen who described sea urchins "moving into" an area, kelp disappearing, and lobster abundance decreasing. They said that if the area were left alone, kelp

eventually reappeared, sea urchins disappeared, and lobster landings increased. The cycle period was reported to be three to four years.

Mann suggested to me that lobsters might be a key predator, for reasons discussed below, and that overharvesting of lobsters might have allowed sea urchins to become abundant. We published support for this hypothesis (Mann and Breen, 1972), and my thesis project was to test it (Breen, 1974).

Although we toyed with the idea of manipulating lobster abundance in fenced-off plots within the Bay, this was clearly unfeasible. If our ideas were correct, the kelp system of the Bay was already out of equilibrium, so results would not be representative of events beginning in a balanced system. As well, such a project would not be possible without the cooperation of the lobster fishermen. Such cooperation could not reasonably be expected, considering that I would remove part of the Bay from their fishing grounds and then remove lobsters from the remaining part for use inside the plots.

Instead, I looked at the individual components of the problem separately, testing whether kelp was in fact disappearing, whether sea urchins were responsible for this disappearance, whether lobster depletion was responsible for urchin increase, whether lobsters had in fact decreased in abundance, and finally, whether fishing could be responsible for lobster depletion. This was the logical series of the project, not necessarily the time series of the work itself.

DISAPPEARANCE OF KELP

During the period of the study, casual observations made throughout the Bay indicated declining kelp beds at many places. In 1973, I re-surveyed six of Mann's (1972a) transects on the western shore of the Bay. The reduction of kelp bed width on these six transects was 53% between 1968 and 1973. During the period of my study, I saw no new kelp beds developing on previously barren rock (except in the study site described below), and none were reported.

Kelp did not disappear completely in all areas. There were refuges of two kinds. Near the intertidal zone of exposed shores, surge apparently prevented sea urchins from grazing and there was a narrow fringe of *Laminaria*. Kelp also grew on boulders in deep water separated from other rocks by wide expanses of soft substrate, which sea urchins apparently did not cross. Since 1974, kelp has continued to decrease in the Bay, and is now nearly absent (Chapman, pers. comm.*).

Chapman, A.R.O., Associate Professor, Dalhousie Univ., Hfx., N.S.

SEA URCHINS AND KELP BEDS

Strong circumstantial evidence linked sea urchins with the demise of kelp. Fishermen had told Mann that sea urchins moved in prior to the decline in kelp. Mann's survey data showed that sea urchins were abundant where kelp was not, and vice versa. Sea urchins were most abundant right at the margins of kelp beds, or at the edges of "holes" in the kelp cover; in other words, at the kelp/barren rock interface. There was evidence of the destructive powers of sea urchins in the literature from California and Britain.

However, it was possible that sea urchins had nothing to do with the decrease in kelp beds: perhaps some substance in the water had interfered with kelp reproduction; perhaps the water temperature had changed at a critical time of year. The pattern of distribution of sea urchins could be explained by saying that for some reason sea urchins stayed out of kelp beds but preferred to feed near them where food was most abundant.

It appeared simple to test the role of sea urchins on kelp grazing by placing them in a healthy kelp bed and also by removing them from barren rock next to a receding bed. The removal yielded clear results: the kelp bed edge stopped receding; and the barren rock was quite quickly covered with algae which, after a year, was dominated by Laminaria. This refuted the hypothesis that something was wrong in the water. However, sea urchin additions were not so successful. I could not establish a patch of barren rock within a healthy kelp bed no matter how many sea urchins I placed at marked locations. The sea urchins dispersed, or apparently were dispersed by the waving action of the kelp in surge. I also found that some urchins were killed by predators (starfish and a crustacean). The general failure of this experiment, coupled with the inability of just a few sea urchins to graze on a blade of kelp waving in the surge, led me to propose a critical density phenomenon. At low densities, sea urchins would be restricted to grazing the understory, but at higher densities they could weigh the kelp down and begin to devour whole plants. When I measured the rate of recession of the edge of a kelp bed at various points, I found no recession where sea urchins were less than 2 kg/m^2, and so this was used as a rough estimate of the threshold density.

The pattern of sea urchins around the disappearing kelp bed was dramatic. Inside the kelp, sea urchins were extremely scarce, and the kelp was dense and lush. At the kelp edge was a narrow band where sea urchins covered the bottom entirely, often several layers deep. There was dense kelp immediately "ahead" of these sea urchins; but on the other side of the

narrow band was only barren rock: even the erect corallines and kelp stipes were grazed away. Sea urchin density reached 400/m^2, and biomass 15 kg/m^2 at the kelp edge. The individuals were large and showed high gonadal indices. As one moved away from the kelp across barren rock, sea urchins became progressively smaller and less abundant.

Repeated sampling showed that the pattern stayed constant as the kelp bed receded. There was always a dense strip of sea urchins at the kelp edge and fewer behind, showing that the concentration of individuals was moving steadily into the kelp and removing all but the encrusting algae. When there was not more kelp, the concentration of sea urchins quickly dispersed. Over the next few months, there was a steady decrease in both density and average size of the urchins. This suggested that the large individuals were either starving or migrating out of the area completely.

Areas in which kelp had disappeared several years previously showed low numbers of small individuals, which were still apparently keeping the bottom in a barren condition. Lang and Mann (1976) continued to look at such areas, and found that sea urchin populations on barren grounds were stable; in other words, that recruitment is sufficient to maintain the populations in their present state.

At this point, I will consider the possibility of reciprocal cycles in the abundances of kelp and sea urchins. If the subtidal communities of Atlantic Canada have flipped into a different and much less productive configuration, one which is going to persist for a long time, we are looking at a major disaster. If, instead, we are observing part of a natural cycle, the situation is much less alarming. There is no way to determine at this point which condition exists. Historical observations on subtidal kelp communities are poor, so the only definitive evidence will be obtained from observing St. Margaret's Bay in the coming years. However, cycles have certainly occurred in the past; but, as discussed below, the present disappearance of kelp does not appear to be part of a cycle.

Scott (1902) spent part of a summer examining the feeding of sea urchins near St. Andrews, N.B., apparently prompted by the claims of local fishermen that sea urchins had become abundant and were destroying the algae locally. He presented an interesting list of arguments to suggest that sea urchins could not be responsible for the reported kelp decrease; but in the process of doing so, he gives a familiar picture:

> "There are now localities where sea urchins are so numerous it would be hard to imagine them more abundant - where they are massed in heaps often obscuring the bottom - and yet in these very places seaweed is equally plentiful, great bunches being found in all suitable places. I have seen boulders covered with seaweed, and yet in the interspaces between the boulders the bottom was literally carpeted with urchins whose intestines contained seaweed alone." (p. 53)

That description applies extremely well to the receding kelp bed/barren rock interface, and suggests that kelp in fact was decreasing. Another of Scott's arguments was that in 1902 seaweed was abundant on the shores of Grand Manad, where Stimpson had reported only carpets of sea urchins in 1851. This is strong evidence that kelp was destroyed in 1851 but had returned by 1902.

More recently, Arnold (1976) reported that sea urchins had become more abundant and denuded a study shore in New Brunswick; later, the sea urchins apparently had diminished again, and seaweeds had returned to the intertidal zone. The story of the fishermen who talked to Mann was that kelp eventually returned to areas denuded by sea urchins. In British Columbia, the same species of sea urchin demonstrates dramatic but temporary "outbreaks", described by Foreman (1977).

As evidence against cycles, several points can be made. Barren grounds now which were established eleven years ago in the Bay are highly stable. The sea urchins are reproductive and their population are in equilibrium. Although their biomass is quite low, they are more than capable of preventing the growth of all macrophytes. Some change in this situtation must occur before the barren grounds can be replaced with a macrophyte community, and this is strong evidence against a simple cycle of sea urchin and kelp abundance. Although historical observations on kelp are poor, one can argue that surely if kelp had disappeared from such a large area before, it would have been noticed by fishermen and reported. Finally, the size of the area affected and the length of time that barren grounds have persisted in the Bay suggest that we have not observed part of a cycle which will reverse itself if we wait a few more years.

LOBSTERS AND SEA URCHINS

If sea urchins were not increasing as part of a simple cyclic interaction with kelp, then another explanation was

needed. We thought, because of the control of sea urhcins by predators in other systems, that a recent release of predation pressure was the most likely cause. We suggested the lobster as the controlling predator: it was a known sea urchin predator; and because of fishing, we could easily suggest a cause for a decrease in its grazing on sea urchins (Mann and Breen, 1972). (The concept of one species being a "controlling" predator of another is without doubt an over-simplification except in a very simple system. Sea urchins have many predators and most of these have many prey. What I tested was the idea that lobster predation was important enough that a great reduction could allow a sea urchin population to escape the influence of the suite of predators.)

The role of lobsters could not be measured directly by manipulation, as discussed in the introduction. Instead, I put all the available information together in a simple simulation model. The purpose of the model was to test whether a lobster population of reasonable size, feeding at known rates and with realistic size interactions with its prey, was capable of limiting the growth of a sea urchin populatin. This was a fair test of the hypothesis - the model might show that only an impossibly dense lobster population would control sea urchins, and the hypothesis would be falsified. If the model showed that a reasonable lobster population could control a realistic sea urchin population, the idea would be tested but not proven.

To make the test fair, I put all the information into the model and then did not change any parameter values once the model ran. This was obviously necessary because I could get any result I wanted from fiddling with parameter values in the model. In cases where I had no idea what a parameter value should be, I set it so as to operate against the hypothesis.

The model contained information on lobster feeding rate as a function of temperature and prey density, water temperature regimes, the size selectivity of various size lobsters, lobster mortality and growth, and sea urchin mortality and growth; later it contained crab feeding rates, size selectivity, growth and mortality rates, and the relative preference of lobsters between crabs and sea urchins. The sources of these data were: first, my own data; second, published values; and third, reasonable guesses.

When just lobsters and sea urchins were considered, the answer was a bit ambiguous. Over the range of lobster and sea urchin population used (these were also determined from field observations and the literature), sea urchins were controlled about half the time. When I included wolffish as an additional predator, there was almost no change. When I included rock crabs, they could not control sea urchins alone, but lobsters

and crabs controlled sea urchins under most conditions. At low lobster density, sea urchin populations exploded.

The hypothesis thus passed its test. I should repeat that the role of lobsters is not proven by the model, but is shown to be plausible.

Further work was carried out by three people. Evans (and Mann, 1977) showed that I underestimated the preference of lobsters for crabs over sea urchins. Drummond* (unpublished MS) showed that I underestimated crab density in the Bay by about 50%. Coleman (1978) then ran the model, incorporating these new data. He found my basic conclusion from the model to be correct, but he also showed that crabs were themselves close to being capable of limiting sea urchins.

(The model was very helpful in sorting out the role of crabs. It was not clear from a trophic diagram, in which lobsters eat crabs and sea urchins, what effect a change in crab abundance would have. Increasing crabs would increase crab predation on sea urchins; but, because lobsters prefer crabs, lobster predation on sea urchins might be reduced and total sea urchin predation could actually be reduced. The model showed that this did not happen - increasing crab abundance was similar to increasing lobster abundance.)

LOBSTER ABUNDANCE AND LOBSTER FISHING

The next step was to determine whether lobster abundance had decreased in St. Margaret's Bay. If it had increased, or remained nearly constant, the idea relating sea urchins and lobsters would have to be discarded. The Bay is part of two statistical areas, so I used tabulated landings from each of 21 ports around the shore.

The landings had decreased by nearly two-thirds between 1959 and 1973. When the number of licensed fishermen (the only available measure of effort) was used to give catch per unit effort, this value had dropped by more than 50%. In 1976, CPUE had dropped to 200 pounds from an average of 700 in 1959-1961. There was a simultaneous decrease in mean seawater temperature in December (when most of the lobsters were caught) in Halifax Harbour (where the nearest series of data were recorded). However, the decrease was too small (1 C) to account for such large decrease in apparent abundance.

The final aspect of my project was to look at whether fishing had caused the decrease in lobster abundance. This dissolved quickly into a semantic problem. Lobsters were once so numerous that they were held in low esteem, considered

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valueless, and were even used for fertilizer (DeWolfe, 1974). When a fishery began around 1870, it quickly peaked, and then landings declined until 1918 (Wilder, 1965). There can be no question that the period before 1918 saw a great decrease in lobster abundance, and that the population changed from one limited by natural factors to one limited by fishing pressure as well.

After 1918, the catch remained steady at around 40 million pounds. Wilder (1965) suggested that the population responded primarily to environmental factors (but without a fishery, would no doubt have increased). This idea was supported by several authors who found correlations between lobster abundance and previous values of temperature or river runoff.

Whether lobsters declined in St. Margaret's Bay after 1959 as a result of fishing or as a result of something else, it is obvious that the population had been kept at well below historical levels by fishing.

DISCUSSION

The change in subtidal communities in St. Margaret's Bay has been massive. Bottom, which once supported 100% Laminaria cover, with a dense understory of erect coralline algae and small fleshy red algae such as Irish moss, now is inhabited only by encrusting red algae and isolated Desmarestia. Fish (especially cunner), crabs, starfish, periwinkles, and other animals have also shown drastic decreases. The barren grounds support sea urchins as the major organism in about the same abundance as they were in the kelp bed community. It is almost certain that disappearance of kelp and its associated fauna has led to the recent drastic decline of lobster stocks. The kelp bed community was both shelter and food supply. The effect on other food chains is not known, because the trophic paths were not known. Kelp is very highly productive, most of the production being detritus, which is processed first by bacteria and then by small organisms such as amphipods and mysids. These may have been important to commercially valuable fish; the kelp itself may have been valuable as shelter for juvenile fish. The loss of so much primary production will no doubt be reflected elsewhere. If not, the loss of the lobster fishery would be bad enough.

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THE DISTRIBUTION OF SEA URCHIN-DOMINATED BARREN GROUNDS ALONG THE SOUTH SHORE OF NOVA SCOTIA

By

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INTRODUCTION

The destructive grazing of macrophytes by the green sea urchin Strongylocentrotus droebachiensis (O.P. Muller) has been documented for St. Margaret's Bay, Nova Scotia (Breen, 1974; Breen and Mann, 1976). This has resulted in the loss of a major input of primary production to the St. Margaret's Bay system (Mann, 1972a; b).

Overgrazing of the seaweed zone has led to the establishment of sea urchin-dominated barren grounds over most of the rocky subtidal zone of St. Margaret's Bay. These grounds appear to possess a degree of persistance, and to date no evidence of regeneration of macrophyte growth has been discovered.

It has been proposed (Breen and Mann, 1976) that the rise in sea urchin numbers prior to destructive grazing is facilitated by the removal of the dominant predator, the American lobster Homarus americanus Milne Edwards, through the activities of a commercial fishery.

The direct relationship between seaweeds and lobsters is not known; however, it is possible that juvenile lobsters require the seaweed for cover and protection from predators. The occurrence of small lobsters in seaweed beds has been reported by Scarratt (1972). The effects of larval survivorship on recruitment to the fishery have been shown by Sutcliffe (1973), and it appears reasonable to assume that factors affecting juvenile survival should be reflected in the commercial catch.

It becomes necessary, therefore, to examine the relationship between lobster abundance and seaweed distribution to ascertain the effects of over removal of lobsters from the system and the subsequent degradation of the seaweed zone.

ST. MARGARET'S BAY, NOVA SCOTIA

Before 1968, the predominantly rocky subtidal substrate of St. Margaret's Bay was covered with macrophytic algal growth down to a depth of about 20 m. The kelps *Laminaria longicruris* Pyl. and *L. digitata* (Huds.) Lamour had a biomass of about 16 kg fresh weight/m^2 and an annual production on the order of 1750 gC/m^2 (Mann, 1972a; b).

Breen and Mann (1976) recorded a 70% reduction of seaweed cover along 15 km of coastline in St. Margaret's Bay in a six-year period. This was accompanied by dense aggregations of the sea urchin *S. droebachiensis*. Removal of sea urchins resulted in a return of macrophyte growth; however, residual populations of sea urchins seemed to be capable of keeping the substrate clear of all growth except coralline algae. It was first thought that after macrophyte removal was complete that populations of sea urchins would die off or migrate away. This was not observed (Lang and Mann, 1976), and known sites of grazing 11 years old are still maintained by urchins in the barren condition. Recent observations (A.R.O. Chapman, pers. comm.) estimate residual kelp cover in St. Margaret's Bay at less than 1%.

Lang and Mann (1976) examined the changes that occur in these sea urchin populations after destructive grazing of the macrophytes has been completed. It was shown that sea urchins grew slower in barren areas (Figure 1), presumably due to a lower abundance of food.

It was also shown (Figure 2) that there was a shift in the size frequency of these populations from larger size classes to smaller size classes accompanied by a recruitment pulse and subsequent increase in density (Figure 3).

This agrees with observations on sea urchin populations in California after cover of seaweeds were reduced (Kelp Habitat Improvement Project Annual Report, 1975), and in Alaska (Estes, 1978).

OBSERVATIONS ON THE SOUTH SHORE OF NOVA SCOTIA

A survey was conducted on the Atlantic coast of Nova Scotia between Halifax and Yarmouth at selected areas with a history of significant lobster catch. This was to quantify the extent of destructive grazing along this section of coast and establish the conditions of sea urchin populations encountered.

The survey consisted of five sites divided into 1/2 x 1/2 nautical mile squares of which 14 or 15 at each site

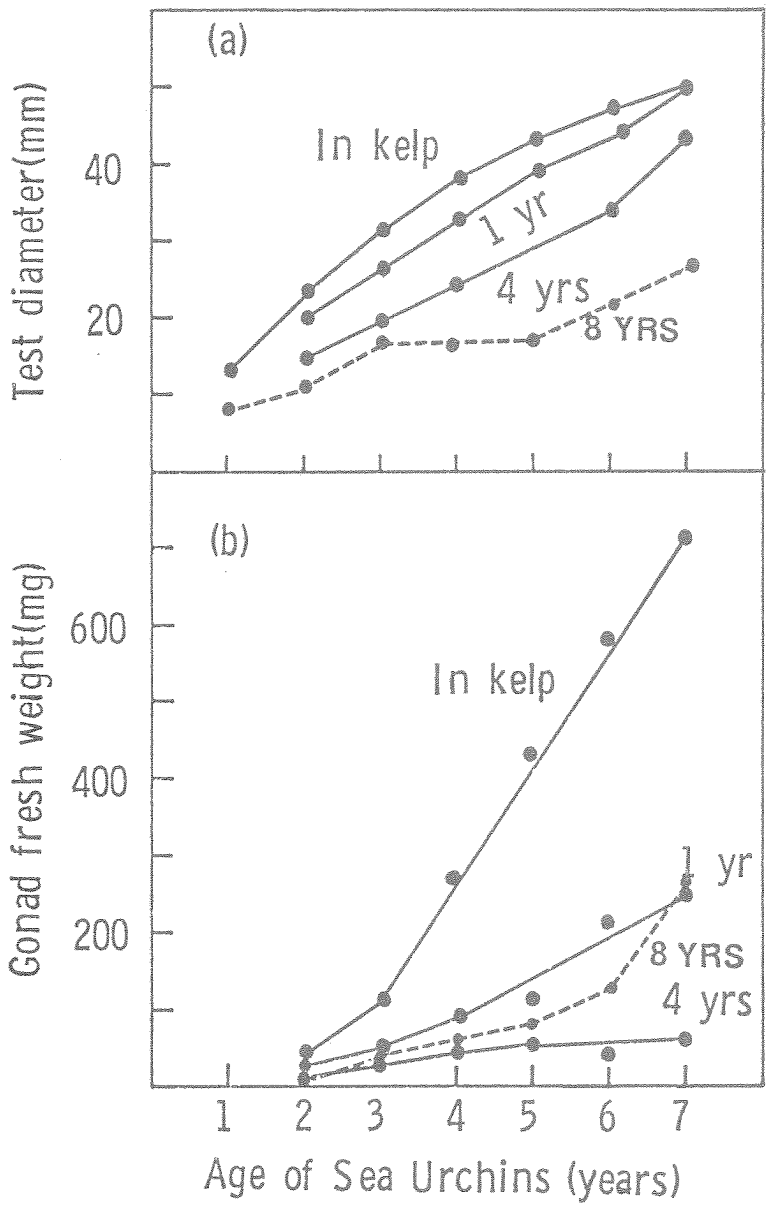


Figure 1. (from Wharton B.Sc. Thesis Dalhousie) Decreases in growth rate and gonad fresh weight with time since destructive grazing.

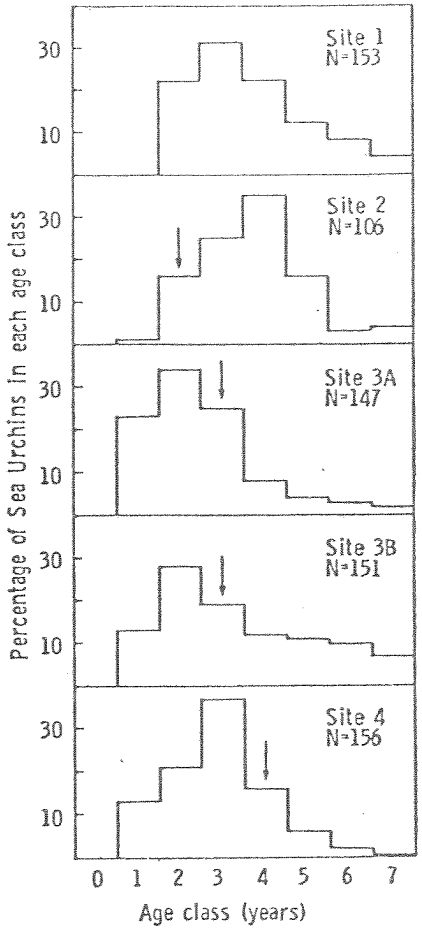


Figure 2. (From Lang and Mann, 1976)

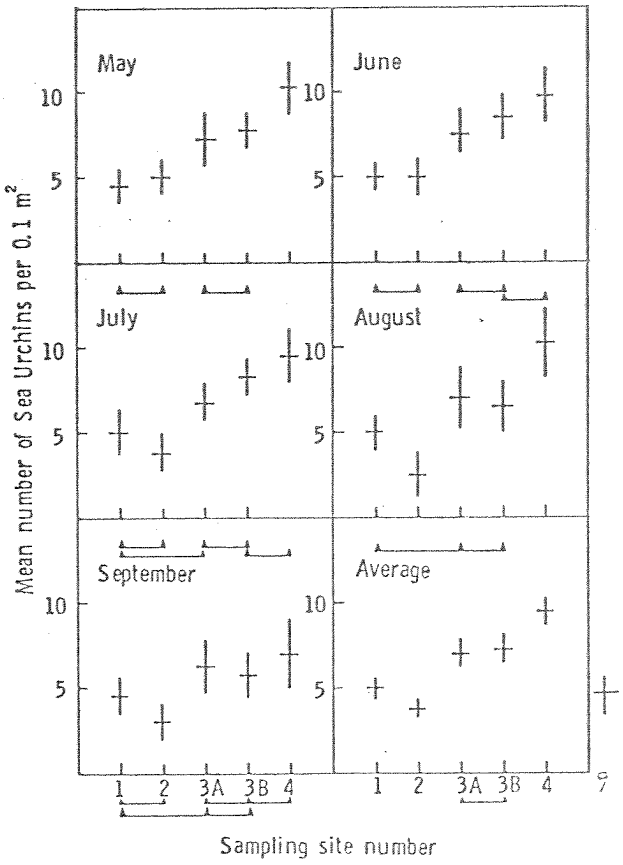


Figure 3. (From Lang and Mann, 1976)

were sampled (Figure 4). At each station within a site three transects were surveyed in a tri-radial pattern, with the centre at 10 m depth. Only squares with depths of 10 m were considered in the station selection process. Along each arm of the tri-radial transect the amount of substrate deemed suitable for macrophyte cover was determined and the percentage that was in fact covered by macrophyte growth recorded. The results of this assessment appear in Table 1 (see also Figure 4).

The area of coastline from the approaches of Halifax Harbour to the western limits of St. Margaret's Bay are well known to the author and other workers at Dalhousie University. Cover of the subtidal by macrophytes in this area could safely be estimated at less than 1%. The rocky subtidal in this area is covered predominantly by the coralline algae with the bulk of the primary production provided by benthic diatoms (A.R.O. Chapman, pers. comm.). Breen (1974) has stated that benthic diatoms were observed as being the early settlers of substrates cleared of sea urchins. It appears that sea urchins in this area are keeping this zone in its earliest successional stages. This zone is referred to as the sea urchin-dominated barren ground.

This was also the situation encountered over much of the first three sites west of Halifax. The amount of substrate that was suitable for cover and actually covered was 3.6%, 8.8%, and 11.5% respectively. The barren areas at these sites bear a striking resemblance to those existing in St. Margaret's Bay. In each of these three sites kelps were encountered, typically in areas of intense water movement. At the fifth site west of Halifax the percentage cover on suitable substrate was in excess of 99%. At the fourth site the overall cover was 74%; however, if the site were divided at Green Island (approximately in half) the percent cover on the eastern side would be 59% and the western side 93%. From this point, they will be referred to as Sites 4a and 4b and dealt with separately.

DIFFERENCES AMONG SEA URCHIN POPULATIONS ALONG THE SOUTH SHORE OF NOVA SCOTIA

The sea urchins encountered at Site 5 were large, sparsely distributed, and confined to stations at the eastern end of the site. Fishermen have reported seeing "pockets" of urchins but none were encountered in the course of the surveys. Much of this area could be described as a healthy kelp bed community.

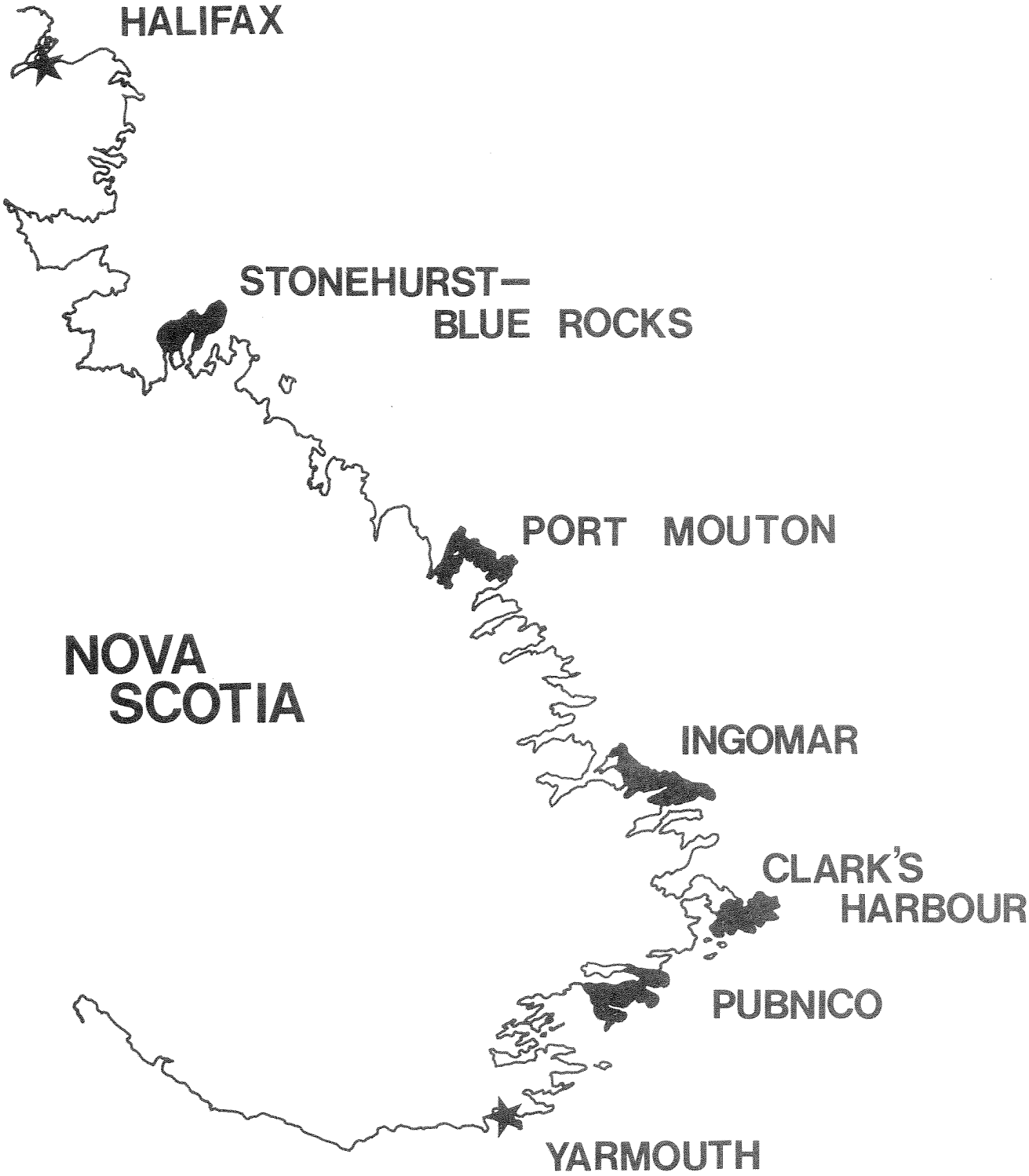


Figure 4. The southern and southwestern shores of Nova Scotia, showing the study sites.

TABLE 1. The percentage of suitable substrate bearing macrophytes.

Site surveyed	% of substrate suitable for cover that was found to be covered by macrophytes
Site 1 (Stonehurst, Blue Rocks)	3.6
Site 2 (Port Mouton)	8.6
Site 3 (Ingomar)	11.5
Site 4a (Clarks Harbour)	59.0 (section of site being actively grazed)
Site 4b (Clarks Harbour)	93.0 (section of established seaweed cover)
Site 5 (Pubnico)	99.4

Sea urchins at Site 4b (93% cover), although more dense than the populations at Site 5 at 2.8 urchins/m^2, were still predominantly large (Figure 5). Site 4a (59% cover) showed marked differences in sea urchin populations with densities averaging 60.7 urchins/m^2, and observation revealed aggregations of urchins and active grazing of macrophytes in a typical front pattern described by Breen and Mann (1976) for St. Margaret's Bay.

Populations at Site 4a also have higher frequencies of sea urchins in the smaller size classes (Figure 6). This shift in size frequencies has also been documented for populations of the Pt. Loma kelp bed near San Diego, California, in association with changes in kelp cover (Kelp Habitat Improvement Project, 1975).

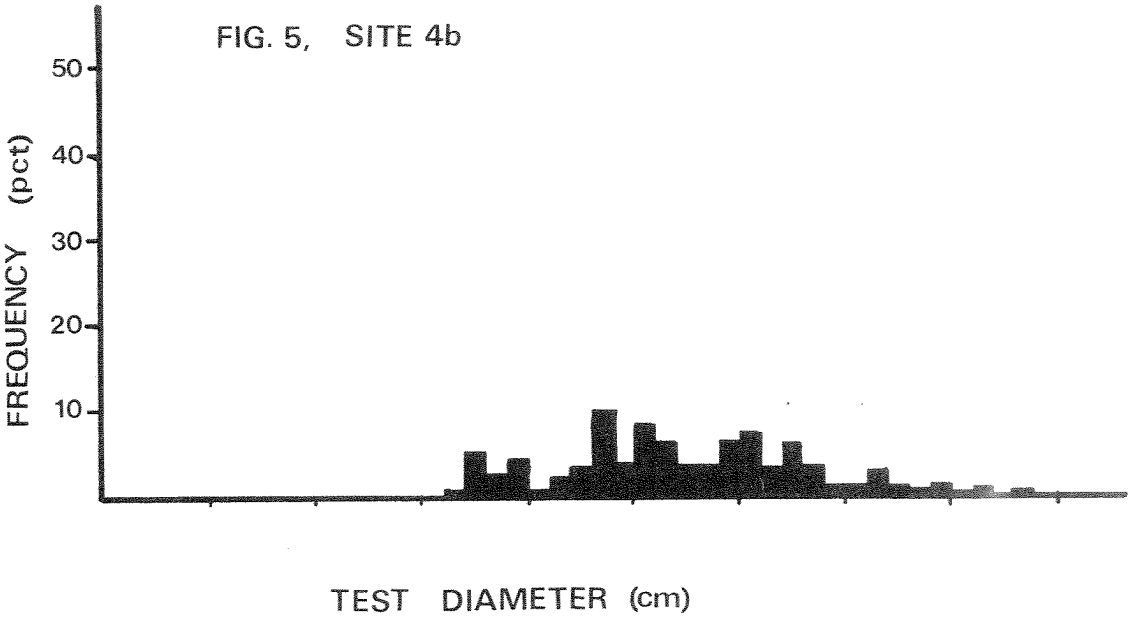
On the basis of this evidence, I believe that the front of grazing at the interface between Sites 4a and 4b is active and that further damage in this area can be expected.

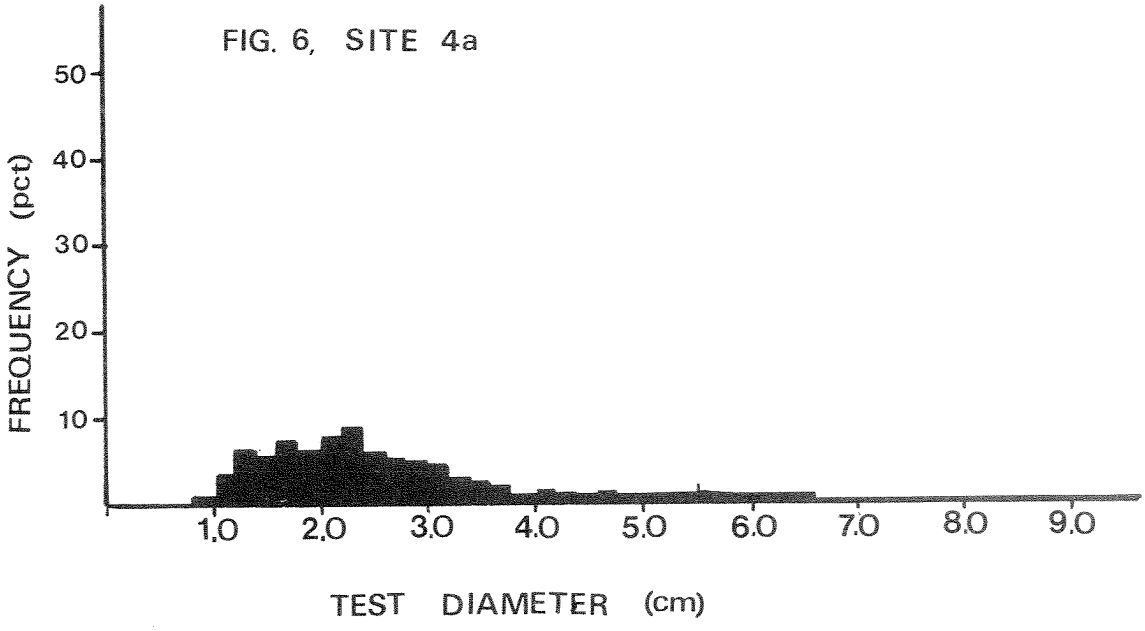
Also of interest in the California urchins is the appearance of a large number of juveniles following the disappearance of kelp. This recruitment pulse has been observed in urchin populations at the three sites west of Halifax (Sites 1, 2, and 3) (Figures 7, 8, and 9). The pulse appears strongest nearest the site of active grazing and seems to be furthest along at the site most distinct from the site of active grazing. Based on this, it appears that the chronological order of destructive grazing, from oldest to most recent, has been Site 1, Site 2, then Site 3 with Site 4 now being actively grazed. Sites 2 and 3 are, however, quite similar and distinction at this time would be mostly conjecture. Comparative growth rate estimates should substantiate this.

Densities at Sites 2 and 3 are 101 and 104 urchins/m^2 respectively, but density of urchins at Site 1 averaged only 62 urchins/m^2. This lower density was also encountered in older established barren sites in St. Margaret's Bay and is most likely a result of urchins approaching a number sustainable on the benthic diatom production.

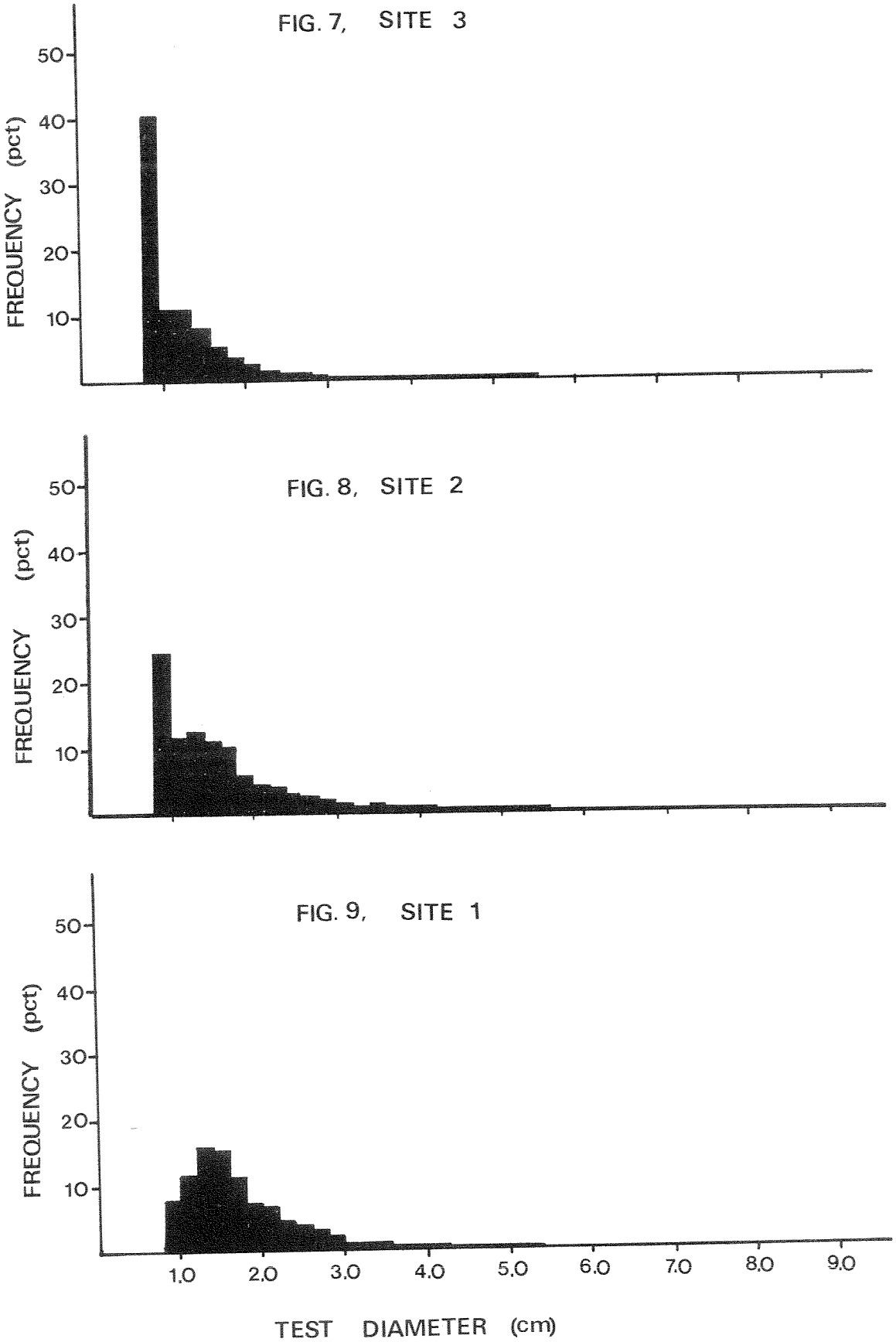
CATCH HISTORY OF LOBSTERS ON THE ATLANTIC COAST OF NOVA SCOTIA

The commercial catch of the American lobster has been on the decline generally in recent years (Robinson, 1979); however, the catch along the Atlantic coast warrants close examination. It can be seen (Figures 10 and 11) that catches appeared to decline first in Guysborough County on the





Figures 5 and 6. Sea urchin size frequencies at Sites 4a and b.



Figures 7, 8, and 9. Sea urchin size frequencies at Sites 3, 2, and 1.

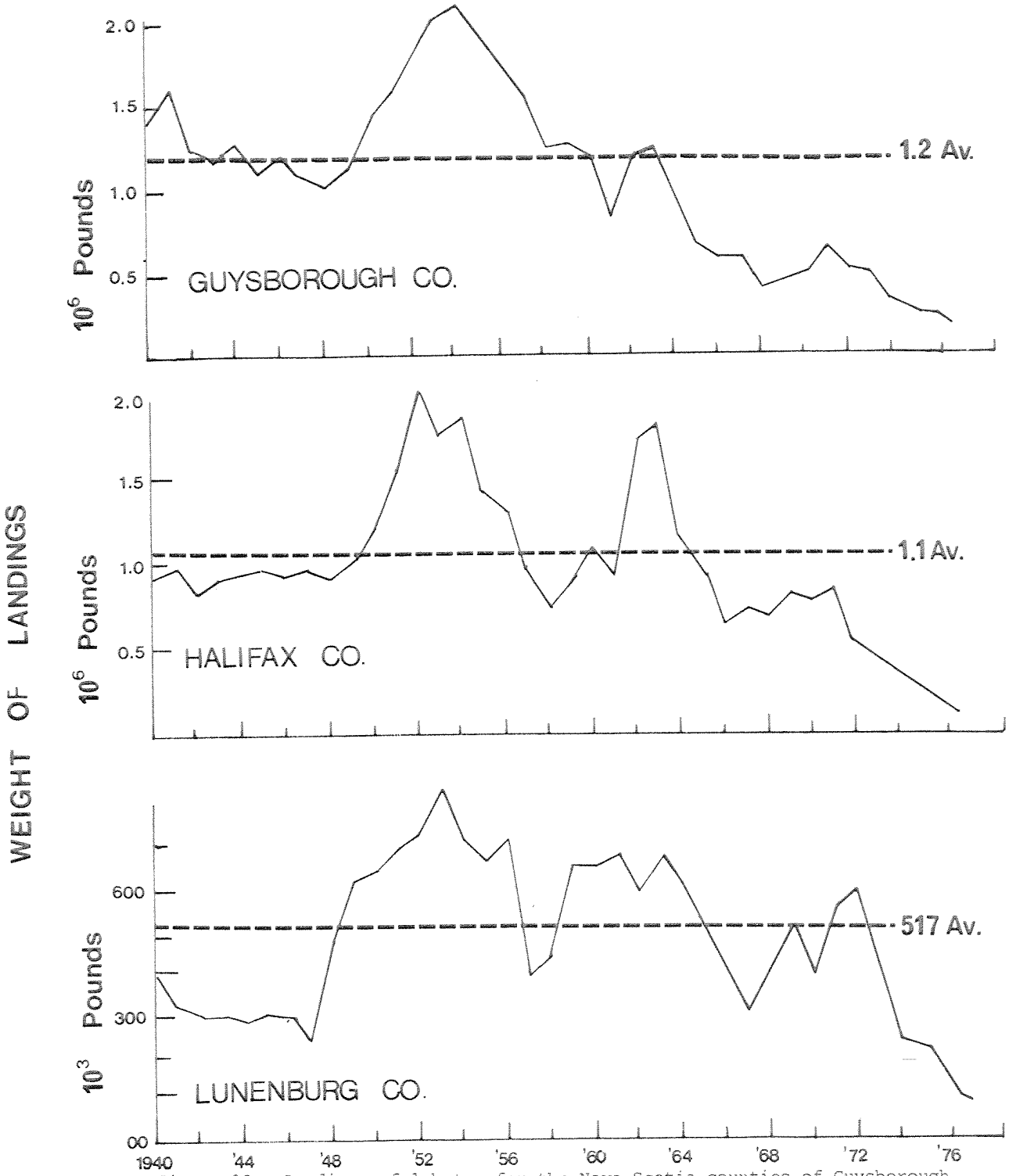


Figure 10. Landings of lobster for the Nova Scotia counties of Guysborough, Halifax, and Lunenburg between 1948 and 1976.

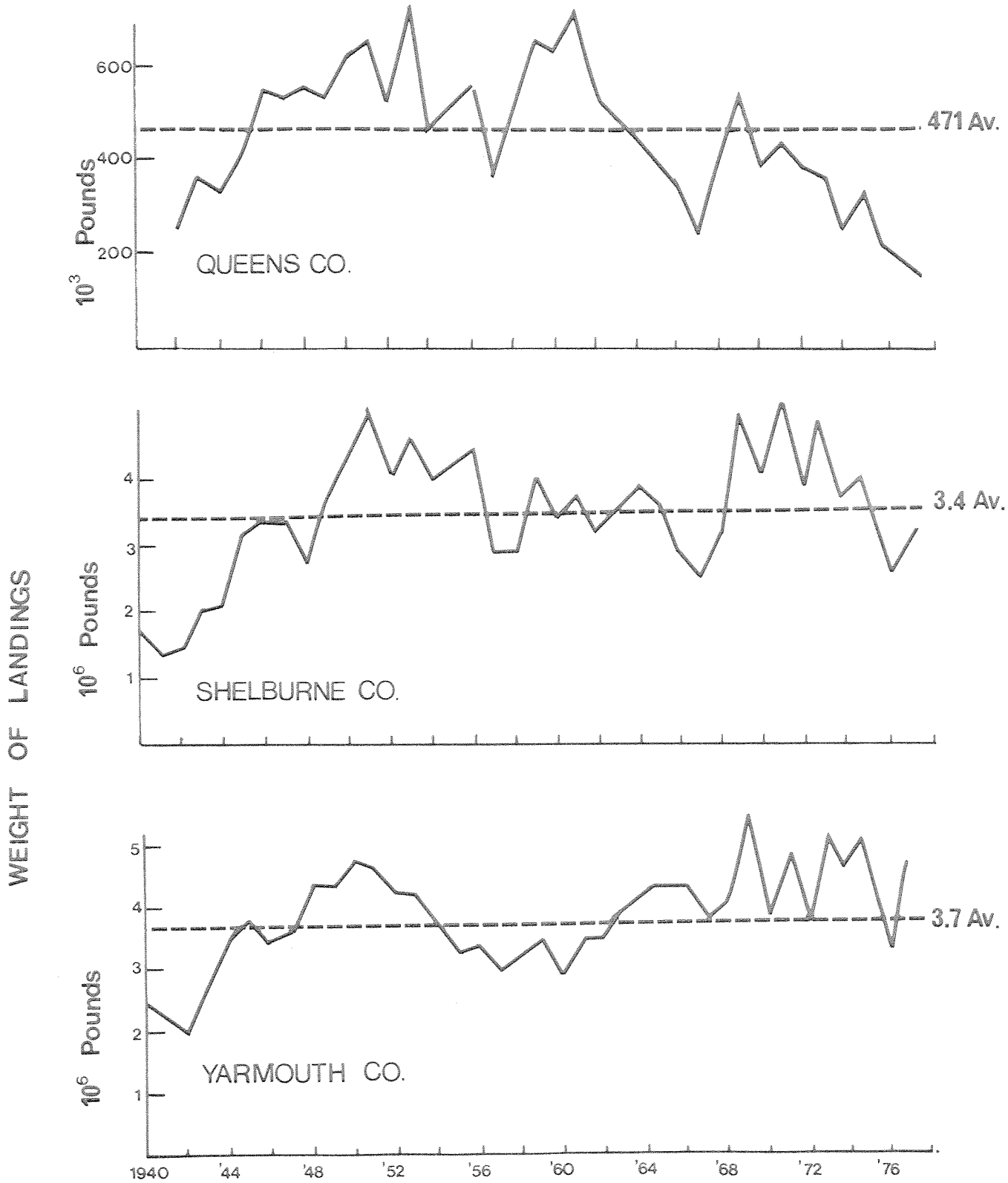


Figure 11. Landings of lobster for the Nova Scotia counties of Queens, Shelburne, and Yarmouth between 1940 and 1976.

eastern shore then Halifax, Lunenburg, and Queens Counties. Catches still appear to be high in Yarmouth County. This corresponds well with the extent and apparent time sequence of destructive grazing observed along the south shore. Although Guysborough County was not included in this survey, extensive damage by sea urchins has been reported. Catches appear to be at reasonable levels in Shelburne County which included Site 3. Site 3 was extensively grazed although this grazing appeared to be of a relatively recent nature. If lobster abundance and the availability of cover by macrophytes is related, then the decrease in catch of lobsters in the Shelburne area may be imminent.

The mechanism involved in the recruitment failure in these areas may well be the increased mortality of juvenile lobsters as a result of predation and the reduced availability of suitable habitat.

PERSISTANCE OF SEA URCHIN POPULATIONS AND EXPECTATIONS FOR REGENERATION OF KELP BEDS

Sea urchins have demonstrated through growth plasticity and availability to utilize diverse food sources that they can persist on these "barren" grounds. Wherever kelp is found in refuge from urchin grazing it is normally surrounded by dense stands of sea urchins presumably living off the detrital production. As this kelp will no doubt provide the spores to facilitate any regeneration, the presence of surrounding urchins may in some way hinder the process.

To this point in time, no evidence of regeneration has been discovered, and even if sea urchin abundance is a cyclical phenomenon it would appear to be one with a long period between times of high macrophyte production and possibly lobster abundance.

CONCLUSION

The destruction of macrophytes has been observed in St. Margaret's Bay, and the subsequent changes in sea urchin populations documented. Damage of the sort observed in St. Margaret's Bay has been found along the south shore of Nova Scotia and damage is presently occurring in the Cape Sable region. The abundance of lobsters in these areas appears to be correlated to the amount of macrophyte cover available, presumably for habitat for juveniles.

Regeneration of kelp has not been observed, and these barren areas appear to possess a degree of local stability.

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PREDATION ON THE SEA URCHIN (*STRONGYLOCENTROTUS DROEBACHIENSIS*) BY THE AMERICAN LOBSTER (*HOMARUS AMERICANUS*) AND THE ROCK CRAB (*CANCER IRRORATUS*)

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ABSTRACT

Thirty-nine percent of the lobsters and 39.5% of the rock crabs investigated fed successfully on sea urchins within a six-day period in the laboratory. Various predation techniques used by these predators to open sea urchins of a range of sizes are reported. All sizes of lobsters and all but the smallest rock crab size class studied were able to exploit the full size range of sea urchins available, including the largest prey of 73 mm in diameter. Given a range of sea urchin sizes, all sizes of lobsters and rock crabs tested attained a similar mean daily predation rate of approximately one sea urchin/predator/day. Mean daily energy intake was similar for both lobsters and rock crabs and appeared to increase with predator size. Given a choice, both lobsters and rock crabs showed preferences for distinct sea urchin size ranges. The size of preferred prey increased with predator size. Lobsters and rock crabs, when given a choice between equal numbers of sea urchin and mussel prey, displayed 1:43 and 1:79 preferences respectively for mussels. Given the low predation rates and preferences obtained, it is difficult to consider sea urchins as major prey items of lobsters and rock crabs, and these predators as major influences on sea urchin population dynamics.

INTRODUCTION

The green sea urchin, *Strongylocentrotus droebachiensis*, is the dominant sublittoral animal along many rocky coastlines of the eastern and western seaboard of North America (Himmelman, 1969; Miller et al., 1971; Vadas, 1968). Studies by Miller and Mann (1973), Foreman (1977), and Vadas (unpublished data) have shown the green sea urchin to be a most important benthic herbivore, controlling the distribution of macroalgae and strongly influencing species composition and diversity in the sublittoral zone. On the Pacific coast of

North America, Foreman (1977) documented periodic S. droebachiensis population outbreaks which led to localized perturbations of the benthic macrophyte community. Foreman (1977) suggested that these outbreaks were environmentally controlled, probably resulting from favourable plankton blooms and cool seawater temperatures. Similar population outbreaks have been described for the east coast of Canada by Mann and Breen (1972). Since 1968 large increases in S. droebachiensis populations along portions of the Canadian Atlantic coastline have led to considerable areas being completely denuded of kelp (Breen and Mann, 1976a,b,; Mann, 1977). Mann and Breen (1972), Breen and Mann (1976a), and Mann (1977) hypothesized that this situation was largely due to a decline in the sea urchin's "keystone" predator (Paine, 1966; 1969), the American lobster (Homarus americanus). Furthermore, Lang and Mann (1976) and Mann (1977) have suggested that the kelp denudation is irreversible as large populations of sea urchins can persist on the barren grounds. The destruction of the kelp beds is believed to be accelerating the decline of lobster stocks still further by decreasing the overall productivity of the inshore system and depriving lobsters, juveniles especially, of spatial refuges (Breen and Mann, 1976a).

Himmelman and Steele (1971) studied a variety of S. droebachiensis predators, including lobsters and rock crabs, and concluded that predation had little significance in controlling population size. Breen (1974), Breen and Mann (1976a), Hirtle and Mann (1978), Evans and Mann (1977), and Reddin (1973) further examined the role of lobsters and rock crabs as sea urchin predators. However, their conclusions frequently conflict and are not always consistent with the concept of lobsters as the green sea urchin's keystone predator. In the present paper, predation behaviour and foraging strategies of lobsters and rock crabs on sea urchins are reassessed. As both edible mussels, Mytilus edulis and horse mussels, Modiolus modiolus, are commonly present in large numbers in association with sea urchins (Mann, 1977; Miller et al., 1971; R.L. Vadas, pers. comm.), the feeding preference by lobsters and rock crabs for mussels and sea urchins was investigated.

Laboratory experiments were performed to determine the following:

1. The techniques used by lobsters and rock crabs to feed on sea urchins of a range of sizes

2. The feeding rate, in terms of numbers of sea urchins eaten and energy intake, by various size classes of lobsters and rock crabs on a size range of sea urchins in unlimiting numbers

3. The preferences by lobsters and rock crabs when offered a choice between equal numbers of sea urchins and edible mussels.

MATERIALS AND METHODS

Lobsters and rock crabs were captured by bottom trawl in Passamaquoddy Bay, New Brunswick, near the mouth of the Bay of Fundy in December 1977. During experiments animals were kept individually in 77 x 32 cm glass aquaria filled to a depth of 37 cm with running sea water at 12.5 $\pm$ 0.5 C. Sea urchins were collected at low tide or dredged from Passamaquoddy Bay using a Digby tumble-drag in January and February 1978. Edible mussels were collected during the same period from a L.W.S.T. sheltered population on pier pilings in Passamaquoddy Bay, thereby standardizing shell characteristics which vary with exposure and tidal level (Elner, 1978; Seed, 1973).

Lobster size was determined by measuring carapace length from the posterior edge of an eye socket to the edge of the carapace parallel to the longitudinal axis. Rock crab size was determined by measuring the carapace width between the tips of the most distal marginal teeth. Sea urchin size, in terms of test diameter, was measured across the widest part of the animal, excluding the spines. Mussels were sized according to shell length.

Predators were starved for two days prior to all feeding experiments to standardize hunger levels. Only undamaged, healthy sea urchins and mussels less than one week in captivity were used as prey. During all feeding experiments sea urchins that had attached themselves to the tank wall, out of reach of the predators, were regularly removed to the tank bottom.

Predation techniques and foraging behaviour of three size classes of lobsters and three size classes of rock crabs on sea urchins from 10-73 mm diameter were observed. Fragments of sea urchin test were collected after each successful attack to aid in the interpretation and description of the predation techniques. Only those predators that had successfully preyed upon sea urchins within a preliminary six-day period were used for further study.

Individual lobsters and rock crabs of three size classes, each size class being composed of five individuals, were presented with sea urchins of six size classes, each represented by three individuals scattered over the tank floor. The number of sea urchins eaten in each size class was

monitored daily for 11 days. Eaten prey was being replaced by ones of similar size to maintain prey availability. Only male lobsters and rock crabs were used to avoid potential bias caused by sexual differences in morphology and predation behaviour. The prey (sea urchin) size classes (test diameter) were 10-19, 20-29, 30-39, 40-49, 50-59, and 60-69 mm. Predator size classes were 55-65, 85-95, 145-155 mm carapace length for lobsters and 50-50, 80-90 120-130 mm carapace width for for rock crabs.

Four male lobsters 85-95 mm carapace length, and four male rock crabs 80-90 mm carapace width were each given ten sea urchins 30-39 mm diameter, and ten mussels 30-35 mm length. The number and species of prey eaten were monitored daily for 11 days, eaten prey being replaced daily. The sizes of sea urchins and mussels used were known to be vulnerable to lobsters and rock crabs of the sizes used.

The energy value of mussel and male and female sea urchin flesh was measured in a Gallenkamp ballistic bomb calorimeter. The flesh from known sizes of mussels and both sea urchin sexes was dried to constant weight at 75 C, enabling regression equations of prey dry weight on size, and hence prey energy content, to be calculated.

RESULTS

Only 21 (39%) out of 54 lobsters and 32 (39.5%) out of 81 rock crabs of the sizes used successfully fed on sea urchins within the preliminary six-day period. All the predators that failed to eat sea urchins opened and ate edible mussels within a six-hour period, indicating that they were in a feeding condition.

Both lobsters and rock crabs appeared to encounter and attack sea urchins randomly. Sea urchins that could not be broken within a short period were rejected. Attack success rate decreased as sea urchin size increased. Before beginning the attack proper, rock crabs and lobsters usually tore the sea urchin away from its horizontal or vertical substrate using their chelae or walking legs. However, both lobsters and rock crabs were occasionally observed feeding off large sea urchins that were still attached to the substrate. Lobsters, unlike rock crabs, are heterochelous and usually used their comparatively massive crusher chela to open sea urchins; the more slender cutter chela served only to manipulate and support prey that was being crushed. Rock crabs demonstrated no such chelal preference. Invariably the sea urchin test would be broken into fragments by both

lobsters and rock crabs before all the soft tissue was extracted. Rock crabs tore away tissue using their chelae and mouthparts, whereas lobsters used only their mouthparts to glean flesh from the broken test.

The following distinct predation methods on sea urchins could be recognized for lobsters and rock crabs. Lobsters indiscriminantly halved or crushed sea urchins small enough to be gripped within the crusher chela. Larger sea urchins, over about 40 mm diameter, were usually held by the third maxillipeds or first pair of walking legs whilst being punctured by a pinching action of the crusher chela. The initial puncture was then enlarged by either chela until the soft tissue inside the test could be extracted. Lobsters were occasionally observed scissoring away the sea urchin's spines before attempting to puncture the test. In a few instances, lobsters punched holes through the test using the tips of one or both their chelae in a stabbing action. Lobsters had difficulty opening the largest sea urchins, over about 65 mm diameter, which were difficult to manipulate and whose size exceeded the gape of the chelae. Several spine scissoring and puncturing attempts were normally required before these prey succumbed.

Rock crabs crushed outright small sea urchins which could be grasped within the chelal gape. Sea urchins larger than about 20 mm diameter were manipulated with the chelipeds and walking legs whilst indiscriminate attempts were made to puncture the test by stabbing and pinching with the chelae. Spines were frequently scissored away, allowing easier puncturing of the test. About half of the crabs observed were more specific in their predation methods and, after turning the sea urchin over, attacked the vulnerable, non-spined, peristomial membrane around the sea urchin's mouth. Even the largest sizes of sea urchin available were vulnerable to predation by this latter method after they had been turned over.

Sea urchin fragments resulting from lobster predation were invariably finer than those left after rock crab attack. In addition, rock crabs that had opened sea urchins through the peristomial region characteristically left the apical half of the test unbroken.

The energy value of mussel flesh was 17.29 ± 1.1 kJg^{-1} ($n = 6$) and the energy value of male and female sea urchin flesh was 16.21 ± 0.20 kJg^{-1} ($n = 6$) and 20.46 ± 2.17 kJg^{-1} ($n = 6$) respectively.

There were no significant differences between the test diameter to flesh dry weight relationships for male and female

sea urchins (slope: $t = 1.28$, $n = 63$, $P = > 0.2$; intercept: $t = 0.10$, $P > 0.9$). Thus, for sea urchin prey a 1:1 sex ratio was assumed with a mean flesh energy value of 18.33 kJg^{-1}, and a test diameter to flesh dry weight (W) relationship of:

$$\ln W(g) = 2.85 \pm 0.14 \ln \text{diameter (mm)} - 10.35 \quad (R^2 = 0.98,\ n = 63).$$

Mussel dry weight (M) was proportional to mussel length according to the equation:

$$\ln M(g) = 2.43 \pm 0.07 \ln \text{length (mm)} - 10.38 \quad (R^2 = 0.96,\ n = 54).$$

All lobsters and all but the smallest size class of rock crab were able to open and eat the full size range of sea urchins available to them. However, from the diet curves (Figures 1, 2), it is apparent that both lobster and rock crabs showed preferences for certain size ranges of sea urchins. Moreover, the size of the preferred prey increased with predator size. Feeding rate, in terms of mean number of sea urchins eaten per day (Figures 3, 4) showed no apparent increase with predator size, although it was variable between individual predators from day to day, and between predators of the same size class. Mean daily energy intake for both lobsters (Figure 5) and rock cabs (Figure 6) (assuming all prey were completely eaten) was again variable, although some increase with predator size was indicated.

When offered a choice between equal numbers of sea urchins and mussel prey, both lobsters and rock crabs showed an overwhelming preference for mussels, both in terms of numbers of prey eaten and energy intake (Table 1).

DISCUSSION

Selected lobsters and rock crabs, of the sizes used, fed successfully on a wide size range of sea urchins, and most were capable of breaking open the largest *S. droebachiensis* available. The predators had several sea urchin opening techniques that varied with prey size. Lobsters and rock crabs both crushed smaller sea urchins outright. However, the flesh of prey larger than the grasp of the predator's chelae could be fully extracted only after the initial puncture hole had been enlarged and the test rebroken into smaller fragments. Some rock crabs showed a preference for attacking the relatively vulnerable peristomial membrane around the

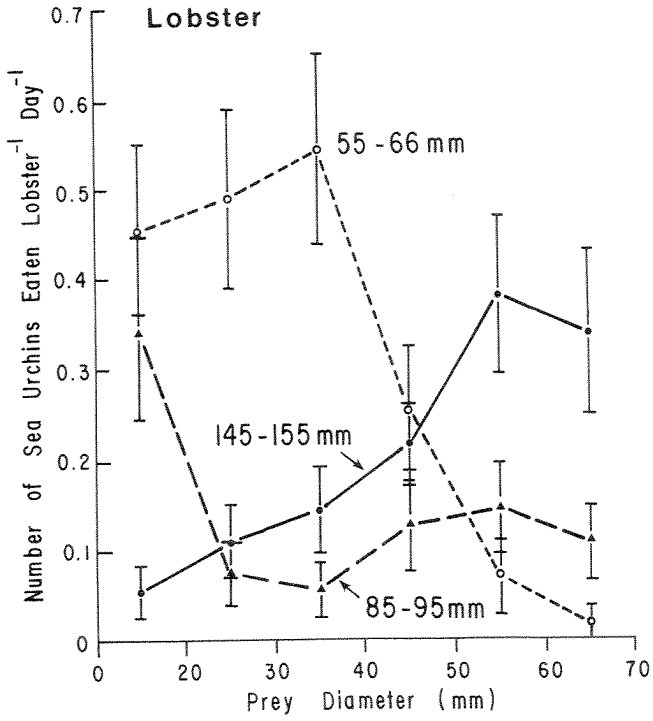

Figure 1. Mean daily sea urchin consumption (± S.E.) plotted against sea urchin test diameter for three lobster size classes.

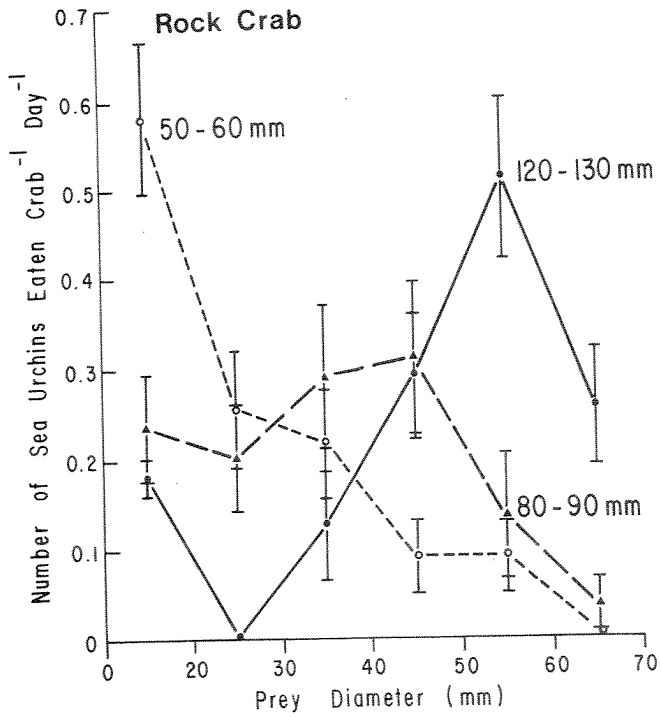

Figure. 2. Mean daily sea urchin consumption (± S.E.) plotted against sea urchin test diameter for three rock crab size classes.

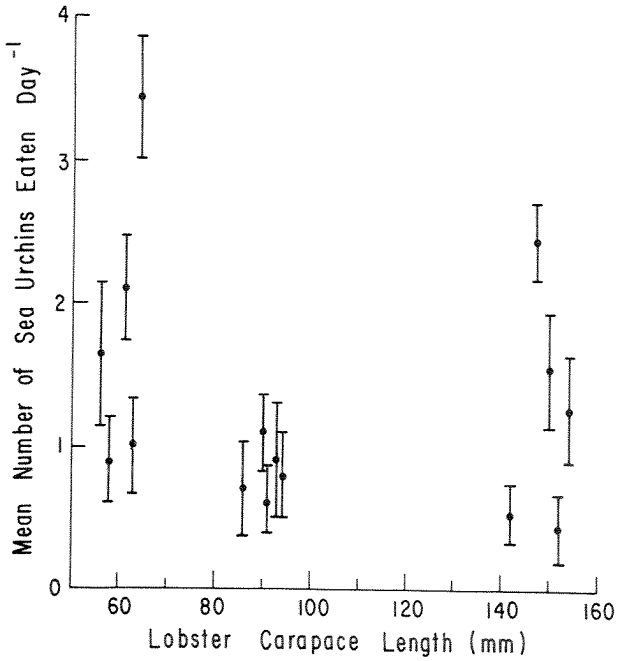

Figure 3. Individual lobster feeding rates, expressed as mean number (± S.E.) of sea urchins eaten per day relative to lobster size.

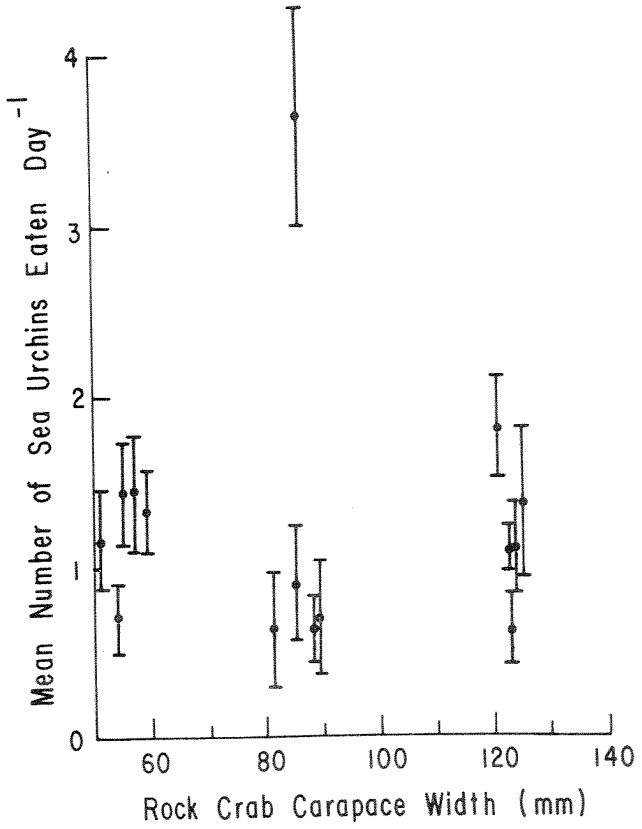

Figure 4. Individual rock crab feeding rates, expressed as mean number (± S.E.) of sea urchins eaten per day relative to rock crab size.

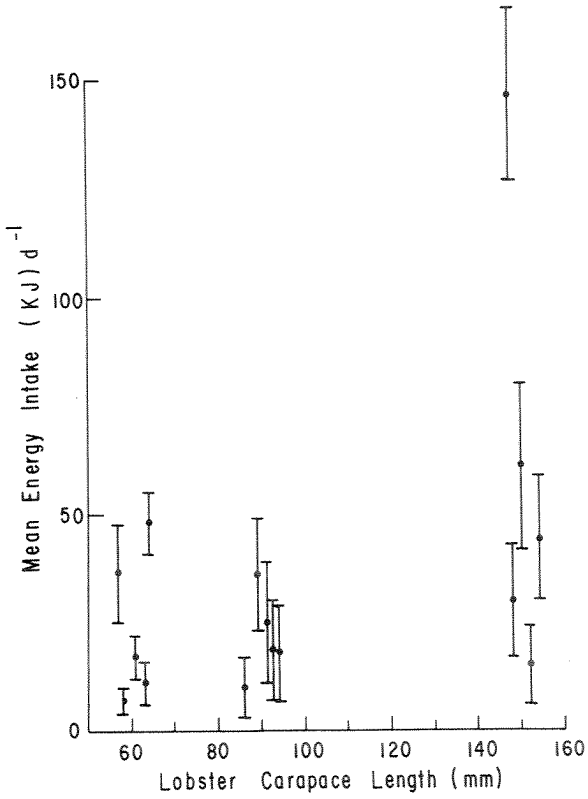

Figure 5. Individual lobster feeding rates, expressed as mean energy intake (± S.E.) per day relative to lobster size.

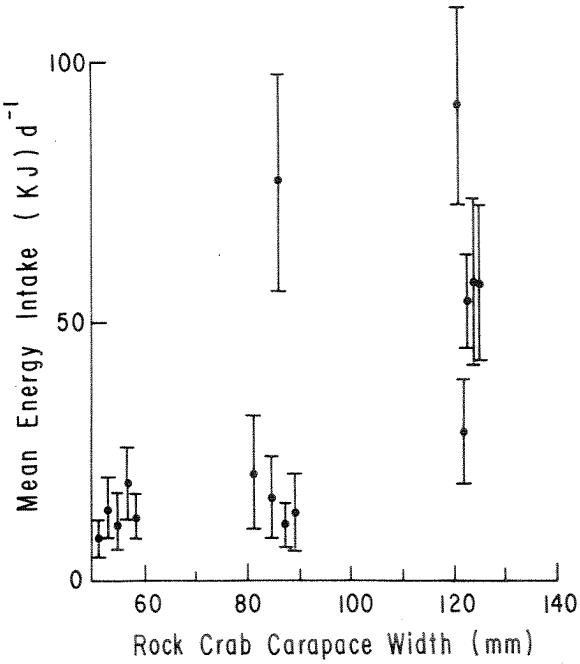

Figure 6. Individual rock crab feeding rates, expressed as mean energy intake (± S.E.) per day relative to rock crab size.

Table 1. Lobster and rock crab predation on a mixed population of mussels and sea urchins. Experiments conducted from February to April 1978.

	Prey numbers	Mean number eaten predator day^{-1} (±S.E.)	Ratio no. of sea urchins: mussels eaten	Total prey energy value (KJ)	Mean energy (kJ) intake predator day^{-1} (±S.E.)
a) Lobsters:					
Sea urchins	10	0.18 ± 0.66	1:43.4	146.1	2.66 ± 0.97
Mussels	10	7.82 ± 0.27		24.07	18.76 ± 0.65
b) Rock crabs:					
Sea urchins	10	0.09 ± 0.04	1:79	146.1	1.33 ± 0.63
Mussels	10	7.11 ± 0.42		24.07	17.07 ± 1.01

urchin's mouth; lobsters showed less specific attack patterns. Himmelman and Steele (1971) and Reddin (1973) infrequently observed Newfoundland lobsters opening sea urchins by first puncturing the peristomial membrane. They also observed Newfoundland rock crabs pinching a hole through the lower edge of sea urchin tests, but not starting at the edge of the peristomial membrane. Himmelman and Steele (1971) also noted, contrary to our observations, that sea urchin test fragments resulting from rock crab predation were finer than those produced by lobsters, and that sea urchins were immune from lobster and rock crab predation as long as they remained attached to the substrate. These regional differences suggest that factors such as learning may be involved in the attack behaviour.

Lobsters probably showed less specific opening techniques than rock crabs because of their larger, more powerful chelae that rendered most sizes of sea urchin vulnerable. Notwithstanding their smaller chelae, rock crabs appeared equivalent predators to lobsters, opening similar sizes of prey at a comparable rate. A similar overlap in lobster and rock crab predatory capabilities was observed for sea scallop, *Placopecten magellanicus*, prey (Elner and Jamieson, 1979) and suggests that lobsters and rock crabs would be direct competitors in limited prey situations. Observations on predation techniques used by various crab species and lobsters to open the sea urchin *Paracentrotus lividus* (Muntz et al., 1965) resemble those noted for *H. americanus* and *C. irroratus* on *S. droebachiensis* prey.

Lobsters and rock crabs showed preferences for specific, comparatively broad sea urchin size ranges; and larger predators showed a preference for prey of a larger size range than smaller predators. Similar, but narrower, more well-defined diet curves have been demonstrated for green crabs, *Carcinus maenas*, optimally foraging on mussels to maximize their energy intake per unit foraging time (Elner and Hughes, 1978), and for lobsters and rock crabs foraging on sea scallops (Elner and Jamieson, 1979). Elner and Hughes (1978) observed that green crabs actively chose prey from an optimal preferred size range. However, because of the broadness of the preferences in these experiments and the associated observations on prey selection behaviour, it is likely that the diet curves reflect only mechanical considerations. It is suggested that preferences are explained by predators, relative to their size, having difficulty and failures in opening larger sea urchins and finding smaller sea urchins more difficult to manipulate and detect.

With unlimited prey availablity, all size classes of lobsters and rock crabs had a similar sea urchin predation

rate of about one sea urchin/predator/day, although because the larger predators opened larger prey their energy intake was greater. By comparison, Himmelman and Steele (1971) observed mean daily predation rates of 0.3 sea urchins/lobster/day and 0.6 sea urchins/rock crab/day. The rock crabs had a higher predation rate but ate smaller sea urchins than the lobsters. Results from Himmelman and Steele (1971) and this study are in general accord, and differences can be accounted for by natural variation and possible prey size and temperature disparities.

Lobsters and rock crabs demonstrated 1:43.4 and 1:79.0 numerical preferences, respectively, for mussels over sea urchins when equal numbers of both species were available. That sea urchins are not a favoured food of lobsters is supported by olfaction experiments (McLeese, 1973) that showed tank water from intact prey and extract of echinoderms was practically non-stimulatory to lobsters whereas extracts of molluscs, crustaceans, and fish were highly stimulatory. Similarly, Hirtle and Mann (1978) concluded that crabs are probably more attractive to lobsters because of their more stimulatory odor and their greater activity, compared to sea urchins or mussels. Evans and Mann (1977) also found that lobsters exhibited a 5:1 preference for rock crab over sea urchin prey when the numerical ratio of sea urchins to crabs varied from 0.25:1 to 8:1. In contrast, Breen (1974) and Breen and Mann (1976a) modelled the interactions between lobsters, sea urchins and rock crabs on the basis that, out of five prey species, sea urchins and rock crabs were preferred by lobsters second only to green crabs and were selected at a higher rate to horse mussels. However, Breen (1974) and Breen and Mann (1976a) used only horse mussel sizes that they considered readily available to lobsters in their area, and it is probable that the mussels were too large for the particular sizes of lobsters to open.

In conclusion, although a proportion of the lobsters and rock crabs studied were sufficiently versatile and adapted to open a wide range of sea urchin prey, they appeared to do so with a low preference and at low rates. Laboratory experiments may demonstrate a particular predator's feeding capabilities on a particular prey, but they do not show that this happens under natural conditions. Indeed, studies by Garnick (1978) indicate that the rate of green sea urchin predation in the field may be below that observed in the laboratory due to *S. droebachiensis* forming defensive aggregations. Nevertheless, with these results it is difficult to attribute increases in sea urchin numbers to a decline in the lobster population alone, or to support the hypothesis that lobsters and rock crabs are a key factor in controlling the populations of such an abundant prey.

ACKNOWLEDGMENTS

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THE FOOD OF LOBSTERS

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ABSTRACT

The stomachs of 2,181 lobsters, 1,757 of which were collected by divers, were dissected and the contents examined. Much of the contents, though chewed, were readily identifiable. Principal prey items are sea urchins, starfish, tunicates, polychaetes, crabs, pelecypods, eelgrass and shell fragments, with groups such as mysids, shrimps, amphipods, isopods, algae, brittle stars, fish and others occurring with varying but lesser frequency. There was no evidence of cannibalism.

Changes in diet with season and with lobster size appear to be related to the abundance or otherwise of suitably sized or preferred food which, in turn, may be related to the settling time and success of many of the prey items. Changes in diet with molt cycle appear to be related only partially to the need for calcium and may more likely reflect changes in predation efficiency. Newly molted lobsters begin feeding within hours of ecdysis but their diet comprises items picked off floor and walls of burrow, and active foraging does not begin until later. Feeding diminishes as the lobster enters proecdysis. Lobsters contain newly ingested food at all times of day but have fullest stomachs in late morning. Maximum stomach content weights are 2.2 to 2.5% of total body weight. Rate of feeding has yet to be determined. Calorific content of diet in fall is higher than in spring, due largely to the increased availability of prey species, such as crabs, with high calorific value.

INTRODUCTION

Herrick (1909) found that the food of lobsters consisted principally of fish and benthic invertebrates, algae, eelgrass, shell fragments, sand, and gravel. The fish were small and were taken alive, independently of fishermen's traps, i.e., they were not bait. Invertebrates were mostly

crustaceans such as isopods and decapods, (principally crabs), molluscs (pelecypods and gastropods), starfish, sea urchins, and hydroids. He detected little change in the food during winter and spring months when samples were taken, but did note that lobsters fed when the water was cold. He also considered that while lobsters were scavengers they probably preferred fresh food. Squires (1970) examined the stomachs of 186 trap-caught lobsters from Newfoundland. Apart from fish (probably bait), which occurred in 50% of the stomachs examined, principal prey were polychaetes, crabs and periwinkles with lesser amounts of lobster shell fragments, whelks, mussels, sea urchins, and other species. Dow (1949) stated that from observations on lobsters in captivity and the experience of commercial fishermen it was believed that lobsters ate fish, molluscs and other invertebrates and small quantities of algae. Lobsters in captivity are extremely cannibalistic and there is a strong popular opinion that this applies in nature as well. Prudden (1962) sums up popular opinion with the unqualified statement that lobsters are scavengers and cannibals.

This paper is based on the analysis of stomach contents of 2,181 lobsters. It describes some aspects of the diet of lobsters and explores briefly the effects of season, lobster size, stage in molt cycle and time of day, and variations from year to year.

METHODS

Lobsters were collected from various localities in Kouchibouquac Bay, N.B. (Figure 1). Most were collected by scuba divers who searched areas of seabed temporarily enclosed by a black nylon net fence fastened to a folding metal frame. The net fence, which was buoyed on the upper edge and weighted on the lower, was about 1 m high. It hindered the escape of lobsters, delimited the area precisely, and encouraged the diver to examine the ground carefully rather than merely pick up the most easily captured lobsters. A number of lobsters were examined from samples taken in Kouchibouquac Bay with a specially designed lobster dredge (Wilder, 1953) which was used to sample small lobsters.

Hand collection eliminates bias that may occur in sampling by trapping when only hungry lobsters might be attracted to a particular bait, or by trawling or dredging when only active or foraging lobsters would be taken. However, hand collection is dependent upon the visual acuity, manual dexterity, patience and endurance of each diver and is undoubtedly biased itself. Apart from the failure to collect

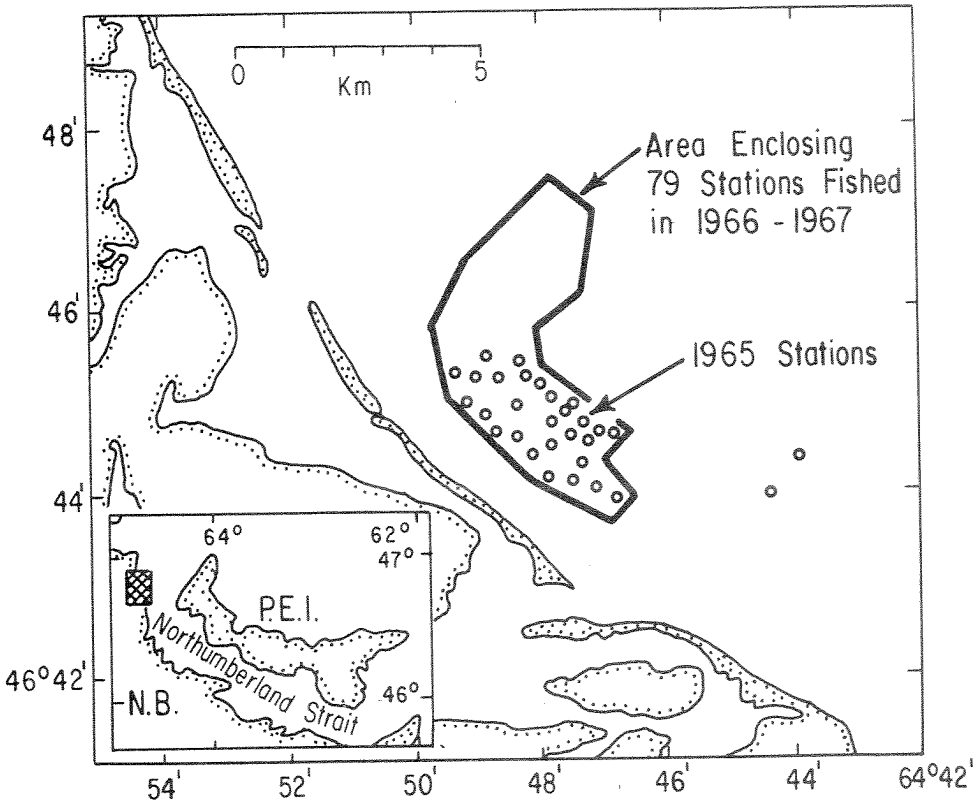

Figure 1. Sampling stations at Kouchibouquac, N.B.

lobsters burrowed under immovable boulders or in deep crevices, the main bias was probably in the underestimation of lobsters smaller than about 30 mm carapace length (Scarratt, 1973). Nonetheless, lobsters as small as 6.8 mm CL were taken although, for practical reasons, the stomach contents of those less than about 15 mm were not examined. The largest lobster was 158 mm CL.

Captured lobsters were placed in a fine-meshed, nylon net bag and brought to the surface where they were killed in a 5% solution of neutralized formalin in sea water. The depth, temperature of the water near the bottom, and the nature of the seabed at each station were recorded. Later the lobsters were sexed, measured, and weighed, and the shell condition and the absence of any walking legs or chelae noted. The carapace of each lobster was removed, the stomach excised and its contents flushed into a petri dish for microscopic examination.

Observations on the 1965 sample were purely qualitative, no attempt was made to estimate the relative amounts of prey items, and only frequency of occurrence is available. In 1966, the intact stomach was weighed with its contents and an estimate was made of the volume of each prey in terms of tenths of the total stomach contents. Individual items occupying less than 0.1 of the total contents were recorded as present in trace amounts. Subjective assessments were also made of stomach fullness to the nearest quarter. (McLaughlin and Hebord [1959] used a similar technique that estimated fullness in 20% increments.) These estimates of stomach fullness were subsequently shown to be inadequate, and in all other samples the stomach was weighed full and empty and, by subtraction, the weight of the contents obtained. From these, the following values were calculated:

1) For all samples, frequency of occurrence of each prey:

$$F = \frac{N_{P_1}}{N} \qquad (1)$$

where N_{P_1} is number of occurrences of prey, and N is number of stomachs examined in the sample.

2) For all samples except during 1965, volume of occurrence (and standard deviation):

$$V_{P_1} = \frac{V_{1_{P_1}} + V_{2_{P_1}} + V_{3_{P_1}} + \text{----} V_{n_{P_1}}}{N_{P_1}} \qquad (2)$$

3) For all samples except 1965, relative proportion of each prey:

$$R_{P_1} = \frac{V_{1_{P_1}} + V_{2_{P_2}} + \text{----} + V_{n_{P_1}}}{N} \qquad (3)$$

4) For 1967 and drag samples only, estimated weight of prey in grams per kilogram total lobster weight:

$$W_{P_1} = \frac{R_{P_1} \times w}{W}$$

where w is total weight of food in the sample and W is total weight of lobsters. This is similar to the method used by Takeuchi (1968) for King crabs.

RESULTS AND ANALYSIS

General Observations

In view of Herrick's 1909 statement that the food is chopped into mincemeat and enters the stomach as a stream of fine particles, it was surprising to find that much of the stomach contents were clearly recognizable and identifiable. Newly ingested polychaetes were frequently entire, though well torn from their passage through the mouthparts. Small tunicates (Molgula spp.) were usually ingested whole; similarly small gastropods, pelecypods, amphipods, copepods, barnacles, etc. Many polychaetes could be identified when almost completely digested by the persistence of buccal teeth, jaws and setae, and crab remains (Cancer irroratus) were frequently identified by the persistent chitinous tips of the walking legs. Tunicate tests, isopod, amphipod and cirripede exo-skeletons could be recognized and occasionally identified after the soft parts had been digested. Flocculent digested tissue was referred to as detritus regardless of its possible origin.

Frequency of occurrence of food items in the samples

Apart from detritus (which included all semi-digested, unidentifiable, flocculent material), the principal items were: eelgrass fragments, usually found in small quantities only; polychaetes, principally nereids but also including

polynoids and polydorids; rock crabs, Cancer irroratus; lobster shell fragments; molluscan shell fragments which, judging by their eroded condition had been picked up off the bottom and not as part of a living mollusc; horse mussels, Modiolus modiolus, which had been living when eaten; starfish, principally Asterias vulgaris; sea urchins, Strongylocentrotus droebachiensis; and tunicates, principally Molgula sp. Other prey species were taken in lesser amounts, and in some instances these have been grouped in Table 1. Admittedly, information on prey identified to species level is lost by this method, but major principles are not obscured since many items were not identifiable beyond family or phylum in the first place.

A number of features are clear. Lobsters enjoy a varied diet. They normally appear to take live food, which includes relatively fast moving creatures such as fish, mysids, shrimps, and amphipods, as well as sessile or slower moving forms. They do take a proportion of inanimate material such as sand and pebbles, and it is clear that this is deliberately eaten and not merely ingested accidentally. They do scavenge, although this is not the main source of their food; and from time to time they ingest some bizarre items such as pieces of plastic, wool, tea bags complete with cotton cover and tea leaves, and in one instance a small iron nail.

There is no evidence that they are cannibalistic in nature. All trace of lobsters found in the stomachs were shell fragments only; by contrast, crab remains consisted of both shell and soft parts.

There appears to be some variation between seasons and also between years; for example, crabs were more frequently consumed in late summer and fall than in the early summer (Figure 2); and tunicates which were commonly present in 1965 and 1966 samples were only recorded in a few samples and in trace amounts in late 1967. Crabs, starfish, and mussels on the other hand, were eaten more frequently in late 1967 than at other times (Table 1). Herrick (1909) stated that the stomachs of soft-shelled lobsters were frequently stuffed with mollusc shells and other calcareous fragments, pointing out the need for a "supply of lime after molting." The fall 1967 sample does contain a lower percentage of hard-shelled lobsters than other samples and, for this reason, changes in diet between years and seasons may be masked by changes due to the molt cycle.

Changes in diet of hard-shelled lobsters, May-October 1966

Each lobster, at capture, was assigned to one of six shell hardness categories: 1) newly molted, shell soft and

Table 1. Percentage frequency of occurrence of food items in lobster stomachs. T = trace.

Year	1965	1966(1)	1966(2)	1967(1)	Diurnal study 1967	1967(2)	Drags(1)	Drags(2)
No. lobsters in sample	229	429	412	412	148	129	209	213
Mean CL (mm)	40.2	40.8	40.3	42.6	40.8	41.5	23.9	24.2
% hard shell	-	84.6	77.2	98.0	95.3	60.5	85.6	84.0
Empty (%)	9.6	11.0	8.0	4.6	4.1	0.8	15.8	11.3
Detritus	6.6	73.0	44.7	53.7	52.0	92.2	41.1	49.3
Liquid		2.1	9.2	5.6	0.7	2.3	2.3	0.5
Sand, pebbles	10.0	7.0	1.7	6.8	6.1	0.8	4.3	7.5
Algae, green		0.2		0.2		0.8	0.5	T
red		1.2	1.0					0.5
brown		0.9	0.7	0.7	2.7	T	2.3	3.7
Vascular plants, eelgrass	21.8	29.8	10.9	26.7	27.0	8.5	3.8	6.1
Foramenifera	0.4	T	0.2	T			1.0	4.2
Porifera		2.1	0.7	0.7			5.3	8.0
Hydroida	2.1	0.5	0.7	2.9	4.1	T	T	1.9
Turbellaria							0.5	
Bryozoa		T	0.2	0.2			T	T
Polychaeta	24.7	8.6	8.4	20.1	27.7	4.7	21.5	18.3
Crustacea								
Ostracoda		T						
Copepoda	4.4	T	0.2			T		
Amphipoda	8.7	2.6	0.9	1.4	0.7		1.4	0.5
Isopoda							0.5	
Cirripeda	3.0	2.9	0.5	2.9			1.4	0.9
Decapoda larvae		T						

Table 1 (cont'd.)

Year	1965	1966(1)	1966(2)	1967(1)	Diurnal study 1967	1967(2)	Drags(1)	Drags(2)
No. lobsters in sample	229	429	412	412	148	129	209	213
Mean CL (mm)	40.2	40.8	40.3	42.6	40.8	41.5	23.9	24.2
% hard shell	-	84.6	77.2	98.0	95.3	60.5	85.6	84.0
Cancer irroratus	9.2	6.1	23.1	7.3	12.2	41.9	13.9	14.6
Homarus americanus shell	3.1	2.1	12.9		1.4	3.9		0.5
Mysidacea			0.2				2.3	11.7
Hyppolytidae	1.7							
Mollusca shell fragments	31.0	9.6	21.6	26.0	14.9	10.1	10.0	10.3
? (chitons)	3.9	2.8	5.1	1.0	0.7	0.8	0.5	
Gastropoda	3.0	0.7	1.2	1.5	2.0	T	1.4	1.3
Pelecypoda general		2.6	4.1	5.4	0.7	0.7	5.3	10.0
Mytillidae		31.0	10.7	15.0	13.5	58.1	35.8	43.2
Echinodermata								
Holothuria			0.7	0.5				
Asteroidea	5.2	4.4	13.8	17.2	1.3	60.5	26.3	13.6
Ophiuroidea	4.8	1.6	1.5	3.4	4.1			
Echinoidea	14.4	36.8	16.7	32.8	26.4	34.9	19.3	17.4
Tunicata	26.6	38.9	18.2	15.5	3.4	T	12.9	18.3
Vertebrata								
Pisces	0.9	2.3	5.6	2.2	2.0	7.8	0.5	0.5
Non marine items	0.4		0.5		0.7	0.8		
Mean no. prey/stomach	2.0	2.8	2.2	2.5	2.1	3.3	2.3	2.5

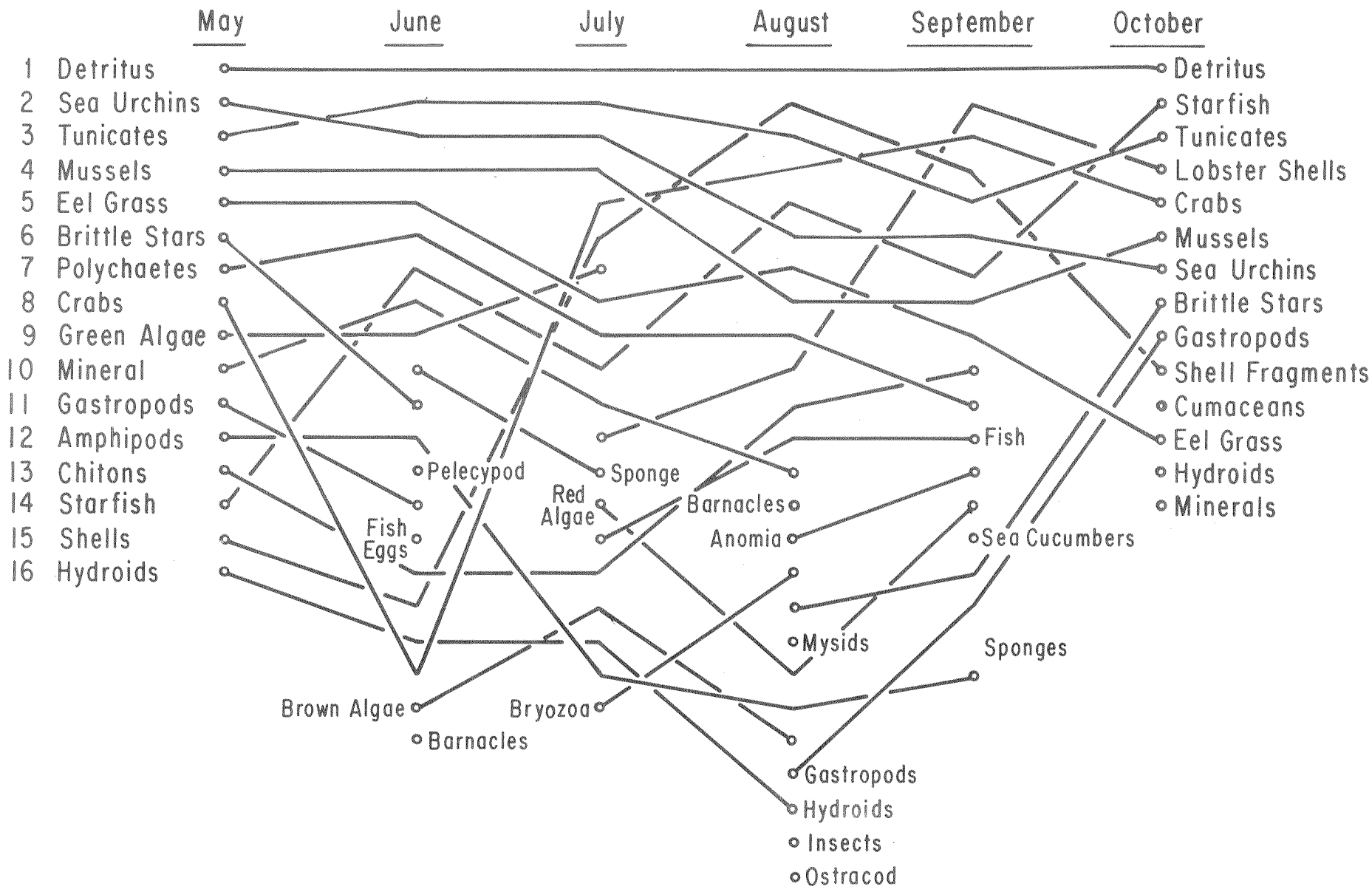

Figure 2. Food items found in the gut of lobster between May and October, 1966.

claws not yet filled out; 2) recently molted, claws filled out but shell still soft; 3) shell firm but yielding to light pressure from the fingers; 4) shell hard, yielding only to moderate pressure; 5) shell hard and rigid; 6) same as 5, but with epiphytic or epizootic growths such as sponges, bryozoans, barnacles. (Regrettably, no attempt was made to distinguish lobsters approaching the molt.) These categories can be approximated with the terminology of Drach and Tchernigovtzeff (1967) as follows:

Shell category	1	2	3	4	5	6
Intermolt stage	A_1	A_2	B	C_1-C_3	C_4	D_{0-4}

For the purposes of investigating seasonal changes in diet categories, 1-4 were considered to represent recently molted lobsters and are ignored for the time being.

Molting began in July and continued at least until October. The frequency of empty stomachs among the hard-shelled lobsters changed from month to month (Table 2). The high number during May when the water was cold is easily understood; thereafter, there was a general decline in the frequency of empty stomachs except in August when it was again high. This high value may be the result of premolt fasting described by Templeman (1936).

The frequency of occurrence of each of the principal prey items also changed throughout the six-month sampling period (Table 2). Thus, crab remains and shell fragments increased significantly, while the incidence of sea urchins rose to a peak in July and then fell away. Starfish reached their peak frequency in August. Mussels had a high frequency in May, declined to a low in August, and thereafter increased slightly.

Frequency of occurrence alone is not enough to demonstrate the full contribution of each prey item to the total food intake of the lobster sample; an estimate of mass is required. In the absence of weights of stomach contents, the relative proportion of each food item in each month's sample was calculated. Thus, selecting a few of the principal prey items: more starfish were eaten by hard-shelled lobsters during August, September, and October, whereas the trend in selection of mussels was quite the reverse, being at its lowest for hard-shelled lobsters in those two months. Sea urchins declined in importance during the six-month period, while crabs increased. Lobster shell fragments were detected only during the molting season. These trends are shown graphically in Figure 2.

Suitably sized samples of soft-shelled lobsters were restricted to August and September. Seasonal change in food

Table 2. Percentage frequency of principal prey in stomachs of hard-shelled lobsters, May-October 1966.

	May	June	July	Aug.	Sept.	Oct.
Number of lobsters examined	80	130	116	166	176	13
Empty	24	9	8	14	7	0
Detritus	60	77	85	48	48	62
Plant fragments	1	8	12	-	-	-
Eelgrass	35	15	18	17	14	-
Sand, pebbles	1	11	10	2	1	-
Polychaeta	6	8	10	10	9	-
Cancer irroratus	5	2	5	21	21	23
Lobster shell	-	-	-	1	12	15
Shell fragments	1	2	10	19	22	8
Mussels	42	40	27	8	12	23
Starfish	1	1	4	22	10	23
Sea uchins	21	36	44	23	12	31
Tunicates	31	45	56	19	21	31
Pisces	-	-	1	5	5	-

selection by soft-shelled lobsters has, accordingly, not been examined.

The effect of molt cycle on food selection

Samples taken in August and September 1966 and in September-October 1967 contained adequate numbers of lobsters within the six, shell-hardness categories described above. The samples were pooled and the relative proportion of each principal prey item computed for each of the six categories (Figure 3). Statistical differences were tested by first computing frequency and mean volume of occurrence of each prey, then performing a 2 x n contingency test on frequencies and a one-way analysis of variance on mean volumes within the shell categories.

This rather oblique approach to assessing the significance or otherwise of observed differences in the total amounts of food eaten by lobsters within a sample is dictated by the impossibility of obtaining weights of prey items in the stomachs, and assessing the differences directly. All principal prey items except tunicates show significant frequency differences among the six shell categories. Only mussels show significant variation in mean volume of occurrence. Mussels and sea urchins have rather unusual curves and will be discussed separately.

It is clear that lobsters begin feeding within a matter of hours of molting, before the lobster has fully grown to its new size (definition of shell category 1). Mostly items of high calcium content are taken; for example, there were only small amounts of partially digested soft parts of prey (referred to as detritus). This suggests that lobsters do not forage and the shell fragments, chitons (and cast shell) are picked up off the floor (and walls) of the burrow. Large meals of mussels were eaten by lobsters in shell category 1 although frequency of occurrence was low. This would be consistent with non-foraging lobsters eating opportunistically on mussel populations in or close to the burrow.

As the shell hardens, foraging is resumed and the incidence of more mobile prey species increases. Crabs and starfish are taken by actively foraging lobsters in the middle-shell hardness categories. The incidence of semi-digested detritus is at its greatest in these groups. Sea urchins follow a similar curve except for the high incidence in shell category 1 which seems to represent selection of cast sea urchin spines and fragments of test off the burrow floor.

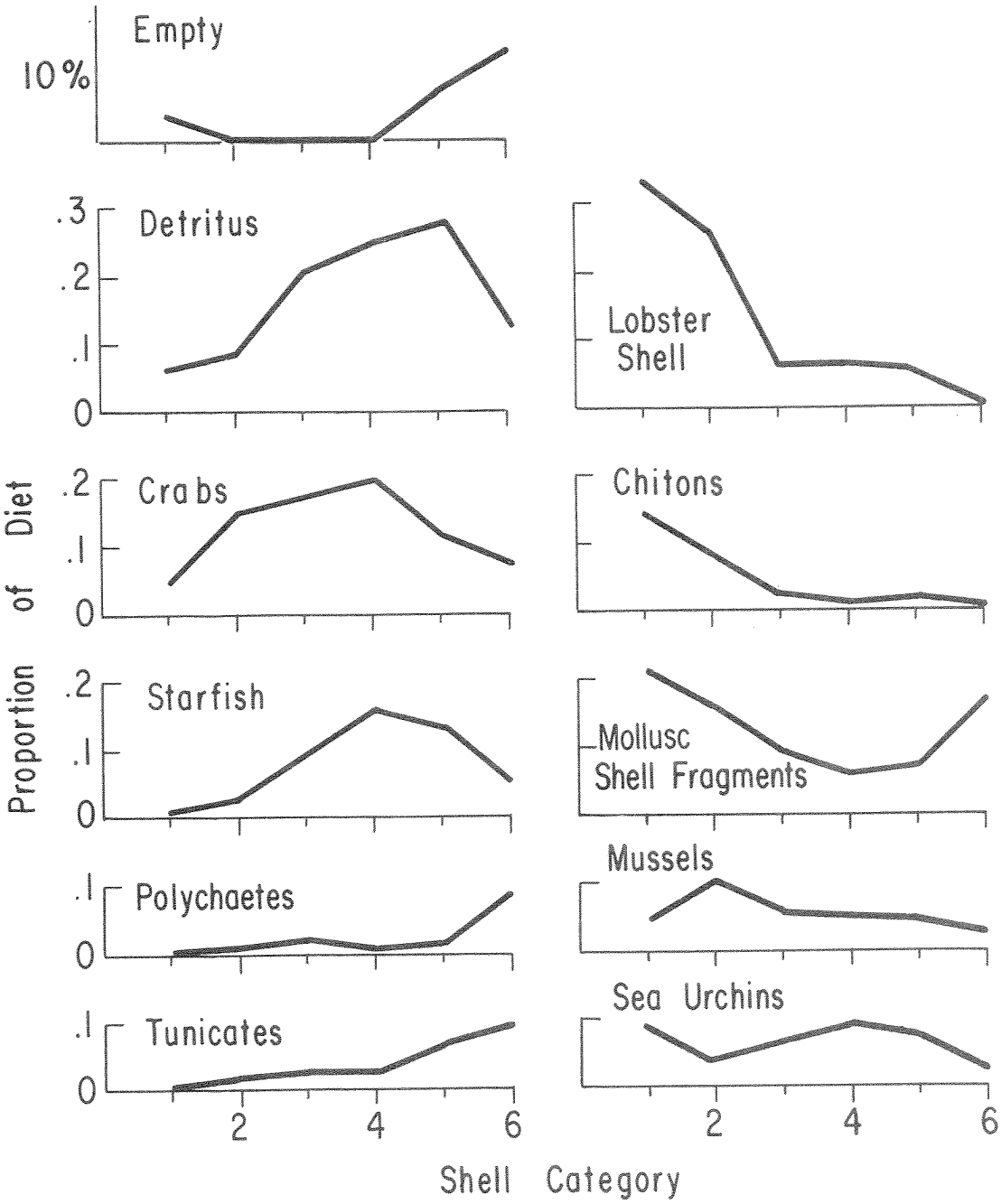

Figure 3. Principal prey items as a proportion of total food at different stages of the lobster molt cycle.

In lobsters approaching premolt, the frequency in occurrence of detritus, crabs, and starfish (the evidence of active foraging) is reduced. Shell fragments are more common than in the stomachs of intermolt lobsters, as are polychaetes and possibly tunicates. It is probably safe to assume a return to a less active foraging behavior pattern, although there does not appear to be the same demand for calcium as in the early postmolt groups. The number of lobsters with empty stomachs is higher.

Changes in Diet With Lobster Size

To eliminate variation due to molt cycle and season, 404 hard-shelled lobsters taken in June 1967 were examined. They ranged from 16-83 mm CL. To determine whether lobsters vary their food with size, the lobsters were grouped into five size groups: below 30 mm, 30-39.9 mm, 40-49.9 mm; 50-59.9 mm, and over 60 mm CL. The number of lobsters in each group containing prey was tested against the number not containing the item (X^2 contingency test). Polychaetes were more frequent in stomachs of larger lobsters (Table 3), as also were crabs, mussels, and fish. Tunicates were taken most frequently by lobsters of intermediate size. There is an impression that starfish were more frequently taken by the smallest lobsters and sea urchins by lobsters of intermediate size, but these results are not statistically significant.

Differences in relative volume occupied by each prey item were explored as before by computing for each prey a one-factor analysis of variance. Sea urchins were eaten in significantly larger amounts by smaller lobsters (Table 4), even though frequency of occurrence within the size groups did not change significantly. Tunicates were taken in greatest quantity by intermediate-sized lobsters, and intermediate-sized lobsters had relatively smaller volumes of mussel remains in their stomachs.

The importance of each prey species to the different size groups is summarized in Figure 4 which, in effect, combines both frequency of occurrence and meal size. Sea urchins formed a significantly smaller part of the diet of lobsters over 50 mm carapace length. There were two peaks in the selection of polychaetes, one by lobsters less than 30 mm and one by lobsters in the 50-60 mm size range, which may represent predation on different-sized species. Tunicates were taken most abundantly by lobsters in the 50-60 mm size range. Mussels were taken in largest amounts by lobsters smaller than 30 mm, and then increasingly by lobsters above 40 mm. This was quite clearly a size selection. The smallest lobsters were selecting recently metamorphosed mussels, while

Table 3. Percentage frequency of occurrence of principal prey in hard-shelled lobsters by size groups, spring 1967.

	Size group					
	1	2	3	4	5	
Size (mm)	<30	30-39.9	40-49.9	>50-59.9	60.0	Signif-
Number	50	117	123	92	28	icant
Empty (%)	8.0	7.7	0.8	2.2	10.7	change
Detritus	50.0	40.2	59.3	63.0	60.7	
Sand	4.0	0.0	6.5	10.9		
Eelgrass	20.0	22.2	34.1	25.0	21.4	
Polychaetes	14.0	12.8	17.0	30.4	21.4	$p < .01$
Crabs	T	2.6	5.7	17.4	14.2	$p < .01$
Shell fragments	24.0	26.5	82.4	25.0	21.4	
Mussels	6.0	4.2	18.7	25.0	28.6	$p < .01$
Sea urchins	28.0	35.9	40.7	26.1	17.8	
Starfish	20.0	21.4	16.3	14.3	3.5	
Tunicates	12.0	13.7	13.0	26.1	7.1	$p < .05$
Pisces	0.0	1.7	0.8	3.2	10.7	$p < .01$

Table 4. Mean relative volume of principal prey species by lobster size groups, spring 1967.

	Size group					
	1	2	3	4	5	F
Size (mm)	<30	30-39.9	40-49.9	50-59.9	>60.0	ratio
Number	50	117	123	92	28	
Empty (%)	8.0	7.7	0.8	2.2	10.7	
Detritus	4.4	5.0	4.9	3.9	5.1	
Sand	3.0	1.8	1.7	1.0	2.5	
Eelgrass	3.2	1.8	2.1	2.1	1.5	
Polychaetes	6.0	3.2	4.1	3.8	2.1	
Crabs	<0.1	3.3	2.8	4.1	5.3	
Shell fragments	2.7	4.3	3.4	2.4	2.7	<.05
Mussels	9.3	2.8	3.4	3.2	4.0	<.01
Sea urchins	6.1	4.7	3.8	2.3	2.6	<.01
Starfish	5.3	5.4	4.7	3.8	4.0	
Tunicates	3.5	3.9	5.0	2.7	3.5	<.05
Pisces	0.0	3.0	1.0	3.3	7.3	

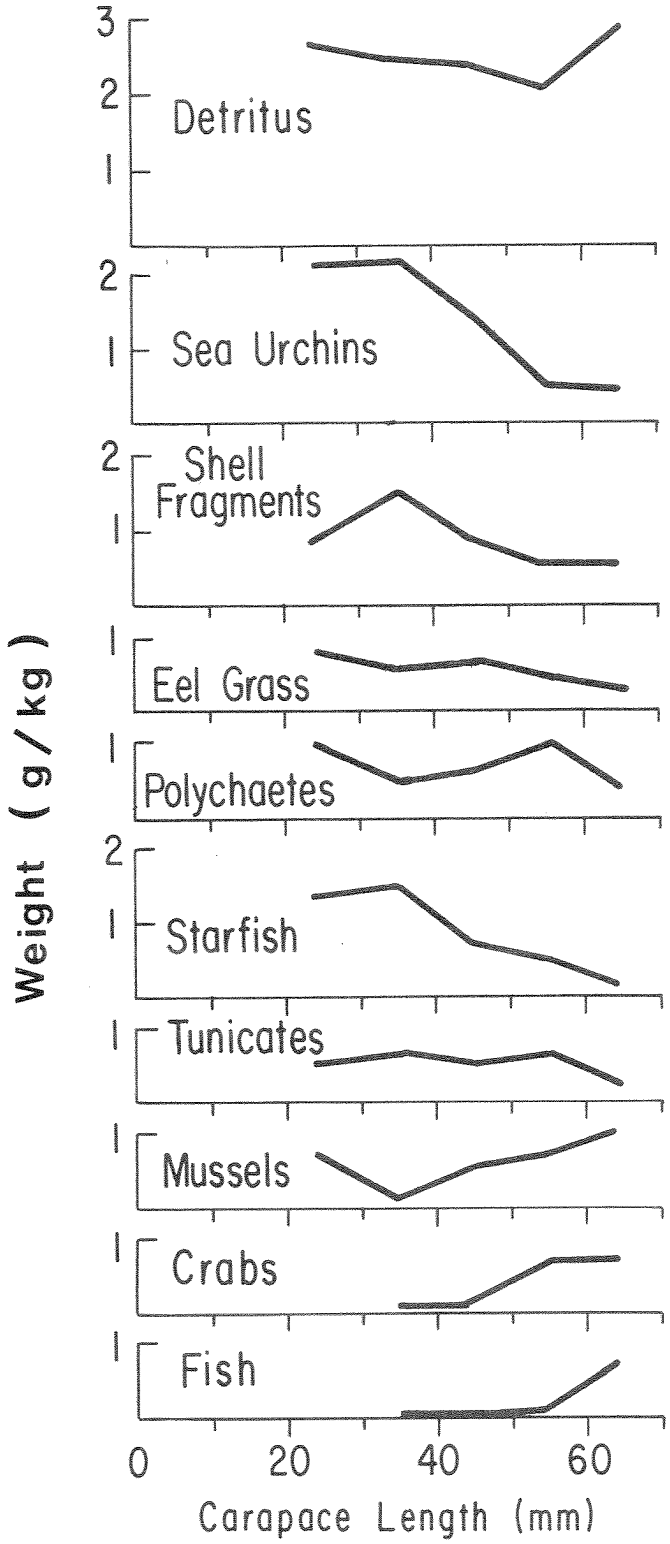

Figure 4. Estimated weights of prey items by size groups.

larger lobsters were eating large mussels only. Crabs and fish remains were found mainly in lobsters over 50 mm CL. Starfish (like sea urchins) appear to be of more importance in the diet of smaller lobsters but neither frequency of occurrence nor mean relative volume show significant differences between the size groups. Both, however, show identical trends. The observed selection is likely real and probably dependent upon the ready availability of small starfish at that time of year.

Sample size in the fall of 1967 was too small for effective statistical analysis, but some corroborative evidence is forthcoming. Crabs were the principal food item, particularly of larger lobsters, but the abundance of newly settled crabs that year enabled the smallest lobsters to add this item to their diet.

Diurnal changes in stomach contents

Three attempts were made to collect samples suitable for the assessment of diurnal changes in stomach contents. On July 5, 1967, sampling began at one station at 10:00 a.m. and thereafter at four-hour intervals until 10:00 p.m. when rough weather terminated the study. The station was in 7 m of water (mean temperature 7.5 C). Subsequently, seven samples were taken from the same station at approximately four-hour intervals between 10:00 a.m., July 24, and 11:00 a.m., July 25 The mean temperature was 6.8 C and the weather was overcast with occasional rain. A further series of six samples were taken at a different station in 9 m of water between 12:00 noo on July 27 and 8:00 a.m. on July 28. Mean bottom temperature was 6.4 C and the weather clear. Ten lobsters were taken in each sample.

The weight of stomach contents relative to total weight when plotted against time of capture gives an indication of periodic changes (Figure 5). The stomachs were at their fullest during the latter part of the night and morning. Little information could be obtained from the appearance of the stomach contents since some newly ingested material was found at all times of the day. In general, all prey species with the possible exceptions of shell fragments were at their maximum values in night and morning and at their lowest during the afternoon and evening.

There is general agreement that lobsters are more active at night, but it is possible that many lobsters may take food back into the burrow to be consumed at leisure. This has been observed among lobsters in the laboratory and may perhaps

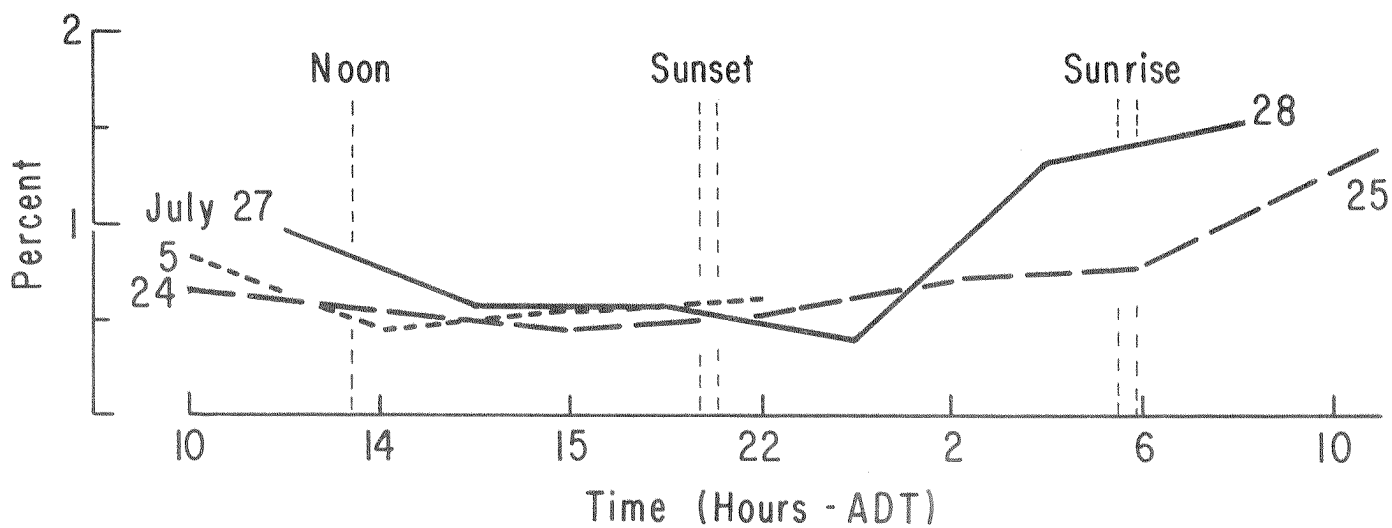

Figure 5. Stomach contents as a percentage of body weight by time of day.

account for the generally higher stomach weight during the morning hours. The low incidence of shell fragments during the night and morning may be due to these items being picked up mainly from the floor of the burrow during the daytime.

Maximum stomach contents

A few of the lobsters examined were completely gorged. One, weighing 92.0 g, had stomach contents weighing 2.5 g or 2.7% of the total weight; another weighing 515 g had stomach contents of 12.7 g or 2.4% of the total weight. The mean value of the 16 fullest stomachs of the 1967 fall sample was 2.2%.

The food of lobsters as a source of energy

Brawn et al. (1968) gave details of the caloric content of several marine benthic invertebrates. Several of these have been identified in lobster stomachs, and generalizations may be made about other prey which have only been identified as far as family or phylum. Thus, polychaetes commonly range between 500 and 800 cal/g live weight; *Asterias vulgaris* between 500 and 600 cal/g; *Strongylocentrotus* around 300 cal/g. With certain assumptions, it is possible to estimate the contribution of each of the principal prey groups to the energy budget of the lobster population (Tables 5 and 6).

The first assumption is that the detritus which for the most part is unidentifiable, partially digested remains of other food, is derived *pro rata* from identifiable food items. If this is so, detritus can be excluded from the calculations and attention focussed on the identifiable prey. The second and more tenuous assumption is that the digestion rates of all prey items are comparable. This is clearly not so, and accepting this assumption will result in underestimation of rapidly digested prey species. However, in the 1967 spring samples starfish and polychaetes, although appearing part way down the relative abundance list, together contributed a major fraction of the energy available to lobsters, with sea urchins, crabs, and mussels contributing somewhat less (Table 5).

In the fall (Table 6), nearly half the energy was derived from crabs, with a large fraction coming from starfish. Other prey with low calorie contents must be eaten largely as a source of calcium carbonate for shell construction. The caloric value of the lobster diet in the fall is approximately 40% higher than in the spring - 650 cal/g compared with 470 cal/g. These data have already appeared in Miller et al. (1971).

Table 5. Caloric content and contribution of principal prey items to energy budget, spring 1967.

Food item	g/kg	Caloric content cal/g wet wt	Contribution cal/kg lobster
Detritus	2.3	-	-
Sea urchin	1.3	300	390
Shells	0.8	0	0
Starfish	0.8	630	500
Polychaete	0.7	700	490
Tunicate	0.5	400	200
Eelgrass	0.5	0	0
Mussel	0.5	500	250
Crab	0.3	1,000	300
Brittle star	0.2	0	0
Sand	0.1	0	0
Fish	0.1	1,000	100
Remainder	0.5	500	250
Liquid	0.3	-	-
Total	8.9 (5.1[a])		2,380

[a]total weight of prey excluding noncombustible material and detritus derived from prey.

Table 6. Caloric content and contribution of principal prey items to energy budget, fall 1967.

Food item	g/kg	Caloric content cal/g wet wt	Contribution cal/kg lobster
Starfish	3.7	630	2,330
Detritus	3.6	-	-
Crab	3.0	1,000	3,000
Sea urchin	1.2	300	360
Mussel	1.1	500	?
Shells	0.5	0	0
Lobster shells	0.5	0	0
Pisces	0.4	1,000	400
Eelgrass	0.1	0	0
Polychaete	0.1	700	70
Remainder	0.1	500	50
Total	14.3 (9.6[a])		6,780

[a]Total weight of prey excluding noncombustible material and detritus derived from prey.

DISCUSSION AND CONCLUSIONS

It is clear that lobsters are most unspecialized feeders. They will consume almost anything, regardless of its possible nutritive value. It is equally clear, however, that their feeding is not entirely random in that there is selection by lobsters of differing sizes and at different stages in the molt. cycle. Differences in diet related to lobster size are probably a function of the availability of different sizes of prey. This was clearly illustrated by predation on the smallest mussels by the smallest lobsters, and by the large numbers of crabs eaten in spring by larger lobsters. The smallest crabs collected by divers at the same time as these lobster sample (Scarratt and Lowe, 1972) were about 22 mm in carapace width and weighed about 2 g. Such a crab would be a full meal for an 80-100 g lobster (C.L. 47-50 mm). Smaller lobsters will only find appropriate-sized crabs during late summer when newly metamorphosed crabs are settling from the plankton. The same argument can explain the occurrence from time to time of lobster stomachs full of small "bite size" tunicates, sea urchins, and other species, and may, to a large extent, explain seasonal differences in diet and possibly differences between years. For example, polychaetes were eaten more commonly in 1967 than in 1966, whereas tunicates were the reverse. Whether these are the result of real changes in the populations of polychaetes and tunicates or are due to sampling bias of some type should be resolved.

Food selection by recently molted lobsters differs from that of hard-shelled lobsters. There is a tendency for soft-shelled lobsters to ignore calcium-poor foods and eat more heavily of calcium-rich foods. However, the pattern is by no means clear cut and may be confused by the availability of prey of a suitable size. Calcium dependence of newly molted lobsters is difficult to resolve accurately because the normal lobster diet is heavily dependent upon crustaceans, molluscs, and echinoderms. Possibly the main part of the immediate postmolt calcium requirements are obtained from the gastroliths and from calcium stored in the hepatopancreas (Passano, 1960) and also from the cast shell which is usually consumed. (Note that parts, at least, of many cast shells are eaten by lobsters other than the original owner.) This may mean that normal postmolt calcium requirements can be met from reserves with only a slight or temporary shift in diet, and the shifts observed may represent predation efficiency changes rather than anything else. For example, examination of the stomach contents of lobsters within 24 hours of molting (shell categories 1 and 2) shows these lobsters feed on such things as shell fragments, chitons, sea urchins, and starfish which are items that can be picked up from the floor and walls of the burrow. The absence of other errant forms and the

general low occurrence of unidentifiable detritus suggests that foraging does not begin until a few days after the molt. Travis (1955) considers that Panulirus argus does not feed for several days (perhaps five or six) following molting. Ropes (1968) similarly states that Carcinus maenas does not feed immediately before or after molting and felt that bits of shell contained in the stomach of newly molted crabs were probably ingested before ecdysis. This seems illogical because the whole of the cuticular lining of the stomach is shed through the mouth at molting and, failing its rupture, anything contained within would be discharged as well. There are general statements that crustacea do not immediately eat before or after ecdysis (Passano, 1960) but evidence points strongly towards lobsters beginning to ingest material shortly after the molt is complete.

Miller et al. (1971) estimated productivity of lobsters and several principal prey species in inshore seaweed zones and concluded that productivity of prey species exceeded requirements of lobsters. However, they speculated that lobster productivity might be limited by the demands of competitors, and might be increased by controlling competitor abundance.

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THE ROLE OF THE GREEN SEA URCHIN, *STRONGYLOCENTROTUS DROEBACHIENSIS*, IN THE ROCKY SUBTIDAL REGION OF NEWFOUNDLAND

By

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ABSTRACT

Populations of sea urchins, *Strongylocentrotus droebachiensis*, were studied in three locations varying in wave exposure. Urchins were most abundant in shallow water or just below the subtidal fringe of *Alaria esculenta*. In the most protected location the density was low but most individuals were large. In the more exposed locations the density was very high, but a large proportion of the individuals was small. This suggests that urchin recruitment and mortality increase as exposure increases.

Urchins feed primarily on algae. Their rate of consumption varies with the season and appears to be related to their annual reproductive cycle. Also, they consume different algae at markedly different rates. When given a choice of algal foods, urchins display strong food preferences. *Laminaria longicruris* and *Alaria esculenta* are highly preferred and consumed at the highest rates. In contrast, *Agarum cribrosum* and *Ptilota serrata* are eaten slowly and only when other foods are not available.

Urchins are an important factor in determining the distribution of macrophytes. In the winter, the distribution of *Alaria* is extended into more protected habitats, where it is not present in the autumn, and in exposed locations the *Alaria* zone is extended to greater depths. This process is favoured by the low winter consumption rate of the urchin, the limitation of urchin grazing by frequent heavy wave conditions, and probably by the rapid growth rate of *Alaria*. During the spring and summer, a marked increase in the consumption rate of the urchin and the increased frequency of calm conditions results in a reduction of the *Alaria* zone by urchin grazing. The survival of *Agarum cribrosum* and *Ptilota serrata* at greater depths, where urchins predominate, is probably due to the marked unattractiveness of these algae to urchins.

An addendum is given discussing the factors influencing the distribution of Laminaria in Newfoundland and the St. Lawrence Estuary.

INTRODUCTION

I became interested in the role of sea urchins in subtidal communities during the summer of 1967 when I was involved in a kelp survey of the west and south coasts of Newfoundland. At this time I was repeatedly impressed by the very high densities of the urchin, Strongylocentrotus droebachiensis, over large stretches of coastline. This situation was frequently associated with a scarcity of macrophytes and generally low diversity of organisms. It seemed obvious that any animal present in such great numbers must have considerable impact on its environment. Thus, I made a study of this problem between June, 1968, and September, 1969, and will here present my major findings.

General Distribution of Organisms in the Subtidal Region in Newfoundland

The distribution of the major benthic species on rocky shores in Newfoundland in relation to wave exposure is shown schematically in Figure 1. In the intertidal region, there is a distinct zonation pattern resulting from the defined vertical limits of barnacles and fucoid algae. Alaria esculenta is the major species making up the subtidal algal fringe. In exposed locations the Alaria zone extends from 1 m or more above lowest water of spring tides (LWST) to a depth of about 6 m below LWST. This zone decreases in width with decreasing wave exposure, and is not present in protected locations. The reduction in the width of the Alaria zone can also be observed along the sides of small inlets and surge channels in exposed locations. Laminaria digitata is a common constituent of the subtidal algal fringe in exposed locations but it rapidly disappears as exposure decreases. Below this subtidal algal fringe and extending from 15 to 25 m depth, there are large numbers of the urchin, Strongylocentrotus droebachiensis. Crustose coralline algae are abundant on stable rock substrates in this region: species which form smooth crusts are common in exposed areas, and nodular forms such as Lithothamnion sp. predominate in more protected locations. Non-calcareous macrophytes are not common in this urchin-dominated region. The major

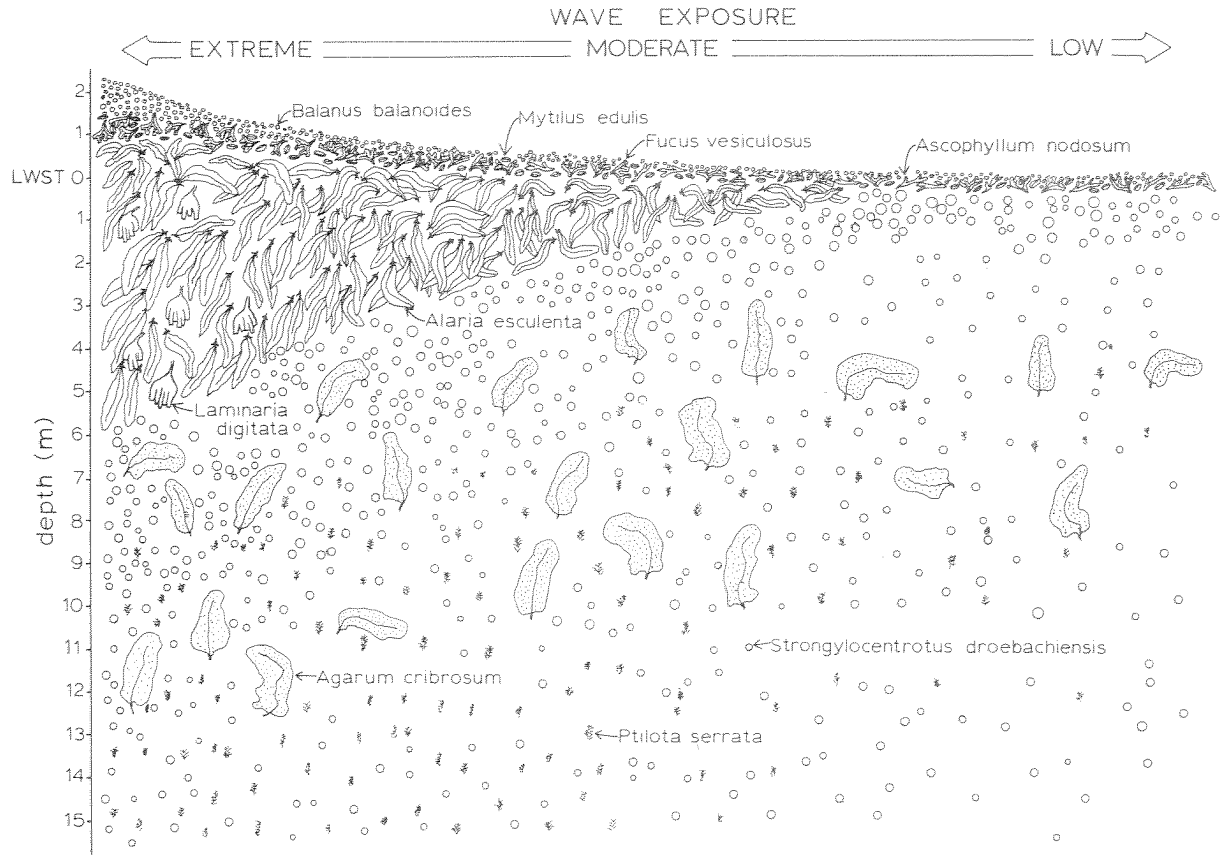


Figure 1. Schematic sketch showing the distribution of the major organisms on rocky shores of Newfoundland in relation to exposure.

perennial forms are Agarum cribrosum, which is usually scattered in its distribution, and Ptilota serrata, which usually forms a sparse undergrowth. The above pattern applies to shores where the substrate is either bedrock or large stable boulders, and this pattern is interrupted when the predominant substrate is sand, pebbles, or cobbles. The latter types of substrate become increasingly more common as exposure decreases.

RESULTS AND DISCUSSION

Distribution of Urchin Populations

To examine the characteristics of urchin populations in relation to depth and exposure, I made vertical transects at three different locations on the Avalon Peninsula, eastern Newfoundland (Figure 2).

(1) Logy Bay. This area faces northeast towards the open North Atlantic and receives heavy wave action. Bedrock is the predominant substrate and extends to a depth of about 18 m. Sampling was started at 4.9 m depth, just below the Alaria fringe, and continued to a depth of 24.4 m.

(2) Portugal Cove. This site is located 21 km inside of Conception Bay and receives moderate wave action. Here there is a mixture of loose substrate areas and bedrock points. One transect was made on bedrock substrate, starting at 3.0 m depth, just below the Alaria zone, and continuing to 15.2 m depth, near the lower limit of bedrock at Portugal Cove. A second transect was made from 0.3 to 21.3 m on loose rock substrate.

(3) Holyrood. This is a protected area located near the innermost part of Conception Bay. The bottom is mostly loose material, boulders, cobbles, and occasionally sand. Samples were collected from 0.3 to 18.3 m depth.

In each transect, samples were systematically taken in horizontal series, usually at 3.0 m depth intervals (Figure 3). In most instances, six samples were collected at each level. A square grid with an area of 0.2 m^2 was used at all locations except Holyrood, where urchin densities were low and 0.8 m^2 and 1.0 m^2 grids were used.

Histograms showing total density and biomass of urchins at each depth sampled in the four transects, and

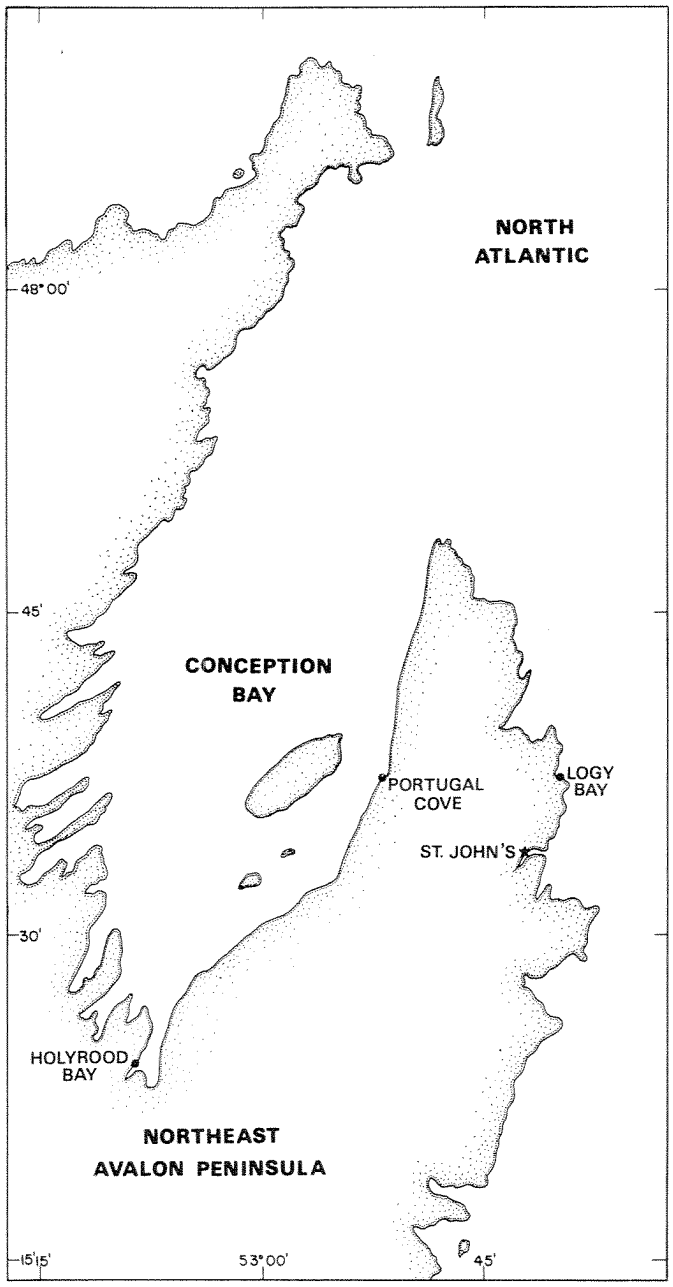


Figure 2. Northeast portion of the Avalon Peninsula, Newfoundland, showing locations where subtidal transects were made.

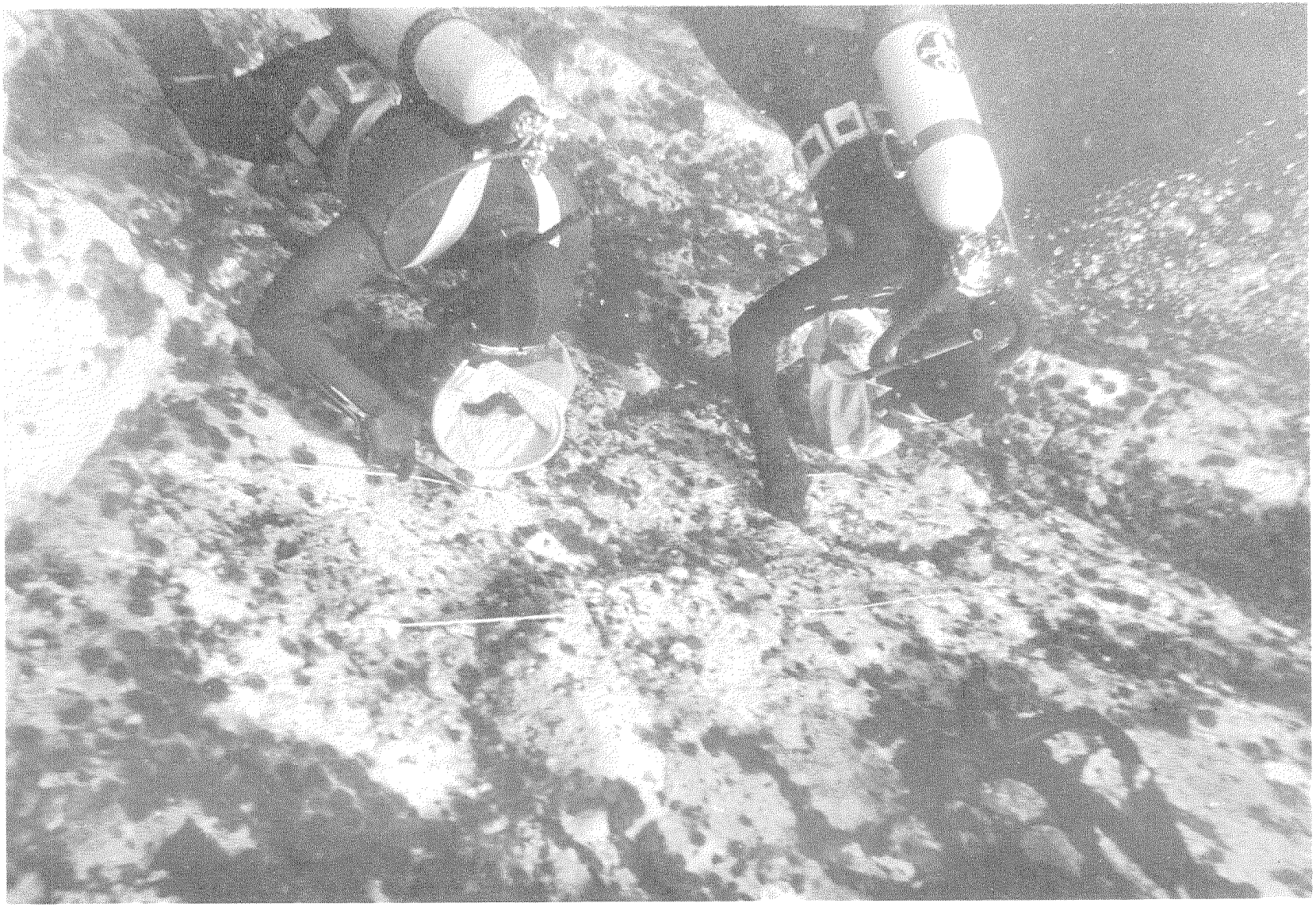


Figure 3. Divers sampling the urchin population at 4.9 m depth at Logy Bay. Urchins grazing on blades of *Alaria esculenta* can be seen at right.

the contribution of small (< 20 mm in test diameter), medium sized (20-40 mm), and large (> 40 mm) urchins to the totals, are given in Figure 4. In the bedrock transect at Logy Bay, density showed a decrease with depth, from 350 urchins m^{-2} at 4.9 m depth to 80-100 urchins m^{-2} at 18.3 to 24.4 m depth. Biomass was greatest at 8.2 m, 2.5 kg m^{-2}, and decreased with increasing depth to 0.6-0.8 kg m^{-2} at 18.3-24.4 m depth. During the sampling period, biomass was slightly lower at 4.9 m than at 8.2 m, and this was due to the greater numbers of large urchins at 8.2 m depth. However, large urchins can move about to a considerable extent. During calm periods, when they move to more shallow water to graze on algae, peak biomass undoubtedly occurs just below the Alaria fringe.

Density and biomass also decreased with increasing depth in the bedrock transect at Portugal Cove. However, at comparable levels, values were generally less than at Logy Bay. Thus, density and biomass at 3.0 m depth at Portugal Cove were similar to the values at 8.2 m depth at Logy Bay. While quantitative samples were not collected from within the Alaria fringe at Logy Bay and Portugal Cove, I observed that densities were low in this habitat. The animals present almost always had short, blunt spines; and the spine breakage is probably due to being battered by algal fronds.

In contrast to the pattern in the above transects, on loose substrate at Portugal Cove density showed an increase with increasing depth to a peak at 15 m depth. This pattern was entirely due to the contribution of small urchins, as medium-sized and large urchins decreased in numbers with depth as in the other transects. The rock material in shallow water in this transect was well scoured due to being moved about by wave action. It is likely that small urchins, if they settle in this area, are crushed. The loose rock material becomes more stable with increasing depth, as was evidenced by the increase in the abundance of crustose coralline algae, Lithothamnion sp.; and these irregular surfaces supported large numbers of small urchins (Figure 5). Small urchins contribute little to total biomass; thus, biomass decreased with increasing depth as in the other transects.

At Holyrood, urchin densities were lower than at Logy Bay and Portugal Cove by an order of magnitude (note change in scale in Figure 4). The peak density was 31 urchins m^{-2} at 0.3 m depth. At 3.0 and 6.1 m depth the substrate was coarser at 12.1 and 18.3 m depth and the density of urchins increased slightly. At Holyrood a peak biomass of 0.8 kg m^{-2} occurred near the level of LWST.

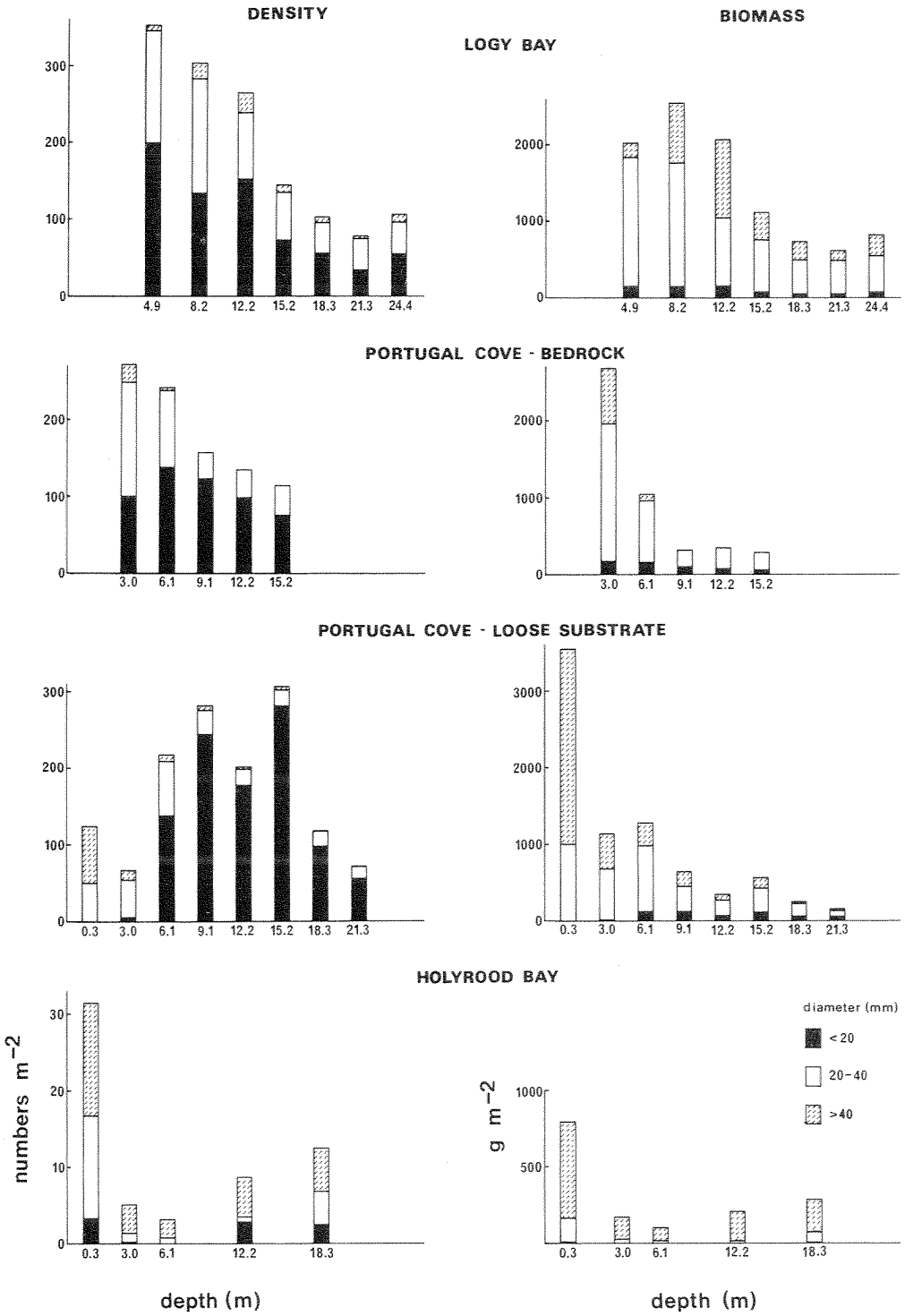


Figure 4. Density and biomass of S. droebachiensis in relation to depth in the four subtidal transects.

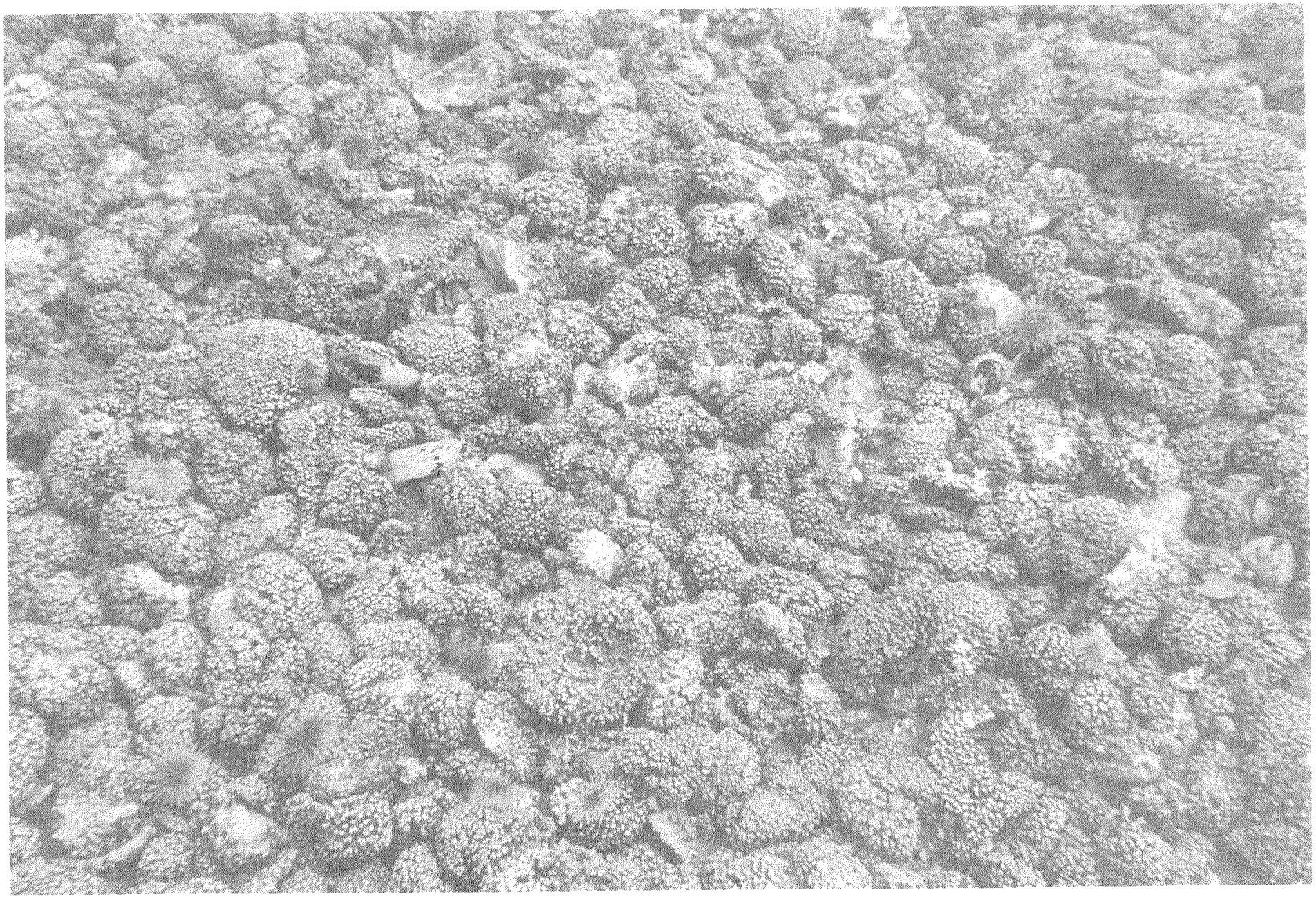


Figure 5. Loose substrate, heavily encrusted with Lithothamnion glaciale, at 15 m depth at Portugal Cove. This type of substrate supports a density of approximately 300 S. droebachiensis m^{-2} but most individuals are less than 20 mm in test diameter.

A number of generalizations about urchin populations are suggested by the transect data: (1) Urchins are most abundant in shallow water, or just below the subtidal *Alaria* fringe. (2) Urchin abundance increases with increasing wave exposure. Thus, at comparative depths, density and biomass were greater at Logy Bay than on bedrock at Portugal Cove, and were least at Holyrood. (3) Recruitment is markedly more successful in exposed and moderately exposed areas than in protected areas. This was indicated by the high density of small urchins at Logy Bay and Portugal Cove compared to the scarcity of small urchins at Holyrood. (4) Mortality increases with increasing exposure. This is suggested by the marked decline in the numbers of small, medium-sized, and larger urchins at Logy Bay and Portugal Cove, compared to an increase in the proportion of individuals in these three groups at Holyrood. Wave action itself, or waves carrying debris, are probably directly responsible for the high mortality in exposed areas. (5) Growth rate increases with decreasing exposure. This was suggested from changes in size-frequency distributions for Logy Bay and Portugal Cove over a period of just over a year (Himmelman, 1969). There was greater modal advancement at Portugal Cove. Increased spine breakage and consequently more energy being needed for spine repair (Ebert, 1968), or colder water temperatures, may be factors causing decreased growth in exposed areas. Greater growth in protected areas would also contribute towards the greater proportion of larger animals in protected areas.

Feeding Activities

Gut analyses: I have previously described the gut contents of urchins collected from shallow water throughout one year at Portugal Cove (Himmelman and Steele, 1971). Brown algae, particularly fucoids and *Alaria esculenta*, always occurred with the highest incidence and also formed the bulk of the gut contents of many individuals. Coralline algae, either pieces of *Corallina officinalis* or scrapings of encrusting corallines, and some animal material, especially small *Mytilus edulis*, regularly were present in small quantities. Various other species of non-calcareous algae occurred from time to time when they were present in the field. The main materials observed in the guts of urchins from deeper water (15 m) were pieces of *Ptilota serrata* and coralline algae.

Food preference. To obtain a relative estimate of the preference of urchins for various algae, an equal bulk of 12 species of algae were placed equidistantly along the edge of a large shallow tank (170 x 84 x 8 cm) containing

110 small urchins (20 mm in test diameter). The number of urchins in contact with each alga, and the rate of disappearance of the various algae was recorded (Table 1). In the first four days of the experiment, large numbers of urchins were grazing on Petalonia fascia, Alaria esculenta, and Halosaccion ramentaceum, and these algae disappeared rapidly. Laminaria longicruris and Chorda tormentosa disappeared on the sixth day. As the most desirable species disappeared, there was an increase in the numbers of urchins in contact with algae of intermediate desirability. Throughout the experiment, only a small number of urchins were in contact with Agarum cribrosum and Ptilota serrata and these algae remained in the tank for several weeks after all other species had been consumed. Similar results were obtained in a second experiment using larger urchins (50 mm in test diameter; Table 2). Laminaria, Alaria, Petalonia, Chorda, and Halosaccion disappeared in the first four to six days, and Agarum was present for two weeks after all other algae had been consumed. Thus, urchins have marked food preferences and Agarum and Ptilota are the least preferred algal foods.

Consumption rates on different species of algae. To obtain the rate at which urchins ingest different algae, a weighed portion of each alga (damp dried) was placed in a tank containing urchins of a specific size (test diameter). The amount consumed each day was divided by the number of urchins present to give the grams consumed urchin^{-1} day^{-1}. Figure 6 shows the consumption rate of 10, 30, and 50 mm urchins on eight species of algae during September, 1968. Laminaria longicruris and Alaria esculenta were consumed at the highest rates; the rates were markedly lower for Ulva sp., Desmarestia viridis, Fucus vesiculosus, and Ascophyllum nodosum and were lowest for Agarum cribrosum and Ptilota serrata. This order of consumption rates closely resembles the results of the food preference experiments. This is to be expected since the latter reflect the ability of urchins to consume the different algae, as well as the purely chemical attractiveness of the various algae. Thus, urchins consume different algae at markedly different rates, even when there is no other food available.

Seasonal rate of consumption. Figure 7 shows the consumption rate of urchins on Laminaria longicruris in February, May, and September. Experimental temperatures were 1.0-1.5, 1.3-2.0, and 11-13 C respectively, similar to sea temperatures at the Marine Sciences Research Laboratory, Logy Bay. There was a sharp increase in the consumption rate between February and May (from 1.0 to 2.2 g 50 mm urchin^{-1} day $^{-1}$), even though there was little

Table 1. Daily record of the number of urchins in contact with 12 species of algae. At the beginning of the experiment, equal quantities of each alga were placed equidistantly along the edge of a large shallow tank which contained 110 20mm urchins. The dashes commence when each alga has been completely consumed.

	May 6 start	May 7	May 8	May 9	May 10	May 11	May 12	May 13	May 14	May 15	May 16	May 20	May 21	May 26	May 27	May 29	May 30	June 3	June 5	June 9	June 16	June 17	June 19	June 20	June 25	June 26
Petalonia fascia		16	16	16	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alaria esculenta		14	15	15	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Halosaccion ramentaceum		20	21	21	19	19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laminaria longicruris		8	9	10	11	8	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chorda tomentosa		4	7	13	14	26	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhodymenia palmata		11	9	9	9	11	11	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chondrus crispus		10	7	2	3	5	12	22	26	27	26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ulva sp.		6	8	8	10	8	8	8	15	22	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fucus vesiculosus		3	3	4	7	10	13	12	10	9	7	7	9	-	-	-	-	-	-	-	-	-	-	-	-	-
Ascophyllum nodosum		8	8	10	8	7	5	5	2	2	4	14	19	13	10	5	5	-	-	-	-	-	-	-	-	-
Agarum cribrosum		8	4	1	0	0	2	0	3	1	3	1	1	4	4	11	7	5	5	5	1	1	1	-	-	-
Ptilota serrata		0	0	0	0	0	0	2	1	1	0	1	2	1	4	1	0	0	0	2	3	2	1	1	1	-
Urchins not feeding		2	3	1	2	16	28	47	53	48	41	87	79	92	92	93	98	105	105	104	106	108	109	109	109	110

Table 2. Daily record of the number of urchins in contact with 12 species of algae. At the beginning of the experiment, equal quantities of each alga were placed equidistantly along the edge of a large shallow tank which contained 42 50mm urchins. The dashes commence when each alga has been completely consumed.

	May 6 start	May 7	May 8	May 9	May 10	May 11	May 12	May 13*	May 14	May 15	May 16	May 20	May 21	May 26	May 27	May 28	May 29	May 30	June 3	June 5	June 9
Laminaris longicruris		2	3	1	4	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Alaria esculenta		5	5	3	3	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Patalonia fascia		3	5	6	4	7	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Chorda tomentosa		4	4	4	7	3	1	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Halosaccion ramentaceum		5	6	4	4	4	2	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhodymenia palmata		2	2	3	4	3	2	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Desmarestia viridis		5	4	5	2	3	3	+	3	2	-	-	-	-	-	-	-	-	-	-	-
Chondrus crispus		3	3	3	4	3	4	+	3	2	2	-	-	-	-	-	-	-	-	-	-
Ulva sp.		5	5	6	6	5	11	+	5	2	12	-	-	-	-	-	-	-	-	-	-
Fucus vesiculosus		3	3	4	4	4	5	+	6	3	3	-	-	-	-	-	-	-	-	-	-
Ascophyllum nodosum		3	2	1	0	0	7	+	8	7	7	3	2	-	-	-	-	-	-	-	-
Agarum cribrosum		1	0	0	0	0	0	+	0	2	0	0	3	3	2	3	3	2	1	1	-
Urchins not feeding		1	0	2	0	10	7	42	17	26	18	39	37	39	40	39	39	40	41	41	42

* Water stopped and urchins discontinued feeding.

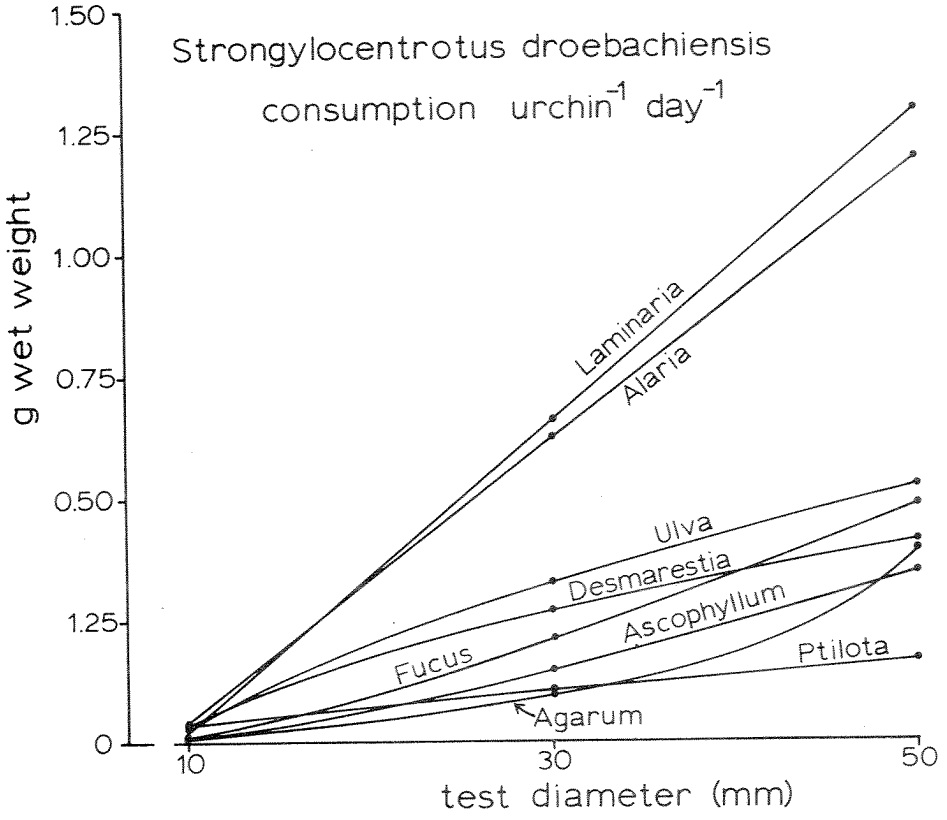


Figure 6. Consumption rate of S. droebachiensis, measuring 10, 30, and 50 mm in test diameter, on Laminaria longicruris, Alaria esculenta, Ulva sp., Desmarestia viridis, Fucus vesiculosus, Ascophyllum nodosum, Ptilota serrata, and Agarum cribrosum during September, 1968.

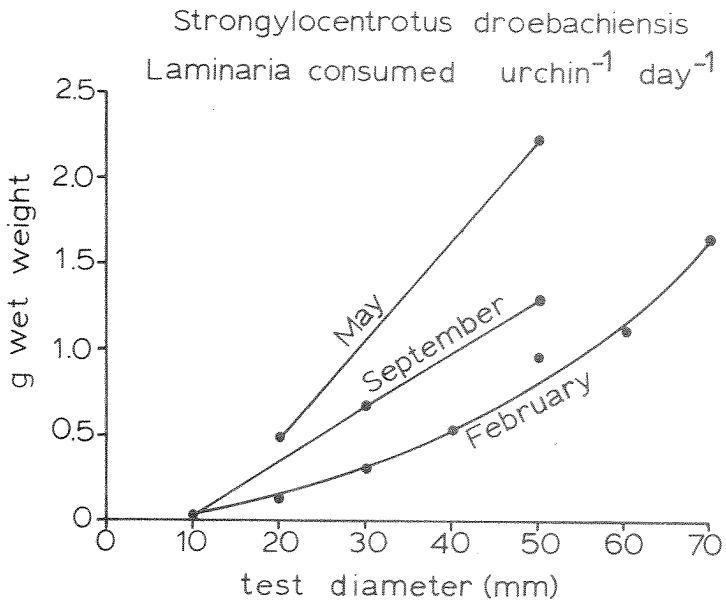


Figure 7. Consumption rate of S. droebachiensis on Laminaria longicruris during September, 1968, and February and May, 1969.

change in temperature. The consumption rate probably declined during the summer (to 1.3 g urchin^{-1}) day^{-1} in September) as temperatures were increasing, and continued to decline in the autumn as temperatures were decreasing. Vadas (1977) reported a similar annual cycle in the percentage of urchins feeding in the field. It appears that the consumption rate is not correlated with temperature. The consumption rate does, however, appear to be related to the annual reproductive cycle. Spawning in S. droebachiensis occurs during late March or April (Himmelman, 1975, 1978) and thus coincides with a period when consumption increases markedly. The gonads are enlarging and developing in the summer and autumn when consumption is decreasing. Fuji (1967) noted that small urchins, which have not reached sexual maturity, do not have a seasonal cycle in consumption. These observations suggest that an endocrine pathway links feeding activity and the annual reproductive cycle. The spring phytoplankton bloom is the environmental cue for spawning in S. droebachiensis (Himmelman, 1975, 1978) and thus may indirectly be the signal for increased consumption in the spring.

Grazing in the Field

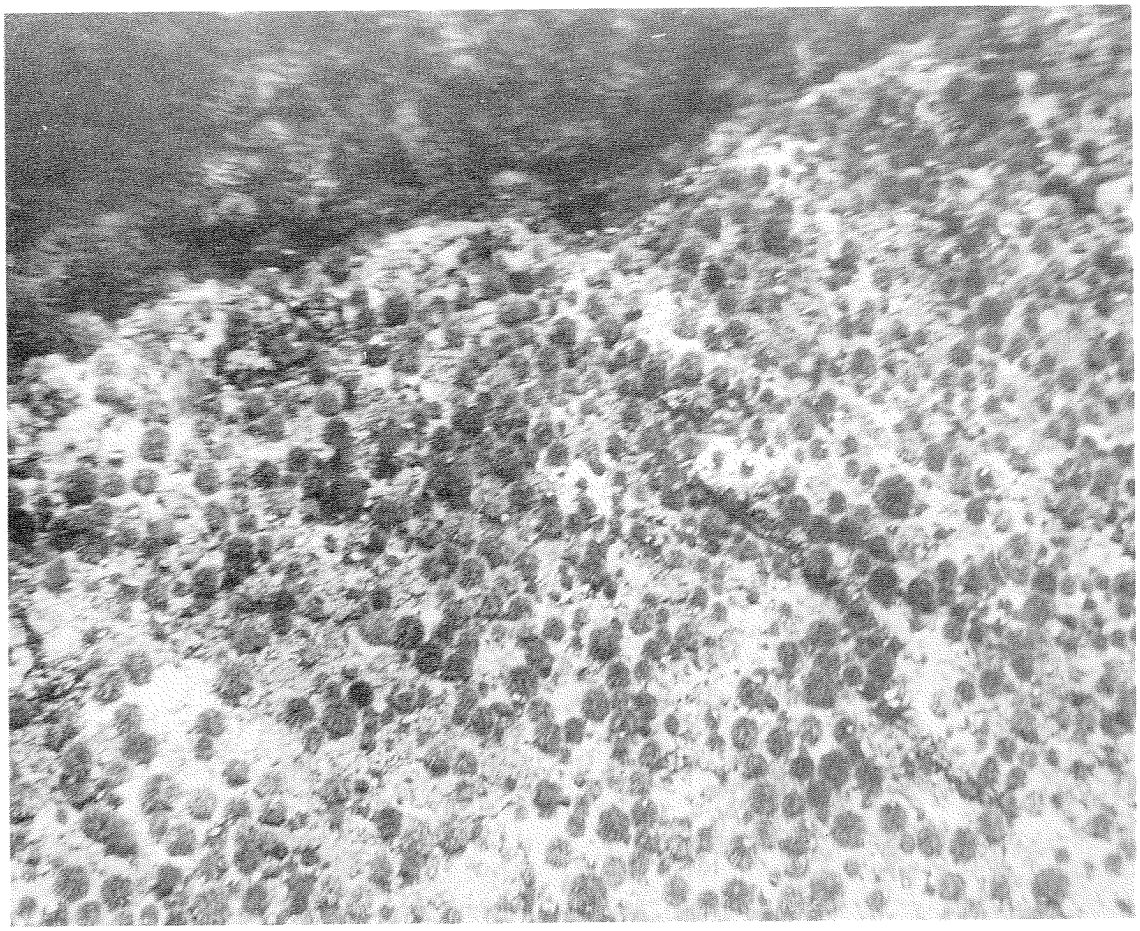
The great abundance of urchins in the shallow subtidal region of Newfoundland suggests that their grazing activities could strongly influence the structure of the subtidal community. An estimate of the grazing potential can be made using the size-frequency data for the field urchin populations and the consumption rates as measured in the laboratory. Thus, in the region just below the Alaria fringe in the bedrock areas at Logy Bay and Portugal Cove, the urchins could potentially consume about 100 g of Laminaria or Alaria m^{-2} daily during September. In February, about 60 g of Laminaria m^{-2} day^{-2} would be consumed and about 160 g m^{-2} day^{-1} in May. A rough estimate for a year would be about 100 kg m^{-2}. In the region where Agarum or Ptilota are common, for example at 9 m depth on bedrock at Portugal Cove, only about 5 g m^{-2} of Agarum or Ptilota could be consumed daily, using the September feeding rates. The food preference experiments demonstrate that these algae would only be consumed if other algae were not present. When an area is denuded of algae, a very low density of urchins will prevent algal colonization. For example, Leighton et al. (1966) estimate that for the related urchin, S. purpuratus which is similar in size to S. droebachiensis, the density must be reduced to 10 urchins m^{-2} for algal colonization to occur. If the feeding rates in the laboratory are at all indicative

of the potential feeding rates in the field, the impact of urchin grazing is considerable.

Drift algae. Whenever pieces of macrophytes break away from the intertidal region or subtidal algal fringe and drift to the bottom at greater depths, urchins quickly find this material and devour it. In the field, one commonly finds aggregations of urchins feeding on the drift algae, especially after stormy periods. On one occasion, I anchored a large clump of *Ascophyllum nodosum*, and another of *Fucus vesiculosus* (each weighing approximately 2-3 kg) at 15 m on the bottom at Portugal Cove. After a few days, urchins were covering this material to the extent that it was barely visible, and after six days only fragments of algae remained. The keen ability of urchins to sense and locate algae was noted in the laboratory. When an urchin is kept in an aquarium (20 l volume) without food, it remains stationary most of the time. However, within minutes after a piece of *Laminaria* is placed in the aquarium the urchin's podia become active and it starts searching for the alga. The alga is usually found in ten minutes.

Wave action and urchin grazing. The importance of wave action in limiting urchin grazing was noted while diving. This was vividly demonstrated by *Desmarestia viridis* growing on vertical rock faces at Logy Bay (Figure 8). The delicate filamentous structure of this algae allows it to be washed about by slight wave action. While during the summer on most rock faces at Logy Bay urchins are abundant and relatively evenly distributed, urchins were notably absent on surfaces which were abraded by *Desmarestia* as it moved in a rotating fashion with the incoming and outgoing surge. A similar urchin-free area was also observed around other algae; for example, *Alaria esculenta*, *Agarum cribrosum*, and *Desmarestia aculeata*, when they were being moved about by waves. When there were calm periods, the urchins approached the algae and commenced grazing (Figure 9). Usually many urchins attack a plant at the same time. As a group they can anchor the plant and prevent further movement of the alga if there is a slight increase in wave action. Thus, urchins move away when they are being abraded by moving objects, and the movement of algal fronds by wave action deters urchin grazing.

Annual extension and recession of the subtidal *Alaria* fringe. A high density of *Alaria* sporelings appeared during the winter of my studies in Newfoundland (1968-1969). In exposed locations the *Alaria* fringe was extended to greater depths and into small inlets and channels where it was previously absent. In more protected



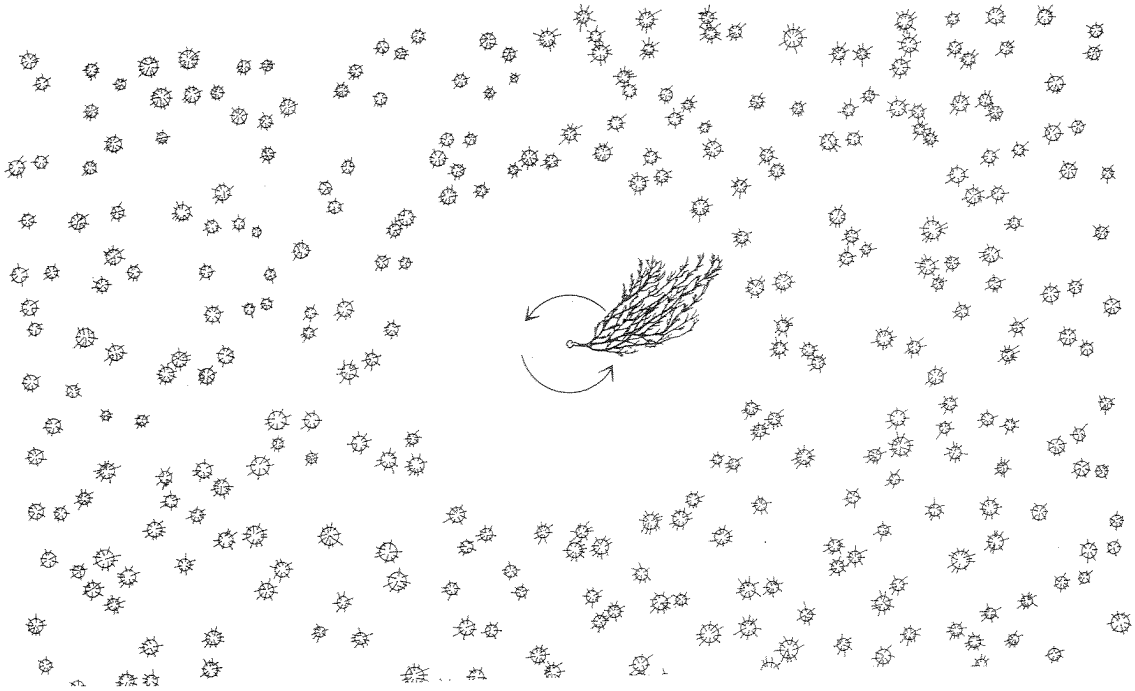


Figure 8. Above: S. droebachiensis on a rock face at 6 m depth at Logy Bay. Below: sketch showing the conspicuous absense of urchins in the area abraded by Desmarestia viridis as it moves with the incoming and outgoing wave surge.

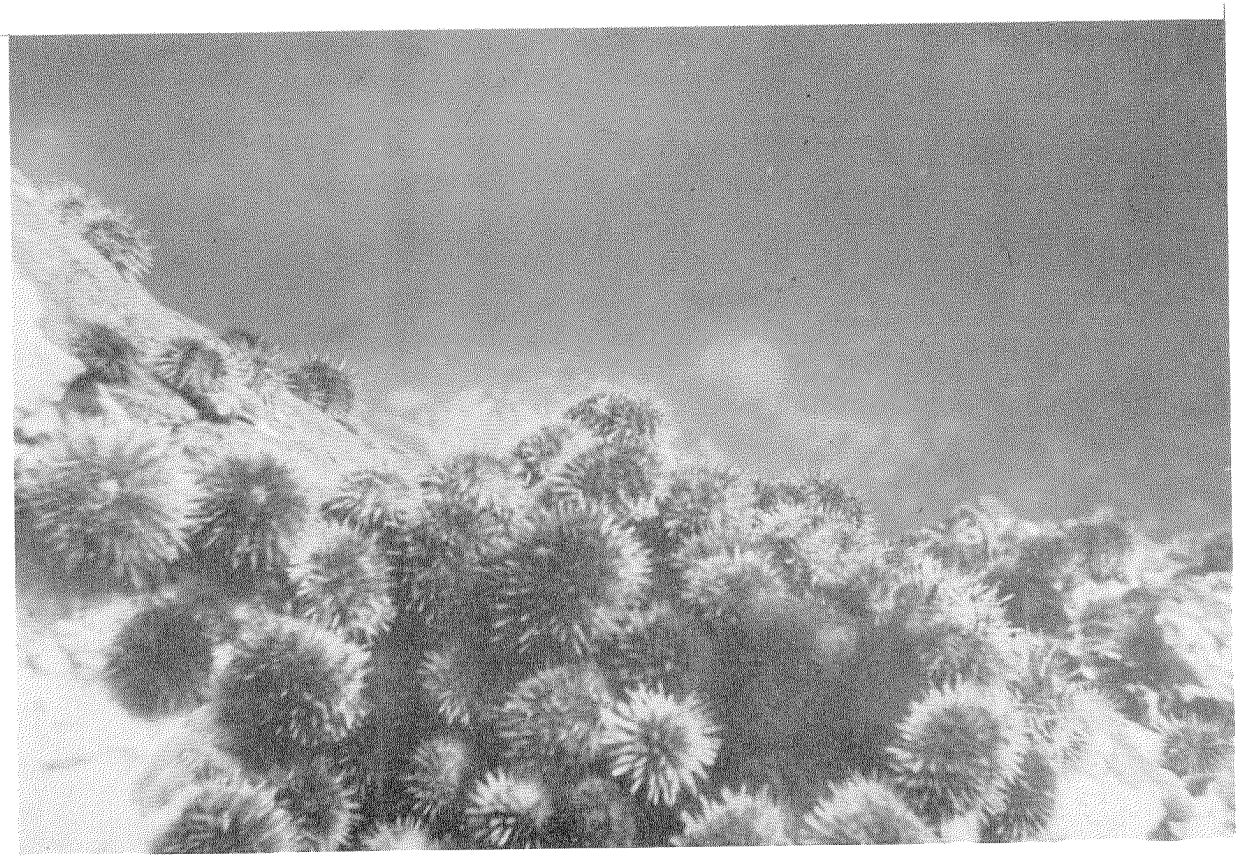


Figure 9. *S. droebachiensis* grazing on *Desmarestia viridis* at Portugal Cove during a calm period in August, 1969.

locations, where there was no Alaria during the previous summer, a shallow zone of Alaria was established. Thus, there was a vertical and horizontal increase in the distribution of Alaria. The sporelings grew rapidly during February, March, and April. During April, May, and June, when there were calm periods, high densities of large urchins were seen in shallow water feeding on the new Alaria plants. There was often a continuous band of urchins, 15-35 cm in width, at the lower edge of the Alaria zone (Figure 10). When there was increased wave activity, the urchins dispersed downwards and the grazing activity was interrupted. By late June, the new growth of Alaria had nearly been eliminated in most locations, and at Portugal Cove urchins were grazing in the lower fucoid zone. Older Alaria were attacked during the summer (Figure 11). Their tougher stipes offer some protection against urchin grazing, but on calm days their blades sank to the bottom and were anchored and devoured by groups of urchins. In some instances urchins will climb and graze on the stipes. Thus, there is a vertical and horizontal extension of the Alaria zone during the winter and it is reduced again by urchin grazing during calm periods in the spring and summer.

Summary of interacting factors influencing the distribution of macrophytes (Figure 12). Urchins, especially large ones, are concentrated in shallow water next to the seaweed zone. There is a seasonal cycle in the rate at which urchins consume macrophytes. This cycle does not appear to be related to the annual temperature cycle, but is probably physiologically related to the annual reproductive cycle. During the winter, Alaria sporelings appear and the distribution of Alaria is extended to greater depths and to more protected areas. During this period, the ingestion of algae by urchins is at its lowest rate, and further urchin feeding is reduced by frequent heavy wave conditions. Buggeln (1974) shows there is a marked increase in the growth rate of Alaria during October and November and rapid growth continues through the winter. These factors favour the extension of the Alaria zone during the winter. In March or April the spring phytoplankton outburst signals spawning in S. droebachiensis (Himmelman, 1975; 1978). Following this there is a marked increase in the rate at which urchins consume algae. This, combined with the increased frequency of calm conditions, results in a reduction of the distribution of Alaria by urchin grazing. Thus, the interaction between urchin grazing and wave action appears to be the main factor in determining the vertical and horizontal distribution of Alaria.

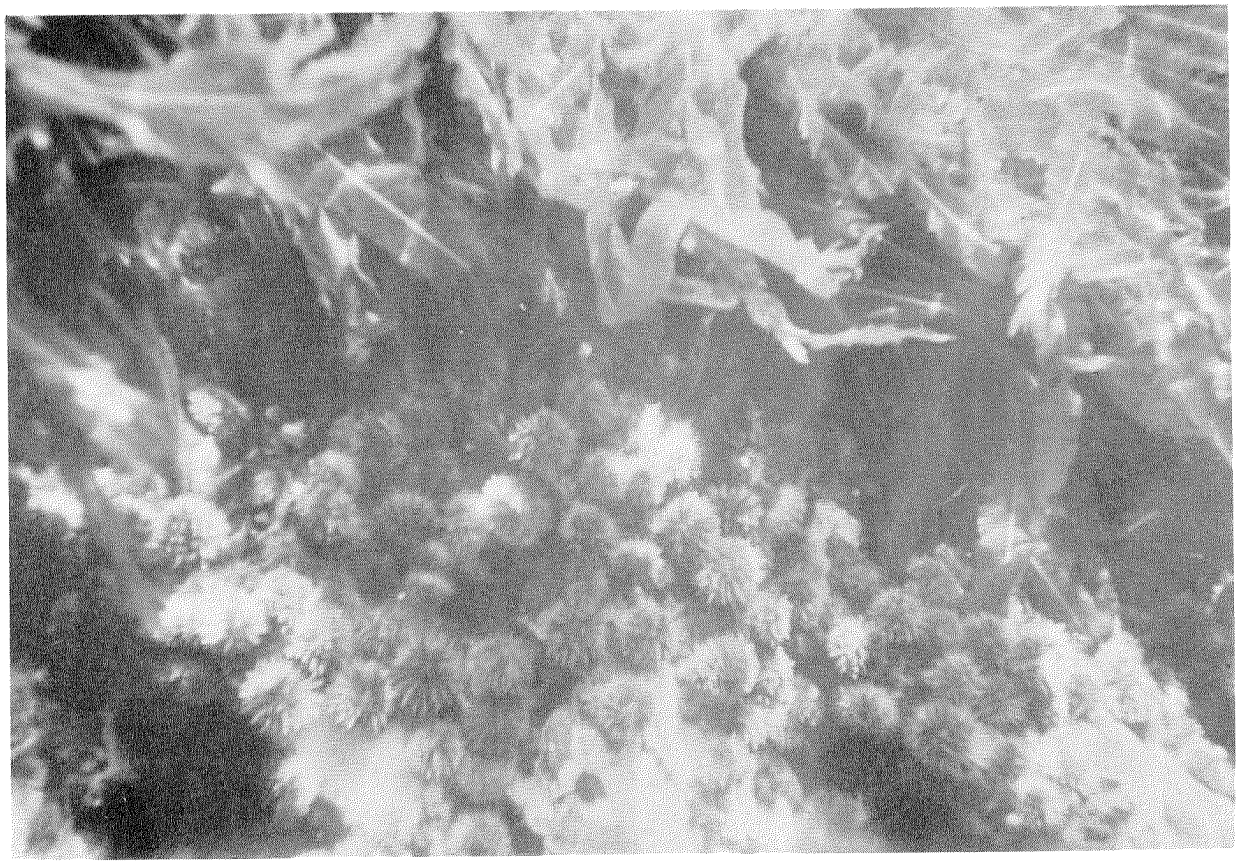


Figure 10. *S. droebachiensis* grazing at the lower edge of the zone of young *Alaria esculenta* at Portugal Cove during May, 1969.

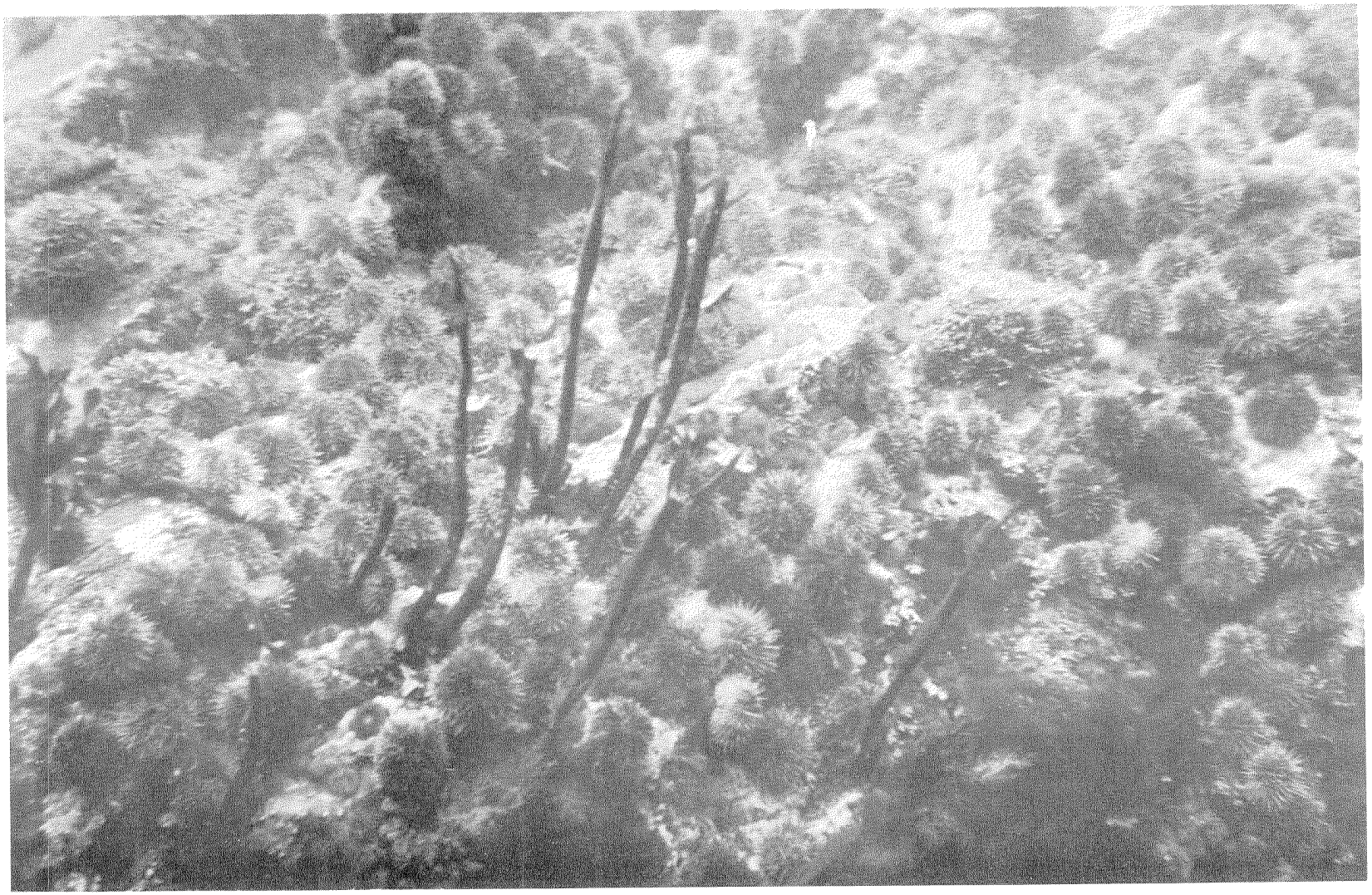


Figure 11. High density of S. droebachiensis (biomass approximately 3-4 kg m^{-2}) at 3 m depth at Portugal Cove in September, 1969. Older plants of Alaria esculenta have been consumed except for the stipes. The stipes show scars from urchin attacks.

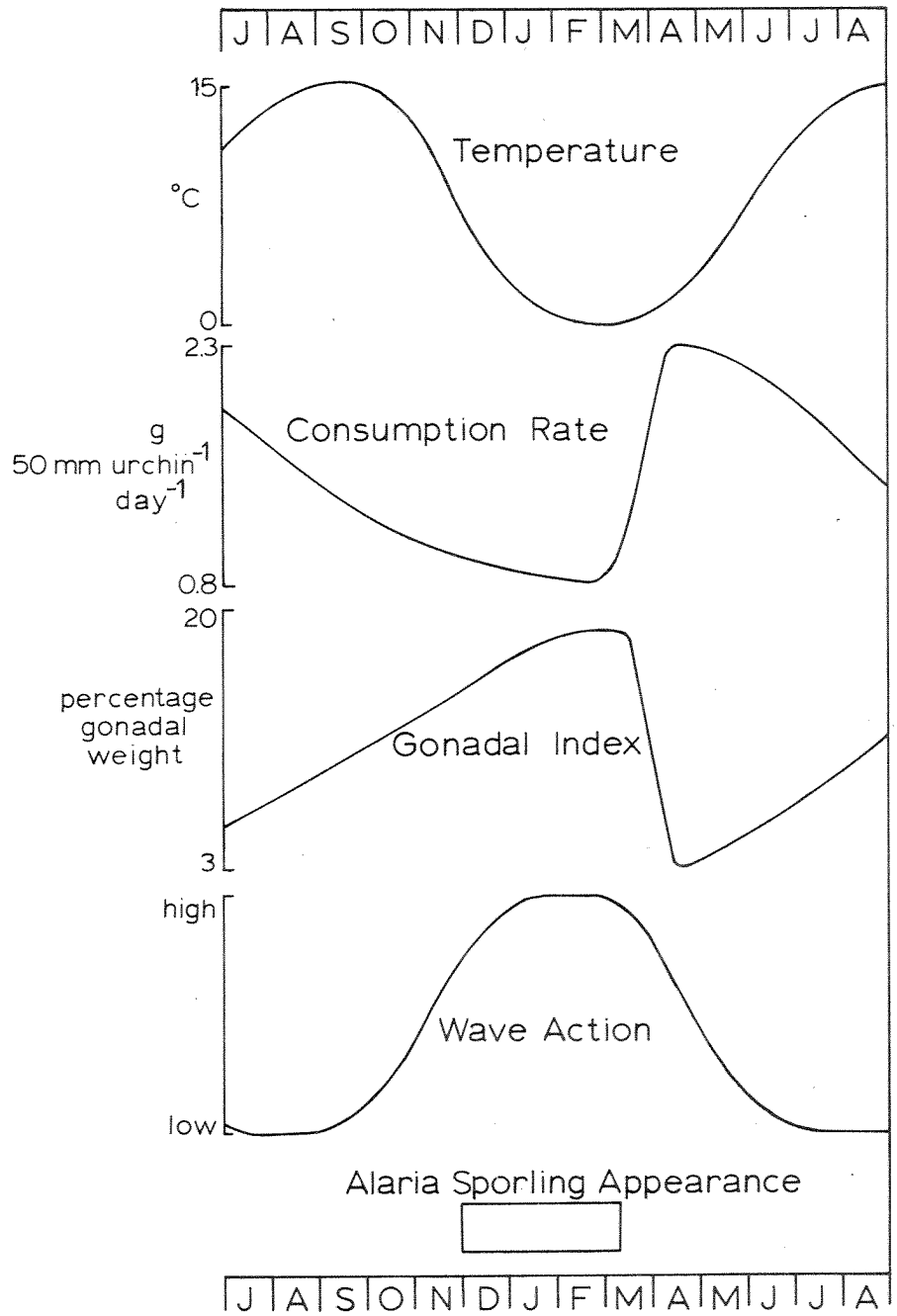


Figure 12. Seasonal changes in factors influencing the feeding of S. droebachiensis and the distribution of Alaria esculenta.

In the urchin-dominated region below the *Alaria* fringe, there is an abundant growth of coralline algae, scattered plants of *Agarum cribrosum*, and an undergrowth of *Ptilota serrata*. The marked unattractiveness of *Agarum* and *Ptilota* to urchins undoubtedly contributes to their survival in this region. Also, the calcareous structure of the corallines prevents them from being consumed at a high rate. Annual species, such as *Monostroma* spp. and *Desmarestia viridis*, appear and flourish for a while during the winter and spring, especially on boulder tops and rocky prominences, but are consumed by urchins during the summer.

ADDENDUM

Distribution of *Laminaria* in Newfoundland and the St. Lawrence Estuary

My observations from the Newfoundland region, primarily the west and south coasts of Newfoundland and the Avalon Peninsula, indicate that beds of *Laminaria longicruris* are uncommon. Three factors appeared to be present where *Laminaria* beds occurred: (1) moderate to slight exposure, (2) good circulation, and (3) suitable rocky substrates (bedrock or boulders). *Laminaria* beds were most common in shallow bays, in passages between islands, and at the entrance to inlets. Strong tidal currents were invariably associated with *Laminaria* beds, and are probably important in supplying nutrients to the plants. Currents may also be beneficial in keeping the fronds suspended and moving, thus preventing attacks by urchins. *S. droebachiensis*, having a keen ability to detect algal foods and being a very mobile urchin, can readily move to a food source. I have often observed that *Laminaria* exists on boulders or small bedrock outcrops which were surrounded by sand or pebbles, while on adjacent areas with more continuous rocky surfaces and high urchin densities, no *Laminaria* was present. Urchins probably have difficulty moving across sand, and the movement or scouring action of fine sediments during periods with increased wave activity may be harmful to urchins. Thus, in certain situations urchin attacks are probably limited by substrate barriers. Another common example of isolated populations of *Laminaria* is on piers. For example, while there was no *Laminaria* in my study area at Portugal Cove, there was a luxuriant growth of *Laminaria* on a pier located 0.6 km away. This situation suggests that hydrographic conditions are suitable for *Laminaria* growth. On piers, *Laminaria* fronds

are always supended and move freely with even slight wave or current action. They are, therefore, less vulnerable to urchin grazing.

While Laminaria digitata is found as an understory plant in beds of L. longicruris, it is most common in association with Alaria esculenta in the shallow subtidal region at exposed locations. Its numbers increase with increasing exposure and in very exposed sites L. digitata can form almost pure stands near low water level. The short, flexible (but strong) stipe and sturdy divided blade of L. digitata and the extremely flexible structure of Alaria esculenta with supporting mid-rib region make these phaeophytes well adapted to withstanding turbulent wave action. In contrast to L. digitata and Alaria, L. longicruris is seldom found in exposed regions of Newfoundland. While the very high urchin densities and urchin recruitment rates in exposed areas may account for the absence of L. longicruris in deeper water, it is less clear why this species is not common in shallow water. Why doesn't the limitation of urchin grazing by wave action allow L. longicruris to become established in the subtidal fringe? It may be that L. longicruris is less successful than Alaria and L. digitata in spatial competition. Another hypothesis would be that L. longicruris is not as capable of withstanding severe beating by waves. Its long hollow stipe, especially in older plants, is considerably less resilient than that of L. digitata and the broad membranous blade is more delicate. L. longicruris may be analogous to the kelps having floatation bladders on the Pacific coast of North America which do not occur in the splash zone. Nereocystis luetkeana and Macrocystis pyrifera are common in exposed locations, but they are usually found a short distance off shore. They are replaced by Lessoniopsis littoralis and Alaria spp. in the low intertidal and upper subtidal regions.

In Nova Scotia, Breen and Mann (1976a, 1976b) documented a marked reduction in the size of Laminaria beds which was the result of attacks by dense fronts of grazing urchins. They hypothesized that this change had been brought about by the reduction in the population of one of the urchin's predators, the lobster. This raises the question as to whether there has been a similar change in the subtidal community of Newfoundland. Considering the lack of L. longicruris in exposed locations during the period of my observations, 1967 and 1968, I suspect that these areas have not supported Laminaria beds in recent history. It is unlikely that there has been such a marked change that former Laminaria beds are now not even found in

a few locations. Large populations of Laminaria longicruris are, however, found on the open coast off southwestern Nova Scotia. This would suggest that they should also be able to exist in exposed areas off Newfoundland. However, several factors may be different. The Laminaria beds off the Nova Scotia coast occur on shallow platforms which extend out a considerable distance from shore. Wave action may be reduced as it passes over this type of area. In exposed areas off Newfoundland, this type of topography is rare. Another favourable factor off southwestern Nova Scotia may be the very strong tidal currents and high nutrient levels, which should stimulate extremely rapid growth.

In the St. Lawrence Estuary, the distribution of Laminaria is very restricted. (Here, lobsters are found only in the outer portion of the Estuary.) In many locations the lack of macrophytes is due to the presence of unsuitable substrates. Locations which have suitable rocky bottoms support high urchin densities, and here the principal perennial algal species are Agarum cribrosum, Ptilota serrata, Phycodrys rubens, and crustose coralline algae. Phycodrys may be an unattractive food for urchins, along with Agarum and Ptilota. In locations where there is moderate to light wave action, and where there is not a great deal of ice movement during the winter, the Agarum/urchin community may extend to the low intertidal zone.

In the Estuary, Alaria esculenta, Laminaria longicruris, L. digitata, L. saccharina, and Saccorhiza dermatodea are found together in the subtidal fringe, although Alaria predominates at higher levels. Laminaria is most common on rocky points where there are strong tidal currents. The subtidal algal fringe is narrow and usually does not extend below 1 m below LWST. The ability of Laminaria and Alaria to grow at greater depths in the Estuary was demonstrated in an experimental situation. Starting in July, 1978, a 20 m stretch of shoreline (bedrock) at Les Escoumins was maintained free of urchins to a depth of about 11 m. During the autumn, 1978, Alaria and Laminaria plants were found in this area to a depth of 8-9 m.

Along rocky points in the Estuary, there is extensive ice scouring during the winter. By spring, organisms are found mainly in crevices. Urchins are not present in shallow water in the spring and have either been crushed by ice or have been driven to deeper water. After the melting of ice, there is a rapid growth of colonial diatoms,

Monostroma, and other small algae, followed by the appearance of large phaeophytes. One finds concentrations of urchins at the bottom edge of this new algal zone during the summer. The algal zone persists through the summer where there is tidal or wave action or where unsuitable substrates for urchins are found below the algal zone.

While ice conditions could account for the destruction of Laminaria during the autumn and winter, observations during the autumn of 1978 indicated that L. longicruris plants were deteriorating before there was significant ice formation. In a population at Pointe Metis there was a striking reduction in biomass by October, when most of the plants were worn down to a short length. While increased wave action could be a factor in destroying the plants, I observed that the stipes became more fragile in the autumn. This condition varied over short distances. For example, in early December in the region of Bic I found that plants in the landward side of a small reef could easily be broken (their stipes were especially brittle), while those on the seaward side were more sturdy. Thus, a structural change may lead to the reduction in Laminaria in the autumn.

A large population of perennial Laminaria observed in the Estuary is in a shallow bay at Ile-du-Bic, near Rimouski. Most of this population occurs from the low intertidal region and down to 1 m below LWST. There is a great deal of water movement in this bay throughout the tidal cycle. A stable ice layer forms over this bay during the winter (approximately 40 cm in thickness, February 1979), thus allowing the survival of the kelp bed.

ACKNOWLEDGEMENTS

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OBSERVATIONS ON ALGAL-GRAZER INTERACTIONS IN NEWFOUNDLAND AND LABRADOR

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INTRODUCTION

Urchin-dominated areas are a common feature of Newfoundland and Labrador coastal marine biology, as are kelp beds. The interaction between the two, not to mention the myriad other species present, is a complex ecological puzzle. To date, little local research has been done apart from Himmelman's (1969) study on sea urchin feeding. During the past nine years we have been examining algal community structure and biogeography in Newfoundland and Labrador. This has included general studies of several hundred sites and regular repetitive studies at several sites. While these studies were not directed towards the sea urchin/kelp bed interaction, they do provide a relatively broad background which may be useful in understanding some aspects of the problem. In addition, nature "designed" some mass mortality experiments on a massive scale which provide some insight into attainment of equilibrium between local algae and grazers.

OBSERVATION AND DISCUSSION

The shallow coastal biota of Newfoundland and Labrador may be classified into a number of geographically and vertically distinct community types. Each type usually reflects a local interaction of physical, chemical, and biological parameters. One particular, vertically zoned community assemblage occupies much of the coast of Newfoundland and southern Labrador. The physical, chemical characteristics of this coast include a bedrock-dominated substrate, considerable exposure to wave energy, a relatively low tidal range (usually less than 2 m), a salinity range between 28 and 32%, a water temperature range of -2 to about 16 C, and a periodic scouring by heavy arctic pack ice.

The intertidal biota of these shores is quite heterogeneous, depending largely on timing and degree of ice action. Immediately following ice action, the intertidal is colonized by diatoms and filamentous algae, usually including *Ulothrix*, *Urospora*, and *Pilayella*. Secondary succession is

more erratic and may be dominated by Halosaccion, Delamarea, Petalonia, Scytosiphon, Chorda, or a number of other annual species. The chief grazers in this community type are usually amphipods, especially Calliopius. Perennial species, including Alaria, Fucus, Balanus, Mytilus, Littorina, Laminaria, and Chondrus, are usually important only a year or more after heavy ice action or in areas relatively protected from the scouring. The low intertidal and upper subtidal are dominated by a kelp bed fringe. The lower limit of kelp is determined by the upper limit of major sea urchin numbers and varies with season and weather. The upper limit of sea urchins is chiefly determined by wave energy and substrate slope and represents only an instantaneous equilibrium boundary point of the kelp bed. The zone, which is alternately dominated by sea urchins or kelps, is rather barren during sea urchin domination, with only a few mainly microscopic and encrusting plants. Below this zone, usually by a 6 to 10 m depth, a permanently urchin-dominated encrusting coralline algal community occurs. These plants, which require surface grazing for success (Adey, pers. comm.*) form a thick (up to 50 cm) profusely branched cover which shelters an extremely abundant and diverse animal community. With increasing depth, sea urchins are less abundant and by 15 to 20 m the coralline algal community gains an important overstory of Agarum and Ptilota. These regions are still thoroughly grazed, although the most important grazers are now Tonicella spp., chitons, rather than urchins.

Areas with extensive subtidal kelp forests in Newfoundland represent a distinctly separate biogeographic unit than the above. Overall diversity is similar, but the flora and fauna are completely distinct. The most obvious features of the mature kelp bed are a complex fleshy seaweed understory, epiphyte communities, and a lack of encrusting corallines. Besides the different biological characteristics, subtidal Newfoundland and Labrador kelp community areas generally possess a narrower seasonal temperature range, less seasonal variation in nutrient concentrations, and considerable water movement by either upwelling or major currents. Such beds occur off Cape Race, the north shore of Fortune Bay, along parts of the Straits of Bell Isle, and at other locations. These areas correspond in some features to the habitat along the Yarmouth coast of Nova Scotia with its major kelp beds.

The central question of this conference is the stability of a kelp and sea urchin community. In the absence of solid historic data, opinions on either side are speculative. One popular hypothesis is that the kelp bed was the prehistoric climax community until lobster fishing reduced predation pressure on sea urchins, permitting sea urchin dominance. This does not seem likely in Newfoundland, based on two circumstantial pieces of evidence. The first is the thick

*Adey, Smithsonian Institute, Washington, D.C.

growth of coralline algae in urchin-dominated communities. Excavation at such sites indicates coralline rhodolith production dating back at least hundreds of years, indicating that these areas were not stable kelp beds before the lobster fishery began. The second is examination of sediments for sea urchin spine and test fragments as an indication of sea urchin abundance. A recent upsurge in urchin abundance should be reflected in recent sediments. Core samples in local waters (Slatt, pers. comm.) do not show this. There is, however, some erratic variation which may correspond to mass urchin mortality, ice damage, or other causes.

On the short-term time scale, we have been observing sites in major kelp and sea urchin-dominated areas for nine years. During this time, some beds have expanded greatly and others have retreated. We have seen no correlation between these changes and lobster populations or the absence of lobster fishing. Labrador, without lobsters, shows similar patterns to Placentia Bay with high lobster populations.

MASS MORTALITY

When sea ice is particularly abundant, virtually all algae and grazers may be removed to depths of 5 to 10 m. Subsequent recolonization depends on many factors. If grazers have actually been killed by crushing or stranding, recolonization may be quite rapid, leading within less than a year to much more extensive kelp beds than before the scouring. These beds may be stable for years or may be quickly eradicated by a tremendous population increase of Lacuna, Margarites, or other prolific grazers. If grazers are merely shoved into deeper water or crevasses, they can crawl out and inhibit or prevent recolonization.

Sea urchins have a poor tolerance for reduced salinity. Unusually rapid spring thaws, heavy rainfall, and some winds can combine to produce a surface low-salinity layer fatal to sea urchins but not kelps or many other species of marine life. This has been observed on several occasions in Newfoundland and Labrador, especially in fiords. The largest example was observed in Kaipokok Bay, an 80 km long inlet in Labrador. In 1976, much of the Bay was urchin dominated. The spring runoff of 1977 killed all urchins to a depth of 12 to 15 m. This was approximately 60 to 75% of the total population in the Bay. The first summer of recovery produced much diatom and small algal growth. Longer-term recovery will be observed. Similar cases were observed in Terra Nova National Park, Bonavista Bay, Aquaforte, and elsewhere where similar effects were observed to depths of 3 to 4 m. The Alexander Bay location developed a

small kelp bed subsequent to the urchin mortality. This persisted for three years before succumbing to a combination of urchins, Littorina spp., and amphipods.

Another unpredictable cause of sea urchin mortality is disease. We have occasionally observed large numbers of urchins dying from some type of unknown infection.

Normal mortality by predation has been observed for all stages of urchin growth. Larvae are eaten in large numbers by many predators. The large scyphomedusa, Cyanea capillata, and smaller medusae can eat vast numbers of larvae. Anemones sponges, tunicates, and larval fish do as well. If planktonic predation is high, low recruitment may occur. Small post-recruitment juveniles are still susceptible to many predators. As the urchins grow, their predators change. Table 1 lists some of the major predation observed but not quantified. The work of Squires (1970) and Ennis (1973), as well as our own observations, suggest that lobsters are not an important urchin predator in Newfoundland.

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TABLE 1. Observed sea urchin predators in Newfoundland waters.

	Sea Urchin Size			
	Larvae	Small (5 mm)	Medium (5+ to 25 mm)	Large (over 25 mm)
Predators	*Cyanea* ctenophores *Ophiopholis* *Metridium* sponges tunicates medusae	*Tealia* flounders gunnels shannies small *Cancer* *Hyas* juvenile lobsters small sea stars juvenile cod	*Tealia* wolffish flounders *Solaster* cod *Leptasterias* *Cancer* sea birds lobster other anemones	wolffish *Solaster* *Tealia* sea birds large lobsters *Cancer*

MULTISPECIES CONSIDERATIONS OF RESOURCE MANAGEMENT IN SOUTHERN CALIFORNIA KELP BEDS

By

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ABSTRACT

Southern California kelp beds, especially those around major metropolitan centers, have suffered from severe episodes of sea urchin overgrazing in the last four decades. The proposal that increases in sea urchin populations leading to this destructive grazing were caused by release from predation by the sea otters is rejected on the basis of historical data. While fluctuations in standing crop have been observed, some kelp beds in this region continue to flourish in the absence of either otter predation or human control of urchins. Abalones, spiny lobsters, and sheephead are other species whose populations have been reduced by fishing and which, by virtue of their trophic relationships with urchins, could be expected to control urchin distribution and abundance patterns. Studies of giant kelp mortality in the Point Loma kelp bed off San Diego provide evidence for the role of lobster and sheephead predation in controlling urchin populations. These biological interactions provide a mechanism for the maintenance of southern California kelp bed communities in a stable configuration after the demise of the sea otter from this region.

INTRODUCTION

Sea urchins are well known for their abilities to control the distribution and abundance of marine plants; and especially where their preferred foods are large kelps, these herbivores can be the major structure-determining factor in nearshore communities. In his recent review, Lawrence (1975) cites reports from several parts of the world where urchins appear to have overgrazed their food supply, leading to urchin-dominated barren grounds. Mann and his associates have documented the decline of kelp beds in St. Margaret's Bay, Nova Scotia, in the face of intense grazing pressure by *Strongylocentrotus droebachiensis* (this work is reviewed by Mann, 1977). This increase in urchin grazing was apparently caused by heavy fishing of an important urchin predator, the lobster *Homarus americanus*.

The urchins, sustained by drift from algal refuges too shallow for urchin grazing, prevent algal recolonization in deeper water. Because of the persistence of this association, Mann (1977) has proposed the hypothesis that the urchin-dominated barren grounds of Nova Scotia are not representative of cyclic changes in the abundance of kelp and associated herbivores but instead are a new, stable configuration of the system. In other words, he is suggesting that overfishing a predator of the major grazer has so perturbed the community that it will not be able to recover to its previous, long-persisting state.

The decline of kelp beds in southern California predates that documented for Nova Scotia by many years; and here as well, sea urchin grazing has received much of the same. I would like to consider the resiliency of these kelp bed communities and the applicability of Mann's hypothesis to southern California. This will entail first a discussion of the history of this ecosystem and the changes which have taken place as a result of human impact on the nearshore environment. Secondly, my own research has dealt with the natural history and population dynamics of two sea urchins, *Strongylocentrotus purpuratus* and especially *S. franciscanus*, which is now the object of a commercial fishery. These two sea urchins are the most important consumers of kelps in southern California; control of their populations is fundamental to the persistence of kelp beds in this region.

SOUTHERN CALIFORNIA KELP BEDS: A BRIEF HISTORICAL PERSPECTIVE

The giant kelp, *Macrocystis pyrifera*, is the most prominent alga of southern California kelp beds. Several other kelps contribute to the diversity of these assemblages, but *Macrocystis* is most important in terms of biomass and its contribution to the spatial structure of the community. Its holdfast, fronds, and canopy furnish food, substrate, or shelter for a variety of organisms. These beds are the location of valuable fisheries for abalone, spiny lobster, fin fish, and most recently, sea urchins. The surface canopy, which forms large offshore beds often covering several km^2, is easily harvested and has been an important resource since the early part of this century (Leighton, Jones, and North, 1966; North, 1971).

When potash supplies became a national concern about 1910, Congress authorized a survey of west coast kelp resources. The beds were mapped during the period of 1911 to 1912 and the total area of kelp beds in southern California (San Diego to Point Conception) was estimated at

253 km^2 (North, 1971). North (IMR, 1963) has used these data to assess subsequent changes, especially the decline of large kelp beds around the two major metropolitan centers of southern California. During the decade of 1940-1950, productive beds around the Palos Verdes peninsula (the site of the Los Angeles County sewer outfall) deteriorated to the point that little or no harvesting was conducted. A decade later, the same changes took place in the Point Loma kelp bed off San Diego (see Leighton, Jones, and North, 1966, for historical variation of the Point Loma beds). In both cases, the historical data indicated that those portions of the beds close to sources of waste disposal were affected first (IMR, 1963).

Early investigations of these once productive beds revealed an abundance of grazers, particularly sea urchins (IMR, 1963). North and his co-workers described barren rock bottoms where grazing pressure prevented algal recolonization. Perhaps the coup de grace was delivered to these communities by the warm-water years of 1957-1959 when abnormally high temperatures prevailed throughout the year. Offshore island beds produced normally in 1957; but by 1958 these were affected, as were the beds along the coast. By 1959, North reports that most of the canopies in kelp beds of southern California had deteriorated and many beds had virtually disappeared (IMR, 1963).

Several authors have proposed that this apparent population explosion of S. purpuratus and S. franciscanus associated with the decline of kelp beds along the coast of southern California (North and Pearse, 1970) was caused by a decrease in predation by the sea otter, Enhydra lutris (McLean, 1962; North, 1965, Lowry and Pearse, 1973). Leighton, Jones, and North (1966) consider the otter to be the only predator capable of controlling urchin populations in California. Sea urchins are a preferred food of sea otters (Ebert, 1968), and otter predation of urchins has been documented as having major effects on kelp community structure in Alaska (Estes and Palmisano, 1974; Dayton, 1975). As the now protected otter has begun to reoccupy part of its former range in central California, urchin densities have decreased and the herbivores are now restricted to deep crevices beyond the reach of the otters (Lowry and Pearse, 1973).

The problem with this hypothesis for the control of urchin populations is that otters were probably gone from southern California 130 to 150 years ago (Ogden, 1941). Hunting is known to have continued up to the time of the Gold Rush in 1848 and sporadically after that; but this most likely took place north of Point Conception where sea

conditions and the coastline are considerably rougher and where in fact a remnant population did survive (Woodhouse, Cowen, and Wilcoxon, 1977). Furthermore, the abalone (another preferred food of the sea otter; Ebert, 1968) fishery dates back to the 1850's around San Diego (Cox, 1960), and large kelp beds were documented in 1913 (North, 1971). According to North, the major decline of surface canopies did not begin until the 1940's (IMR, 1963). These historical data strongly suggest that factors other than otter population have controlled urchin populations in southern California.

SEA URCHINS AND THEIR INTERACTIONS WITH OTHER SPECIES

Since sea urchins can be considered a foundation species (Dayton, 1972) in these communities, any factors which affect their birth or death rates are likely to be important to the maintenance of community structure. I have been studying sea urchin recruitment, competition, and mortality patterns to determine what disturbances may have prevented urchin domination in the past. An obvious consideration is those species which, in addition to sea otters, have been fished.

While several benthic invertebrates graze on attached or drift *Macrocystis* (Leighton, 1971), the abalones, by virtue of their physical size (*Haliotis rufescens* attains sizes up to 30 cm; Cox, 1960) and the magnitude of their populations, require consideration as competitors of the sea urchins. Seven species are found in southern California; all are subject to both sport and commercial fisheries. While abalone shells are common in Indian middens dating back more than 7,000 years, the recorded history of the abalone fishery in California begins with the Chinese in the early 1850's (Cox, 1960). These immigrants, collecting primarily green and black abalones in shallow water around San Diego, built up an industry to over 4.1 million pounds per year in 1879. When coastal counties made it unlawful to fish for abalone in shallow water, Japanese hard hat divers, later followed by Caucasians, took their place subtidally and extended the fishery throughout the state (Cox, 1960).

While landing records indicate that all commercial species have suffered major declines in standing stock, data are presented in Figure 1 for the pink abalone, *H. corrugata*, the second most valuable species, because the northern limit of its range is Point Conception (Cox, 1960). Interpretation of these data is not yet confused by the range extension of the sea otter. The pink abalone's range was opened to commercial fishing in 1943. After 1952, the catch declined

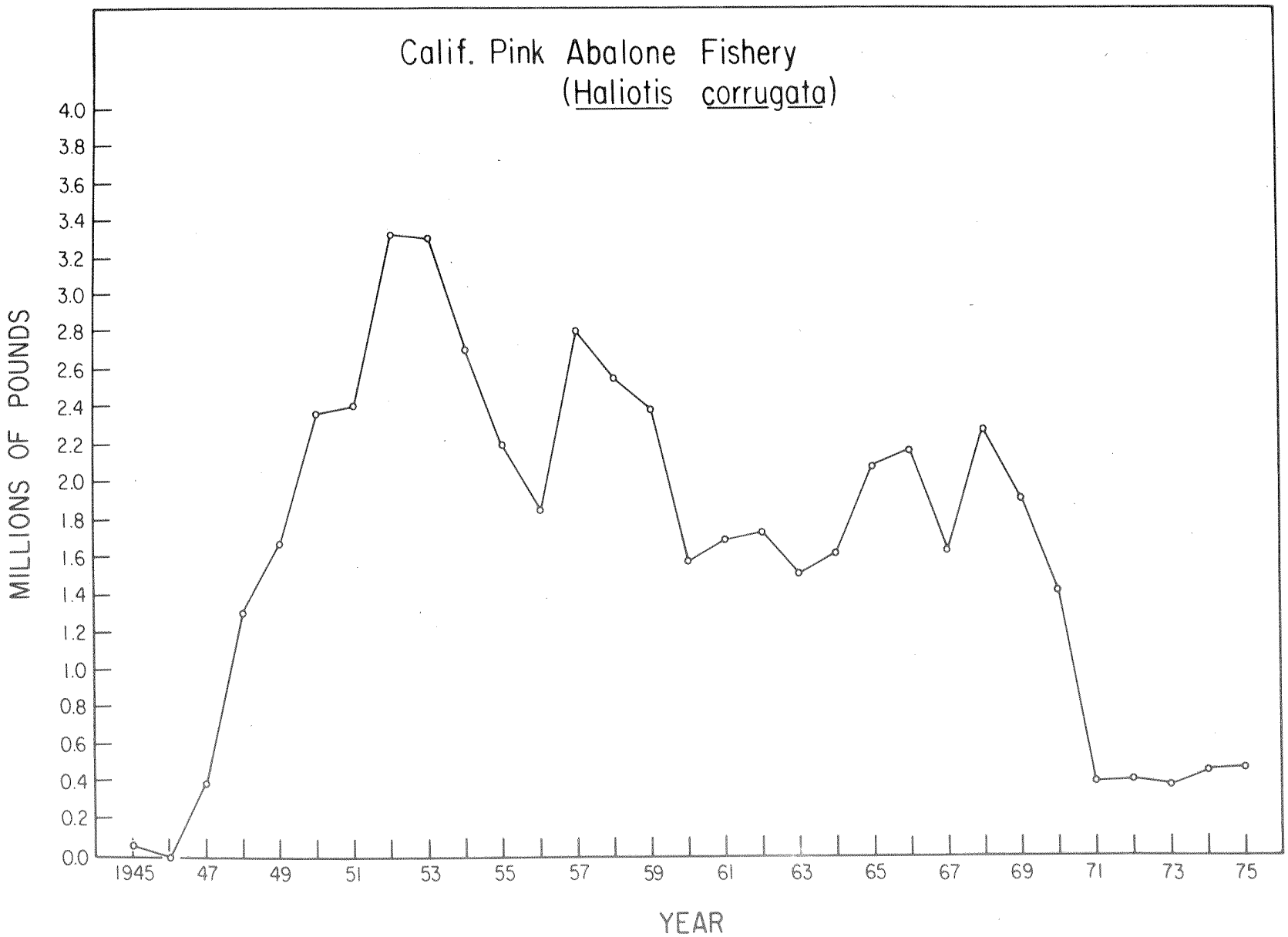

Figure 1. Commercial pink abalone, Haliotis corrugata, landings. Data are compiled from various California Department of Fish and Game sources.

as virgin stocks were depleted (Cox, 1960). The average catch of recent years is a small percentage of peak yields.

The abalones, especially those found subtidally, share very similar food (Leighton, 1966) and habitat preferences with the two strongylocentrotids. Under optimal conditions, both groups feed on drift algae carried by currents and surge. While urchins are well known to attack attached plants when drift becomes limiting, red, pink, and white abalones have also been observed foraging on *Macrocystis* holdfasts (Leighton, 1971; personal observations).

Considering that these herbivores share both food and habitat resources and that abalone standing stocks have been greatly reduced by fishing, it is tempting to speculate that the urchin population growth may have been caused in part by a release from competition. It has been suggested that abalones out-compete urchins for space (Lowry and Pearse, 1973) but that where food is limiting, urchins may be able to displace abalones by differences in feeding habits (Shepherd, 1973). We have been conducting studies of exploitive competition between red urchins, *S. franciscanus*, and red abalones, *H. rufescens*, in the laboratory (Tegner, unpublished data). Under conditions of limited food supply, the urchins have proven to be superior exploiters capable of scavenging all the food they need for growth, despite the presence of abalones. Red urchins and red abalones exhibit virtually identical resistances to starvation. Behavioral observations support the contention that urchins are better foragers. When presented with the scent of *Macrocystis*, starved abalones assume feeding posture and wait for the food to drift to them; starved urchins move toward the source of the scent (Tegner, unpublished data).

Field observations of habitat partitioning suggest that abalones may be superior in interference competition in the presence of adequate food supply (Lowry and Pearse, 1973; personal observations). Manipulations of the densities of these two herbivores are planned to study competition for space. The effects of this hypothesized interaction may be most obvious where predators (urchins and abalones share many of the same predators) restrict the herbivores' foraging patterns.

More clearly than competition, predation is important for regulating the abundances of the two strongylocentrotids. Sea urchin predators in southern California today include three asteroids (*Pycnopodia helianthoides*, *Astrometis sertulifera*, and *Dermasterias imbricata*), cancer crabs (*Cancer antennarius*, *C. productus*), the spiny lobster (*Panulirus interruptus*), the horn shark (*Heterodontus*

francisci), and three labrids of which the California sheephead (Pimelometopon pulchrum) is most important (Leighton, Jones, and North, 1966; Winget, 1968; Rosenthal and Chess, 1972; Tegner and Dayton, in preparation). Two of these predators are subject to fishing pressure. Spiny lobsters are taken by both commercial fishermen and sport divers; sheephead are a sport fish taken by anglers and spear fishermen. Commercial lobster landings data are presented in Figure 2. Data are not available for the sport catch of either species.

To analyze urchin predation patterns, 200 m^2 transects were established at three depths (10, 15, and 20 m) in the Point Loma kelp bed. Urchin populations were censussed and the tests of dead sea urchins collected as often as possible. While we were not able to visit these areas with sufficient regularity to establish rates of predation, some interesting patterns emerged (Tegner and Dayton, in preparation). Morphological differences between purple and red urchins suggest different susceptibilities to predation. S. purpuratus is smaller, with a maximum test diameter in this area of about 70 mm, and has short spines relative to its test size. S. franciscanus reaches about 140 mm locally, has long spines relative to its test size, and has a considerably thicker test than S. purpuratus. While all of the predators cited take purple urchins, only the spiny lobster and sheephead prey on adult S. franciscanus.

Male sheephead feed on large red urchins by turning the animal over and using dog-like teeth to puncture the oral surface. The oral surface of the urchin is bitten in a regular, characteristic pattern (which allows identification of the predator when such tests are found) to give the fish access to the soft tissues inside. The advantage of long spines is seen in how these predators handle S. purpuratus; the purple urchins are attacked from any angle and often the entire test is consumed (Tegner and Dayton, in preparation). Sea urchins are the major dietary constituent of sheephead larger than 30 cm (McCleneghan, 1968, unpublished M.Sc. thesis).

Winget (1968) reported that the spiny lobster, P. interruptus, feeds on sea urchins but assumed that only S. purpuratus was taken. Molluscs were most heavily consumed, followed by sea urchins and crabs. Because of the problems of observing a skittish, nocturnal predator in the field, we conducted feeding tests in the laboratory. The lobster was capable of handling full-size red urchins, generally by inverting its prey and using its third maxillipeds and anterior walking legs to pierce the test (Figure 3). Irregular holes, occasionally in the aboral surface, were made in most tests; however, some urchins were consumed by

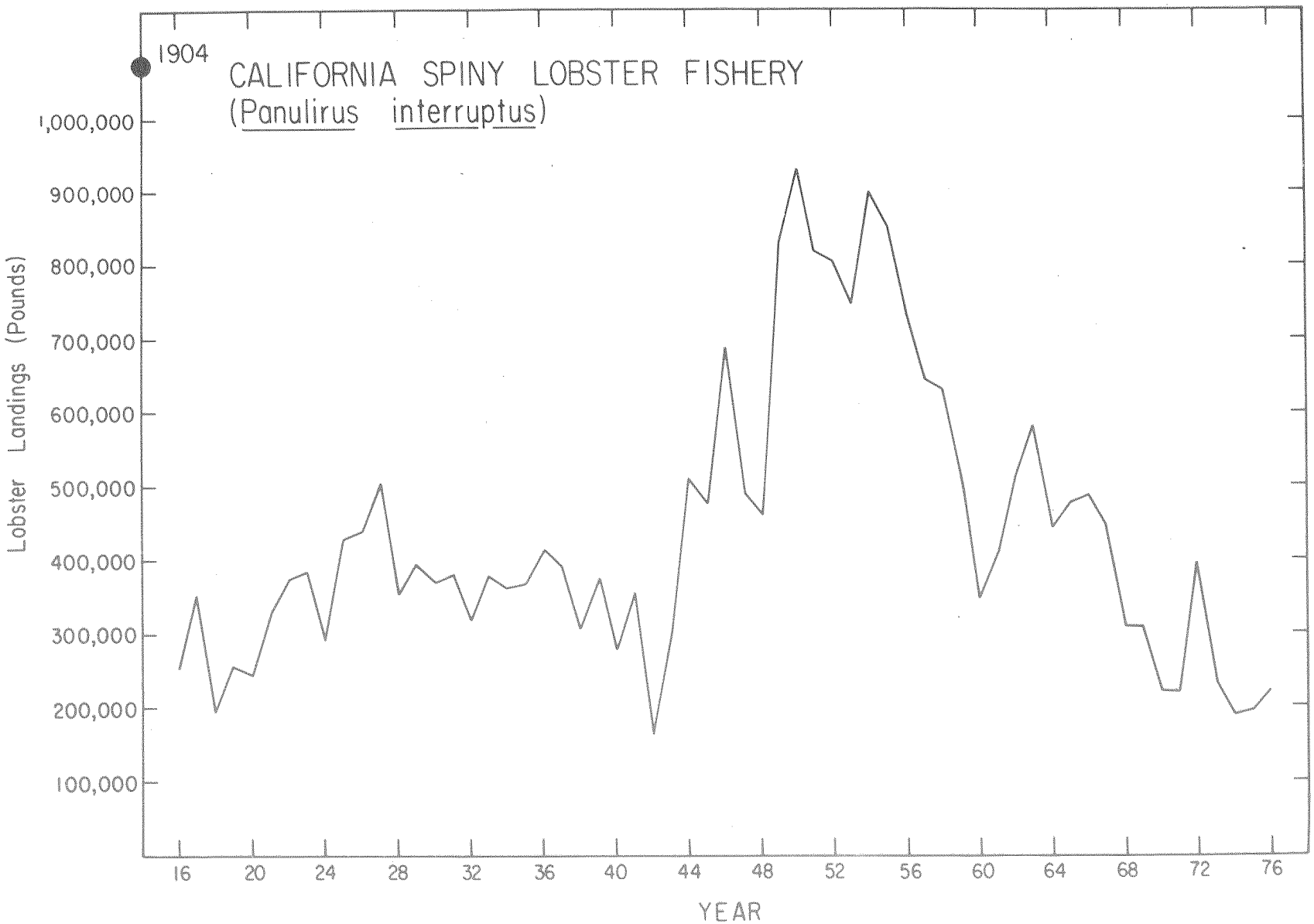

Figure 2. Commercial spiny lobster, Panulirus interruptus, landings. Data are compiled from various California Department of Fish and Game sources.

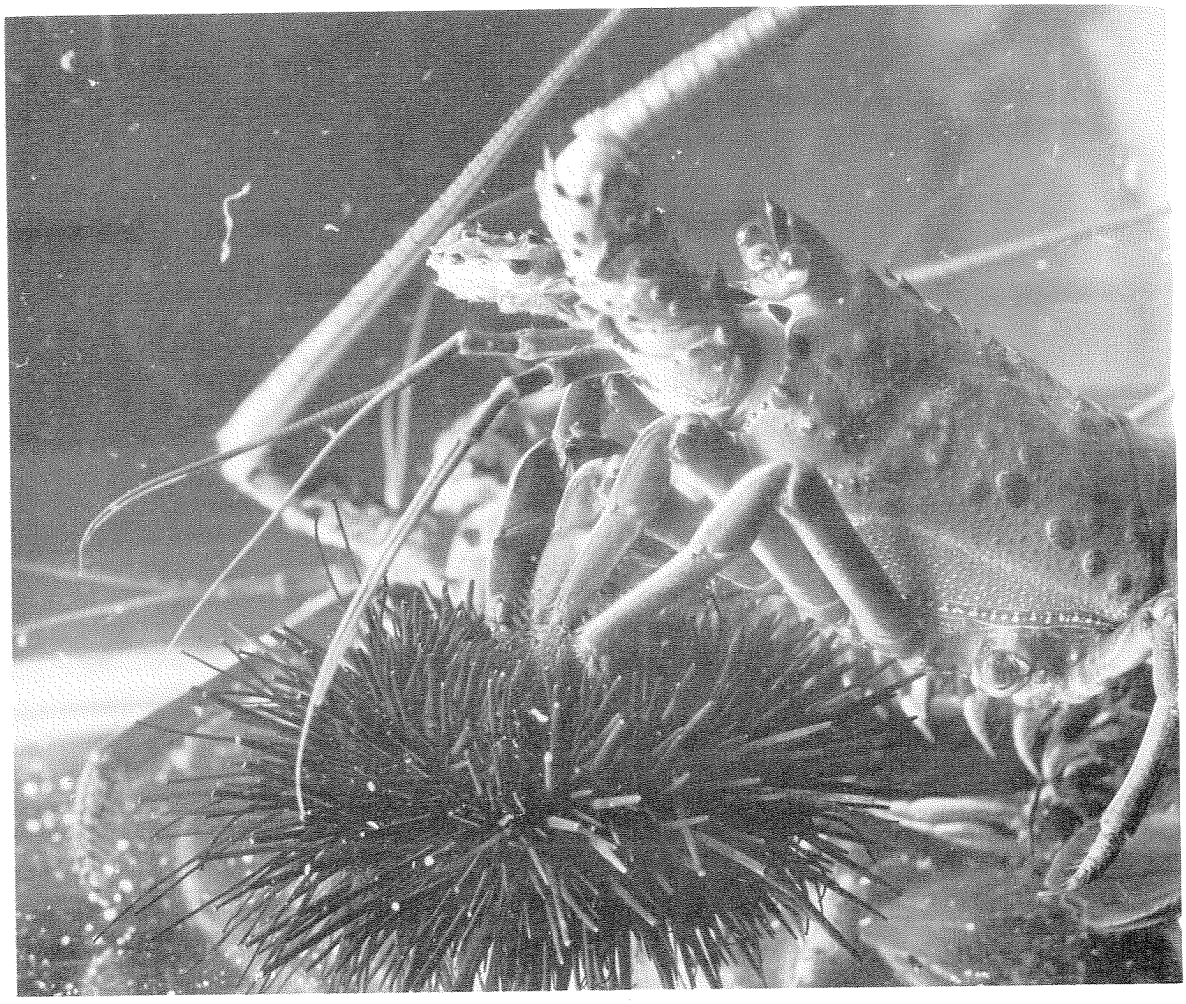

Figure 3a. The spiny lobster, Panulirus interruptus, using its anterior walking legs and third maxillipeds to break into the surface of the red sea urchin, Strongylocentrotus franciscanus.

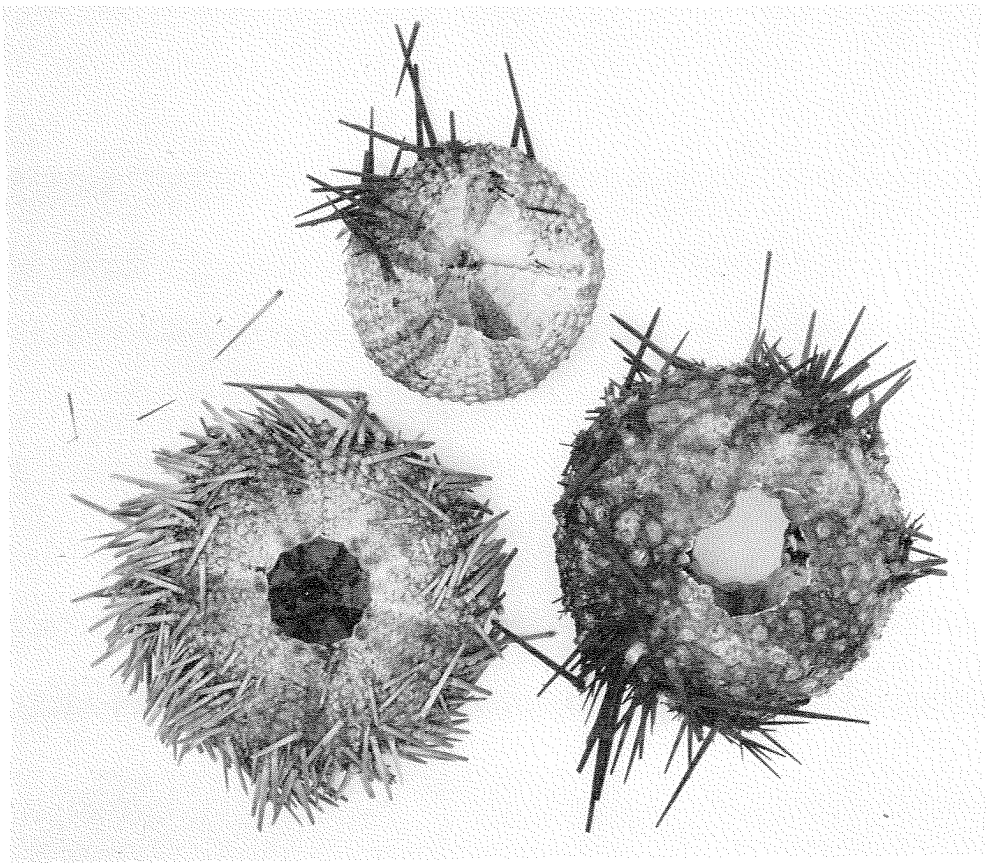

Figure 3b. Recovered tests of S. franciscanus following consumption of soft parts.

simply removing the peristomial membrane. Again, S. purpuratus were attacked from any angle and the entire test consumed (Tegner and Dayton, in preparation).

Sheephead (and lobsters to some degree) are far more common at offshore locations such as San Clemente Island and Tanner Bank. Several effects can be noted in the urchin populations of these areas. Compared to the coastline, the short-spined purple urchins are more cryptically located and the purple to red urchin ratio is much lower. Size-frequency distributions of red urchin populations suggest that the predators are having a major impact on the 30 to 60 mm size class where recruits are no longer sheltered by the spine canopies of adult urchins (Tegner and Dayton, 1977; in preparation). While the effects of increased predation can be observed in these urchin populations, some episodes of overgrazing have been reported for San Clemente Island (McPeak, pers. comm.). It should be noted that extensive abalone and lobster fisheries are conducted there so large lobsters are not common.

Thus, competition with abalones and predation by spiny lobsters and sheephead are proposed as biological interactions which may have regulated sea urchin abundances in the past. In 1971, a commercial fishery began harvesting sea urchins around the Northern Channel Island; this fishery spread to San Diego in the second half of 1976. Only the red urchin is large enough to be commercially feasible for the export market at this time. The fishery has grown rapidly; about 12 million pounds were landed in 1977 (Figure 4). The value of this resource suggests that major episodes of red urchin overgrazing in the future are unlikely.

RESILIENCY OF THE POINT LOMA KELP BED

Given these biological interactions which may have controlled urchin population after the demise of the sea otter, I would like to go back to the question of the resiliency of southern California kelp bed communities by considering our study areas off San Diego. After the Macrocystis canopy of the Point Loma kelp bed reached a recorded low in 1960, a program of urchin control by quicklime was organized and started late in 1962. In 1963, the City of San Diego moved its sewer outfall to deeper waters. By 1964, considerable restoration of the canopy had occurred (Leighton, Jones, and North, 1966). Today, after extensive urchin control efforts by the Kelp Habitat Improvement Program and Kelco, the Point Loma bed once again covers a large area. From a low of 0.03 sq. mi. in 1960, the canopy has grown to 3.2 sq. mi. in 1978 (McPeak, pers. comm.).

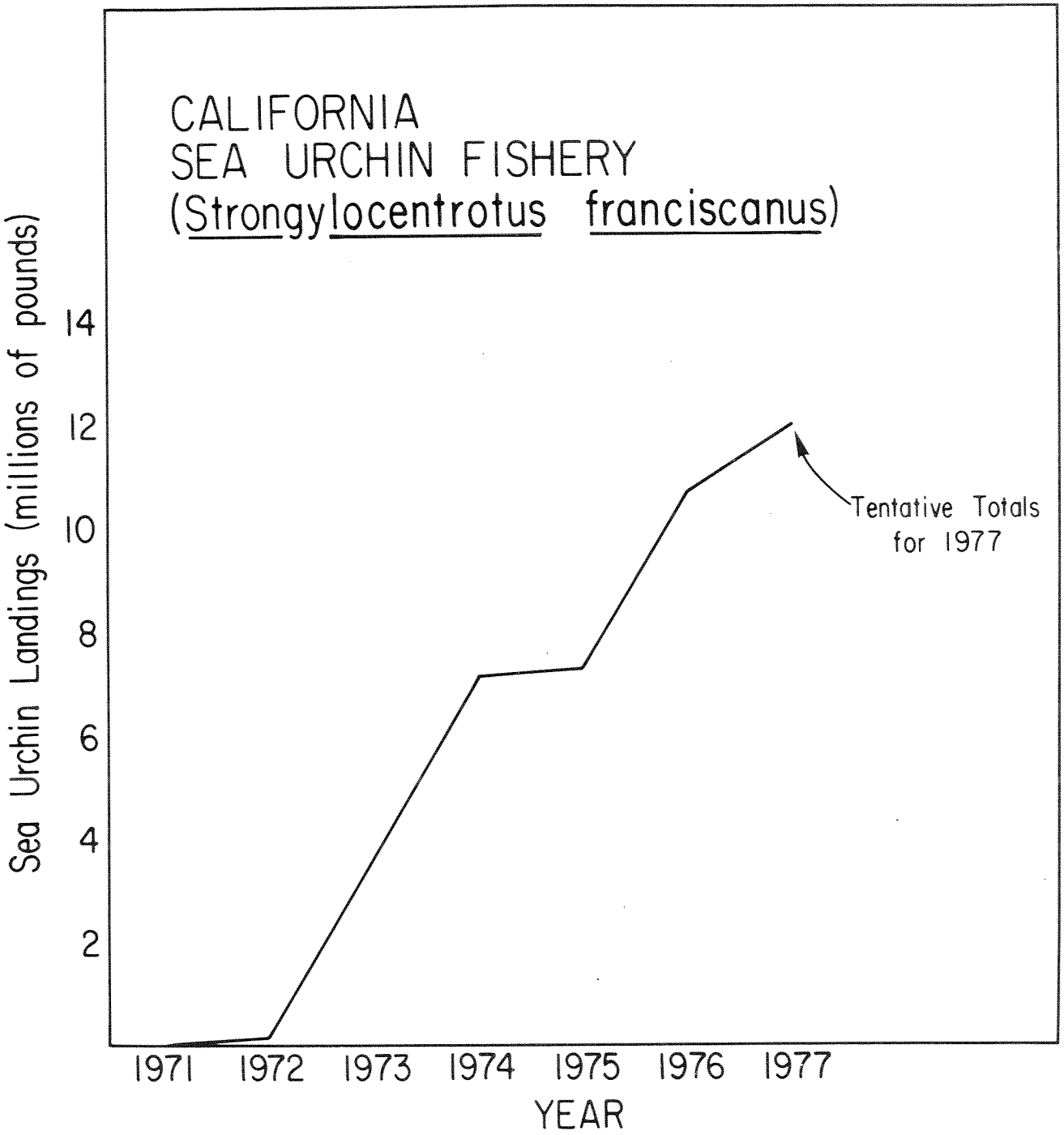

Figure 4. Commercial red sea urchin, Strongylocentrotus franciscanus, landings. Data are compiled from various California Department of Fish and Game sources.

In recent years, certain areas of the Point Loma bed have remained unstable, suffering major losses of canopy and requiring continual urchin control (McPeak, pers. comm.). Other areas of the bed have exhibited fairly stable canopies; these have varied in percent cover with time but have not gone through drastic declines. My colleague, Paul Dayton, has been studying Macrocystis mortality in the Point Loma kelp bed since 1970 at sites which Kelco has graciously allowed us to study in an unharvested state. These are the same three sites where I have been following sea urchin predation. All three sites have significant urchin populations within or adjacent to Dayton's plant transects. The deeper two sites are characterized by extensive vertical relief, reefs and boulders, while the third is mostly flat pavement rock with a few low ledges and boulders. The amount of vertical relief appears to be important to urchin populations for two reasons. First, vertical relief makes it easier for urchins to snare and hold down drift kelp, especially in surge conditions. Where urchins can be sustained by drift kelp, they are less likely to attack attached plants. Secondly, both lobsters and sheephead are dependent upon vertical relief, forming caves or ledges. The nocturnally foraging lobsters require shelter (from sheephead, among other predators) during daylight hours, and the sheephead need a place to sleep at night. Sheephead are common and lobsters are present at both of the study areas with extensive vertical relief. I have never observed either predator at the third site. Dayton's Macrocystis data indicate that 100% of the observed mortalities at both sites with extensive vertical relief was caused by entanglement with other drifting plants. At the flat site, 50-70% of the kelp mortality was due to urchin grazing and the remainder was caused by entanglement. Macrocystis densities at all three sites have shown considerable variation over the years of the study but only the flat site went through a virtually complete loss of plants (Dayton, in preparation). It is interesting to note that although no urchin control measures were used, a massive Macrocystis germination restored the canopy in a little over a year.

This episode provides further evidence in support of a relationship between Macrocystis and urchin settlement which affects urchin population size proposed by Pearse, Clark, Leighton, Mitchell, and North (1970). They observed that barren mode populations of S. franciscanus apparently consisted of continuously recruiting small animals but that after an area became reforested with Macrocystis, the size frequency distribution of the population shifted to the right as the animals present grew and recruitment declined. They proposed that filter feeding organisms associated with the canopy were effectively minimizing larval settlement. The

largest pulse of red urchin recruitment observed at our flat site in three years of study was after the Macrocystis canopy was eliminated by grazing. After the canopy returned, recruitment rates went back down. At another location, settling experiments detected red urchin recruitment at both edges of a dense 100 m canopy, but almost no settlement was observed at a reef inside the bed (Tegner and Dayton, in preparation). Thus, in an indirect manner, Macrocystis apparently affects the population size of a major grazer.

Eight years of relatively stable canopies and Macrocystis mortality caused only by entanglement with drifters indicate that sea urchin populations were being controlled in these two areas of extensive vertical relief. At both sites, red urchin recruitment was observed in all three years of this study at fairly constant rates (Tegner and Dayton, in preparation). Predation was also significant in these areas, suggesting that these urchin populations have been in a steady state. Our sampling program at the third site, which underwent an episode of urchin overgrazing, ruled out the possibility of increases in urchin abundance caused by recruitment but did not test for immigration. While one explanation of this episode would be an increase in urchin populations, an alternate hypothesis would be a decrease in the supply of drift kelp. This grazing episode took place during the time of year when Point Loma is most susceptible to surge conditions which can make it very difficult for the urchins to trap drift. At any rate, Macrocystis rapidly recolonized the area and the grazing cycle was completed.

Other examples of cycles of sea urchins overgrazing their food source, followed by algal recolonization, are available. Foreman (1977) documents a massive outbreak of S. droebachiensis in the Strait of Georgia where a combination of environmental factors favored urchin recruitment. His results indicated that S. droebachiensis undergoes periodic outbreaks which are responsible for localized perturbations of the kelp community and that about 8 to 12 years are required to complete the cycle. North (1971) records algal recolonization after urchin grazing has destroyed kelp beds when urchin concentrations are reduced by starvation or migration. Pearse, Costa, Yellin, and Agegian (1977) document two incidences of localized mass mortalities of S. franciscanus caused by disease, another mechanism which could complete cycles of urchin grazing. We have observed similar outbreaks of disease at Point Loma.

DISCUSSION

Whether the conditions of 1960 were evidence of a massive cycle of urchin grazing or represented a new stable configuration of these ecosystems is subject to debate. The kelp beds around the major metropolitan centers of Los Angeles and San Diego may well have deteriorated so far that these areas could not have recovered on their own; since extensive urchin control efforts were expended in both areas, the question cannot be answered. The Point Loma bed showed significant recovery one year after urchin control measures were started (Leighton, Jones, and North, 1966); but it took seven years of effort until the first growing bed stabilized at Palos Verdes in 1974 (Wilson, Haaker, and Hanan, 1978). However, Palos Verdes is the site of the largest sewer outfall in southern California, and large-scale ecological changes have occurred in this area (Grigg and Kiwala, 1970).

Of more biological interest is the history of kelp beds less heavily impacted by waste disposal. Rosenthal, Clarke, and Dayton (1974) reported on a bed off Del Mar, California, which has undergone major fluctuations in relative kelp harvest. During their six-year study, there was a pronounced oscillation in Macrocystis standing crop, apparently caused by storms. There was little indication that urchin grazing contributed to kelp mortality. Other beds, in coastal areas distant from metropolitan centers or offshore island sites, have recovered from the warm-water years to become major producers of kelp without either otter predation or human activities to control urchins (McPeak, pers. comm.). A notable example is the large bed around San Nicholas Island. The higher priced shellfish, abalones and lobsters, are both harvested intensively; but since San Nicolas is the farthest of the Channel Islands from any mainland port, urchin divers have only recently begun to investigate this area. Local areas of the San Nicolas bed have undergone cycles of urchin overgrazing leading to losses of Macrocystis standing crop; but, as we have observed at Point Loma in recent years, the large beds of this island have persisted (McPeak, pers. comm.).

The persistence of kelp beds in southern California well over a century after the demise of the sea otter from this region clearly indicates that other factors have controlled sea urchin populations and thereby maintained the structure of this community in a stable configuration. Southern California kelp beds have suffered from urchin grazing, environmental perturbations such as the warm-water years, sewage disposal, and heavy human use. Natural recovery from such stresses in many areas illustrates the resilience of the ecosystem. However, continued problems, such as at Palos Verdes, suggest that there are limits to the ability of the

system to resist and recover from severely disturbed conditions. Hopefully, our recognition of these limits is a major step toward protection of the nearshore environment.

I have proposed biological interactions, predation by spiny lobsters and sheephead, and possibly competition with abalones, as the factors which have controlled sea urchin abundance and distribution patterns since the time of the sea otters in southern California. These interactions provide mechanisms for the maintenance of kelp community structure and are fundamental to the system's resilience to external perturbations. The populations of spiny lobsters, abalones, and to a lesser degree, sheephead, have all been reduced by fishing. A knowledge of the functional relationships between these species and sea urchins would have predicted that external perturbations favorable to urchins and/or unfavorable to Macrocystis could lead to the destructive overgrazing episodes of the late fifties. The biology and history of this complex community underscore the need for a multispecies approach to the management of resources.

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THE BENTHIC ALGAL BIOMASS, COMMERCIAL HARVESTING, AND *CHONDRUS* GROWTH AND COLONIZATION OFF SOUTHWESTERN NOVA SCOTIA

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ABSTRACT

Studies were carried out in the southwestern Nova Scotia area concerning *Chondrus crispus* and its relationship to other benthic algae. Standing crop, harvesting areas, growth, reproduction, and succession were monitored. Out of 30 genera of algae, *Ascophyllum*, *Chondrus*, and *Laminaria* spp. made up 74.2% of the biomass at the transect sites. *Fucus* spp., *Phyllophora* spp., *Corallina officianalis*, *Chaetomorpha* spp., and *Desmarestia* spp. made up 23.8% of the biomass. Two percent (2%) was composed of 21 other genera of algae. Sixty-one (61) commercial *Chondrus* beds were located and approximately 650 harvesters utilized these beds. *Chondrus* was found to grow from a spore to a reproductive plant in two years. Succession on a concrete block took approximately three years for *Chondrus* establishment. It is estimated five to ten years will be required to re-establish *Chondrus* in barren areas.

INTRODUCTION

Marine plants are harvested commercially from a number of areas in the Maritime provinces (Ffrench, 1971; Pringle, 1976); but one of the most important areas is southwestern Nova Scotia, between Cape Sable Island and Pinkney Pt. (Figures 1, 9, and 10). Here, approximately 7,800 acres of ocean bottom have a minimum of 40% *Chondrus* cover (Haggerty and Hellenbrand, 1976). The large tides, nutrient-rich waters, extended growing season, and relatively ice-free conditions promote a luxurious standing crop of benthic algae. One result is a commercial marine plant industry based on three genera: *Laminaria* Lamouroux, *Chondrus* Stackh., and *Ascophyllum* Stackh., which has been ongoing for approximately 45 years, 40 years, and 20 years respectively. The first two genera are harvested in the subtidal; consequently, the observations by Breen and Mann (1976), of local overgrazing by the sea urchin *Strongylocentrotus droebachiensis* (O.P. Muller) of benthic algal populations, are of extreme concern to those involved in the marine plant industry.

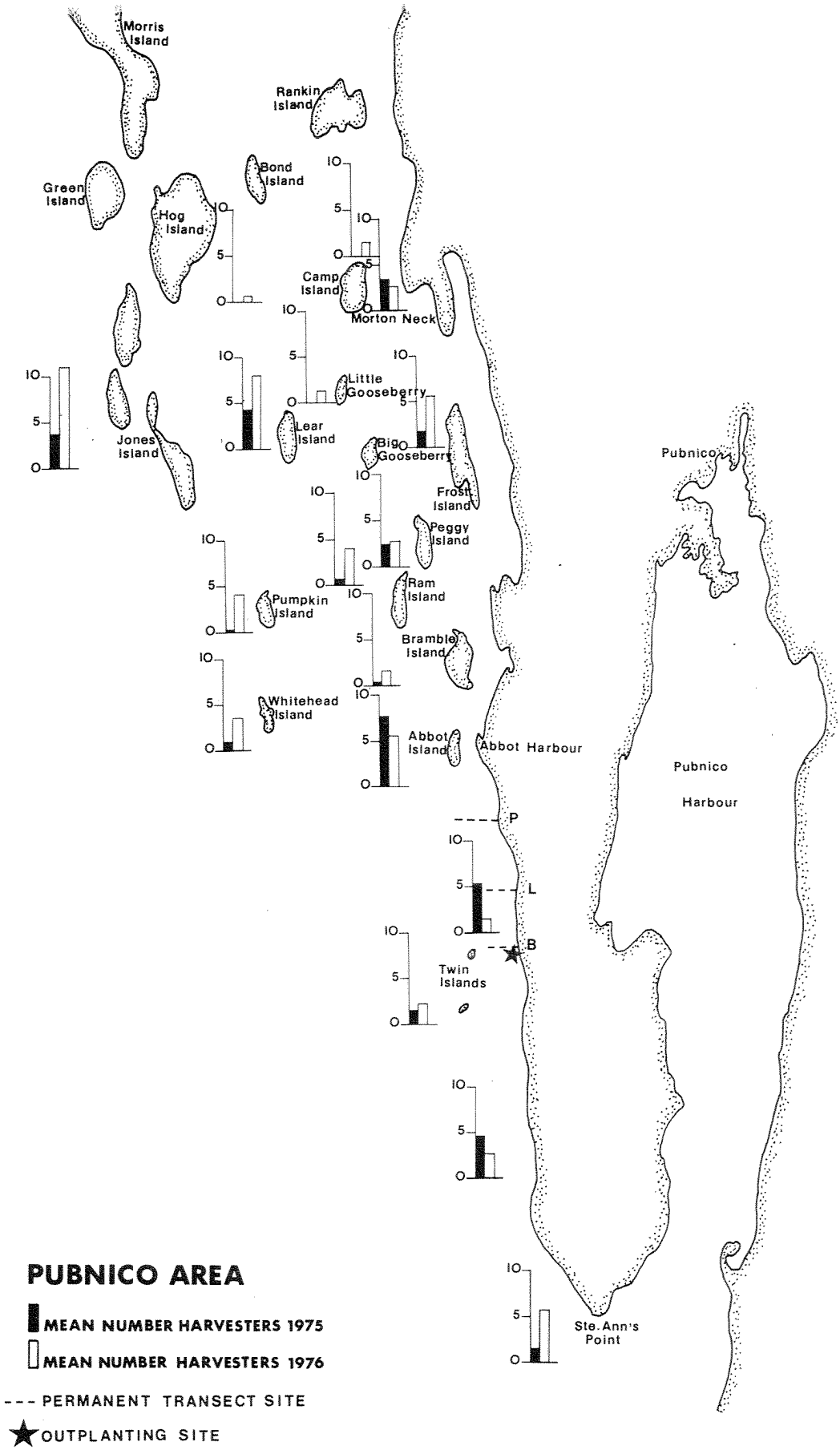

Figure 1. The commercially important beds of Chondrus in the Pubnico area and the daily mean number of harvesters observed/bed during 1975 and 1976. Shown as well, the location of permanent transects B, L, and P and the outplanting site.

This paper is presented to give delegates to the workshop information on both the ecology of the commercially important benthic algae of southwestern Nova Scotia and Irish moss harvesting. For details on the standing crop of *Laminaria* spp., see McPeak (1980); Sharp (1980) reviewed the history of *Laminaria* harvesting.

1. STANDING CROP

METHODS

Chondrus and *Ascophyllum* harvesting takes place along the west side of the West Pubnico peninsula (Figure 1). As a result, three representative study sites were chosen. A stainless steel cable, marked at 1 m intervals, was layed along the ocean bottom at each site vertical to the shore, extending through the algal zone. Above the high tide mark, each transect was permanently marked and a bearing taken with a surveying transit to determine the angle of the transect. All macrophytes within a 0.25 m^2 area (sampling unit) were collected at 5 m intervals (3 m intervals for Transect B) along the transect line. The time and depth from surface were recorded; and using Canadian Tide and Current Tables (Anonymous, 1975), the level of each station with respect to chart datum was calculated.

The plants were placed in polyethylene garbage bags, kept on ice, and transported to the laboratory where they were stored at -5 C. The plants from each sample unit were sorted to at least genus and often to species and weighed. *Ascophyllum* and *Chondrus* were dry weighed as well. The data from each transect were pooled and mean values determined.

RESULTS AND DISCUSSION

General Distribution

Thirty genera of benthic algae were identified; their distribution, relative to chart datum, is shown in Figure 2. The mean total biomass for a 0.5 m wide by 131.7 $\pm$ 21.9 m long strip through the algal zone off the West Pubnico peninsula was 368.0 $\pm$ 86.3 kg wet weight (Table 1). The mean weight (wet) of *Ascophyllum*, *Chondrus*, *L. longicruris*, and *L. digitata* in this strip was 102.9 $\pm$ 76.5 kg, 83.7 $\pm$ 19.3 kg, 31.4 $\pm$ 26.3 kg, and 55.9 $\pm$ 85.8 kg respectively (Figure 3). Figure 4 shows the percentage of the total standing crop based

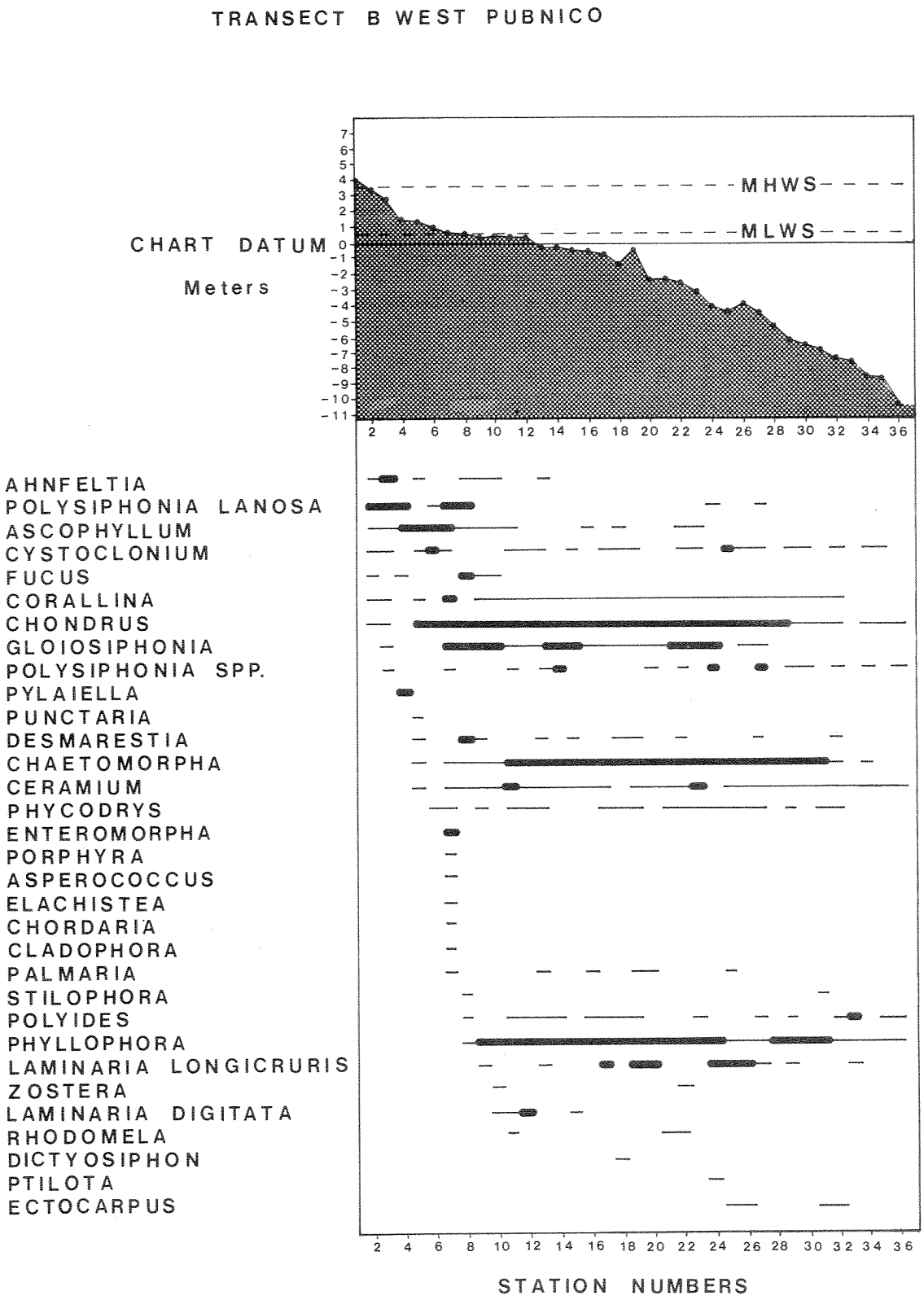

Figure 2. The vertical distribution of identified taxa along Transect B off West Pubnico during August, 1975.

TABLE 1. Total biomass data for each transect B, L, and P and the biomass of *Chondrus*, *Ascophyllum*, and *Laminaria* spp.

Transect	Biomass (wet kg)				
	Total	*Chondrus*	*Ascophyllum*	*L. longicruris*	*L. digitata*
B	268.4	90.8	56.3	34.0	7.4
L	416.0	61.8	191.2	3.8	5.3
P	419.7	98.5	61.2	56.3	154.9
Mean	368.0	83.7	102.9	31.4	55.9
S.D.	± 86.3	± 19.3	± 76.5	± 26.3	± 85.8

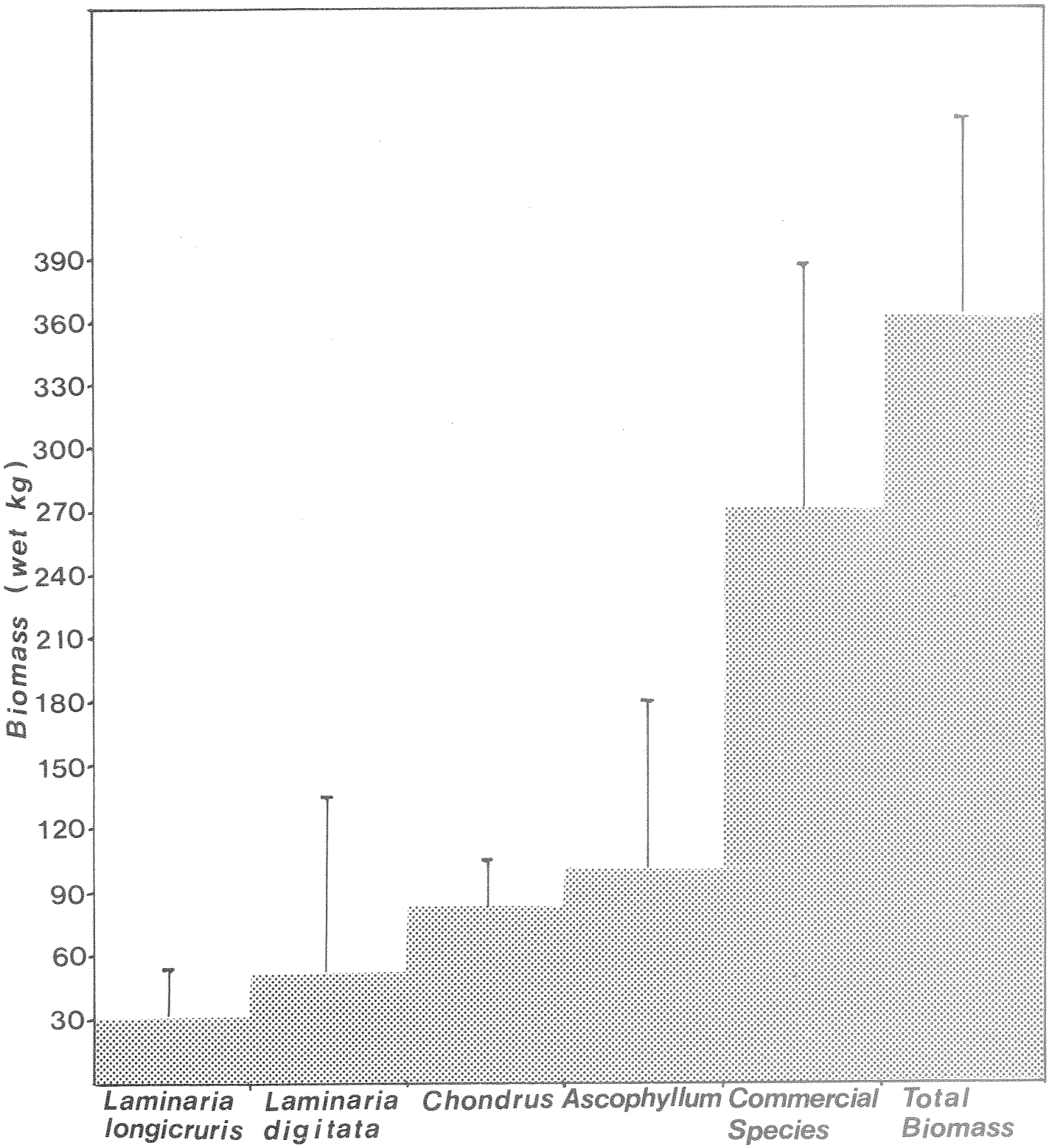

Figure 3. The mean biomass for a 0.50 m wide strip through the benthic algal zone off the West Pubnico peninsula during the summer, 1975.

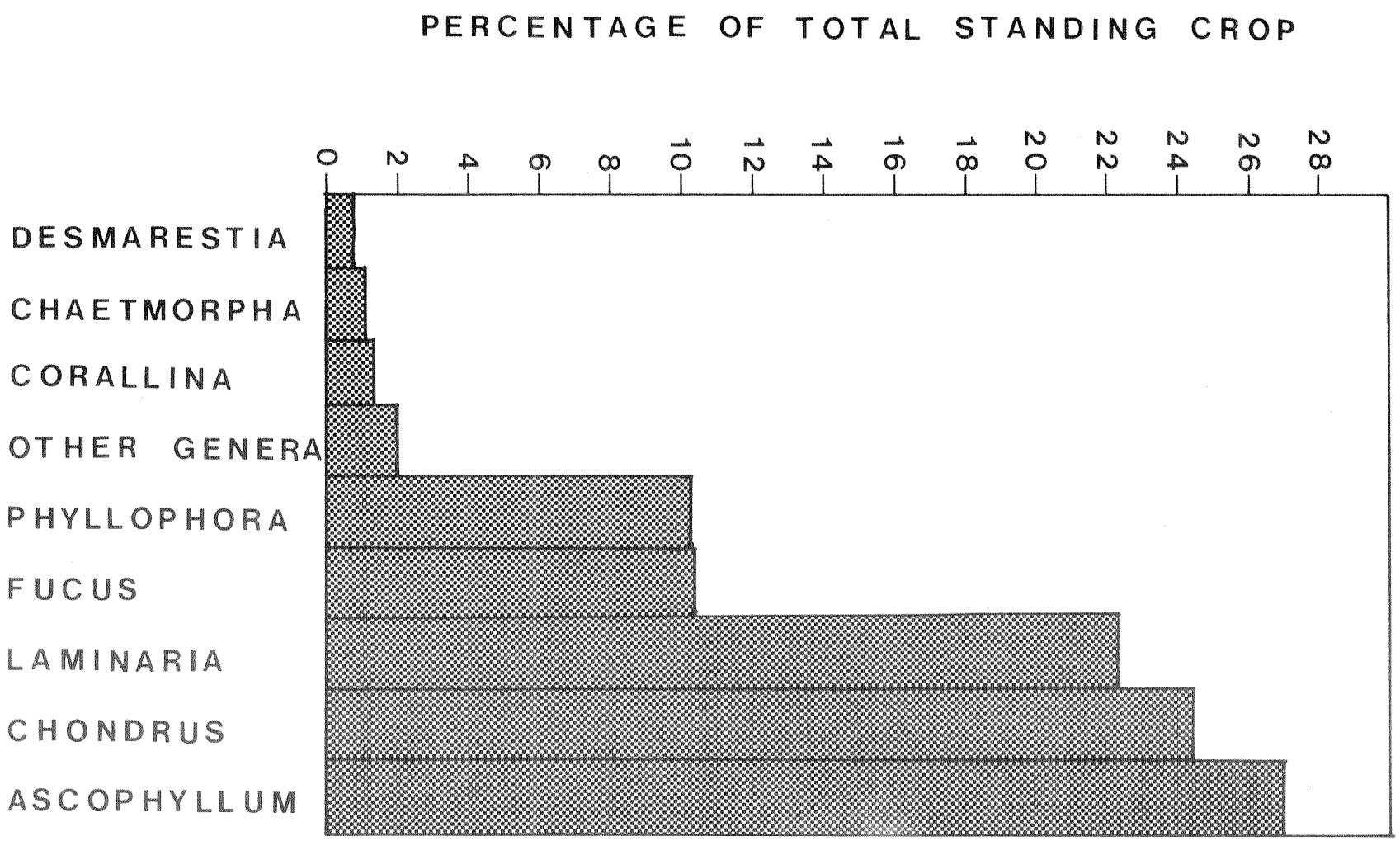

Figure 4. The percentage, by weight, of each of the eight most abundant genera from a 0.50 m wide strip through the benthic algal zone off West Pubnico during summer, 1975.

on weight for the eight most abundant genera. Note that Ascophyllum, Chondrus, and Laminaria spp. make up 74.2% of the biomass. Five other genera: Fucus Linnaeus spp., Phyllophora Greville spp., Corallina officianalis L., Chaetomorpha Kutzing spp., and Desmarestia Lamouroux spp. make up 23.8% of the remaining biomass and "other" taxa represent the remainder (2%).

Ascophyllum begins at 3.5 m above chart datum (Figure 5, Table 2); between 3.5 and 3.0 m the mean standing crop was 3.2 ± 2.0 g wet weight/m^2. Between 2.5 m and 0.5 m the mean wet weight/m^2 was 6720 ± 5171.2 g; this decreased to to 31.0 ± 105.6 g wet weight/m^2 between chart datum and 6 m below chart datum. The mean standing crop for the entire Ascophyllum zone was 1700.8 ± 3804.8 g wet weight/m^2.

Chondrus ranged in distribution from 3.5 m above chart datum to 10.5 m below chart datum (Figure 6, Table 2). Between its upper limit and 2.0 m, the mean standing crop was 130.0 ± 156.0 g wet weight/m^2. This increased to 1057.6 ± 820.0 g wet weight/m^2 between 1.5 m and -7.0 m and decreased to 54.8 ± 54.8 wet weight/m^2 between -7.5 and -10.5 m. The mean standing crop for the entire Chondrus zone was 1054.8 ± 952.0 g wet weight/m^2.

L. longicruris Pyl. ranged from 2.0 m above chart datum to -8.5 m below (Figure 7, Table 2). Mean standing crop from the upper limit down to chart datum was 65.6 ± 142.4 g wet weight/m^2 between -0.5 and -8.0 m. The mean standing crop throughout the zone was 944.0 ± 2243.6 g wet weight/m^2.

L. digitata (Huds.) Lamour. ranged from 1.0 m above chart datum to -7.5 m below, and between its upper limit and -1.5 m the standing crop was 123.6 ± 187.6 g wet weight/m^2 (Figure 8, Table 2). This increased to 615.6 ± 975.2 g wet weight/m^2 between -2.5 m and -7.0 m. The mean standing crop throughout the zone was 416.0 ± 785.4 g wet weight/m^2.

The Pubnico area (Figure 1) has approximately 17.2 km of commercially harvestable shore that is likely similar in both physical and chemical ecological parameters to the shore surveyed off the West Pubnico peninsula. Using the data above, the total standing crop of benthic algae in this area was calculated at 12622 MT wet weight. Of this, Ascophyllum, Chondrus, L. longicruris, and L. digitata would make up 3529.5 MT, 2870.9 MT, 1077.0 MT, and 1917.4 MT respectively.

Our data for the Barrington (Figure 9) and Wedgeport (Figure 10) areas are not complete but the quantities/km of shore are likely similar to the Pubnico area. Haggerty and Hellenbrand (1976) suggested that there was 23500 MT of

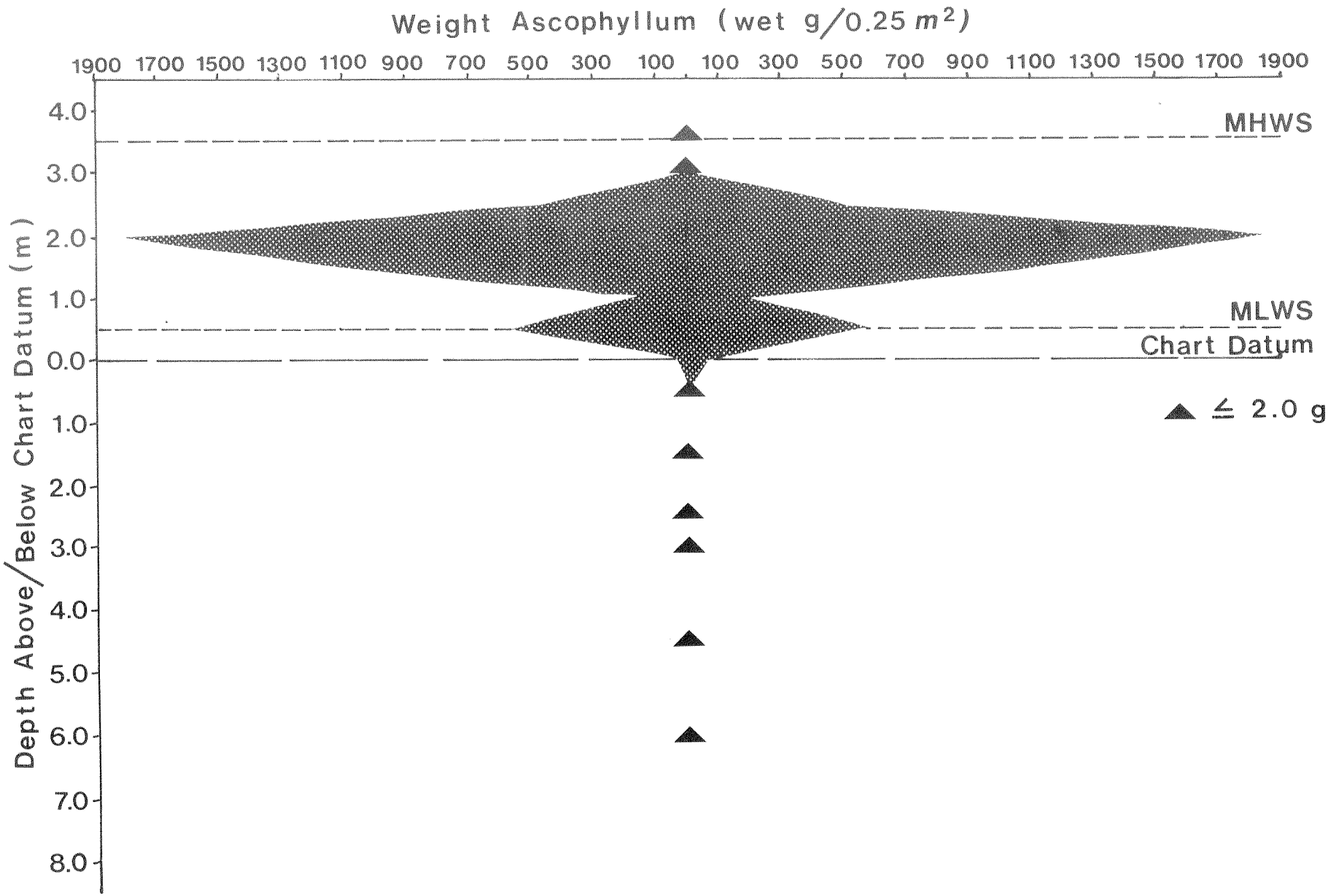

Figure 5. The distribution, by weight, of A. nodosum in relation to chart datum along the West Pubnico peninsula.

TABLE 2. Mean standing crop of *Chondrus*, *Ascophyllum*, *L. longicruris*, and *L. digitata* between certain depths off the West Pubnico peninsula in August, 1975.

Chondrus	Depth ranges (m)	3.5-2.0	1.5-(-)7.0	-7.5-(-)10.5	3.5-(-)10.5
	Standing crop (wet g/m^2)	130.0 ± 156.0	1057.6 ± 820.0	54.8 ± 54.8	1054.8 ± 952.0
Ascophyllum	Depth ranges (m)	3.5-3.0	2.5-0.5	0.0-(-)6	3.5-(-)6
	Standing crop (wet g/m^2)	3.2 ± 2.0	6720.0 ± 5171.2	31.2 ± 105.6	1700.8 ± 3804.8
L. longicruris	Depth ranges (m)	2.0-0.0	-0.5-(-)8		2.0-(-)8
	Standing crop (wet g/m^2)	65.6 ± 142.4	1258.8 ± 2561.2		944.0 ± 2243.6
L. digitata	Depth ranges (m)	1.0-(-)1.5	-2.5-(-)7		1.0-(-)7
	Standing crop (wet g/m^2)	123.6 ± 187.6	615.6 ± 975.2		416.0 ± 785.4

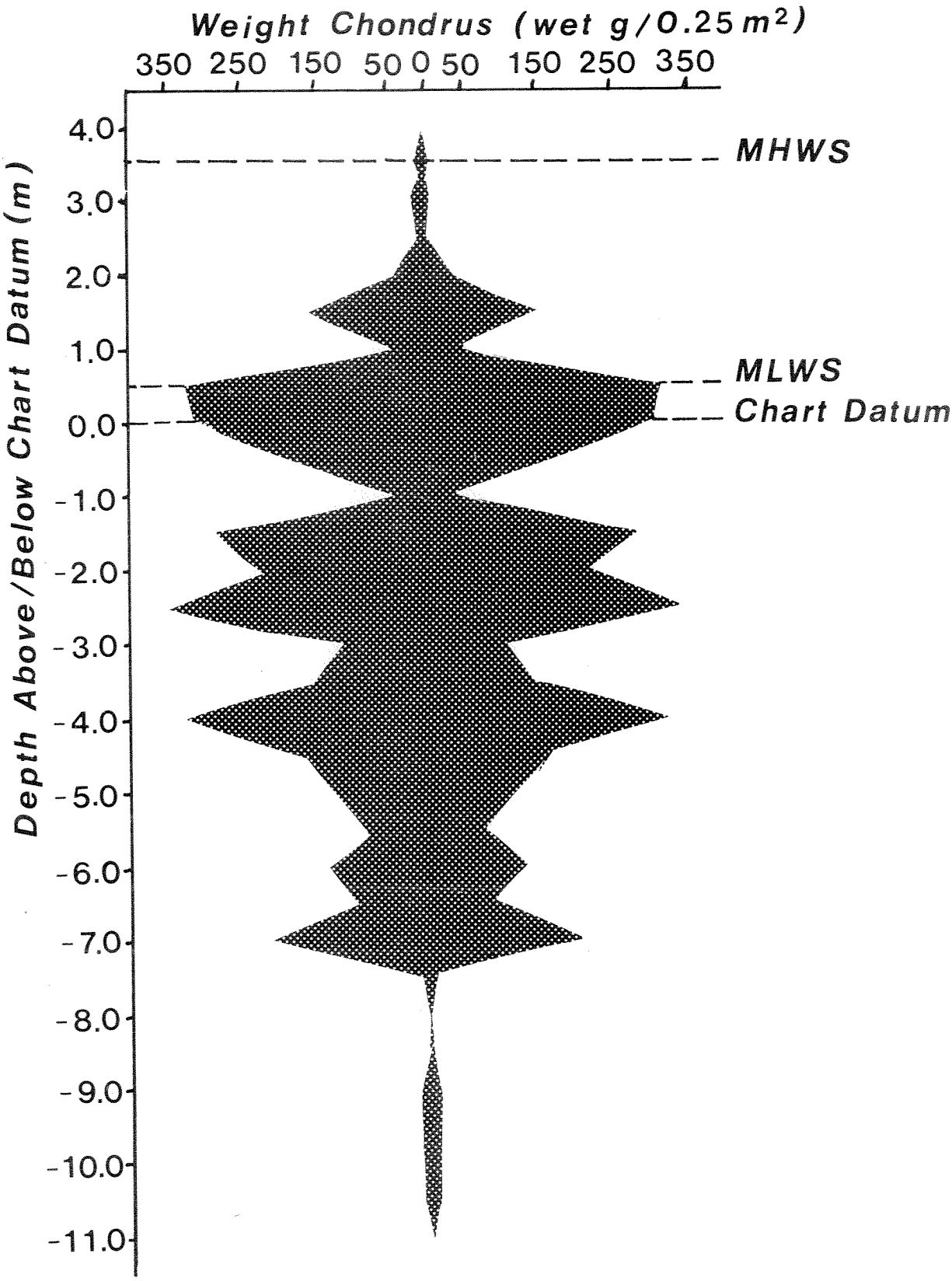

Figure 6. The distribution, by weight, of C. crispus in relation to chart datum along the West Pubnico peninsula.

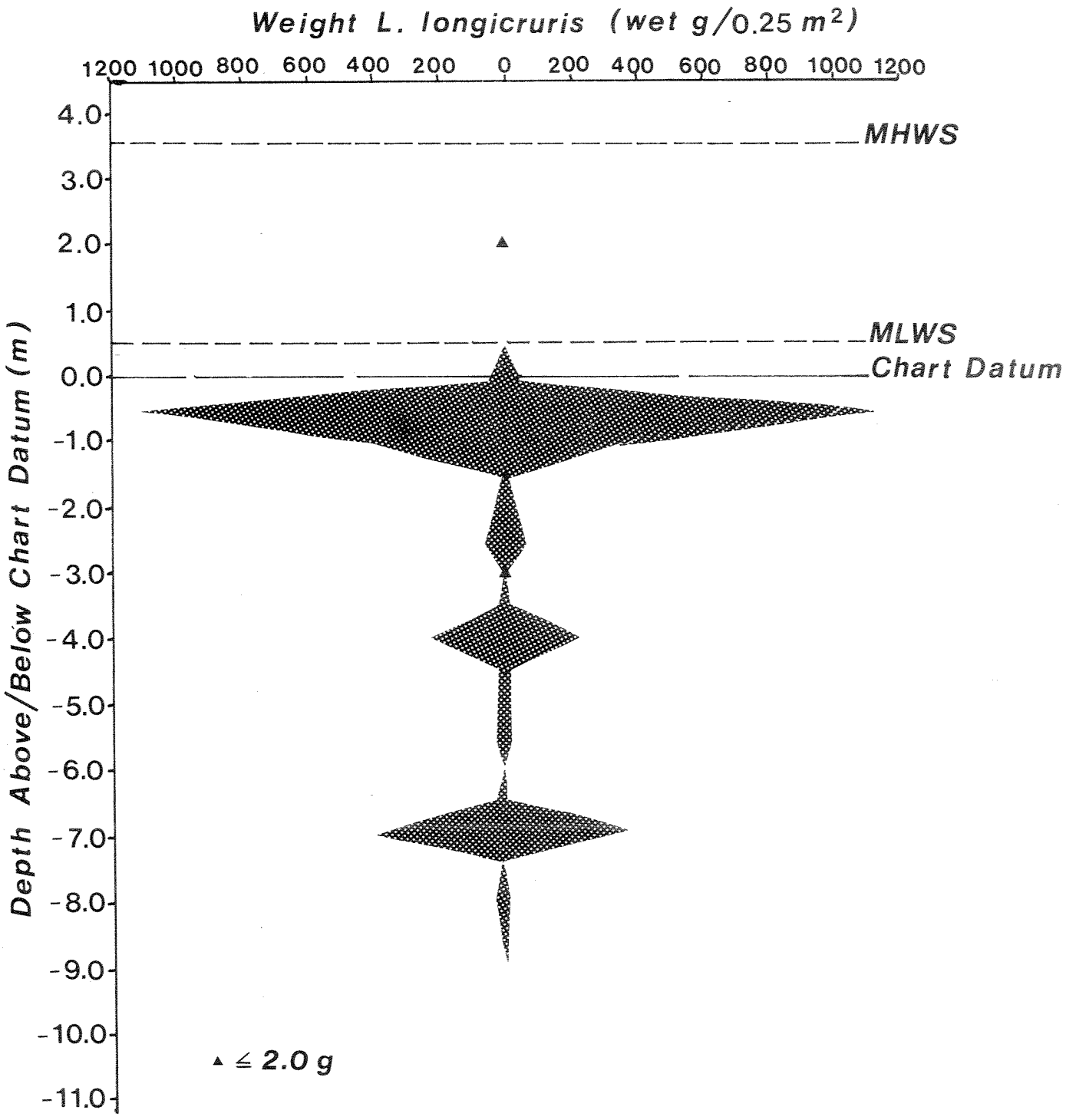

Figure 7. The distribution, by weight, of L. longicruris in relation to chart datum along the West Pubnico peninsula.

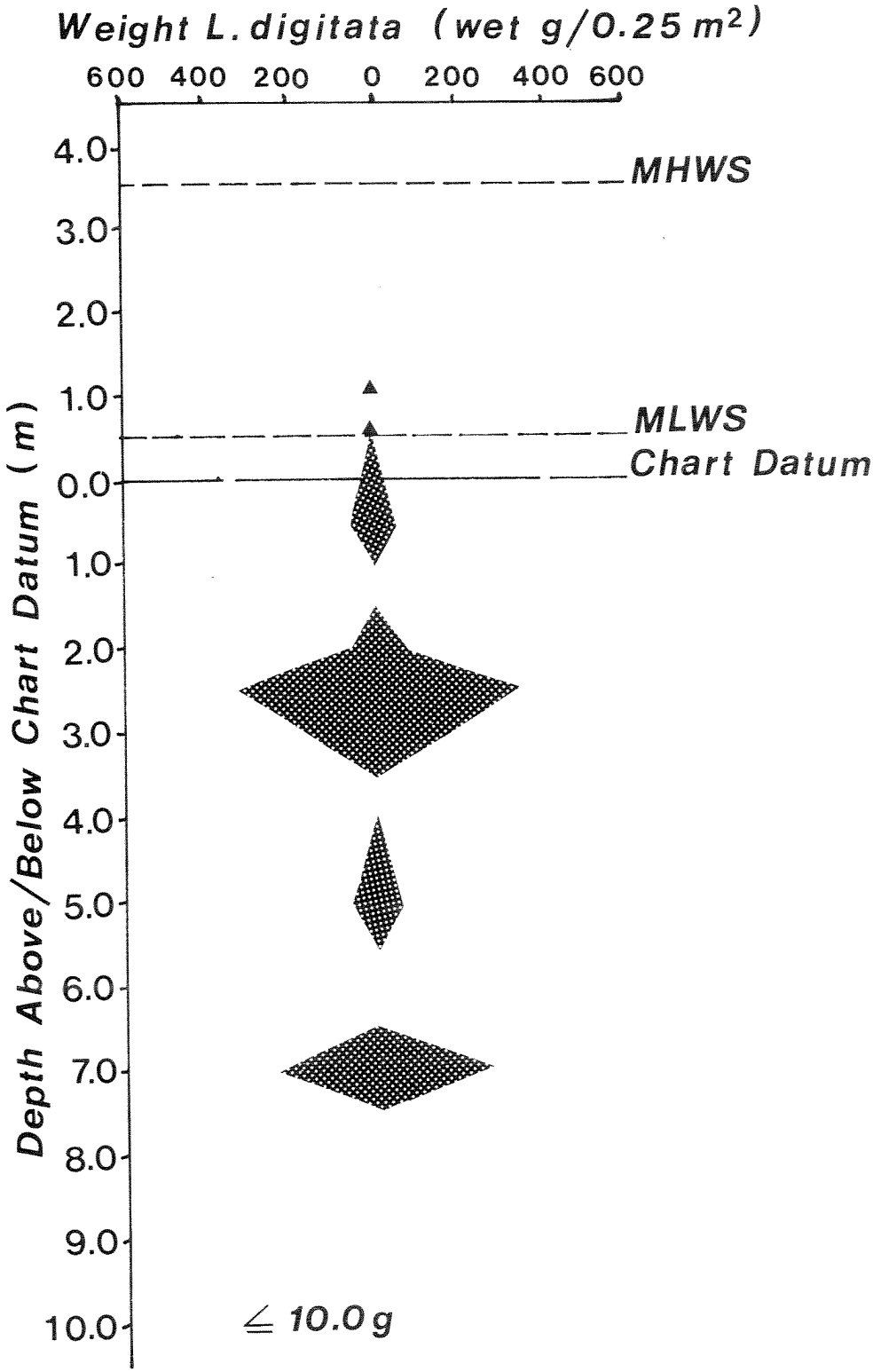

Figure 8. The distribution, by weight, of L. digitata in relation to chart datum along the West Pubnico peninsula.

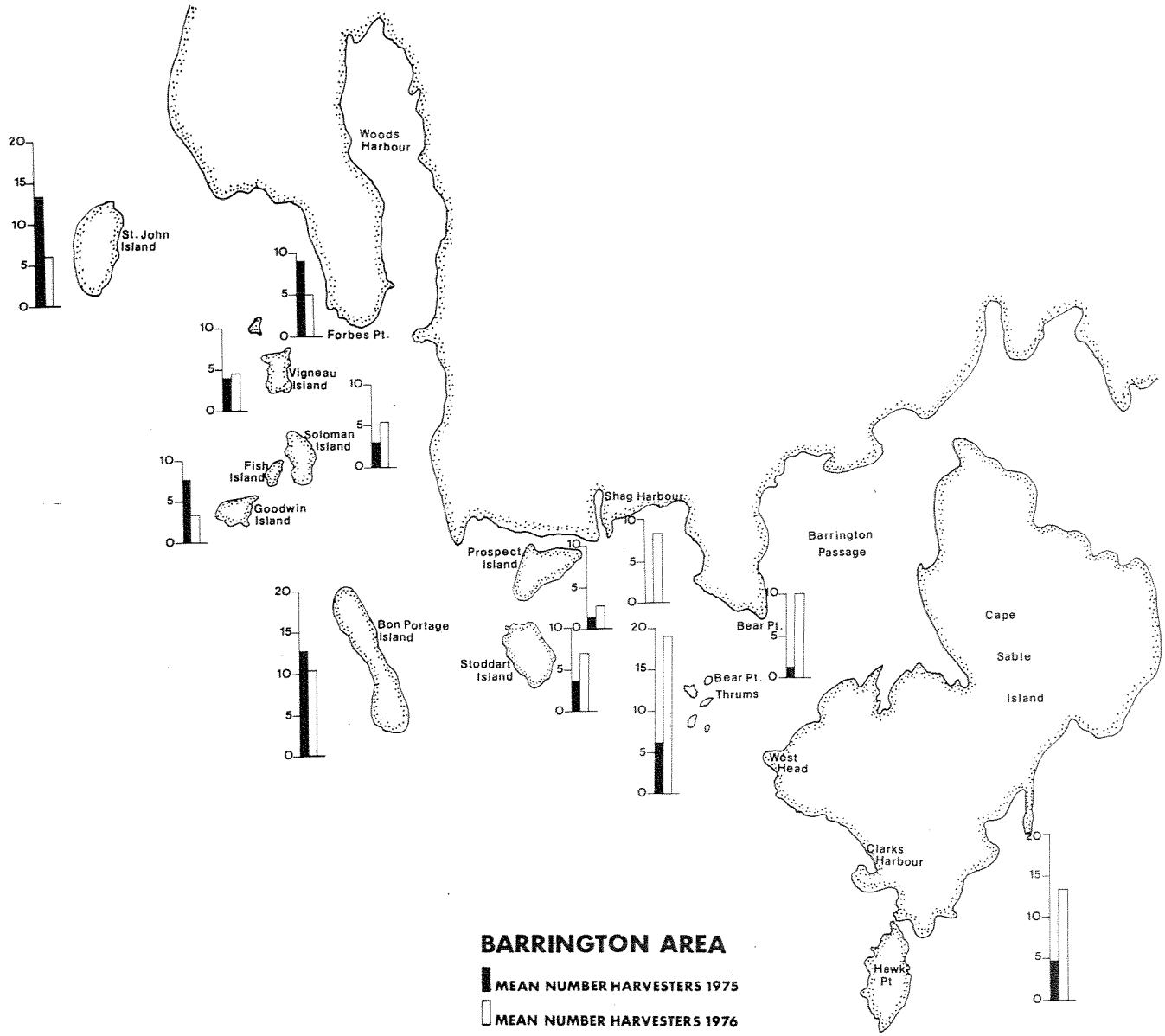

Figure 9. The commercially important beds of Chondrus in the Barrington area and the daily mean number of harvesters observed/bed during 1975 and 1976.

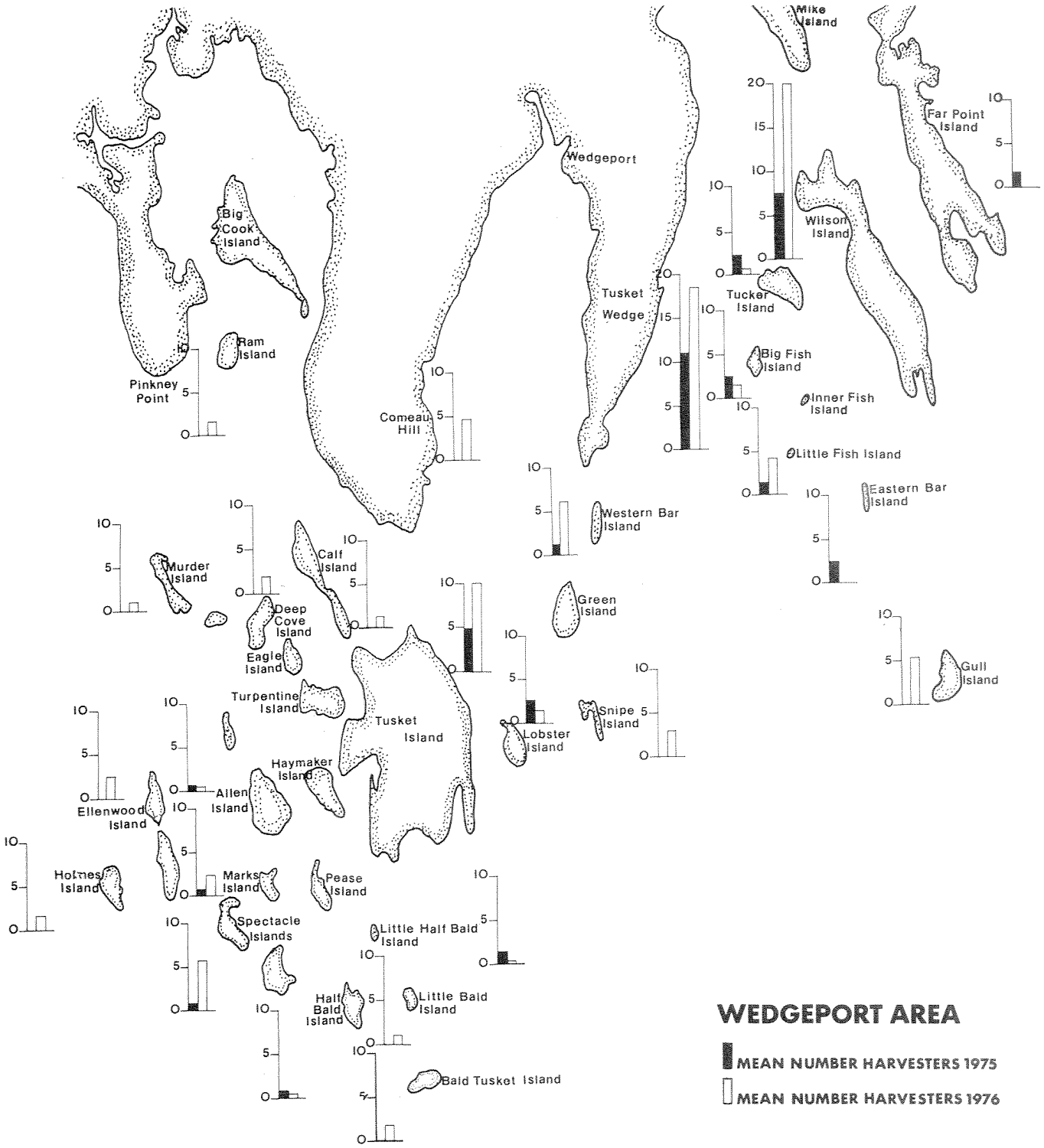

Figure 10. The commercially important beds of Chondrus in the Wedgeport area and the daily mean number of harvesters observed/bed during 1975 and 1976.

Chondrus between Cape Sable Island and Pinkney Pt. (ca. 400 km of shore) and this was in beds with greater than 40% coverage. The harvest in 1950 was approximately 3000 MT (MacFarlane, 1952) and the latter author noted, "...it is estimated that the total of nearly eight million pounds probably represents about one-third of the available Chondrus in this part of Nova Scotia." This would be approximately 9700 MT. The mean annual crop of Chondrus for the period from 1974 to 1978 was 11100 MT wet weight (Figure 11), only slightly more than the suggested "available" crop calculated by MacFarlane (op. cit).

2. CHONDRUS HARVESTING

During 1975 and 1976, between Cape Sable Island and Pinkney Pt., surveys were made along the coast during the harvesting season to determine the following: the location of the economically important beds, the harvesting effort, and the proximity of the beds to individual harbours. Sixty-one (61) beds (Figures 1, 9, and 10, Table 3) were identified and 40 separate harbours (Table 4) noted. Approximately 650 boats were counted in harbours during a period in mid season when it was too rough to harvest (Table 4). The annual value of the industry to the harvesters is approximately $2 million.

3. GROWTH AND REPRODUCTION

It was felt that aspects of the biology of Chondrus could best be attained by outplanting; thus, techniques were developed that could be employed in commercially important beds (Hanic and Pringle, 1978). A concrete outplanting block was secured to the ocean bottom off the West Pubnico peninsula (Figure 1) at 0.5 m below chart datum. The outplants were observed at regular intervals and growth was initially assessed by increase in length (Figure 12). Classes I-IV in Figure 13 refer to Prince's (1971) morphological classes.

The plants increased in length by a factor of two between August and October, 1976. Thereafter, the rate of increase was constant to July, 1977; the rate increased again between August and November. The first dichotomy was observed in October, 1976, the second in late March, and the sixth by November. Carposporangia were first observed in late August, 1977, when coincidentally the first Class III plants were observed (Figure 12).

The data presented here compare favourably with estimates made by Rosenvinge (1931), Taylor (1959/60), and Pybus (1977). The former estimated that mature fronds on the Danish coast were two to three years old. Pybus (op. cit.) calculated the

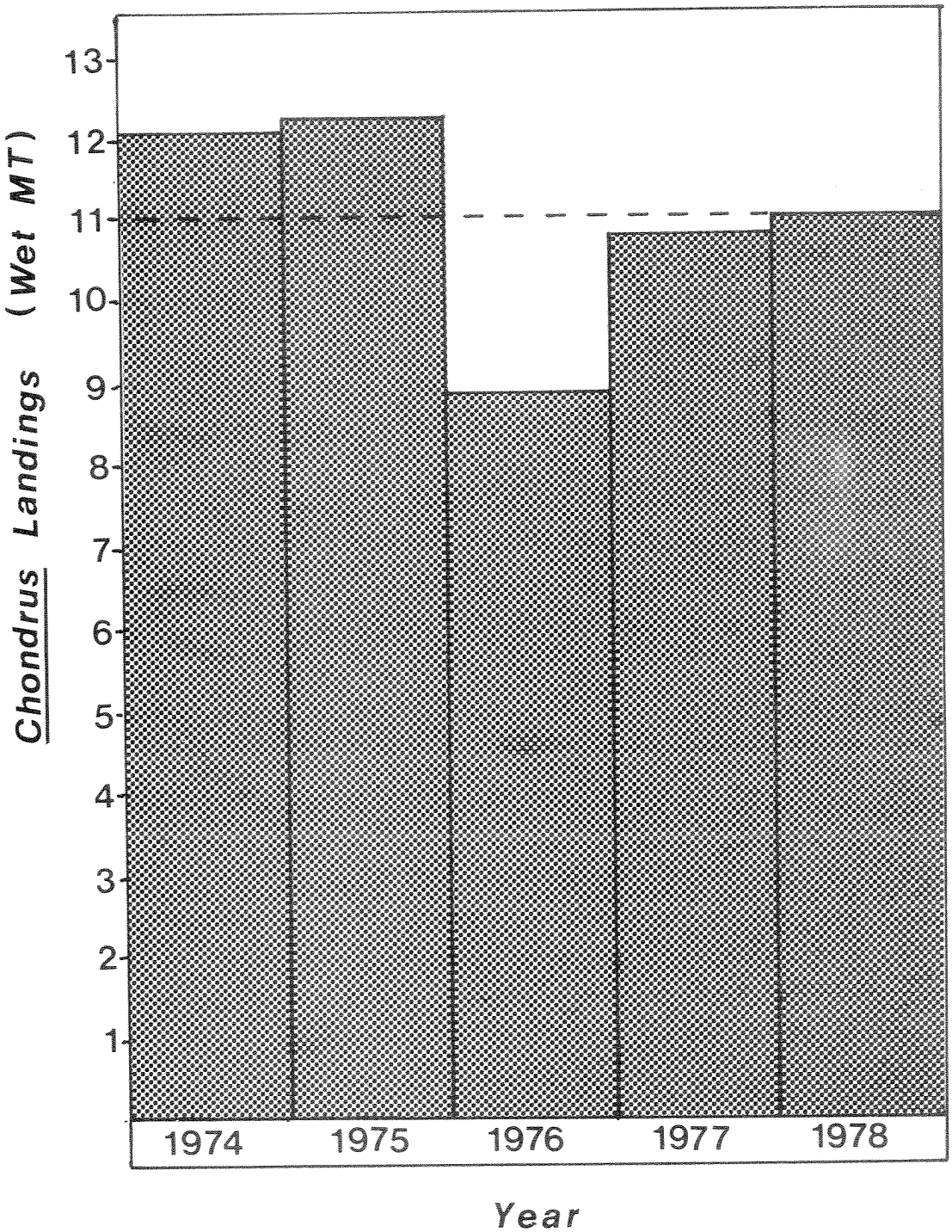

Figure 11. The commercial landings of Chondrus for the years 1974 to 1978 in Marine Plant Harvesting District 12.

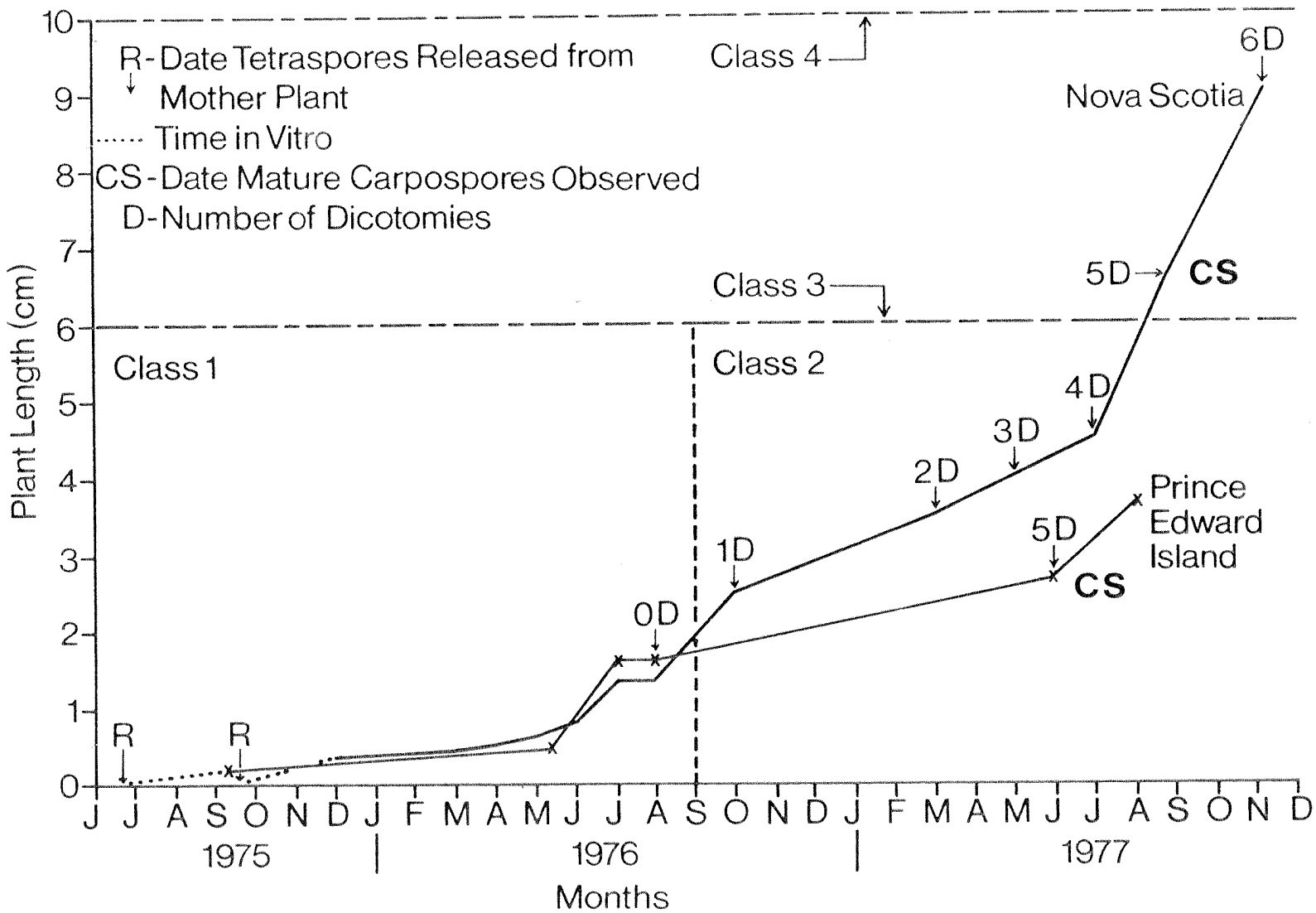

Figure 12. The increase in outplant length with time; the length of time for the occurrence of both plant dichotomies and mature carposporangia and the approximate time isolates remained in each of Classes I-III [Prince's (1971) morphological classes: Class I, no dichotomies; Class II, dichotomies but plant < 6 cm in length or > 6 cm in length but with ≤ 3 dichotomies; Class III, between 6 cm and 10 cm in length with > 3 dichotomies; and Class IV, ≥ 10 cm in length).

TABLE 3. The location of commercially important *Chondrus crispus* beds off southwestern Nova Scotia.

Wedgeport Section	Pubnico Section	Barrington Section
Allen Island	Abbott Harbour	Bald Bar
Big Fish Island	Argyle Sound	Barrington Passage
Big Fish Reef	Camp Island	Bear Point
Eastern Bar	Frost Island	Bear Point Thrums
Far Point Island	Jones Island	Bon Portage
Far Point Island Ledge	Lear Island	Egg Island
Fish Ledge	The Thrum Island	Fish Island
Green Island	Ledge Harbour	Forbes Point
Green Island Ledge	Lower Argyle	Goodwin Island
Half Bald Island	Morton Neck	Green Ledge
Inner Fish Island	Peggy Island	Lower Woods Harbour
Little Bald Island	Pubnico Harbour	Outer Island
Little Fish Island	Pubnico Stretch	Prospect Island
Lobster Island	Ram Island	St. John Island
Lobster Island Ledge	St. Ann Point	St. John Ledge
Mark's Island	The Twins	Shag Harbour
Mike Island		Solomon Island
Spectacle Island		Stoddard Island
Tucker Island		Vigneau Island
Tusket Island		West Head
Tusket Wedge		Whale Island
Western Bar		
Wilson Island		
Wilson Point		

TABLE 4. The number of *Chondrus* boats observed/harbour on a day in mid-*Chondrus* season when it was too rough to harvest.

Harbour	1975 Count	1976 Count
The Hawk, Cape Sable Island		6
Clarks Harbour, Cape Sable Island	17	19
Swims Point, Cape Sable Island	17	13
West Head, Cape Sable Island	12	15
Newellton, Cape Sable Island		16
Orion Wharf, Cape Sable Island	14	18
Cripple Creek, Cape Sable Island	4	5
Causeway, Cape Sable Island		7
Doctors Cove		4
Bear Point	31	35
Shag Harbour	25	24
Prospect Point	20	20
Lower Woods Harbour	21	22
Woods Harbour	51	41
Forbes Point	12	11
B.C. Packers Wharf	8	20
Ledge Harbour	14	27
Dennis Point	15	11
Abbot's Harbour	26	25
Argyle Sound	15	18
Lower Argyle	10	35
Camp Cove, Lower Argyle	43	13
Glenwood	3	3
Rocco Point	5	2
Abrams River	4	7
Surretts Island	13	7
Morris Island	22	11
Lower Surretts Island	20	20
Sluice Point	47	39
Muise Point	9	5
Hubbards Point	1	
Robards Island	5	
Eel Brook	1	
Wedgeport (Public Wharf)	33	15
Wedgeport (Doucet Wharf)	13	4
Wedgeport (Tuna Wharf)		52
Wedgeport (Cape Wharf)	26	3
Little River	16	19
Comeau Hill	12	16
Pinkney Point	41	63
TOTALS	626	671

growth (increase in length) of tagged plants on the west coast of Ireland and then estimated that mature plants had been initiated two years previously from the basal disc.

MacFarlane (1968) estimated that "fruiting bodies" are developed five years after spore germination in plants off coastal New Brunswick and Nova Scotia. From the data presented here it appears MacFarlane's (op. cit.) estimate can be reduced by two to three years.

4. PLANT SUCCESSION

Concrete outplanting blocks were put in place (Hanic and Pringle, 1978) in July, 1975, at various depths off the west side of the West Pubnico peninsula. It was originally planned to quantify plant succession on a regular basis but time was not available. However, the blocks were photographed regularly and scrapings from their surface were occasionally made.

The observations presented below were made on Blocks 2 and 2a, located 5 cm above chart datum.

By mid December (four months after placement) only a small percentage of the blocks were covered with macroalgae and they were ephemerals (Table 5). Similar cover was present in March and April (Table 5). The number of taxa present in May and June increased markedly (Table 5, Figure 13), and by August much of the block was covered with *Ceramium rubrum* (Figure 14). *Chondrus* germlings were first observed at this time and were about 1.5 cm long. They no doubt originated from spores discharged sometime between September and December. The macroalgal diversity increased by a factor of two between April and May (Table 5) and, at this time, the first dichotomy was observed on the *Chondrus* plants, now about 2.0 cm long. *L. longicruris* plants were first noted at this time (Table 5). After 38 months the blocks were covered by perennials such as *Chondrus*, *Laminaria*, and *Fucus* (Figure 15), the former being the most abundant.

Thus, at this particular site, it takes about three years to acquire a relatively dense bottom cover of *Chondrus* on concrete blocks. The succession on the granitic outcrops would likely be similar. Although a few plants are harvestably mature the bulk are not, and it would take a minimum of another year to attain a relatively dense bed.

The succession on "barren" grounds would likely be considerably slower. These blocks were placed in the middle of dense *Chondrus* beds; consequently, spore settlement would

TABLE 5. The occurrence of macrophytic benthic algae on Block #2 off West Pubnico between December, 1975, and July, 1976

Taxa	Date Observed				
	8/12/75	24/3/76	21/4/76	26/5/76	27/7/76
Chaetomorpha melagonium (Weber et Mohr) Kützing	X				
Monostroma pulchrum Farlow		X			
Ulva lactuca Linnaeus	X			X	X
Spongomorpha arcta (Dillwyn) Kützing				X	
Asperococcus echinatus (Mertens) Greville					X
Chordaria flagelliformis (Müller) C. Agardh					X
Eudesme virescens (Carmichael) J. Agardh				X	X
Fucus distichus Linnaeus			X	X	X
Laminaria longicruris De la Pylaie				X	X
Leathesia difformis (Linnaeus) Areschoug					X
Petalonia fascia (O.F. Müller) Kuntze			X		
Punctaria plantaginea (Roth) Greville	X		X	X	X
Scytosiphon lomentaria (Lyngbye) C. Agardh				X	X
Ceramium rubrum (Hudson) C. Agardh	X	X	X		
Chondrus crispus Stackhouse			X	X	X
Cystoclonium purpureum (Hudson) Batters			X	X	X
Gloiosiphonia capillaris (Hudson) Carmichael				X	
Polysiphonia sp.	X	X			
Polysiphonia harveyi Bailey		X		X	X
Polysiphonia nigrescens (Hudson) Greville					X

Figure 13. Block #2A, Pubnico, N.S., on June 22, 1976, almost 11 months after placement, showing light recruitment of ephemerals.

Figure 14. Block #]a, Pubnico, N.S., on August 25, 1976, filmed 12-1/2 months after placement, showing almost complete coverage by Ceramium with some Fucus and Laminaria present.

Figure 15. Block #2A, Pubnico, N.S., on September 19, 1978, filmed 25 months after placement, showing the establishment of perennials, such as Chondrus, Laminaria, and Fucus.

likely be heavier than on barren grounds. As a result, the pattern of succession might be different and the time to acquire a mature Chondrus bed following urchin removal could be eight to ten years.

CONCLUSION

There is a luxurious standing crop of macroalgae in southwestern Nova Scotia that likely contributes significantly to the primary productivity of the area. The four commercial species, A. nodosum, C. crispus. L. longicruris, and L. digitata, make up 74.2% of the standing crop. There are approximately 650 fishermen in the area that supplement their income by harvesting Chondrus. The harvesting and extraction of algin from Ascophyllum is an important local industry. Consequently, it would be unfortunate to permit the decimation of these beds of benthic algae by sea urchins, particularly when it takes a minimum of three years to attain a harvestably mature Chondrus plant from a spore and possibly from five to ten years to develop a dense bed on barren grounds.

ACKNOWLEDGEMENTS

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HISTORY OF KELP HARVESTING IN SOUTHWESTERN NOVA SCOTIA

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INTRODUCTION

One of the aims of this workshop is to provide a strong scientific basis for management of our remaining kelp resources. An impending question is: to what extent should kelp harvesting be permitted in southwestern Nova Scotia (S.W.N.S.)? Prior to the existence of any governmental control or scientific investigation, a kelp harvesting industry existed in S.W.N.S. from 1940 to 1949. The Algin Corporation of America obtained its raw material from S.W.N.S. for an alginate extraction plant at Rockland, Maine. Through interviews with fishermen, former company officials, and limited published information, I have obtained a reasonable history of this industry.

DEVELOPMENT OF THE INDUSTRY

There were two principal harvest areas centered around collection centers. Holding tanks were constructed at Clarks Harbour on Cape Sable Island by 1940 and at Dog Island in the Tusket Islands by 1943 (for location, see Figures 9 and 10, pages 157 and 158 respectively, of this volume). Initially, all kelp was delivered directly to the tank site; however, due to excessive delays in unloading, the buyer provided floats for off-loading at numerous wharves in each area from which he collected the harvest. In addition, the harvesters were provided with 500 lb capacity net bags to facilitate handling material to and from the tanks.

During the first three years of harvesting, the harvest methods consisted of cutting with sickles or scythes at low tide, using grapnels and gathering storm-tossed material. These methods harvested mainly *Laminaria digitata* (Huds.) Lamour. (horsetail kelp). The buyer again improved the harvest technology by introducing a large dragrake to harvest the deeper populations of *Laminaria longicruris* De La Pylaie (broadleaf kelp). It consisted of a 1.5 m-1.8 m piece of oak with steel rods 30 cm-45 cm long, spaced 7.5 cm-12.5 cm apart as tines (Figure 1). This was dragged over the bed by lobster boats 9.2 m-12.3 m in length, equipped with winches. Usually two men were required to handle this equipment.

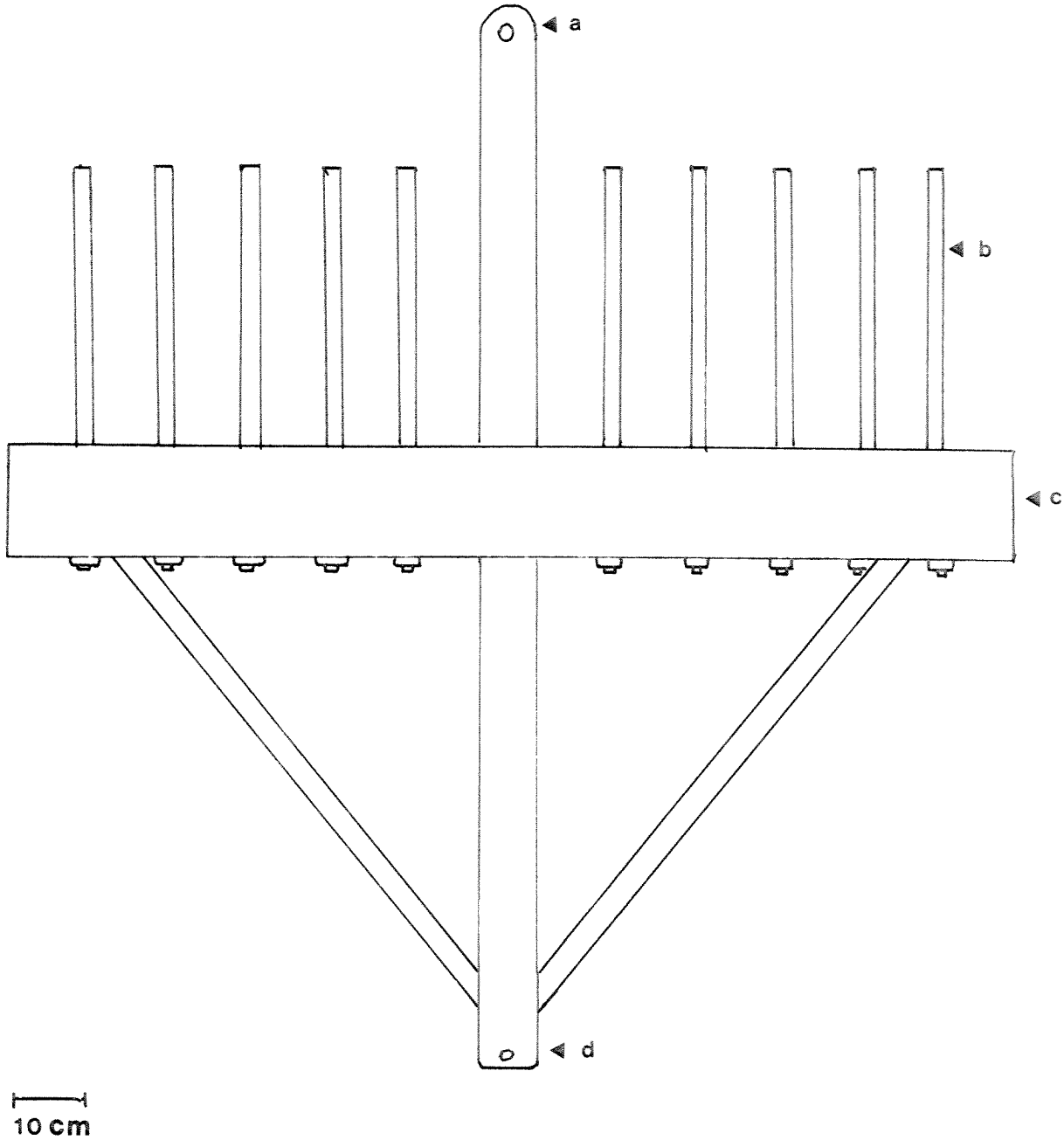

Figure 1. Kelp dragrake as used in southwestern Nova Scotia in the 1940's.

a) towing point (flat bar steel)
b) rake tines (mild steel rod)
c) main beam (hardwood)
d) trip point

The main harvest began in the early summer after the end of the lobster season and continued well into the winter months. Storm-tossed material was principally gathered in the fall and early winter. Each boat could hold 10 to 12 tons; and due to the ease of harvest, some harvesters made two trips, harvesting 20 tons per day. Although we only have rough estimates of the tonnage per day landed by these early kelp harvesters, recent studies on the economics of kelp harvesting in the Grand Manan area provide more precise data. Using a steel dragrake (Figure 2), harvest rates were from 1/4 ton to 6 tons per hour depending on the harvest area (Table 1). It was found tows of less than four minutes filled the rake tines. Divers observing the action of the rake in the bed noted 10% of the plants in the path of the rake were removed, the majority slipping through the tines. The holding capacity of the harvesting vessel and the distance to the kelp beds were the limiting factors rather than efficiency of the gear (Sharp and Neish, 1976). The price to the fishermen in the 1940's began at $5 per wet ton, and reached a maximum of $8 per ton. This price was very competitive with lobster, which at the beginning of this industry ranged from $.17 to $.30 per pound and was subject to gear loss and weather limitations. Irish moss harvesting did not become a competitive industry until after 1945 when the price was $.05 per pound for dried Irish moss and $.01 per pound wet.

The harvest of kelp offered many advantages over mossing and lobstering. The weather was rarely a problem since the archipelago offered sheltered harvest areas. A 10 to 12 ton harvest could be obtained in two to four hours with any tide level. No further processing or holding of the harvest was required by the harvester. These advantages encouraged 20 to 30 boats into the industry on a part-time basis in each area.

Concrete holding tanks 4.6 m x 4.6 m x 1.2 m and larger were constructed at the collection sites, holding 40 to 60 tons. Six of these tanks held the harvest at Dog Island in a 18-20% salt solution. During the height of the season a 29 m company boat was used to transport the kelp to Rockland, Maine, two times per week, carrying 100 tons per load. Other boats were chartered as the harvest demanded. The harvest had no restrictions placed upon it. The amount of harvesting in a bed depended entirely on its distance from a collection center, its wave exposure and the harvest per unit effort considered economical by the fishermen. During the course of this operation, the estimated peak year of harvesting was 5,000 to 6,000 wet tons of kelp. Exact records of exports are only available from the Clarks Harbour operation for 1942 to 1949 (Table 2).

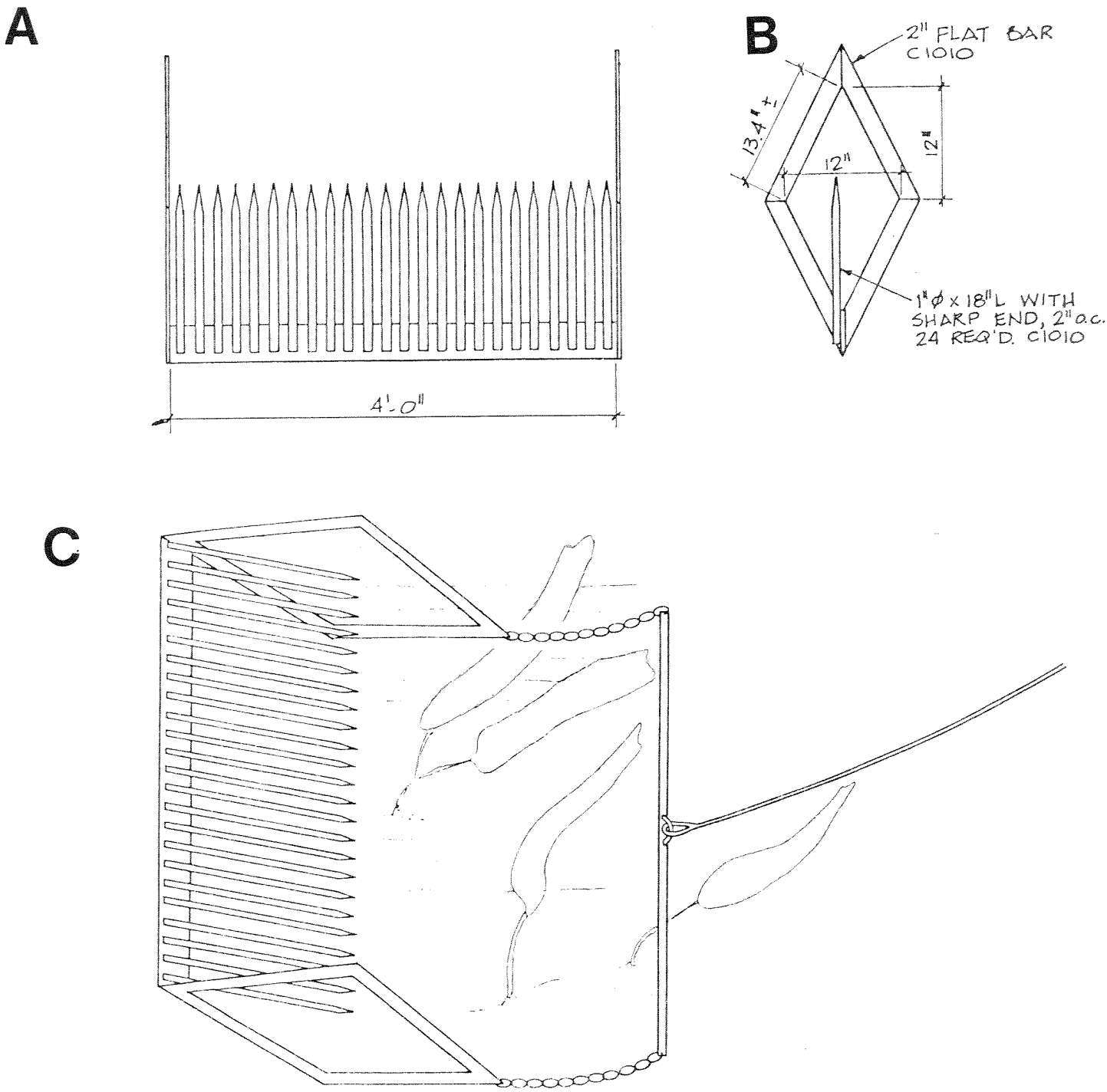

Figure 2. Kelp dragrake used in Grand Manan harvesting trials (Neish and Sharp, 1976).

a) top view
b) side view
c) *in situ*

Table 1* A. Kelp yield/tow - Oxhead, Grand Manan

Tow no.	Kelp wet weight (lbs/kg)	Duration of tow (minutes)
1	73/33	4
2	105/48	1
3	0/ 0	1
4	32/15	1
5	61/28	1
6	48/22	1

B. Kelp harvest rates in Grand Manan kelp beds.

Trial	Locale	Kelp wet weight (lbs/kg)	Duration (hours)
1	Grand Harbour	320/145	0.5
2	Green Island & Oxhead	2,000/909	0.3
3	Sheep Rock Channel	378/172	0.5
4	Sheep Rock Channel	260/118	0.5

*Neish and Sharp, 1976.

Table 2. Kelp exports - Clarks Harbour, 1942-1949*.

Year	Wet weight (tons)	Operational period (months)
1942	2,400	6
1943	2,700	6
1944	3,000	6
1945	3,000	6
1946	2,200	5
1947	860	3
1948	1,050	3
1949	1,020	3

*C. MacFarlane, 1952a.

The Clarks Harbour operation provided a more consistent harvest than the Dog Island site. The tanks in the Dog Island site were uncovered, allowing freshwater dilution of the preservative solution and freezing. Production from this area was intermittent, and in only one season did it reach the level of Clarks Harbour's production.

Until 1947, 95% of the raw material needs of the Rockland American Algal Corporation plant was provided by S.W. N.S. kelp. Imports of dry kelp from South Africa and Ireland supplemented this source after 1946.

An explosion and fire which destroyed the Rockland plant in May, 1946, lead to the eventual demise of kelp harvesting in N.S. In 1947, Irish moss processing was begun at the new plant as the Algin Corporation of America was becoming less competitive in the alginate market against Kelco of the U.S.A. and Alginate Corporation of the U.K. Operations at the Dog Island site ceased at this time. The Clarks Harbour operation continued until the final switch to full carrageenan production in 1949.

The industry developed, in 1946, a new harvest technology in the form of a mechanical harvester. A mowing device was constructed to fit on the back of a Cape Islander (Figure 3). This consisted of a chain-driven reciprocating cutter on a spring-loaded frame. The frame could be raised and lowered to avoid rocks and to replace the net bag used for collecting the severed kelp. This machine had numerous problems and was only partially successful. It is interesting to note that the subjective observation was made that regrowth of the bed was faster after cutting than dragging. A 20 m boat was under construction to act as a packer and harvester in 1946.

DISCUSSION

The impact of this harvest on the kelp beds and associated resources is one of conjecture. Although there was no shortage of raw material in some specific areas there were reports of harvested populations not recovering at all or not reaching former standing crops. Some fishermen attributed lower lobster landings to this harvest.

It would appear that 5,000 to 6,000 tons per year is an insignificant cropping in S.W. N.S. when compared to the surveyed standing crop of 900,000 tons (MacFarlane, 1952b).

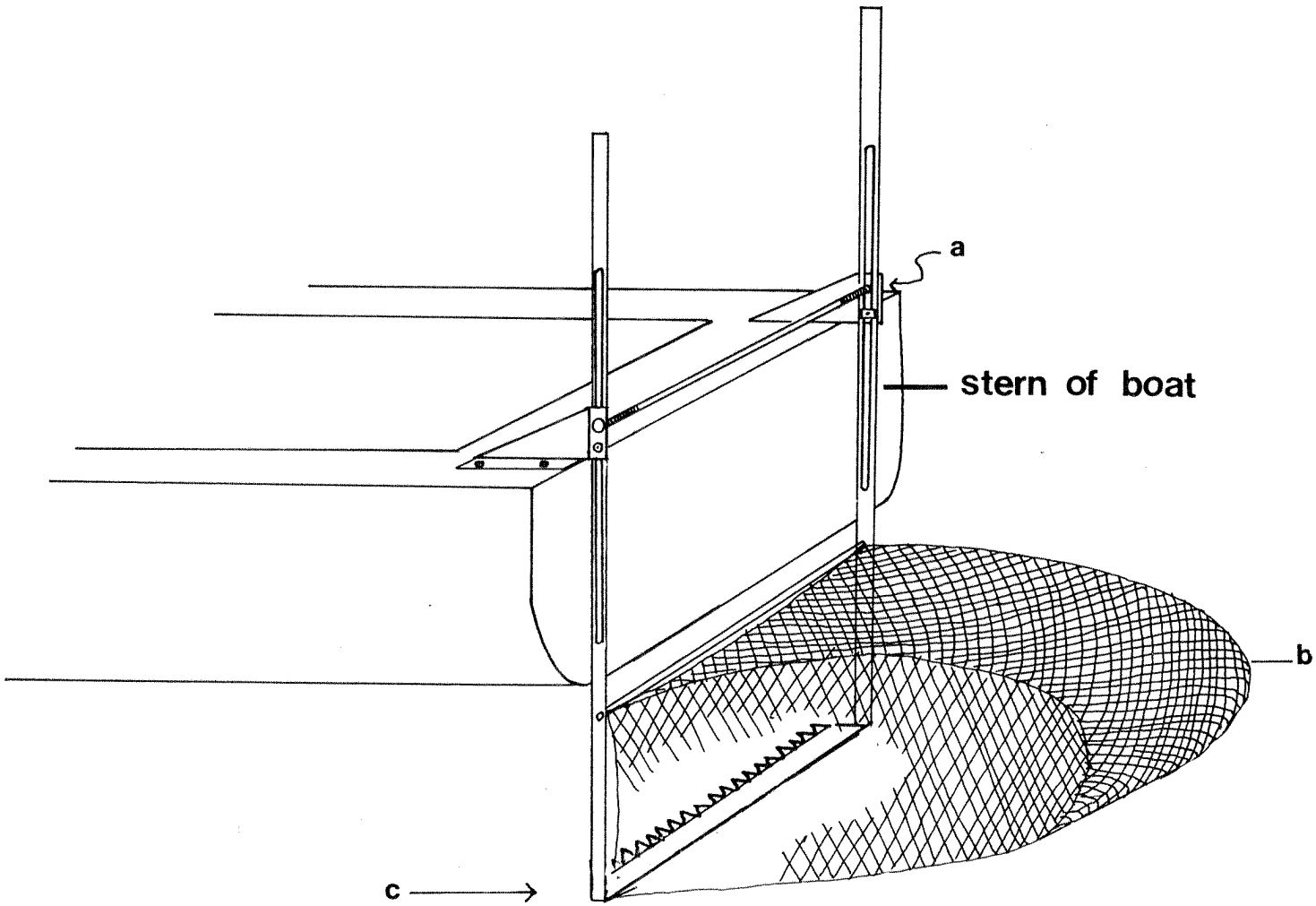

Figure 3. An approximate sketch of a mechanical kelp harvester underdevelopment in 1946.

a) spring-loaded lifting
b) removable net bag
c) mower blade chain drive from main engine.

Little Half Bald Island and Spectacle Island and ledges, which were areas most certainly harvested between 1943 and 1946, had a total of 26,400 tons when surveyed between 1948 and 1950. The ledges near Cape Sable Island were reported to have 29,000 tons of standing crop after seven to nine years of harvesting. Perhaps the inefficiency of the dragraking harvest method as described earlier contributed the sustained harvest in these areas.

In the period since 1949 there were periodic small-scale harvests of kelp for health food and meal. Bonda Seafoods purchased kelp for meal in the mid 1960's. Argosy Seaweeds purchased approximately 20 tons at $40 per ton in 1974. More recently, Marine Colloids have purchased several hundred tons for a dried food product in 1978. It is noteworthy that this recent harvest was completed with a dragrake derived from the design used thirty years ago. The harvest of 9 tons for four hours of towing is also similar to earlier catch per unit effort levels. We understand that an increasing market for dried kelp products will lead to greater harvests in the coming year by Marine Colloids.

In conclusion, we have records of a fairly low level but sustained harvest from two areas of S.W. N.S.; however, no records were made of the impact on the kelp beds or associated resources. Fortunately, we are now in a position to both monitor the impact of kelp harvesting and control the level and means of harvest.

ACKNOWLEDGEMENTS

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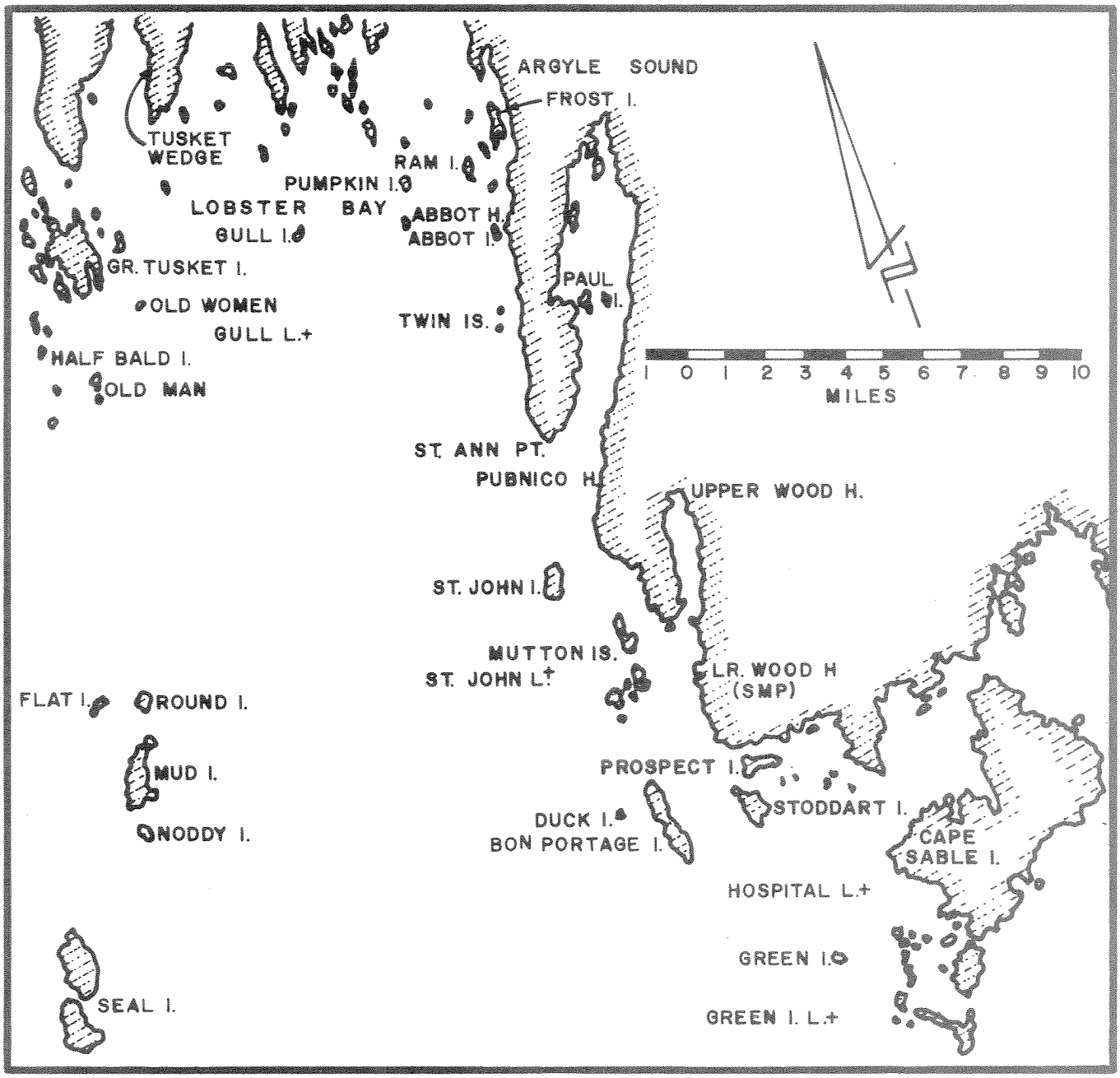

Figure 1. Southwest Nova Scotia. The Laminaria resource from the following areas was surveyed during July, 1977: Seal Island, St. John's Ledge, Duck Island, Green Island, and Twin Islands.

dominated the bottom to depths of 15 m: Laminaria longicruris De la Pylaie and Laminaria digitata (Linnaeus) Lammouroux. These species comprise the bulk of commercially utilizable kelps. Three additional kelps were observed during diving surveys: Alaria esculenta (Linnaeus) Greville, Agarum cribrosum (Mertens) Bory, and Saccorhiza dermatodea (De la Pylaie) J. Agardh. Desmarestia spp. were also collected at a variety of sites.

Several papers deal with the systematics or ecology of Nova Scotia seaweeds (MacFarlane, 1961; Mann, 1972, 1973; Taylor, 1957; Lang and Mann, 1976; Breen and Mann, 1976). Mann (1972) found that Laminaria at St. Margaret's Bay, Nova Scotia, grew rapidly from January through April, and slowly from July through October. He estimated that summer biomass turnover was four to ten times during the year. Chapman and Craigie (1977) determined that the onset of winter growth in L. longicruris correlated with increased dissolved nitrate. Reserves of nitrogen were accumulated during winter months within the plants and were subsequently depleted following reduction of nitrate in the water column.

METHODS AND MATERIALS

Scuba equipment was used when diving, and unisuits (Poseidon Co. Ltd.) provided warmth in the 10 C Nova Scotia waters. The diving tender was a leased 8.5 m Cape Island fishing vessel. Diving operations were limited to depths ranging from 0 to 15 m relative to mean sea level during periods of slack tide. Areas for general assessment were determined by evaluating charts and fathometer tracings. A Farallon underwater propulsion vehicle was used for general surveys to evaluate the substrate and extent of kelp beds over large areas. Areas surveyed by MacFarlane (1952) and information from local sources helped determine site location. The following sites were surveyed: Seal Island, Green Island, St. John's Ledge, Twin Islands, and Duck Island.

Kelp plant density and wet weights were determined from material collected along a 50 m transect line at five randomly selected 1 m^2 areas defined by square quadrats. All conspicuous brown algae were collected from the quadrats and placed in mesh bags. Laminaria was divided into two size classes: harvestable and non-harvestable. L. longicruris with a stipe longer than 1 m in length and L. digitata with stipe diameters greater than 1.5 cm were considered harvestable. Wet weights were measured on an Ohaus scale at SMP. In a few instances density estimates

were obtained by counting plants *in situ* rather than collecting within the square meter quadrats.

To gain an idea of the variability of standing crop and plant density, standard errors (SE) were calculated for each data set using appropriate statistical transformations. The variance increased with the size of the mean, and thus detailed comparisons between areas using data collected in this study are not possible with any statistical precision.

RESULTS

The bulk of the *Laminaria* resource existed between 2 to 10 m below mean sea level. Dense stands were also present to depths of 15 m at Seal Island, where water clarity was better than near the mainland. At sites other than Seal Island, red algae became dominant at depths greater than 10 m.

Sea urchins (*Strongylocentrotus droebachiensis*) were abundant at Green Island and were rare or absent at the other areas. The highest density of *Desmarestia* spp. was noted at Green Island and Hospital Reef where sea urchins were abundant. At Twin Island, *Chondrus crispus* (Stackhouse) appeared to be in greater abundance than *Laminaria* in some shallow rocky areas.

Seal Island

Seal Island was the most extensive kelp community observed during the two-week survey. Approximately 1,200 ac of *Laminaria*-dominated substrate occured on the west side of Seal Island. Here, dense beds of *L. Longicruris* and *L. digitata* were noted to depths of 15 m. No diving was done on the east side of Seal Island.

The substrate was rocky and contained numerous large boulders (to 2 m in height) scattered throughout. Good substrate, high water clarity, and strong currents probably contributed to the large size and abundance of kelp at Seal Island. *L. longicruris* was especially abundant atop boulders, whereas *L. digitata* and *Alaria esculenta* were often found in depressions. *L. longicruris* plants were exceptionally large with many stipes reaching 5 m in length and lamina up to 7 m long. An occasional sea urchin was noted during survey dives.

Two transect lines were sampled at Westside and Division Point. Density and biomass were determined at

Westside, while only density was determined at Division Point. Density estimates (plants/m^2), for both transects together, averaged 6.5 for L. longicruris and 7.1 for L. digitata. All kelp, including juveniles of these species, averaged 32.20 plants/m^2 (Table 1). Biomass at Division Point was estimated by multiplying density by the average weight per plant (grand mean) as determined in other transects (Table 2). Harvestable plants of L. longicruris and L. digitata at Westside averaged 1.91 kg and 1.06 kg, and yielded 3.82 and 5.28 kg/m^2 respectively (Table 3). Harvestable plants of L. longicruris and L. digitata at Division Point averaged 7.37 and 9.20 kg/m^2 respectively (using the grand mean weight per plant). The average standing crop of kelp at Seal Island was 68.33 T/ac; therefore, a maximum resource of 87,736 T may be available (Table 4). Approximately 84% of the biomass was large plants and considered harvestables; therefore, a maximum harvestable resource of 73,600 T was available.

Green Island/Hospital Reef

Two transects were completed in the Green Island/Hospital Reef area where approximately 650 ac of bottom appeared suitable for kelp. The area was dotted with numerous shoals and shallow areas. Dense fog, during the survey, prevented more extensive study.

Substrate at Hospital Reef was rocky and contained areas of large boulders interspersed with sandy patches. L. longicruris dominated the rocky substrate while Chorda filum (Linnaeus) Lammouroux and Zostera marina L. dominated sandy areas. Desmarestia spp. and several species of red algae were also common on the rocky bottom. The largest concentrations of sea urchins (average of 10/m^2) observed during the study were seen at Hospital Reef. L. longicruris was the dominant kelp at Green Island. Stands of A. esculenta, A. cribrosum, L. digitata, and S. dermatodea were also observed.

Harvestable L. longicruris and L. digitata in the Green Island/Hospital Reef area averaged 5.60 and 0.30 plants/m^2, respectively, with an average weight per plant of 0.55 kg and 0.98 kg, respectively. Biomass of harvestable L. longicruris and L. digitata averaged 2.87 and 0.29 kg/m^2, respectively. The average standing crop of all kelp was 3.97 kg/m^2 or 17.70 T/ac. The 647 ac near Green Island would yield a maximum of 11,450 T of kelp, 79.6% or 9,100 T of which is considered harvestable.

TABLE 1. Kelp density (plants/m^2) estimates based on counts in five randomly placed 1 m^2 quadrats along 50 m transect lines.

		Seal Island (2 transects)		Green Island/ Hospital Reef (2 transects)		St. John's Ledge (3 transects)		Twin Island (1 transect)		Duck Island (2 transects)	
		$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
L. longicruris (harvestable)	1)	6.50	-	5.60	-	1.27	-	2.00	-	2.10	-
	2)	4.04	2.50	4.29	1.82	0.85	0.43	1.69	0.96	1.39	0.85
L. digitata (harvestable	1)	7.10	-	0.30	-	3.26	-	2.00	-	1.90	-
	2)	5.92	1.97	0.18	0.20	2.80	0.70	1.58	1.04	1.42	0.69
All kelp 3)	1)	32.20	-	17.20	-	15.53	-	6.20	-	14.00	-
	2)	30.30	5.31	15.22	3.94	14.61	2.06	5.53	2.18	11.06	4.21

1) Based on untransformed quadrat counts.
2) Based on transformed (i.e. x+0.5) counts, backtransformed for presentation in this table.
3) Includes: *Agarum cribrosum*, *Alaria esculenta*, *Saccorhiza dermatodea*, and all harvestable and unharvestable *L. digitata* and *L. longicruris*.

TABLE 2. Average weight (kg) per plant from study sites in southwest Nova Scotia - July, 1977

	Seal Island Westside	Green Island/ Hospital Reef	St. John's Ledge	Duck Island	Grand Mean
L. longicruris (large)	1.91	0.55	0.58	0.61	0.67
L. longicruris (medium to small)	0.06	0.06	0.07	0.16	0.07
L. digitata (large)	1.06	0.98	1.09	0.47	1.00
L. digitata (medium to small)	0.12	0.18	0.15	0.09	0.13

TABLE 3. Average kelp wet weight standing crop (kg/m^2), based on harvests from five randomly placed quadrats along 50 m transect lines.

	Seal Island* Division Pt. (1 transect)		Seal Island Westside Area (1 transect)		Green Island/ Hospital Reef (2 transects)		St. John's Ledge (3 transects)		Twin Island (1 transect)		Duck Island (2 transects)	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE		
L. longicruris (large)	7.37	-	3.82	2.06	2.87	1.06	0.74	-	1.34	-	1.17	0.58
L. longicruris (medium to small)	0.11	-	0.07	0.04	0.55	0.23	0.11	0.04	0.14	-	0.37	0.15
L. digitata (large)	9.20	-	5.28	1.84	0.29	-	3.55	0.78	2.00	-	0.90	0.31
L. digitata (medium to small)	2.48	-	1.26	0.19	0.24	-	1.35	0.32	0.03	-	0.42	0.13
Others	0.81	-	0.21	-	0.02	-	0.13	-	-	-	-	-
All kelp	19.97	-	10.64	3.70	3.97	1.32	5.88	0.649	3.51	-	2.86	0.82
T/ac	89.13	-	47.48	-	17.70	-	26.24	-	15.67	-	12.76	-

*Used Grand Mean weight per plant for each species to calculate standing crop from density estimates.

TABLE 4. Comparison of kelp resource availability based upon MacFarlane (1952) and present (1977) survey (wet wt.).

Location	MacFarlane - 1952				Present Study - 1977					
	Area (acres)	Kg/m^2	Tons/ ac	Est. Biomass (tons)	Area (acres) Min.	Max.	Kg/m^2	Tons/ ac	Est. Biomass (tons) Min.	Max.
Seal Island	1,590	26.88	120.00	190,800	500	1,284	15.31	68.33	34,200	87,700
St. John's Ledge	350	18.43	82.28	28,800	335	350	5.88	26.24	8,800	9,200
Twin Islands	70	21.68	96.80	6,780	65	186	3.51	15.67	1,000	2,900
Total	2,010			226,380	900	1,820			44,000	99,800

St. John's Ledge

St. John's Ledge is a permanently bouyed rocky reef approximately 350 ac in size. The northeast side of the ledge was surveyed at depths between 5 and 15 m and apparently was unsuitable for dense Laminaria growth. Substrate shallower than 10 m was cobble and silt, providing a poor habitat for plant attachment. Boulders dominated the substrate at 15 m. Red algae, A. cribrosum and scattered L. digitata plants were observed. Kelp was not in commercial quantities, presumably because of siltation and/or poor light.

The southwest corner of St. John's Ledge in contrast to the northeast side was well suited for Laminaria growth. Most of the substrate was solid and contained large boulders (about 2 m in height). Three transects were completed in this area. L. digitata dominated the samples. Desmarestia spp. and a variety of red algae were also present as subcanopy.

Harvestable L. longicruris and L. digitata at St. John's Ledge averaged 1.27 and 3.26 plants/m^2, with an average weight per plant of 0.58 kg and 1.09 kg, respectively. Biomass of large L. longicruris and L. digitata averaged 0.74 and 3.55 kg/m^2, respectively. The average standing crop of all kelp was 5.88 kg/m^2 or 26.24 T/ac. The maximum standing crop from 350 ac near St. John's Ledge would be approximately 9,200 T. 73.0% or 6,700 T is considered harvestable.

Twin Islands

Twin Islands, on the northwest side, (also referred to as "The Brothers") are surrounded by approximately 185 ac of suitable substrate at depths from 2 to 10 m. About 60 ac may support commercially important quantities of kelp; the remainder is dominated by Chondrus and sand.

Dense patches of harvestable L. longicruris were observed on isolated boulders. L. digitata was also observed scattered throughout the surveyed area. A subcanopy of low-statured filamentous algae and articulate corallines occurred among Chondrus. Sea urchins were occasionally observed.

The survey of Twin Islands was quite limited and may be the least accurate of the five stations because only a small area was surveyed. Harvestable L. longicruris and L. digitata averaged 1.34 and 2.00 kg/m^2 or 15.67 T/ac.

A maximum of 186 ac of kelp substrate at Twin Islands would yield approximately 2,900 T or 2,760 T of harvestable kelp.

Duck Island

This small island was located approximately 0.8 km west of Bon Portage Island. Two transects were completed along the east side where approximately 70 ac of harvestable kelp were reported. Most of the surrounding area was surveyed by Farallon and much of the bottom was cobble and sand, providing poor substrate for kelp attachment. C. filum and Z. marina were abundant in the sandy areas. Harvestable L. longicruris and L. digitata averaged 2.10 and 1.90 plants/m^2, with an average weight per plant of 0.61 kg and 1.00 kg, respectively. L. longicruris and L. digitata wet weight standing crop averaged 1.17 and 0.90 kg/m^2, respectively. The average standing crop of all kelp was 2.86 kg/m^2 or 12.76 T/ac. The maximum standing crop from 67 ac near Duck Island would be approximately 860 T or 620 T of harvestable kelp.

Total Yield

The total yield per acre at the five study sites ranged from 12.76 to 68.33 T. Harvestable (large) L. longicruris and L. digitata represented 82.3% of the total biomass (Table 3) and non-harvestable L. longicruris and L. digitata averaged 15.2%. Other species of kelp averaged 2.5% of the total biomass. A minimum of 51,500 T and a maximum of 112,100 T of Laminaria were estimated for the five sites.

Harvestable Yield

The commercially important question is - what percentage of the kelp resource is actually harvestable? A maximum of 92,500 T of Laminaria would be available at the five sites if all "large" Laminaria were harvestable. The July survey was conducted during periods of low tidal amplitude at slack tide. Tidal currents would likely cause L. longicruris to orient horizontally along the bottom, making harvesting more difficult. L. digitata would also be affected by currents.

MacFarlane (1952) estimated 400,000 T of Laminaria from twenty sites studied in southwest Nova Scotia during the summers of 1948 to 1950. She estimated another 500,000 T of available kelp in areas not specifically studied. Most of the kelp resource was reported from the following areas:

Seal Island (190,400 T), St. John's Ledge (28,800 T), Old Woman Shoal (25,100 T), Gull Island and Bar (22,600 T), and Spectacle Island area (17,400 T). The estimated yield/ac ranged from 26 to 128 T and averaged 73 T/ac at the study sites.

MacFarlane estimated an average (grand mean) yield of 112 T/ac from Seal Island, St. John's Ledge, and Twin Islands. The 1977 estimated yield, from the same areas, averaged 54 T/ac (Table 4). There are several possible explanations for the difference in biomass estimates:

1) The 1977 samples underestimated the standing crop because random samples were collected from areas of low plant density, whereas surrounding areas supported higher densities. Diving observations did not indicate sampling was biased toward low densities.

2) The standing crop was overestimated during 1948 to 1950 while sampling with the modified Peterson grab. A larger biomass per area would result if the Peterson grab sampled all Laminaria attached within the 1/2 square yard plus any Laminaria attached outside the sample area but laying within the sample area.

3) The 1948 to 1950 data may have been collected in shallower water, supporting higher standing crops, than the depths surveyed in this study.

4) The 1948 to 1950 standing crop may actually have been much higher than during 1977. Standing crops in three beds studied during two consecutive years by MacFarlane varied by a factor of 2 to 3.

MacFarlane (1952) suggests the size of harvest would vary from year to year; for instance, she estimated a total of 12,000 T of Laminaria in three beds during the 1950 survey. By 1951 the estimate had increased to 30,800 T for the three kelp beds. Additional annual estimates of standing crop are necessary to determine more adequately the potential available Laminaria biomass. MacFarlane (1952) conducted harvesting studies during the summer of 1948 off northern Twin Island. All sporophytes were removed from an area approximately 0.07 acres in size (324 m^2). The harvested area was resurveyed during the autumn of 1949 and there was no detectable difference in general appearance of the harvested area or biomass/m^2 when compared to a nearby control.

In conclusion, it appears that commercially important quantities of Laminaria exist in Nova Scotia. Before

attempts to harvest it are made, however, quarterly studies by experimental harvesting should be conducted to determine a harvesting strategy which would permit an annual maximum sustained yield. Harvested areas should be sufficiently large to approximate a commercial harvest. Kelp recruitment and seasonal changes in available biomass at different geographical locations should be determined while testing harvesting equipment. These studies would result in development of a prudent resource management strategy for the harvest of the *Laminaria* resources in Nova Scotia.

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ENVIRONMENTAL CONTROL OF KELP GROWTH IN ST. MARGARET'S BAY AND ON THE SOUTHWEST SHORE OF NOVA SCOTIA

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INTRODUCTION

Dense kelp forests occur in the sublittoral regions of the southwest shore of Nova Scotia. In contrast, the Atlantic shore from Cape Sable to Halifax supports sparse populations of kelp and the sublittoral is dominated by sea urchins. Observations in St. Margaret's Bay over a period of 11 years (1968-1979) by associates of Dr. K.H. Mann at Dalhousie University have shown that grazing by sea urchins has destroyed most of the kelp forest. Breen (1974) believes that overfishing of commercial carnivores (especially lobsters) which prey on sea urchins has resulted in the destruction of the kelp forests. If this is so, why do kelp forests persist in southwest Nova Scotia where there is intense commercial fishing activity? Our observations have shown that sea water in the kelp forests in southwest Nova Scotia is much higher in dissolved nitrate than water in St. Margaret's Bay. Is it possible that the high nutrient levels promote a greater primary productivity on the southwest shore and that this in turn makes the benthic system more resilient to intense fishing? As a first step toward testing this hypothesis, it is necessary to develop an understanding of the factors which control the growth of kelp. This paper synthesizes work carried out by the Dalhousie research group over the past five years.

MATERIALS AND METHODS

Methods used to examine plant growth (in *Laminaria longicruris* De la Pylaie), photosynthesis, respiration, tissue analysis, sea water analysis, and *in situ* irradiance are reported by Chapman, Hoyt, and Paton (1976), Chapman and Craigie (1977, 1978), Hatcher (1977), and Hatcher, Chapman, and Mann (1977). Since 1977, irradiance (as photon flux density) has been integrated using a Lambda instrument LI-500 integrator. Methods for experimental analysis of the role of dissolved nitrate on plant growth are reported by Chapman, Markam, and Luning (1978).

Study sites are situated in St. Margaret's Bay (Fox Point, 44°37'N, 64°03'W; Boutliers Point, 44°35'N, 63°56'W) and on the southwest shore (Sandy Cove, 44°30'N, 66°06'W; Centreville, 44°33'N, 66°02'W; Pubnico, 43°39'N, 65°49'W).

RESULTS

Seasonal growth patterns of *Laminaria longicruris* at three depths at Fox Point in St. Margaret's Bay are shown in Figure 1. The significant features are as follows. First, a period of rapid growth began in mid winter and continued until late spring. Secondly, the rate of growth was found to drop sharply through the summer, fall, and early winter.

Fluctuations in dissolved micronutrients are shown in Figure 2. Only dissolved nitrate showed a distinct seasonal availability which might relate to seasonality of plant growth. Nitrate was available only during the winter and spring. During most of the summer and fall, levels were below the limit of detectability.

Nitrate in the plant tissues was found to vary greatly through the year. In winter, NO_3 occasionally exceeded 150 μ moles per g fresh weight which is ca. 28,000 times higher than ambient seawater levels and represents a nitrogen reserve of 2.5% of the total tissue dry weight. Seasonal variations at 9 m are shown in Figure 3, along with seasonal fluctuations in plant growth rate and ambient nitrate. Of special interest is the fact that NO_3 is available in plant tissues for up to two months after depletion from the water column.

Results of experimental analyses of the relationship between plant growth and nitrate availability are shown in Figures 4 and 5. Figure 4 shows the effects of *in situ* fertilization of a kelp bed at Fox Point with sodium nitrate. Tissue nitrate in the fertilized plants increased to 20 μ moles g^{-1} fresh weight in comparison with a maximum of 1.0 μ moles g^{-1} fresh weight in controls. The effect on summer growth was very marked and in the period August to September, 1975, plants achieved normal winter growth rates. Figure 5 shows a Michaelis-Menten kinetic analysis of the effect of nitrate substrate concentration on specific growth rate of *L. saccharina* (closely related to *L. longicruris*) in culture. Again, the relationship between growth and nitrate levels in the environmental range is very striking.

The source of carbon for winter growth was determined first by measurement of the levels of laminaran in the tissues. Laminaran is the major convertible carbohydrate reserve of

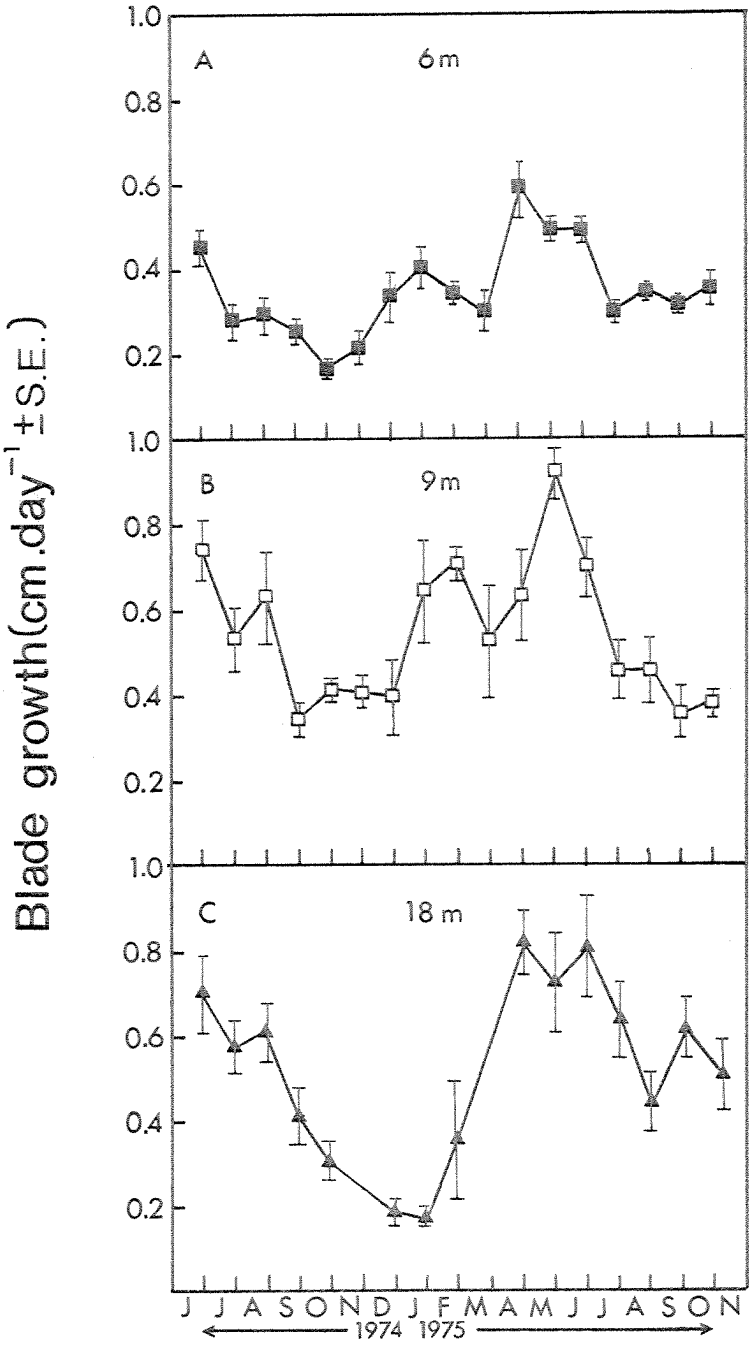


Figure 1. Seasonal growth rates of Laminaria longicruris at 3 depths at Fox Point, St. Margarets Bay.

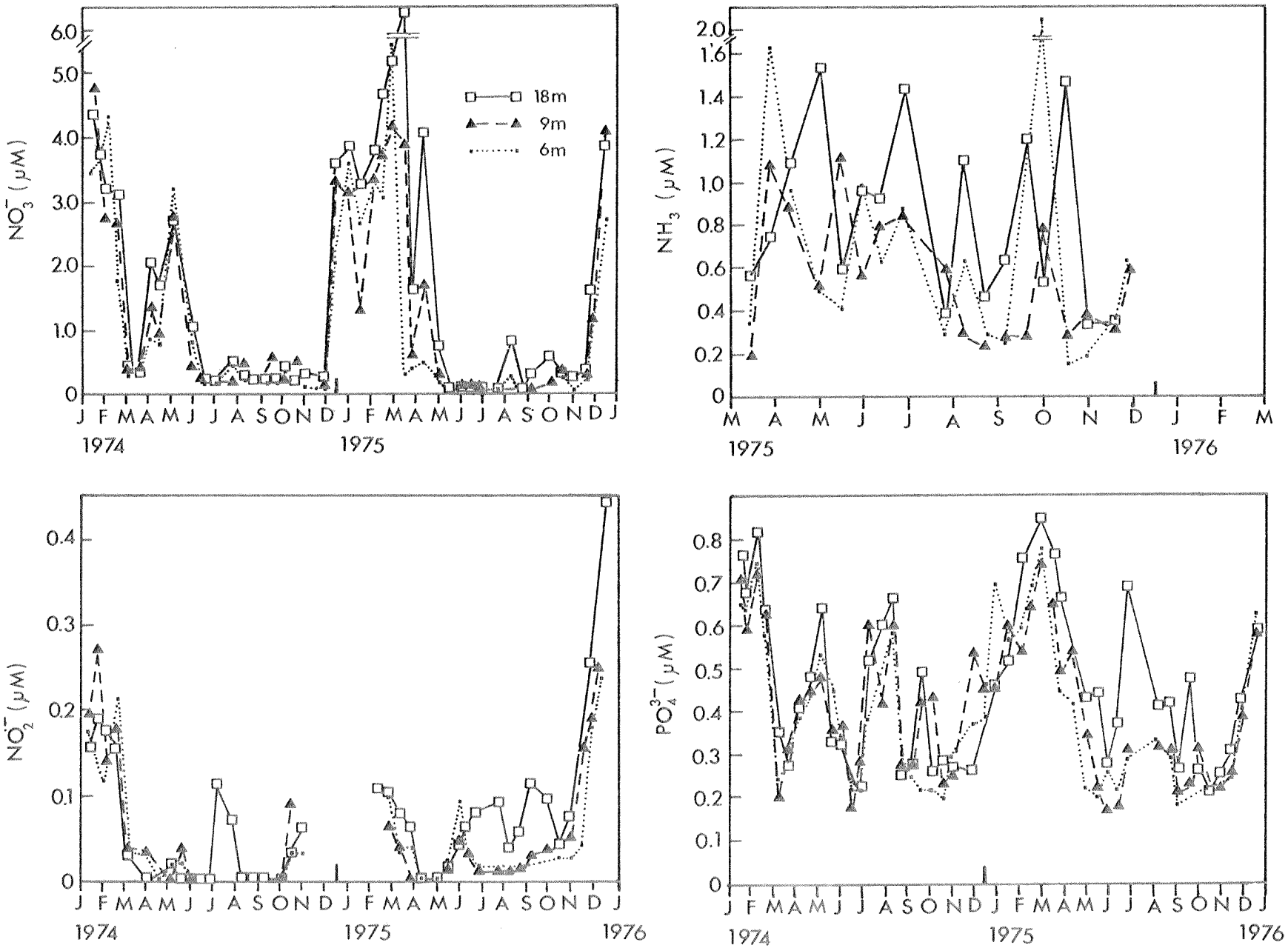


Figure 2. Concentrations of dissolved micronutrients at 3 depths at Fox Point.

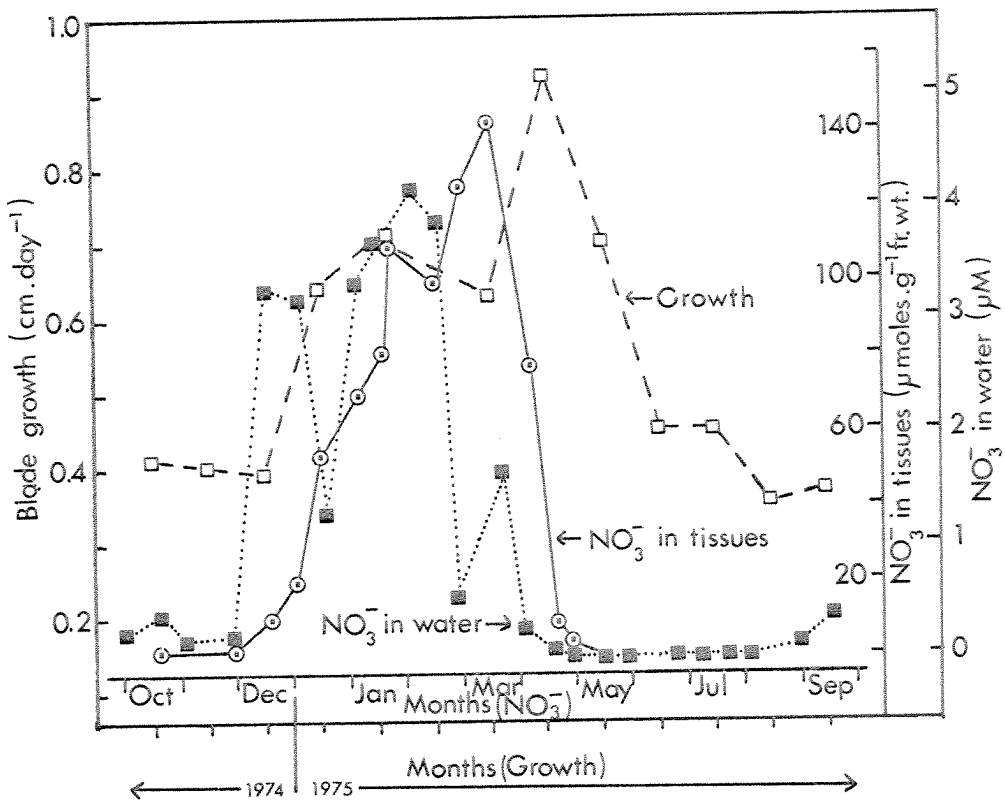


Figure 3. Seasonal changes in growth rate, ambient nitrate, and tissue nitrate at 9 m at Fox Point. Growth rates are integrated over months; nutrient levels are shown for single points in time.

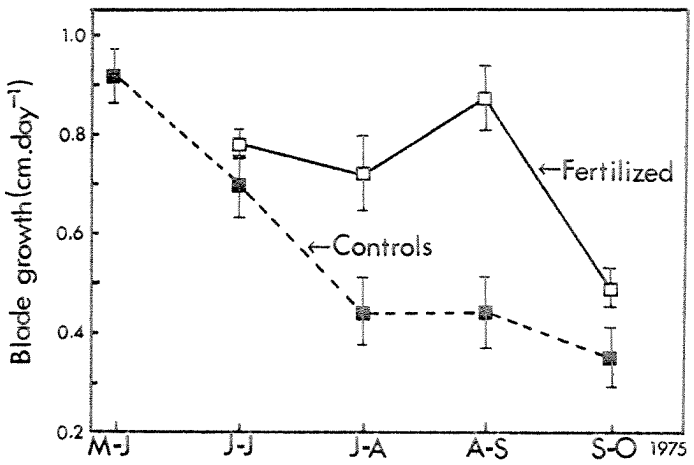


Figure 4. Effect of sodium nitrate fertilization on summer growth rates of plants at 9 m depth. Means ± 2 standard errors are shown.

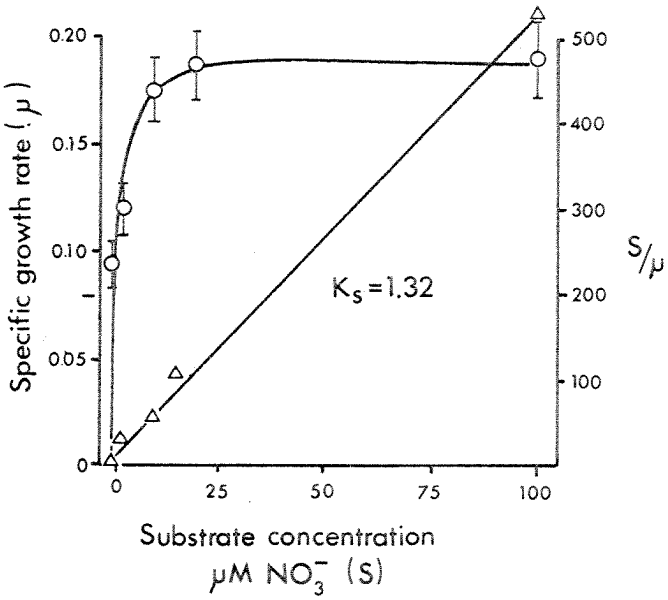


Figure 5. Specific growth rate (μ) of Laminaria saccharina in continuous flow culture under various NO_3^- concentrations (S). Means ± 95% confidence limits are shown. Curve of the reciprocal plot S/μ was derived by linear regression.

Laminaria. Figure 6 shows clearly that by early February, when rapid growth was beginning, laminaran reserves were low and almost certainly could not provide sufficient carbon for the subsequent growth of plants. The relationship between phyotsynthetic carbon fixation and the demand for carbon by growth is shown in Figure 7. Except for the period October through early January, the carbon content of new tissue was below that of diel net assimilation. Therefore, during the period of rapid growth in the first half of the year, there was enough carbon provided by photosynthesis to support growth. In the last three months of the year, photosynthesis was inadequate and laminaran reserves were exhausted, supporting the growth of plants.

All of the results to this point refer to Fox Point in St. Margaret's Bay where nitrate is present in small quantities between April and December. Figure 8 shows NO_3^- levels and growth rates of L. longicruris during the summer of 1975 at Sandy Cove, which is situated on Digby Neck on the Bay of Fundy. During that summer, ambient nitrate levels did not fall below 2.0 μ M and high growth rates were maintained through to June/July. At all times the summer growth rate was higher than any rate measured in the previous two years in St. Margaret's Bay.

Figure 9 shows the results of in-progress observations of the growth of L. longicruris at two sites on the southwest shore of Nova Scotia (Centreville and Pubnico) in comparison with Boutlier's Point in St. Margaret's Bay. In September, growth rate was highest at Centreville, similar at Pubnico, and lower in St. Margaret's Bay. Subsequently, during the following winter, growth rates at Centreville fell sharply in comparison with the other two sites. Nitrate concentrations at all three sites rose through the winter and by December, Centreville and Pubnico levels were markedly higher than those on St. Margaret's Bay. Irradiance levels at all three sites fell through the winter. The decrease at Centreville was more marked than at the other two sites and this may account for the more rapid drop in growth rate.

DISCUSSION

The objective of this work is to determine the factors which control the growth of kelp. Having done this, it may be possible to explain the occurrence of dense kelp forests in southwest Nova Scotia. Our early studies in St. Margaret's Bay show clearly the importance of the available dissolved nitrate on the growth of L. longicruris. During six months of the year, severe nitrate limitation depresses growth rates. For three of these six months, irradiance levels are low and

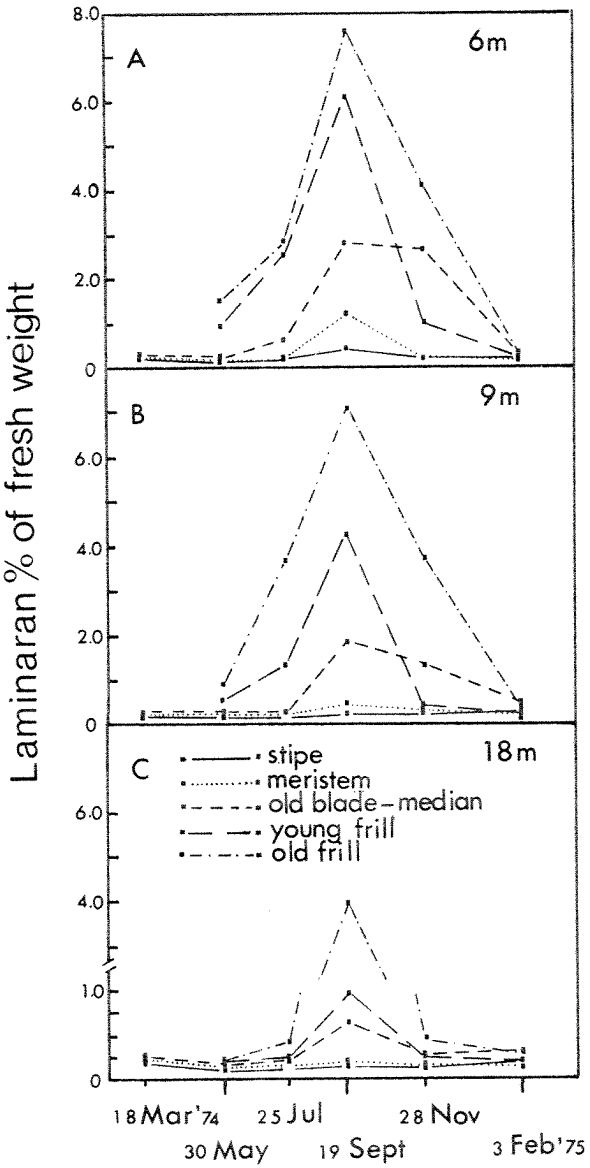


Figure 6. Seasonal variation in laminaran content in 5 tissue sections from plants of L. longicruris at 3 depths at Fox Point.

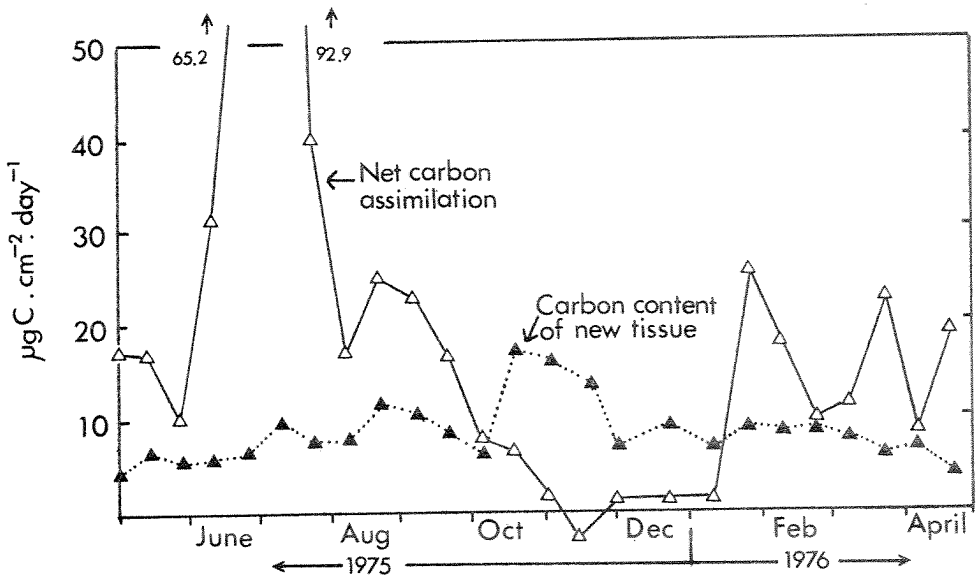
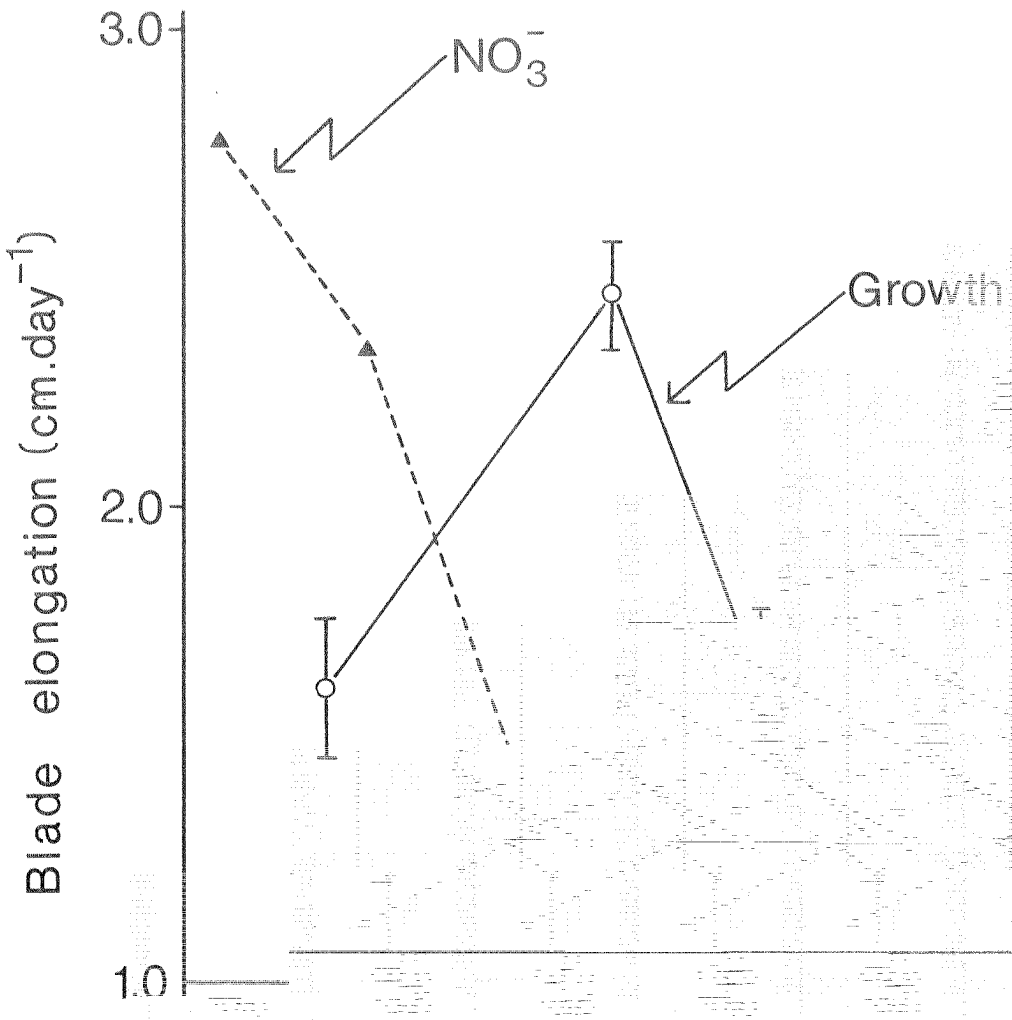


Figure 7. Mean diel net assimilation of whole L. longicruris plant, and carbon content of new tissue calculated for 2-week intervals.


3.0
2.0
1.0
7.0
6.0
NO_3^-
Growth
Blade elongation (cm.day^{-1})

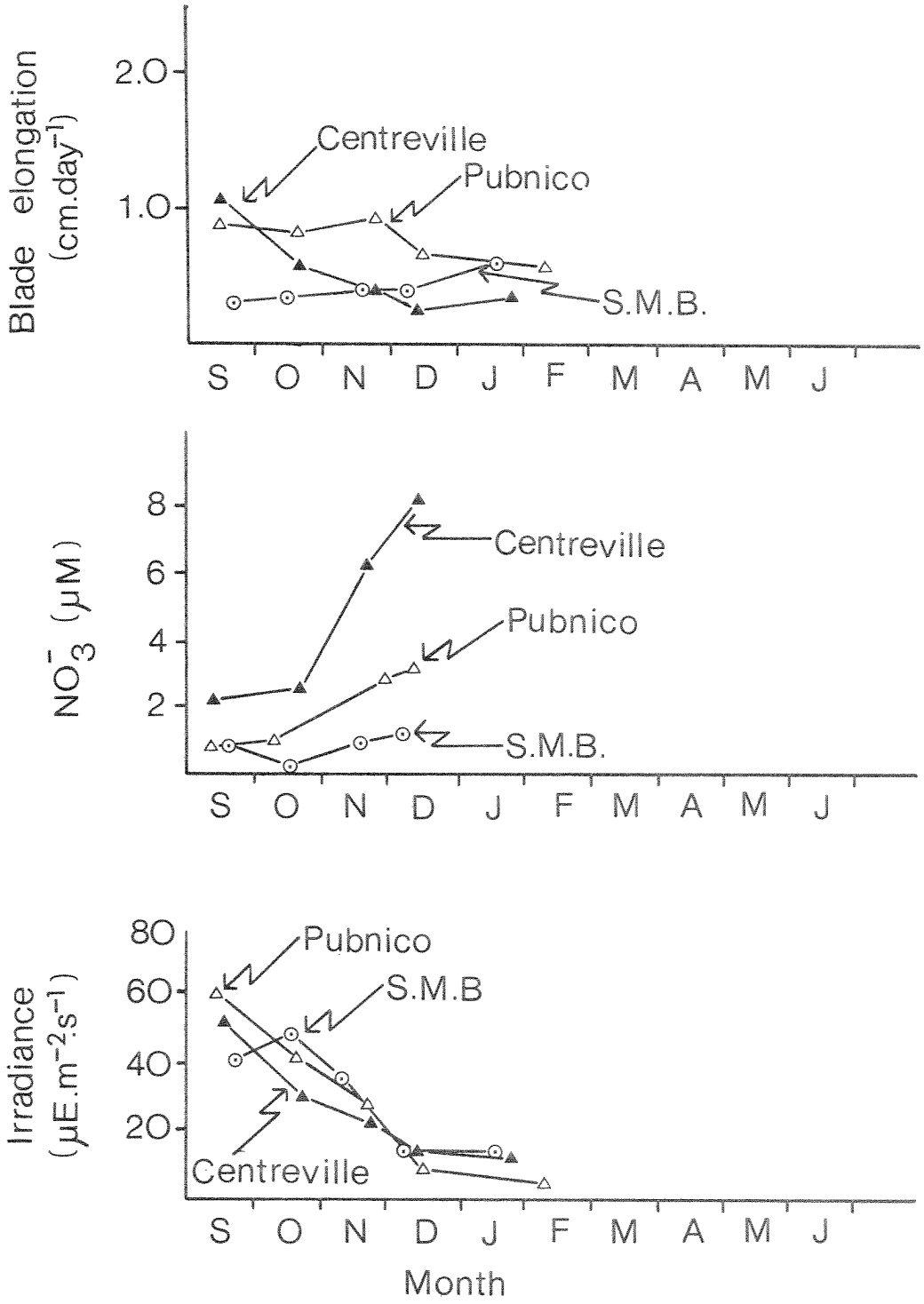


Figure 9. Comparative growth rates (means) at Centreville and Pubnico on the south shore and at Boutliers Point in St. Margarets Bay (S.M.B.) in relation to changing NO_3^- and irradiance levels at the 3 sites.

there is insufficient photosynthetic carbon production to support the carbon demand of growth. During this time, carbohydrate reserves built up during the summer are exhausted. Experimental work has shown that, during summer nitrate limitation of growth, laminaran reserves are accumulated (Chapman and Craigie, 1977). If nitrate limitation is ameliorated experimentally, laminaran accumulation is reduced and growth is depressed below that of control plants during the last two or three months of the year when light is limited. Between late January and early spring, nitrate and irradiance conditions improve and rapid plant growth ensues. Accumulated nitrate in the tissues allows an extension of rapid growth into early summer.

At Sandy Cove on Digby Neck, nitrate levels were found to be relatively high through the summer and presumably this accounts in part for the rapid growth of kelp. However, subsequent winter work at Centreville (ca. 6 km from Sandy Cove) showed that growth was depressed below that at other sites examined. This may be a reflection of minimal carbohydrate accumulation during the summer because of high nitrate availability. Information on this point will be available later this year. At the present time, it is not clear whether or not net annual kelp production is higher in areas of high nitrate availablity. A clear answer to this question should be formulated by the fall of 1979.

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AN OVERVIEW OF LOBSTER LIFE HISTORY AND FISHERY IN SOUTHWESTERN NOVA SCOTIA

By

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ABSTRACT

The life history, ecology and fishery of the lobster, Homarus americanus, is summarized for Southwestern Nova Scotia (S.W.N.S.). The hypothesis that inshore and offshore (beyond the 93 km or 50 naut. mile limit) stocks are interdependent to some unknown degree, is briefly discussed. Overall landings in S.W.N.S. (Lobster District 4) have been relatively stable since the late 1940's. However, more detailed comparison of inshore landings between the early 1960's and 1977-78 shows a general decline east of Cape Sable Island, a recent downturn in Lobster Bay just west of Cape Sable Island, and no change on the west shore at Port Maitland. Seasonal catches and effect of weather on fishing are discussed for Statistical District 32.

INTRODUCTION

In the nearshore areas of S.W.N.S. (Figure 1), the most valuable fishery species is the lobster. Its habitat includes areas covered by Laminaria, as well as areas denuded of vegetation as a result of sea urchin grazing. The effect on lobster of such alteration of habitat constitutes one of the themes of the present workshop. This paper briefly describes some aspects of the life cycle and ecology of lobsters and the lobster fishery in S.W.N.S., Lobster District 4.

LIFE HISTORY AND ECOLOGY

The habitat of lobsters off S.W.N.S. ranges from low tide to depths of over 400 m. Rocky areas appear to be the preferred habitat, but lobsters are also found on sandy and mud substrates (Stasko, 1976; Cobb, 1977; Cooper and Uzmann, 1977).

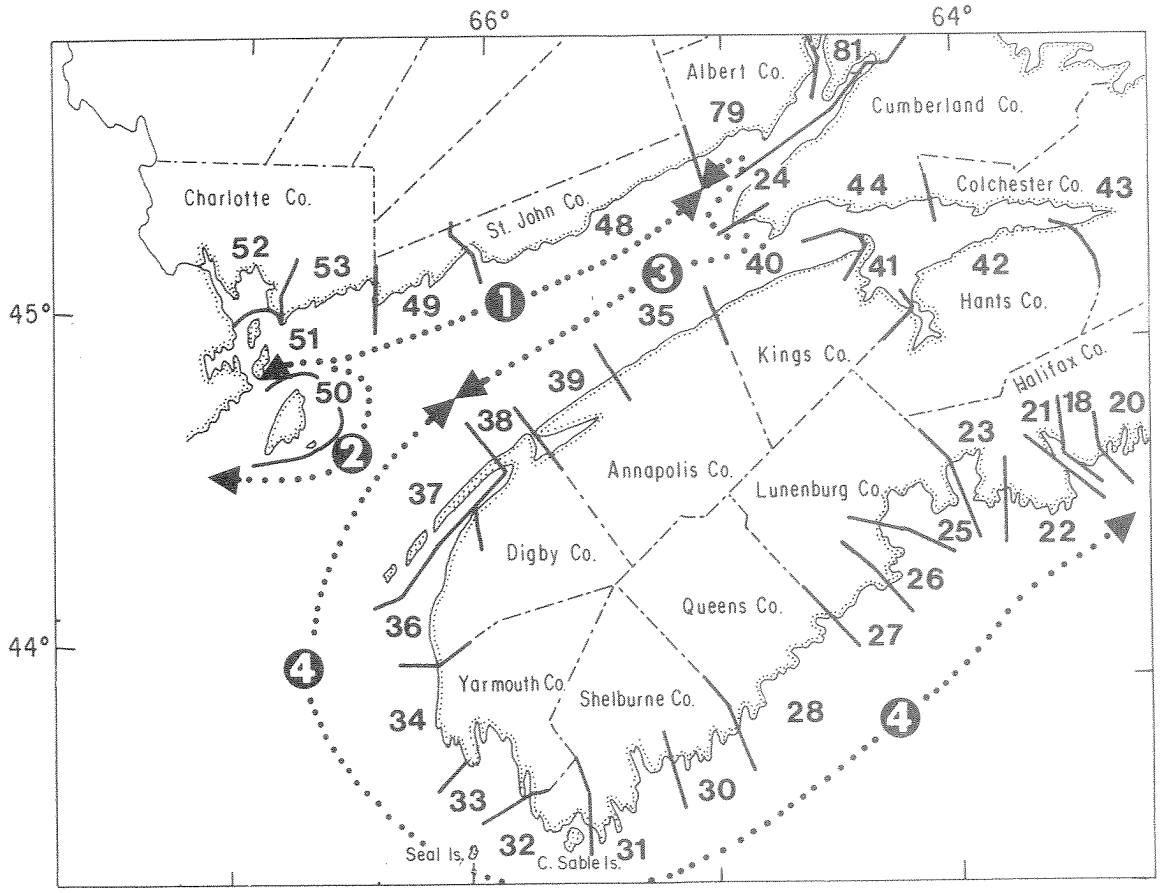

Figure 1. Counties, fisheries statistical districts and lobster fishing districts in western Nova Scotia and southern New Brunswick. Dotted lines with circled numbers denote lobster districts.

In S.W.N.S., lobsters reach the legal size of 81 mm carapace length (CL, measured from posterior margin of eye socket to posterior margin of carapace parallel to longitudinal axis of the body) at an estimated age of six to eight years (Wilder, 1953; Flowers and Saila, 1972). At this size lobsters moult on the average approximately once a year with a growth increment of 14% CL per moult (Wilder, 1953). Moulting is more frequent for smaller animals and presumably less frequent for larger ones and for mature females (Aiken, 1977). Most females reach maturity at a size of about 100 mm CL, based on the presence of external eggs (Templeman, 1936a; unpublished data). Copulation usually occurs while the female's shell is soft after moulting (Templeman, 1936a; Dunham and Skinner-Jacobs, 1978). The female stores the sperm internally to fertilize its eggs at the time of extrusion (Templeman, 1936a). Fertilized eggs are extruded from August to October and deposited on the swimmerets on the underside of the abdomen where they are carried through the winter until they hatch the following summer.

There are few berried (egg-bearing) females in inshore areas; less than 1% of females in commercial traps are berried (except in the small sample from Stonehurst [Table 1]). This is probably the result of heavy fishing pressure and a minimum legal size (81 mm CL) that is below the size of maturity. By contrast, an average of 19% of females were berried in 18 samples (9,537 females sampled) from offshore areas beyond 93 km (50 naut. mi) from shore (Stasko, 1978).

Most lobster eggs in S.W.N.S. hatch in July and August (Stasko, in press a). Larvae rise to the surface and remain in surface waters 1-2 months, depending on water temperatures (Templeman, 1936b), before settling to bottom some time during Stage IV (Scarratt, 1973).

Little is known of the early benthic stages of lobsters, especially off S.W.N.S. Larvae settle to the bottom in late summer (Stasko, in press a). Early post-larval lobsters are generally considered to be burrowing animals (Cobb, 1977; Scarratt, 1972). Small lobsters below 40 mm CL do not usually enter traps. This appears to be a behavioral characteristic, since late June to early September 1977 at four study areas around S.W.N.S. no lobsters less than 40 mm CL were caught (Figure 2) in traps that were designed to retain lobsters as small as 35 mm CL.

In S.W.N.S., lobsters below the minimum legal size of 81 mm CL are common in inshore waters, but are practically absent from traps in deeper or more offshore waters (Stasko, 1978). Conversely, there are few lobsters over 120 mm CL (approximately 1.4 kg) trapped in inshore areas (Figure 2),

Table 1. Summary of at-sea lobster samples (includes beginning and end-of-season samples of year) on commercial boats from selected ports in SW Nova Scotia (Lobster District 4) during the 1940's and 1977-78.

Port (Stat. Dist.)	Years	No. of boat trips	No. of traps hauled	Total no. of lobsters caught	Females % of total	Berried % of females	Berried No./trap haul	Sublegal (shorts) % of total	Sublegal (shorts) No./trap haul	Sublegal (shorts) Avg. weight kg	Legal No./trap haul	Legal Avg. weight kg	% first molt[a] of total legals
South Shore													
Port Mouton(28)	1942-47	80	7235	10780	49.65	0.54	0.004	40.45	0.60	0.28	0.61	0.57	73.0
Stonehurst (26)	1977-78	2	235	76	47.37	5.56	0.008	38.16	0.12	0.32	0.20	0.66	42.2
Lobster Bay													
Abbots Har.(33)	1942-49	114	18102	27349	48.24	0.26	0.002	51.33	0.78	0.28	0.74	0.54	76.9
Argyle and Lr.W. Pubnico(33)	1977-78	6	1018	1443	44.69	0.47	0.003	47.88	0.68	0.34	0.76	0.66	61.0
West Shore													
Port Maitland(34)	1944-50	126	13199	30758	51.73	0.08	0.001	38.62	0.90	0.30	1.51	0.54	74.1
" "	1977-78	18	1987	5571	53.24	0.24	0.004	55.36	1.55	0.34	1.25	0.59	71.7

[a]81-92 mm carapace length.

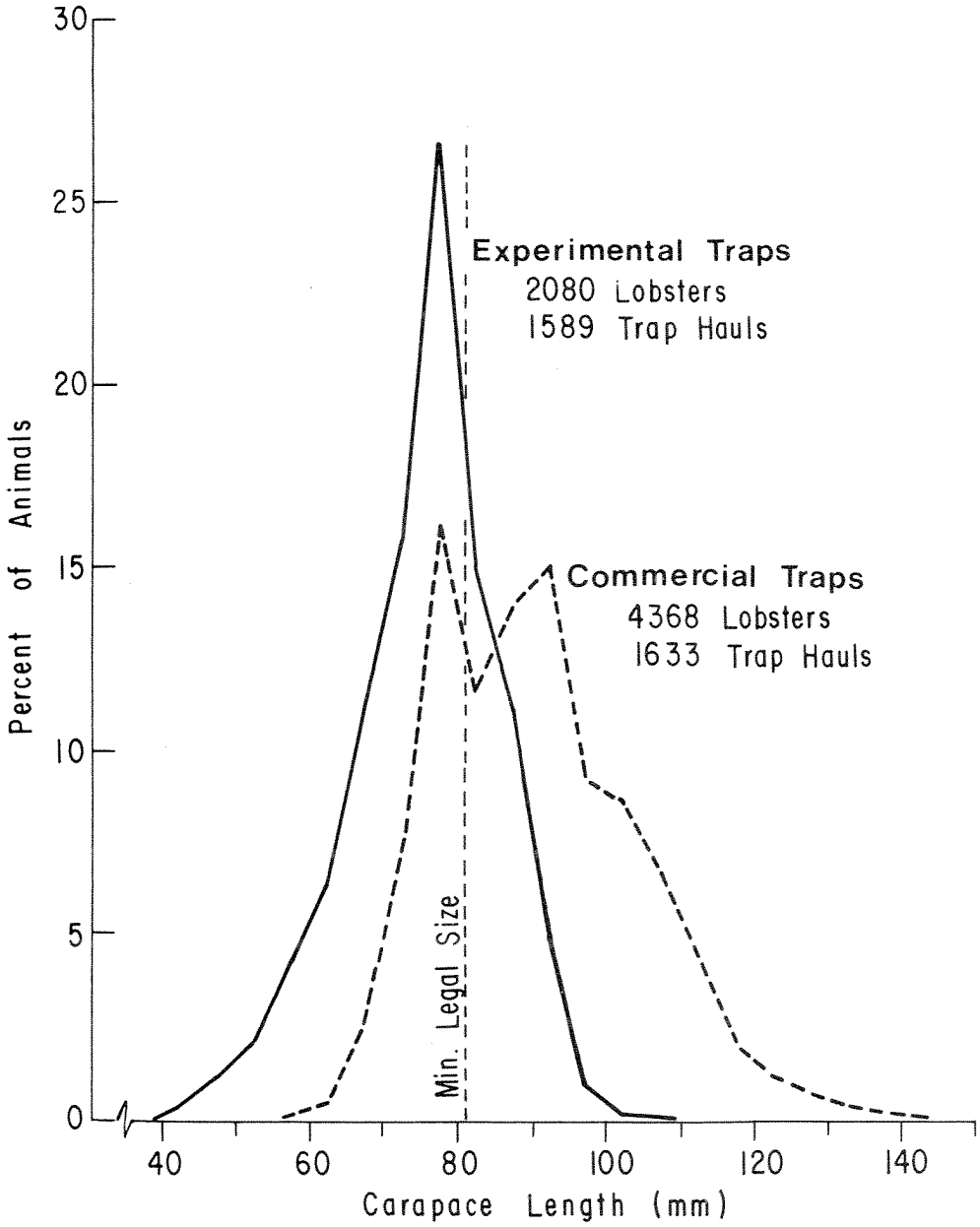

Figure 2. Size-frequency distribution of lobsters trapped in SW Nova Scotia (Port Maitland, Lower West Pubnico, Mud Island north of Seal Island, and Port LaTour) during July and August, 1977. The small traps, with 20-mm lath spacing and 76-mm diameter entrance ring, were designed to exclude large lobsters and retain lobsters as small as 35 mm CL. The commercial traps had 30-40 mm lath spacing and approximately 120-mm diameter entrance rings. The double peak for commercial traps and corresponding bulge in the other curve are presumed to result from combining samples from different areas and from pre and postmoult periods.

although in the late 1870's the average weight of commercially caught inshore lobsters in this area was approximately 1.1-1.4 kg (2.5-3.0 lb) (Venning, 1910), which converts to 112-121 mm CL (Wilder, 1953). The average size of lobsters in the Canadian offshore fishery, beyond a line approximately 93 km (50 naut. mi) from shore, is at present approximately 115 mm CL (Wilder, 1974; Stasko, unpublished data).

The apparent absence of small lobsters and abundance of berried females offshore, and the abundance of sublegal females inshore, lead to the hypothesis that the inshore and offshore (beyond the 93 km line) lobster stocks off S.W.N.S. are to some degree interdependent. This hypothesis gains further support from larval surveys and tagging studies. Lobster larvae are found from shore to the edge of the continental shelf beyond Browns Bank (Stasko, in press a). Summer surface currents from the Browns Bank area move northward (Figure 3), thus providing a transport mechanism to deliver passively drifting larvae from the Browns Bank area to inshore fishing grounds. There is also some indication that adult lobsters off S.W.N.S. can disperse considerable distances and that some do move from the Seal Island area to Browns Bank and beyond (Stasko, in press b; Stasko and Graham, 1976).

Additional larval contribution from the south shore of Nova Scotia (east of Cape Sable Island) by means of the westerly currents (Figure 3) is possible, although berried females east of Cape Sable Island have been just as scarce, except for a possible recent increase in 1977 that is based on a small sample (Table 1).

THE LOBSTER FISHERY

Fishing for lobsters off S.W.N.S. occurs mostly on inshore grounds from a few meters below low tide to a depth of about 30 m. Since 1971, an offshore fishery has developed beyond 93 km (50 naut. mi) from shore (see offshore landings in Figures 4, 5). Only a few boats have fished the area in between, though the number appears to be increasing.

The inshore lobster fishing season in Lobster District 4 (Figure 1) is open from the last Tuesday in November to the end of May. However, most of the fishing is done before and after the cold mid-winter period; i.e., during the first few weeks at the start of the season, and again from late April to the end of the season. Historically, in S.W.N.S., the first restriction of the fishing season was a closed season during July and August introduced in 1874, shortened to July 10 to August 20 in 1876, and further shortened to August 1 to August 31

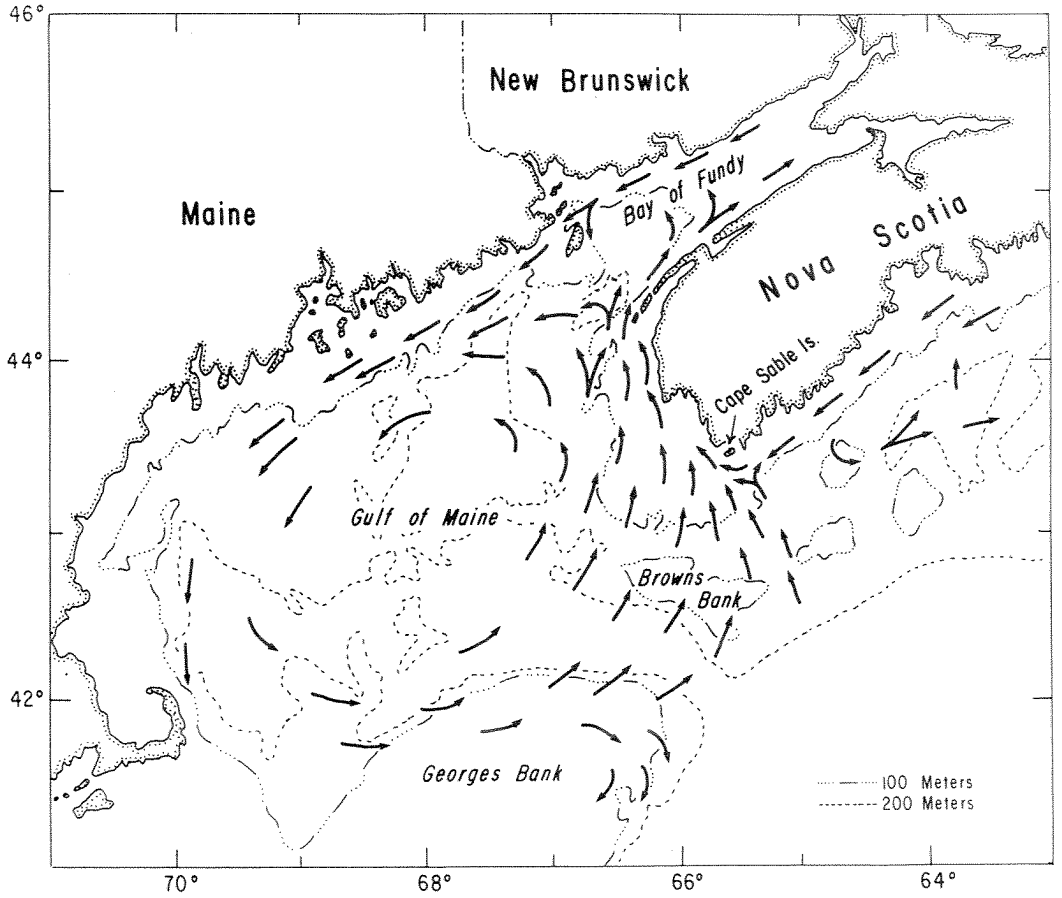

Figure 3. Pattern of summer surface currents off western Nova Scotia (after Bumpus and Lauzier 1965; Trites and Stasko, unpublished data).

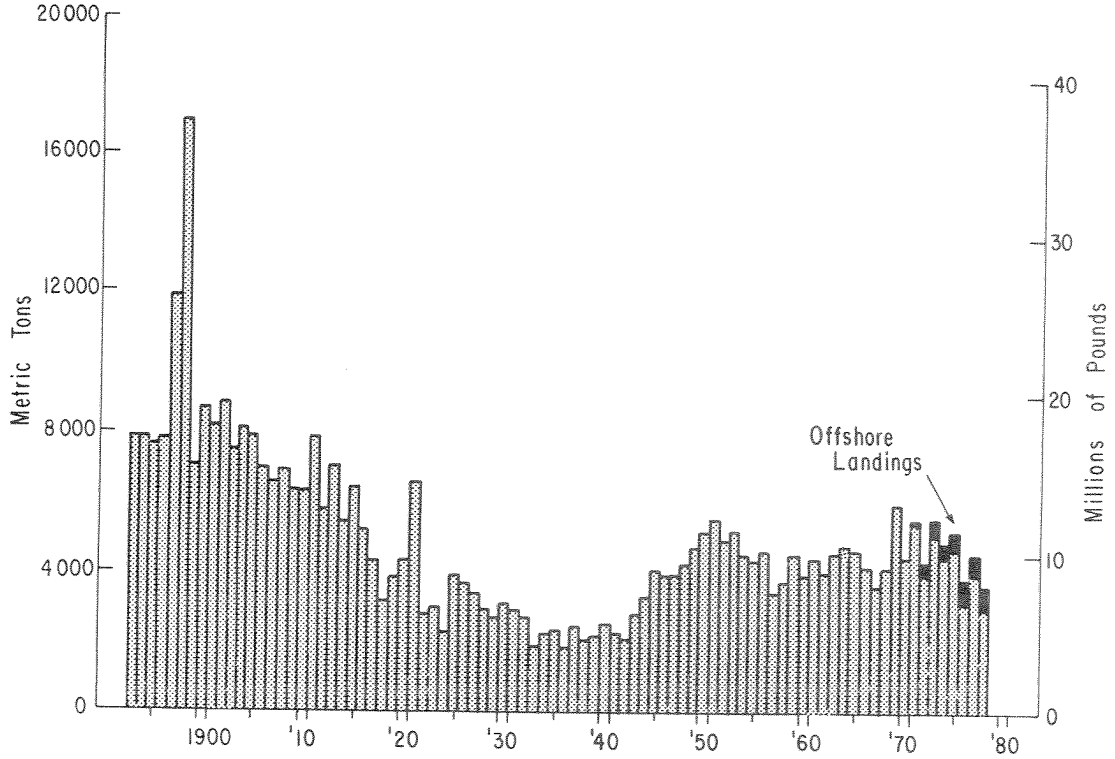

Figure 4. Annual lobster landings for western Nova Scotia (Digby, Yarmouth, Shelburne, Queens and Lunenburg counties) which approximate Lobster District 4.

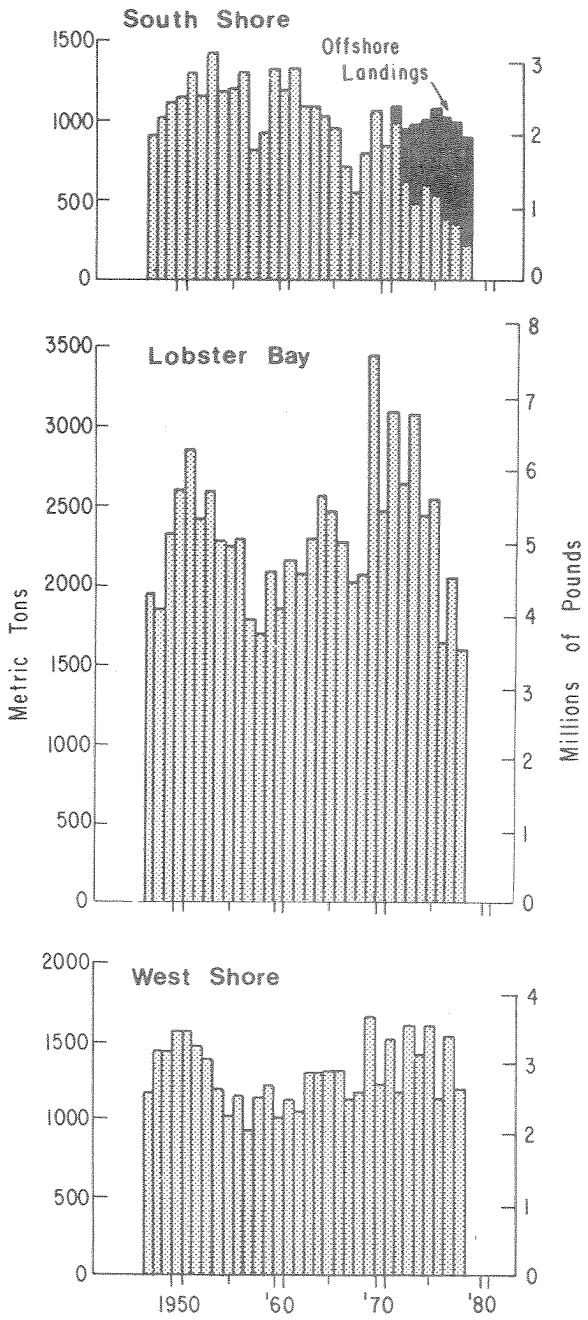

Fig. 5. Annual lobster landings by region within Lobster District 4 after 1947 when the detailed statistical districts were established.

in 1877. In 1879, the closed season was April 1 to August 1, making this in effect a fall fishery. By the turn of the century this became a late fall and spring fishery open December 15 to May 31, and with minor modifications has remained so to the present.

The minimum legal size since November, 1951, has been 81 mm (3 3/16 in.) CL. Historically, the minimum legal size was approximately 94 mm CL (0.7 kg) from July 7, 1873; approximately 79 mm CL (9 in. total length) from October 19, 1923; 77.8 mm (3 1/16 in.) CL from January 25, 1934; and 79.4 mm (3 1/8 in.) CL from November 11, 1941 to November 6, 1951.

The boats now used in inshore areas are generally 10-13.5 m long Cape Island-type boats. With the gradual increase in average boat size over the years and introduction of hydraulic trap haulers, depth sounders, radar, and LORAN, the fishing efficiency and daily travel range have increased. During the 1977-1978 fishing season there were 2,532 registered lobster boats in Lobster District 4. Almost all commercial traps are wooden, either half-cylindrical or box-like in shape with base wider than top, with three or four bows 0.8-1.2 m in length, with an entrance ring 12-14 cm in diameter and lath spacing of 3-4 cm. The bait normally used is salted herring, frozen mackerel, fresh gaspereaux, fish heads, etc. - whatever is locally available at low cost. On S.W.N.S. inshore grounds, traps are generally set singly with a buoy for each trap. Offshore traps, which are larger than inshore ones, are usually set on a trawl line of 50 traps per trawl.

Lobster landings in S.W.N.S. rose to about 8,000 MT per year around the turn of the century, and gradually declined to lows of about 2000 MT in the 1930's. Since the late 1940's landings have been relatively stable at around 4000-5000 MT (range approximately 3500-6000 MT) (Statistics Branch, Dept. of Fisheries and Oceans). During 1978 in Lobster District 4 the catch of 3653 MT, valued at $21.5 million, was 19.1% of the total Canadian lobster landings. The comparable average percentages for five-year periods since 1950 (i.e., 1950-54, 1955-59, 1960-64, 1965-69, 1970-74, and the three-year period 1975-77) are 23.9, 19.9, 21.4, 26.5, 31.5 and 26.

The relative stability of landings since the late 1940's has not been geographically uniform. East of Cape Sable Island, in Statistical Districts 18 and 21-31 (south shore), landings of inshore lobsters have declined since the 1950's to a fraction of former levels (Figures 1, 5). A comparison of the commercial port and at-sea samples at Stonehurst

(Statistial District 26) during 1950-51 versus 1977-78 and at Port Mouton (Statistical District 28) during 1942-47 versus 1978 (for commercial samples see Campbell, in press; for at-sea data see Figure 6, Table 1), indicates that fewer lobsters are moulting into legal size now than in the 1940's-50's. This suggests that recruitment of lobsters into the fishery has declined on the south shore since the 1940's. This declining trend in landings may now be ending. Recent landings along the south shore have increased slightly from 386 MT during the 1977 fall fishing season to 395 MT during the 1978 fall season.

In Lobster Bay (Statistical Districts 32, 33) landings have been higher than in any of the statistical districts in S.W.N.S. However, in recent years (1970-77) landings in Lobster Bay have declined (Figure 5). Reports from fishermen indicate that the decline has been greatest in the nearshore areas, but the true magnitude of the decline has been masked by good catches of boats fishing more than 15 km from shore at Seal Island and other distant areas. A reduction of recruitment in Lobster Bay is indicated by fewer shorts caught and by a decrease in the percentage of animals in the first moult size range above legal size during the 1977-78 fishing season compared to the 1940's (Table 1, Figure 6).

Along the west shore (Statistical Districts 34-38), landings have remained relatively stable (Figure 5) though the ratio of shorts to legal-size animals has increased (Table 1, Figure 6). The slight increase in average weight of lobsters from the 1940's to 1977-78 (Table 1) may be due to the increase in minimum size limit from 79.4 to 81 mm CL in 1951 (Figure 6).

Seasonal catches, along with total landings in the most productive area (Statistical District 32), are graphed in Figure 7. Since 1957 (when statistical districts were last modified) there was a gradual increase in landings (on a fishing season basis as opposed to a calendar year), with a rapid increase in 1968 and a rapid decline after 1976. In the fall of 1967 a trap limit was introduced, but this resulted in increased fishing effort since prior to fall 1967 few fishermen fished the new 375 trap limit.

Along with the increase in landings after 1968 came a change in the pattern of fall-spring catches. Prior to 1968 the fall and subsequent spring catches increased and decreased independently of each other. After 1968 an increase in fall landings was followed by a decrease in landings the following spring, a decrease in fall landings by an increase the following spring.

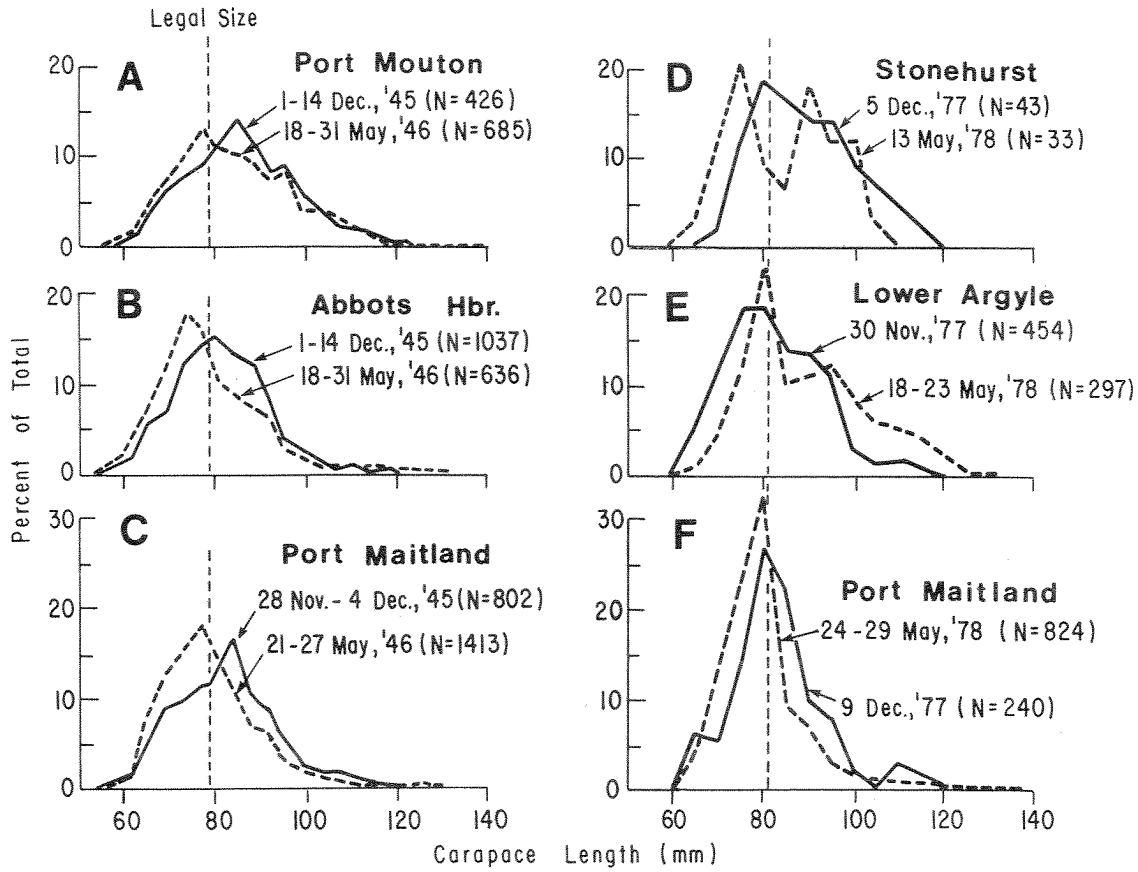

Figure 6. Size-frequency distributions of lobsters (expressed as percent of total catch) from at-sea samples from selected ports in SW Nova Scotia at the beginning and end of fishing seasons 1945-46 and 1977-78. Data from the 1945-46 samples were converted from total lengths to carapace lengths (Wilder 1953) giving lowest increments of 3-4 mm, whereas for the 1977-78 data the lowest increment was 1 mm. Size groupings used in graphs were 3-4 mm for 1945-46 and 5 mm for 1977-78 data, giving the impression of higher values for the 1977-78 data.

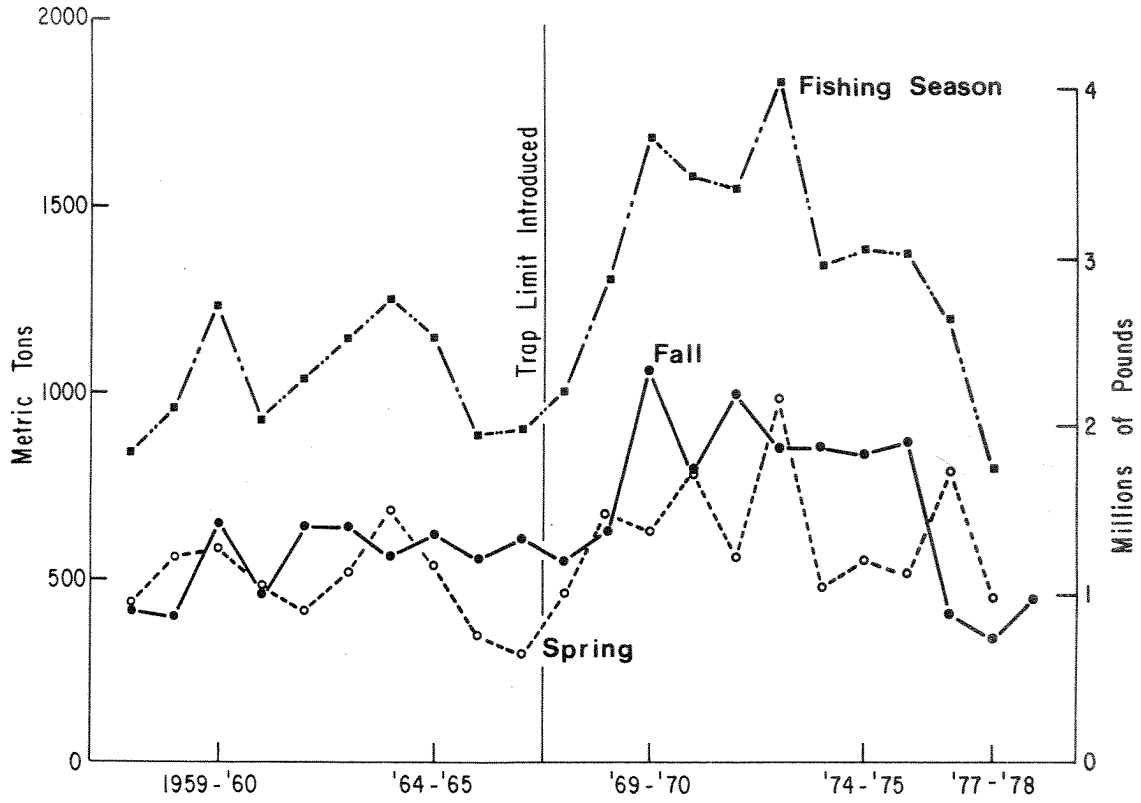

Figure 7. Lobster landings for Statistical District 32 on a fishing season basis. The fishing year is from late November to end of June, but landings data to 31 October were used to allow for sale of lobsters held in pounds. "Fall" includes landings recorded November-February; "spring" includes March-October.

Table 2. Wind speed and air temperature in S.W. N.S. (Yarmouth airport) as possible factors in fishing success. Suitable weather for fishing was arbitrarily defined as having average wind of less than 16 knots and peak gusts of less than 40 knots. For each year the number of fishing days from start of lobster season on last Tuesday in November to the end of December were counted, excluding Sundays when lobster fishing is prohibited. Temperatures shown are averages of daily mean temperatures from start of lobster season to end of December.

	1974	1975	1976	1977
No. of low-wind (fishing) days	23	25	13	26
Average air temperature (°C)	+0.4	-0.2	-2.2	+0.6

In the fall of 1976 landings dropped to about half the previous level. At least part of the fall 1976 decrease can be explained by windy, cold weather in the fall of 1976 (Table 2). However, increased landings in the spring of 1977 did not fully compensate for this; and annual landings continued to decline in 1977-78, with no real improvement in the fall of 1978. This decline comes approximately one lobster generation time after the high landings reached in 1969-70.

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SEA URCHIN (*STRONGYLOCENTROTUS DROEBACHIENSIS*) DISTRIBUTION AROUND WESTERN NOVA SCOTIA

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ABSTRACT

Sea urchin (*Strongylocentrotus droebachiensis*) distribution and abundance were estimated around western Nova Scotia by interviewing lobster fishermen and by compiling bycatch data from lobster traps sampled at sea. Sea urchins are present in all shallow areas except the upper reaches of Annapolis Basin and St. Mary's Bay, and on mud bottom such as east of Mud and Seal Islands. They are also found on shallow areas of Browns and Georges Banks. Abundance along the Fundy shore of Nova Scotia increases from few at Halls Harbour to abundant at Digby, decreasing to few in Lobster Bay (southeast of Yarmouth), and increasing to abundant east of Cape Sable Island. Sea urchin distribution data sampled by lobster traps have serious limitations and should be confirmed by diver observations.

INTRODUCTION

There is a dearth of information in the literature on sea urchin (*Strongylocentrotus droebachiensis*) distribution and abundance in the Maritimes region (New Brunswick, Prince Edward Island, and Nova Scotia). Such information is of increasing interest because of possible effects the sea urchins may have on marine plants and, indirectly, on lobsters.

Mann and his associates (e.g., Mann, 1977) have studied localized sea urchin ecology in St. Margaret's Bay and on the south shore of Nova Scotia. Some data on sea urchin abundance in Northumberland Strait (Gulf of St. Lawrence) are contained in Stasko et al. (1977). Neish (1973) and MacKay (1976) surveyed sea urchin distribution from Grand Manan Island to Cape Spencer, N.B. We could find no reports on sea urchin distribution from southwestern Nova Scotia and the Nova Scotia shore of the Bay of Fundy.

This paper presents the results of a survey (interviews) of fishermen and a compilation of sea urchin bycatch data from lobster traps sampled around western Nova Scotia during 1977-78 with some additional sampling at Grand Manan. Although our methodology does not indicate the absolute abundance of sea urchins in an area, it provides a rough indication of their distribution and relative abundance.

METHODS

Three approaches were taken: interviewing fishermen, summarizing bycatch data from commercial lobster traps sampled at sea during 1977-78, and summarizing bycatch data from traps fished during research cruises in summer, 1977.

Two or three inshore lobster fishermen per port were interviewed at selected ports around western Nova Scotia from Halls Harbour on the upper Bay of Fundy to the Shelburne area (Figure 1). In addition, we interviewed lobster fishermen and a few scallop fishermen who fish deeper waters beyond the normal inshore grounds, including the Browns Bank area and northeast Georges Bank.

The bycatch of sea urchins in commercial lobster traps was recorded as part of at-sea lobster sampling on commercial lobster boats during the lobster fishing seasons in 1977 and 1978. Many sea urchins were small enough to easily pass through the lath spaces in the commercial traps.

Further data on sea urchins were collected during the closed lobster season on research cruises in summer 1977 at four sites: Port Maitland, Lower West Pubnico, Mud Island (north of Seal Island), and Port LaTour (Figure 1). Two types of traps were used: (1) local wooden commercial lobster traps (Su) with 30-40 mm lath spacing and entrance ring approximately 120 mm in diameter; and (2) smaller experimental traps (Ex) with approximately 20 mm lath spacing and 76 mm entrance ring designed to retain lobsters down to a size of approximately 35 mm carapace length (CL) and exclude large lobsters. These traps were fished at a number of stations at each site, from shallow water in bays to a depth of approximately 25 m. One commercial and one experimental trap were set approximately 10 m apart on a single buoy. Bait was frozen mackerel with all old bait removed and new bait added each time the traps were hauled. Soak time was usually 24 h.

Frequency distribution of the number of sea urchins per trap haul was compared (Figure 2) with the negative binomial distribution which is defined by two parameters, the

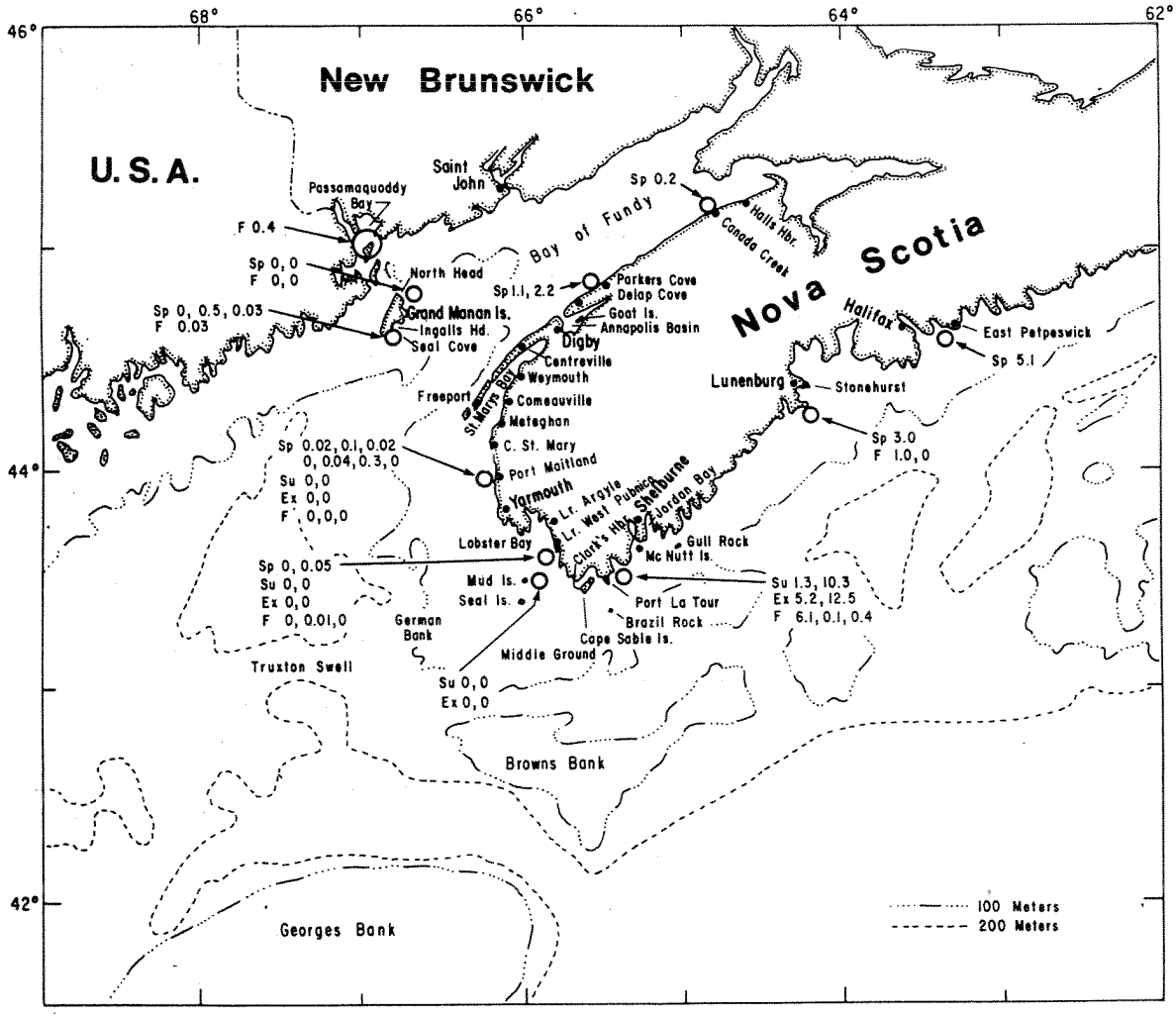

Figure 1. Map of Bay of Fundy and SW Nova Scotia showing sampling locations for both at-sea samples and interviews. The numbers represent bycatch of sea urchins (avg. no./trap haul) in lobster traps sampled at sea in 1977 and 1978 in lobster districts 1 to 4. In the 50 samples, most (76%) had 75-200 traps (range 23-247 traps) per sample. Seasons are indicated as: Sp - spring (commercial lobster fishery mid April to mid June), Su - summer (research fishing mid June to early September), F - fall (commercial lobster fishery November-December). The traps used were local commercial lobster traps, except those marked "Ex" which were experimental traps designed to retain small lobsters down to 35 mm carapace length and fished alongside the summer traps in 1977.

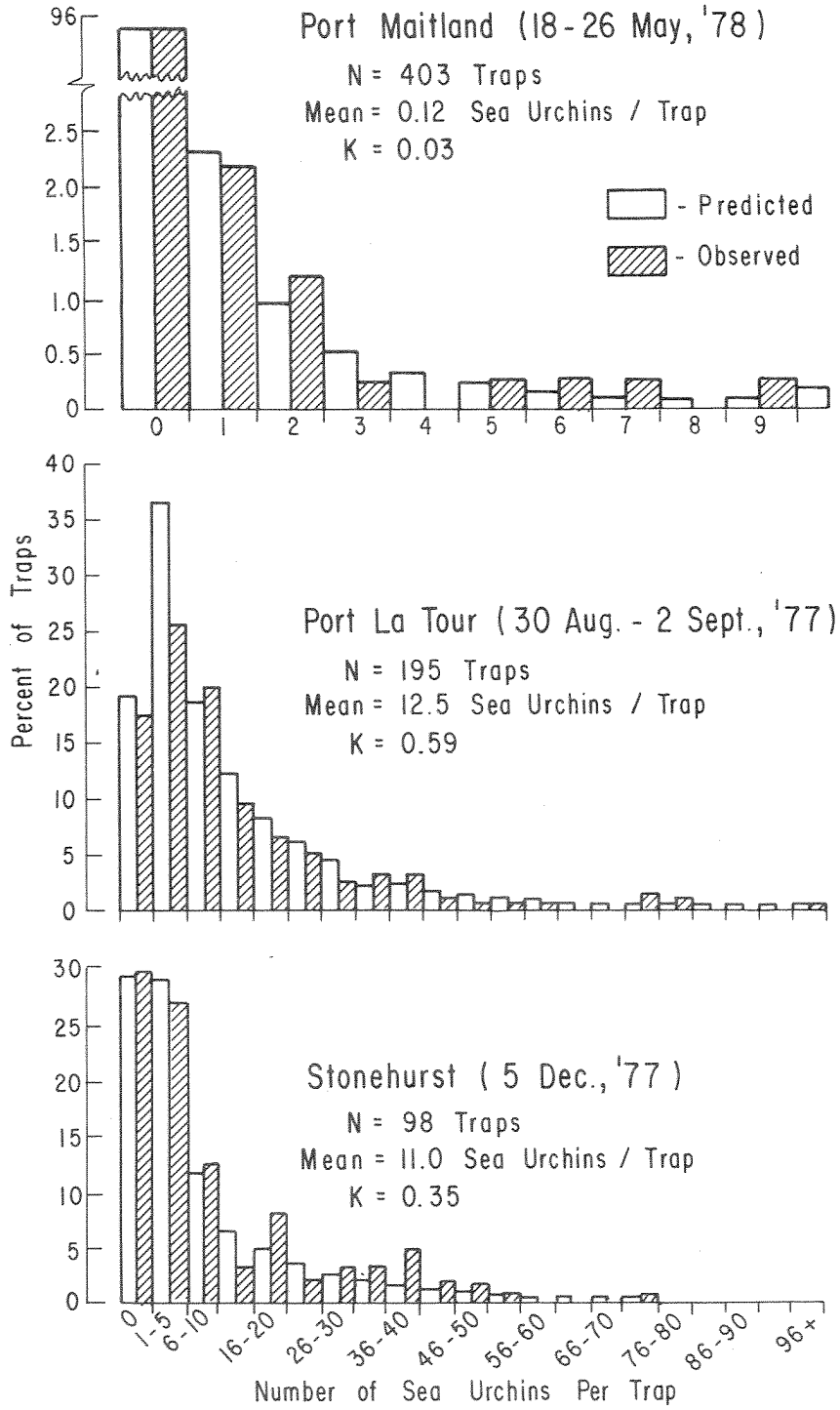

Figure 2. Catch-per-trap frequency for three areas using samples with large number of sea urchins. Shaded histogram shows observed values; blank histogram shows values predicted on the basis of the negative binomial distribution. "K" is the exponent of the negative binomial distribution.

arithmetic mean ($\bar{X}$) and the exponent (K), using a computer program described by Davies (1971). Differences between the observed distributions and the predicted negative binomial values were not significant ($P > 0.10$), using the chi-square test.

RESULTS

Interviews

Fishermen reported sea urchins along the whole Nova Scotia coastline except in a few isolated pockets (Table 1). One such pocket is the upper Annapolis Basin where muddy bottom and low salinities may be factors in limiting sea urchin presence. Another area lacking in sea urchins is Lobster Bay just off Lower West Pubnico, although nearby fishermen from Argyle did report a few. None were reported from east of Mud Island where the substrate is soft. At the other extreme, fishermen in some areas reported catching hundreds of sea urchins per day in 250 to 375 traps, with occasionally 15 to over 1,000 sea urchins per single trap. Such areas of sea urchin abundance extend from the Digby shore to Port Maitland (except for the upper Annapolis Basin and upper St. Mary's Bay), and the coastline east of Cape Sable Island. Few sea urchins were reported from the northern half of Lobster Bay.

A few sea urchins are occasionally seen in lobster traps fished in the shallower areas distant from shore. Some have been noted as distant as Browns Bank and northeast Georges Bank. In fact, scallop fishermen report that on the shallower areas of Georges Bank sea urchins are plentiful in some locations.

A general conclusion, agreed to by all fishermen, is that sea urchins are found on hard bottom. Large sea urchins were noted along the Fundy shore whereas smaller ones were found from St. Mary's Bay south.

Observations on changes in abundance (Table 1) are probably more suspect than fishermen's descriptions of present occurrence of sea urchins. Aside from the fishermen attempting to recall events over a number of years, there is the problem of their estimation of sea urchin size. A few large animals may be more noticeable than a large number of small animals, and changes in size over the years might be interpreted as changes in numerical abundance. Based on the interviews, there is no change in abundance of sea urchins in the upper Bay of Fundy, a decrease in the Digby area, an

Table 1. Distribution and relative abundance of sea urchins in western Nova Scotia from the upper Bay of Fundy to the Shelburne area, based on interviews with fishermen. Two or three lobster fishermen were interviewed in selected ports. Their replies are based on commercial lobster traps fished in late fall and in spring.

Location	Depth a) m	Depth a) (fath)	No. animals/ b) day/fisherman	Max.c) no./trap	Changes in last 5 yr	Remarks d)
NEAR-SHORE AREAS						
Halls Harbour, to ½ km from shore	4-46	(2-25)	4-5	1	No change	Most abundant at Isle Haute; large animals.
Digby area, Fundy shore	9-18	(5-10)	1000	25-30	Decrease	
Digby Gut to Goat I.	9-18	(5-10)	1000	25-30	Decrease	Both sides of gut; large animals. Fishermen land sea urchins to reduce their number.
Annapolis Basin NE of Goat I.	-	(-)	None	None	No change	Mostly mud bottom in this area.
Centreville, Fundy shore	18-55	(10-30)	300	100	Increase	Fishermen land sea urchins to reduce their number.
Freeport, Fundy side to ½ km from shore	18-55	(10-30)	300	100	Increase	Most abundant fairway buoy to Grand Passage.
Weymouth to head of St. Mary's Bay	-	(-)	6-12	1-2	Increase	Most abundant in middle of bay on hard bottom; small animals.
Comeauville to Meteghan	27-64	(15-35)	100-300	10-15	No change	
Meteghan to Cape St. Mary	4-37	(2-20)	50-100	6-10	Increase	None here 2 yr ago.
Port Maitland area	5-46	(3-25)	25-200	30-60	Increase	More abundant on Frenchman shoal at Trinity Ledge.
Yarmouth area	33-73	(18-40)	6-12	1	No change	Most abundant at Gannet Rock and Dry Ledge, few in shallow water.
Lobster Bay (Argyle)	-	(-)	1-5	1	No change	
" " (Lr. W. Pubnico)	-	(-)	None	None	No change	
Mud Island, west	37-55	(20-30)	6-12	1	Increase	Small animals.
Mud Island, east	-	(-)	None	None	No change	Mostly soft bottom.
Seal Island, west	-	(-)	1-6	1	Increase	
Seal Island, southeast	18-55	(10-30)	25-30	12	Increase	The further to the SE the more abundant; rocks cleaned of kelp, more small animals now.
Clarks Harbour	13-37	(7-20)	4-10	1	Slight increase	Small animals west of Green Island.
Port LaTour	-37	(5-20)	300-500	20	Increase to 1977	
Shelburne	4-15	(2-8)	100-300	25	then decrease	Most abundant around McNutt Island.
Jordan Bay	-	(-)	300-500	15	" " "	Most abundant around Gull Island.
DISTANT AREAS (15+ km from shore):						
German Bank	51-64	(28-35)	None	None	-	
Middle Ground (E. of Seal I.)	27-46	(15-25)	5	-	-	Small animals; 180-200 traps per day.
Truxton Swell	128-165	(70-90)	Occasional	-	-	350-400 traps/day; 5-6 d trips.
Top of Browns Bank	29-55	(16-30)	20	2	-	200 traps/d.
West of Browns Bank	146-183	(80-100)	None	None	No change	350-400 traps/d.
S.W. Browns Bank	146-183	(80-100)	Occasional	-	No change	" "
S.E. Browns Bank	128-366	(70-200)	None	None	No change	" "
N.E. Georges Bank, shallow	64-82	(35-45)	Occasional	-	No change	" "
N.E. Georges Bank, deep	119-183	(65-100)	None	None	No change	" "

a) Depth range at which sea urchins are reported as most abundant, except on distant grounds where depth denotes the range of depths fished with traps.

b) The trap limit for inshore fishermen is 375 traps in SW Nova Scotia, 300 in upper Bay of Fundy east of Digby, and 250 east of Cape Sable I.

c) Estimate based on one night soak time.

d) In all interviews fishermen identified hard bottom as the substrate on which sea urchins are found.

increase in St. Mary's Bay to Port Maitland, no change in Lobster Bay, an increase at Mud-Seal Island, an increase to 1977 with subsequent decrease (smaller sizes?) east of Cape Sable Island, and no change in areas distant from shore.

Bycatch in Lobster Traps

In the Bay of Fundy along the New Brunswick shore, sea urchins were found in low concentrations, but were absent in deeper areas off the northeast side of Grand Manan Island (Figure 1). On the Nova Scotia side of the Bay there were few sea urchins at Canada Creek, with greater abundance in the Digby area, and few around the tip of S.W.N.S. The greatest abundance was found east of Cape Sable Island. Variations in sea urchin bycatch between traps and between samples were considerable.

In the summer 1977 trapping study there were fewer sea urchins in the local commercial-type traps (labelled Su) than in the same type of traps fished commercially during the spring and fall lobster fishing seasons (labelled Sp and F) (Figure 1). At Port Maitland, in Lobster Bay, and at Mud Island no sea urchins were caught. At Port LaTour sea urchins were abundant.

The results from the experimental traps showed a similar trend but were more extreme than those obtained by the other two approaches (interviews and commercial fishery); no sea urchins were caught northwest of Cape Sable Island while many were caught in the Port LaTour area. Comparison of the two trap types (Table 2) shows that the experimental traps caught more sea urchins than the commercial traps. During the first sampling period (July 4-8) the mean number of sea urchins per trap in the commercial versus experimental traps was 1.3 versus 5.2 ($P < 0.01$, two-way analysis of variance), while during the second period (Aug. 30-September 2) the difference (10.3 versus 12.5) was not statistically significant. For the other species recorded, the experimental traps caught more of the smaller species but fewer of the large ones (lobsters and jonah crabs).

There was great variability in catches of sea urchins in both trap types during the summer research cruises as well as in the commercial trap during the spring and fall commercial lobster fishery. This is illustrated in Figure 2 where the proportion of traps is plotted against the number of sea urchins per trap for three locations with large catches of sea urchins. Most traps in each of the three samples caught none or very few sea urchins, while a few traps caught large numbers. The observed values closely follow the negative

Table 2. Total number of animals caught in commercial and experimental lobster traps fished at Port LaTour during research cruises in summer 1977.

Trap type	No. of traps	Sea urchins	Whelks	Hermit crabs	Rock crabs	Jonah crabs	Lobsters
Survey 1 (4-8 July)							
Commercial	200	253	0	0	2	1	97
Experimental	199	1025	0	0	63	0	52
Survey 2 (30 Aug.-2 Sept.)							
Commercial	199	2055	1138	17	34	5	90
Experimental	195	2432	3196	59	199	3	47

binomial distribution, with low "K" values (exponent of the negative binomial distribution) indicating a non-random or contagious distribution (Poole, 1974).

DISCUSSION

Of the three approaches used, interviewing fishermen was the most subjective. Some problems with this sampling technique are site selection to place traps for best lobster catches, avoidance by fishermen of sea urchin concentrations, variations in type of bait, not clearing out sea urchins at each haul, inattention to sea urchin numbers, effect of sea urchin size on subjective impressions of abundance, and differences in memory of the individual fisherman. Some of the subjectivity is removed in at-sea sampling of commercial traps by research personnel who actually count the sea urchins.

A further improvement is achieved on research cruises where trap location is determined without reference to lobster abundance, traps are completely cleared at each haul, and the same type of bait is used consistently. A further improvement was gained by use of the experimental small traps that caught fewer lobsters and thus, presumably, reduced the effects that predators (lobsters and crabs) in a trap would have on presence in traps of their prey (sea urchins). Lobsters are known to feed on sea urchins (Himmelman and Steele, 1971; Miller et al., 1971; Elner, 1980).

Although the three approaches, all based on traps primarily fished for lobsters, are not the best for surveying sea urchins, they can be used as a rough guide to sea urchin distribution and abundance. The confidence in the results is increased if the three approaches show similar trends at similar sites. A crude comparison among the three approaches is shown in Table 3 where the subjective criteria of sea urchin abundance are simplified - none, few, medium and abundant. Admittedly, there are problems of site comparability and differences in time of year that sampling was done. Nevertheless, some general conclusions seem to be warranted.

Starting in the upper Bay of Fundy, sea urchin abundance increases toward Digby, is medium toward Port Maitland, is reduced to scarce at Mud and Seal Islands and in Lobster Bay, and increases to abundant east of Cape Sable Island. Sea urchins are also found in shallow areas of offshore banks, but not in deep water even near shore. Fishermen interviews indicate recent decreases in abundance where abundance was

Table 3. Summary of sea urchin abundance estimated by the three approaches: interviewing lobster fishermen, sampling commercially fished lobster traps, and sampling traps on research cruises. Recent change is based on interviews only.

	Interviews	Commercial fishery	Research trapping	Recent change
Grand Manan, shallow	-	few, none	-	-
Grand Manan, deep	-	none	-	-
Upper Bay of Fundy	few	few	-	no change
Digby area	abundant	medium	-	decrease
St. Mary's Bay	medium	-	-	increase
Port Maitland area	medium	few	none	increase
Lobster Bay	few	few, none	none	no change
Mud and Seal Island	few	-	none	increase
E. of Cape Sable I.	abundant	abundant	abundant	increase to 1977, then decrease
Offshore, shallow	few	-	-	-
Offshore, deep	none	-	-	no change

greatest a few years ago. This could possibly be due to reduction in size of individuals rather than reduction in number of animals. An increase was reported in most other areas but not in Lobster Bay.

Other conclusions are that sea urchins and lobsters are not mutually exclusive, even within one trap. The abundance of sea urchins is not necessarily inversely related to lobster abundance, since more lobsters are caught in the Digby area where sea urchins are abundant than in the upper Bay of Fundy where sea urchins are scarce. Nevertheless, east of Cape Sable where sea urchins are abundant, lobster catches are small, and vice versa in Lobster Bay. One general observation is that sea urchins are abundant on hard bottom and absent on muddy bottom and in the upper reaches of estuaries. The non-random statistical distribution of sea urchins in the traps suggests that they are found in aggregated pockets of abundance on the sea bottom.

Where data from lobster traps indicate few sea urchins in shallow areas around Grand Manan Island, diving surveys (Neish, 1973; MacKay, 1976) in the same areas show sites ranging from no sea urchins to abundant, with most of the sea urchins found on substrate within the first few meters below the surface where lobster traps are not normally fished. Neish (1973) suggests that in coastal areas of Charlotte County, N.B., sea urchin populations are increasing, as evidenced by absence of subtidal seaweed in many areas. MacKay (1976) argues that there is no sea urchin explosion in Charlotte County.

Although some qualitative indication of sea urchin abundance may be derived from trap surveys, actual observations underwater are still needed

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AN UPDATE ON THE RELATIONSHIP BETWEEN COMMERCIAL LOBSTERING AND URCHIN AND MACROALGAL DENSITIES

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Halifax, Nova Scotia

INTRODUCTION

As pointed out in the "Introduction to the Workshop," the latter was taken from a review paper based on the workshop which was written by the editors. (This paper was presented at a "Multispecies Workshop" in November, 1979, at St. John's, Newfoundland, and will appear *in toto* in the proceedings.) Presented below is the remainder of this paper which appears in two parts. The first section is based on Session IV and includes each statement as presented by the session chairman, a summary of the discussion that followed, along with a pertinent literature review and the conclusions arrived at following the statement discussion. The second section consists of a general discussion of the workshop theme which includes both information presented at the workshop and that published elsewhere.

Laminaria

Statement - "There has been a significant decline in *Laminaria* along the Nova Scotia coast in recent years."

The marked decline in the size of the *Laminaria* beds in St. Margaret's Bay (Breen and Mann, 1976) was accepted, as it had been well documented since 1968 (Mann 1972). Wharton's hypothesis (Wharton, 1980) that there had been similar declines in *Laminaria* cover west of Halifax was less acceptable. His conclusions are based on present kelp cover as a percentage of suitable substrate availability. His findings were as follows: Lunenburg Co., 3.1%; Queens Co., 8.8%; and eastern Shelburne Co., 11.5%.

It was pointed out by both Himmelman (1980) and Hooper (1980) that much of the Newfoundland coast supports few *Laminaria* beds; the most frequent kelps are *Alaria* and *Agarum* and they are not abundant. In St. Margaret's Bay, refuge

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populations of Laminaria are found in the surf zone where urchin grazing is not possible (Breen, 1980). There are no such kelp refuges in Newfoundland, which led Himmelman (op. cit.) to conclude that the urchin-dominated areas "...have not supported Laminaria beds in recent history". Similarly, Hooper (op. cit.), for the following reasons, felt Laminaria had not been a part of the climax community for hundreds of years: First, the coralline rhodolith layers are meters thick in many areas and one does not find extensive coralline populations as an understory of kelp; and secondly, sea urchin spines and tests do not increase in the sediments of the recent past.

This discussion pointed out a problem in using the term "urchin-dominated barren grounds", which was believed to have been coined by Lawrence (1975). These areas in Newfoundland and Nova Scotia are markedly different both in diversity of flora and fauna and period of barrenness. Apparently, the urchin-dominated areas in Newfoundland have diverse benthic flora and fauna, whereas this is not the case in St. Margaret's Bay (A.R.O. Chapman, pers. comm.).

Conclusion - "For some areas there has been a significant decline in kelp biomass over the last decade. For many other areas information is lacking, but circumstantial evidence (mainly anecdotal) suggests there has been a general decline, at least east of Cape Sable."

Statement - "The changes in density of Laminaria in St. Margaret's Bay are a consequence of abiotic and/or biotic factors."

J. Caddy (pers. comm.) pointed out that domestic sewage in coastal California waters appeared to benefit the urchins more than the kelp; could this be the situation here? This possibility was rejected for St. Margaret's Bay, as apparently nutrient levels are not high (A.R.O. Chapman, pers. comm.). However, St. Margaret's Bay is closed to shellfish harvesting due to high faecal coliform counts (T. Rowell, pers. comm.). Breen (1974) showed that kelp recolonized a bottom where urchins were excluded by cages. C. Lobban (pers. comm.) pointed out that the latter does not preclude the possibility that some factor(s) may be operating which makes the kelp more susceptible to grazing. R. Welsford (pers. comm.) noted that McBride* had recently discovered a disease that affects local populations of Laminaria longicruris. Apparently, Littorina sp. selectively graze the diseased area and may in turn be the vector of the disease.

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Conclusion - "In areas where they have been observed, e.g. St. Margaret's Bay, sea urchins have eaten kelp beds and are the proximate cause of the decline. The data are not sufficient to claim they are the sole cause as there have been environmental changes."

Urchins

Statement - "Increases in sea urchin abundance along Nova Scotia's Atlantic shores have occurred in recent years."

Discussion on this topic pointed out the lack of information available on both the natural history and population dynamics of the local sea urchin. There was little doubt that at certain locations biomass of urchins had increased, e.g. the grazing front in St. Margaret's Bay. However, it was not known whether numbers had increased along the coast. These fronts may be due to immigration and not to recruitment. Unfortunately, neither long-term adult movement patterns nor distribution of the planktonic stages are known. In western Russia (J. Himmelman, pers. comm.) urchin larvae are known to remain planktonic for two to three months. Consequently, local urchin recruitment could be from great distances, given the long-shore current patterns of the area. It was suggested from personal observations that urchins might be invading the coast from headland to headland (D. Pace, pers. comm.). What has been observed both locally (Lang and Mann, 1977; Wharton, 1980) and in California (Tegner, 1980) is an urchin recruitment pulse following frontal grazing. Wharton (op. cit.) has observed this pulse in a number of sites along the coast west of Halifax. However, the nature of this pulse was queried as Wharton inferred urchin age from urchin size.

Conclusion - "It appears there has been an increase in the biomass of the urchin. Whether there has been an increase in total numbers cannot be answered with the meagre data base."

Statement - "Control of urchin abundance is principally by a) lobsters, b) crabs, c) fish, d) other organisms, or e) food supply."

Breen and Mann (1976) used a simulation model "...to test whether a lobster population of reasonable size, feeding at known rates, and with realistic size interactions with its prey was capable of limiting the growth of a sea urchin population." They showed that "...lobsters and crabs controlled sea urchins under most conditions. At low lobster density, sea urchin populations exploded." There was some concern about the lobster densities employed in the

model as the latter are largely unknown. As well, it was felt insufficient weight was given to other predators. It was pointed out that in other ecosystems small changes in predator density readily control prey populations (R. Foreman, pers. comm.). Hooper (1980) pointed out a complex predator/prey system off coastal Newfoundland. He identified a minimum of 30 species (Table 1) that prey on urchins of various sizes, from larvae through to adult. Included were commercial groundfish and wolffish. P. Breen (pers. comm.) noted that wolffish came into St. Margaret's Bay for three months and individuals "...ate horrendous (sic - speaker meant large) numbers of sea urchins..." but their densities were so low they had little effect on the total urchin population. It was noted (J. Caddy, pers. comm.) that wolffish densities dropped markedly in the late 1960's, as have most inshore commercial species such as cod and haddock. The extent of their influence on urchin populations is unknown.

Crabs consume urchins (Elner, 1980) and they are not commercially harvested in St. Margaret's Bay; however, J. Pringle (pers. comm.) noted that lobster fishermen kill crabs caught in lobster traps as they feel they are in direct competition with lobsters. G. Roach (pers. comm.) verified this for Guysborough and Richmond Counties (see Figure 1 in Introductory paper). Here, the fishermen had agreed among themselves to bring all captured crab inshore. Robinson (1980) pointed out that a lobster trap is designed to catch lobster and may not be an adequate mechanism for sampling urchin and crab populations. Consequently, without experimental evidence, in an area of low lobster density the return of crabs and urchins in the traps should not be interpreted as an increase in their population density.

Elner (1980) presented laboratory data on urchin, mussel, and crab predation by lobsters. Lobsters and crabs had respectively 1:43 and 1:79 preference for mussels over urchins. Each lobster and crab consumed, on average, one urchin per day. The author concluded that "...it is difficult to attribute increases in sea urchin numbers to a decline in the lobster populations alone, or to support the hypothesis that lobsters and rock crabs are a key factor in controlling the populations of such an abundant prey."

In a similar study, Evans and Mann (1977) showed that lobsters preferred crabs over urchins by 5:1, but if urchin densities were markedly higher than those of crabs then more urchins were eaten. They concluded that, "It is still possible to think of the lobsters as controlling factors in the abundance of urchins..."

TABLE 1. Observed sea urchin predators in Newfoundland waters.

	Sea Urchin Size			
	Larvae	Small (5 mm)	Medium (5+ to 25 mm)	Large (over 25 mm)
Predators	*Cyanea* ctenophores *Ophiopholis* *Metridium* sponges tunicates medusae	*Tealia* flounders gunnels shannies small *Cancer* *Hyas* juvenile lobsters small sea stars juvenile cod	*Tealia* wolffish flounders *Solaster* cod *Leptasterias* *Cancer* sea birds lobster other anemones	wolffish *Solaster* *Tealia* sea birds large lobsters *Cancer*

Hooper (1980) noted that urchins have a low tolerance for decreased salinities and he has observed mass mortalities off coastal Newfoundland due to a combination of rapid spring thaw, heavy rainfall, and wind. He also noted large numbers of urchins dying of disease, as has been observed off California (Tegner, 1980).

R. Foreman (pers. comm.) felt predation on juvenile lobsters and urchins is important but little studied. Similarly, data are lacking on both in situ predation rates by lobsters and other predators on urchins and gut analysis of lobsters. G. Ennis (pers. comm.) determined that 4% to 7% of the food in lobster guts was urchin derived.

The sea otter has been cited (Mann and Breen, 1972) as that predator which controlled urchin populations off coastal California. Tegner (1980) explored the decline of the California kelp beds and the population explosion of urchins. She noted the otter was eliminated by 1850 and yet there were large, healthy kelp beds in 1912 and up to the mid to late 1940's. Also, during the 1950's, kelp was adversely affected by warm water and water pollution. The urchin explosion was first observed in the early 1960's. Tegner (op. cit.) gave evidence of a complex predator/prey system operating in California kelp beds. One urchin predator, the spiny lobster, and a competitor for space and food, the red abalone, are commercially important; the landings for these fisheries peaked in the 1950's. The California sheephead fishery peaked in the 1960's. She concluded that "...competition with abalones and predation by spiny lobsters and sheephead are proposed as biological interactions which may have regulated sea urchin abundances in the past."

Conclusion - "There was insufficient evidence at present to claim that lobsters were the primary predators of sea urchins and that urchin populations exploded due to a release from predation by lobsters. Also, with the paucity of data on each species, the ranking of predators with respect to importance was impossible."

Statement - "The present abundance of sea urchins and lowered densities of *Laminaria* in St. Margaret's Bay is a permanent phenomenon."

Empirical data only go back ten years for St. Margaret's Bay (Breen and Mann, 1976) - insufficient time to observe this particular cycle. A large amount of anecdotal evidence was presented suggesting that *Laminaria* beds are ephemeral. Scarratt (pers. comm.) noted little kelp in a portion of Northumberland Strait, where it now is apparently a nuisance factor to the lobster fishermen (R. Henry, pers. comm.).

Similarly, G. Roach (pers. comm.) claimed that fishermen of both Richmond and Guysborough Counties have noticed in the past a synchronous decline in kelp and lobster and an increase in urchins. They now find signs the reverse is true. Breen (1980) outlined similar anecdotal evidence, particularly in the Bay of Fundy. The only long-term data for kelp might be old admiralty charts which often included kelp beds (D. Pace, pers. comm.).

Hooper (1980) and Himmelman (1980) both noted that urchin-dominated areas appeared to be a permanent mode for many areas off coastal Newfoundland. Consequently, it could be argued that the Laminaria community observed in St. Margaret's Bay was a unique phenomenon and the present urchin-dominated beds are the more normal mode.

Tegner (1980) outlined cyclic patterns between urchins and kelp off California; they had periods of 12 years. She also outlined studies by her colleagues at Scripps which pointed out the importance of geomorphology in these cycles. Beds in rugged terrain were occupied by spiny lobsters and sheephead which tended to keep the urchin population under control; hence, these populations did not oscillate. Kelp populations on flat bottom with no lobsters or sheephead oscillated with urchin abundance.

Conclusion - "There appears to be a degree of cyclicity between populations of urchins and kelp in certain areas of the northwestern Atlantic, based on anecdotal evidence only. It would appear the present situation in St. Margaret's Bay may be a little more severe but it does not imply that it is permanent."

Statement - "Declines in lobster and inshore fish abundance along Nova Scotia's eastern shore has occurred in recent years. For lobsters, this is due to changes in environmental factors, overfishing or other predators, food shortages, or lack of cover."

Changes in environmental factors were shown to correlate to fluctuations in lobster landings along the Quebec coast (Sutcliffe, 1973). Sutcliffe showed a nine-year lag between landings and St. Lawrence River discharge volume. D. Robinson (pers. comm.) feels the river has an effect but only for annual fluctuations, not the long-term decline in lobster stocks. Upwelling of nutrient-rich waters in southwestern Nova Scotia (S.W. N.S.) as compared to lower nutrient levels along the southeastern shore (Chapman and Gagne, 1980) may provide the high productivity required to prevent the decline in landings experienced on the eastern shore. As well, current patterns may supply larval recruitment from offshore banks in the S.W. N.S. area (Stasko, 1980).

Overfishing was the most strongly supported factor for the decline in lobster landings: "...there definitely has been over the last forty years...high overfishing of 70 to 75%" (A. Campbell, pers. comm.). The current size limit of 81 mm carapace length is well below the average size of female maturity, which is 100 mm carapace length (Stasko and Campbell, 1980).

The decline in lobster stocks off Guysborough and Richmond Counties brought about the introduction of larger traps. This permitted the capture of jumbo lobsters, possibly accelerating the final decline in landings (G. Roach, pers. comm.). Fishing pressure was reduced from 120 fishermen to 20 for this area. There was a recent increase in juvenile (less than 81 mm) lobsters, which suggests a recovery of stocks. However, areas where catches have been stable in S.W. N.S. have recently shown declines, e.g. Lobster Bay (Stasko and Campbell, 1980).

The introduction of market size limits in 1933 (22.5 cm total length) removed fishing pressure on young recruits and resulted in stabilization of the catch until recently (Robinson, pers. comm.).

Robinson (1980) noted that in general, "...the fisherman of today is a far more efficient predator of lobsters than any of his predecessors." Introduction of radar, larger boats, and hydraulic hauling gear are some of the advances.

Food supply was not considered to be a limiting factor. Declining lobster populations would quickly stabilize any food to lobster biomass imbalance.

The importance of Laminaria and other benthic plant species as protective cover for juvenile and mature lobsters has not been directly investigated. Indirect information comes from benthic studies investigating other problems. For instance, in studies of lobster feeding in the Gulf of St. Lawrence, "We found that on those Chondrus beds, lobsters tended to move onto them as the season (summer) approached, and tended to vacate as winter approached...we seem to find most of our new set of lobsters 6-9 mm carapace length in the 4-8 fathom range" (D. Scarratt, pers. comm.). This was confirmed by divers doing algal studies in this area (J. Pringle, pers. comm.). Studies of scallop beds deeper than the commercial Chondrus beds found "large numbers of lobster less than 20 mm carapace length" (G. Jamieson, pers. comm.). An abundance of juvenile lobsters (20 juveniles per diver hour) were reported for areas devoid of macroalgae in Placentia Bay (J. Carter, pers. comm.). Coastal British Columbia macrophyte beds were reported to provide complex habitats for both prey and predator (R. Foreman, pers.

comm.). In reference to crabs, "...the juveniles are in the rocky seaweed-dominated areas." Studies in South Africa found "...large numbers of invertebrates in the holdfasts of kelp and it is difficult to find the young lobsters there too" (J. Field, pers. comm.).

The opinion that habitat area increases for lobster in a kelp bed was expressed by Scarratt "...within the Laminaria forest you may well find increase in the availability of suitably sized crevices which small lobsters might exploit."

Conclusion - "Overfishing of lobsters appears to have been a major factor in the decline in landings. No overwhelming evidence is available that environmental factors, food, or plant cover were important factors in population declines."

GENERAL DISCUSSION

There is an unfortunate lack of quantitative, ecological data for subtidal communities along northwestern Atlantic shores. MacFarlane (1952) surveyed commercially important, subtidal plant populations for the shores of Shelburne, Yarmouth, and Digby Counties (Figure 1). However, it was not until Mann's (1972) study of St. Margaret's Bay that quantitative data were available east of Shelburne County. The ecosystem as it existed 25 to 100 years ago is unknown. During this period lobster, groundfish, and pelagic fish have been extensively harvested. Furthermore, along these shores human densities have increased, industrialization has occurred in limited areas, and major ecological perturbations such as the Canso Causeway (Figure 1) have taken place. Given the above, it was difficult to accept Mann's hypotheses that: 1) the lobster is a keystone predator of the kelp bed ecosystem and by overharvesting it has caused Laminaria densities to drastically decline along hundreds of miles of the western Atlantic shore (Evans and Mann 1977); and 2) that urchin-dominated barren grounds constitute a stable ecosystem (Mann 1977).

There is little doubt the kelp bed ecosystem observed by Mann (1972) in the late 1960's is all but gone. We know that similar kelp bed ecosystems are not present on much of the available substrate along coastal Guysborough, Halifax, Lunenburg, Queens, and Shelburne Counties (Wharton, 1980); but evidence they were there in the past is lacking. This gap in the data base is particularly unfortunate, as Hooper (1980) and Himmelman (1980) noted that much of the coast of Newfoundland, Labrador, and Gaspe are similarly lacking a kelp bed ecosystem. They presented good evidence that these

coasts may never have supported kelp beds as observed by Mann (1972) in St. Margaret's Bay. We were also presented with anecdotal evidence going back to 1851 (Breen 1980) that urchin populations periodically overgrazed large stretches of the subtidal in the Bay of Fundy.

The urchin-dominated areas of Newfoundland and Nova Scotia are different in structure to those observed off Nova Scotia. On the Newfoundland coast, coralline communities are well developed, some with rhodoliths meters thick. This apparently is not the case off Nova Scotia (St. Margaret's Bay) where A.R.O. Chapman (pers. comm.) noted that on average, coralline plant density was approximately $1/m^2$. Thus, there is the possibility the south Newfoundland coast was perturbed many years ago and the Nova Scotia coast only recently, both flipping from a productive kelp bed ecosystem to a less productive coralline/urchin system. Local kelp beds may not have the resiliency of those in the eastern Pacific. Off Pt. Loma, California, the kelp beds were reduced to 0.03 square miles during the early 1960's but now measure 3.2 square miles (Tegner, 1980). Foreman (1977) noted a similar recovery in Nereocystis beds off British Columbia.

Given that something has perturbed the system, it would be appropriate to learn its nature and, if possible, take remedial action. If it is disease, as affected eelgrass along the northwest Atlantic, it would likely have to run its course. If it is allocthonous then the source could be curtailed. If, however, it is due to the commercial overharvesting of carnivores then a multispecies resource management program should be implemented immediately in an attempt to "stem the tide."

Tegner (1980) presented a well-documented argument outlining poor resource management as the major cause of destructive grazing by urchins off California. She suggested commercial overharvesting of the spiny lobster, the red abalone, the California sheephead, and the otter, extreme warm waters during the late 1950's, and allocthonous substances from industrial Los Angeles and San Diego as causes of kelp destruction. It appears it was not only the otter, as suggested by Leighton et al. (1966). Similarly, the overgrazing of macrophytes in St. Margaret's Bay was likely not due solely to commercial overharvesting of the lobster. The density of many other commercial species has been reduced markedly.

It is a well-known ecological concept that the simpler the trophic pyramid the more productive the system. However, organization theory shows this leads to a system with wild annual oscillations in population numbers (Watt, 1968). The

original kelp bed ecosystem, as it existed 400 years ago, was likely more complex and hence more stable than at present. Man began extensive fishing off coastal Nova Scotia and Newfoundland during the 17th century, taking large catches of haddock, cod, halibut, pollock, etc. - all known urchin consumers at a stage of their life cycle. Lobsters were first fished commercially during the late 19th century, and within 20 years the point of the maximum sustainable yield had been surpassed (Robinson, 1980). CPUE data are not available for this period but if landings reflect lobster densities then there were periods betwen 1912 and 1924 when densities were comparable to present day.

In summary, what may have happened was that a complex kelp bed ecosystem was transformed into a simple system and, over the last 50 to 70 years, lobster and crab (incidental harvest) were the major carnivores due to commercial overharvesting of other fish species, the hunting of ducks (R. Vadas, pers. comm.) and seagulls having a better source of food in man's wastes. Being a more simple system, small perturbations such as a single-year recruitment failure of lobster along with intense commercial pressure causes wild oscillations.

The above suggests a "boom and bust" fishery which has not been managed for maximum sustainable yield. As has been concluded for California (Tegner, 1980) likely holds for the northwest Atlantic; the overgrazing by urchins is due to the removal of a number of carnivores, the lobster being only one of them. Consequently, Mann's hypothesis of the lobster as a keystone predator is rejected. However, his ecosystem approach to resource management is not. What apparently is required to maintain a stable ecosystem is a high degree of stability at the carnivore level which would encourage stability at the herbivore level "...by damping the oscillations of increasing amplitude inherent in a predator/prey system with delayed negative feedback" (Holling in Watt, 1968). Thus, to manage the resource for maximum sustainable yield all trophic levels and predators must be considered. This points up Watt's (1968) contention that most resources have rarely been managed scientifically "...even in instances where it was generally considered that this was being done." Watt (op. cit.) concluded that management practices must be carefully conceived regarding basic ecological principles if productivity and stability are to be maintained at optimum levels. Due to the complexity of ecosystems, with their attendant physical and chemical parameters and the difficulty in defining optimum management strategy, one is forced to resort to complicated systems analysis and simulation procedures.

Recognizing the complexity of this problem and the large number of data gaps, implementation of coordinated programs of experimentation and observation are necessary. However, the acquisition of useable data from such studies ranges from one to ten years from initiation, depending on generation time of the study organism and rates of colonization and succession. Within this time frame the commercial inshore fishery could collapse completely (many fishermen claim it has already). We must act upon our present state of knowledge. The most obvious area for potential correction is recruitment of lobsters. The first step would be an increase in size of first capture to the age of first maturity.

At present, the number of urchins in certain areas is so great it will require more than one year of high predator recruitment to reduce urchin densities significantly. Hence, destructive grazing of macrophytes will continue for some time beyond the recovery of predator populations. Remedial measures must be taken to reduce urchin densities where macrophyte destruction is transitional to a barren mode. Development of economical restoration methods can be instituted in chronic barren grounds.

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APPENDIX I

Workshop Attendees

Speakers

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14. Dr. Aivars Stasko	Fisheries and Oceans Canada, Biological Station, Brandy Cove Rd., St. Andrews, N.B. E0G 2X0

15. Dr. Mia Tegner	Scripps Institute of Oceanography, University of California, LaJolla, California 92093
16. Dr. Bob Vadas	Biology Department, University Maine, Orono, Maine
17. Mr. Gary Wharton	Biology Department, Dalhousie University, Halifax, N.S.

Chairmen of Sessions

Dr. John Caddy	Fisheries and Oceans Canada
Dr. John Pringle	Fisheries and Oceans Canada
Mr. Glyn Sharp	Fisheries and Oceans Canada
Dr. Bob Vadas	University of Maine

Other Delegates

1. Ms. Robin Anderson	Biology Department, Laval University, Ste. Foy, P.Q.
2. Dr. Fritz Axelsen	Service de Biologie, Ministere de l'Industrie et du Commerce, 2700 Einstein, Ste. Foy, P.Q.
3. Dr. Andre Cardinal	Biology Department, Laval University, Ste. Foy, P.Q.
4. Mr. Jean Carriere	College de la Gaspesie C.P. 596, Gaspe, P.Q.
5. Mr. John Carter	Martec Ltd., 1526 Dresden Row, Halifax, N.S.
6. Mr. Ward Cunningham	Stauffer Chemicals, Pubnico, Yarmouth Co., N.S.
7. Dr. G.P. Ennis	Fisheries and Oceans Canada, Northwest Atlantic Fisheries, Center, P.O. Box 5667, St. John's, Nfld.
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9. Mr. Jacque Gagne	Biology Department, Dalhousie University, Halifax, N.S.
10. Ms. Mary Guerinot	Biology Department, Dalhousie University, Halifax, N.S.
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18. Dr. Chris Lobban	Faculty of Science, University of New Brunswick at Saint John, Saint John, N.B.
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20. Dr. Dick McBride	Biology Department, Dalhousie University, Halifax, N.S.
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30. Dr. Robin South	Biology Department, Memorial University of Newfoundland, St. John's, Nfld. A1E 3Y2
31. Dr. D.H. Steele	Biology Department, Memorial University of Newfoundland St. John's, Nfld. A1E 3Y2
32. Mr. Rick Wellsford	Biology Department, Dalhousie University, Halifax, N.S.
33. Ms. Barb Williams	Biology Department, Dalhousie University, Halifax, N.S.
34. Mr. Scott Wilson	Biology Department, Memorial University of Newfoundland, St. John's, Nfld. A1E 3Y2

APPENDIX II

Workshop Program

PROGRAM

Welcome Address
- Dr. B.S. Muir, Director, Resource Branch, Department of Fisheries and Oceans

Session I: Background to the "Commercial Overharvest/Urchin/Algal Hypothesis" in Northwest Atlantic Waters
- Chairman - Dr. John D. Pringle

1. History of the lobster fishery on the eastern shore of Nova Scotia
   - Mr. Douglas G. Robinson

2. Relations among lobster, sea urchins, and kelp in Nova Scotia
   - Dr. Paul A. Breen

3. The relationship between certain commercial finfish species and urchins in St. Margaret's Bay
   - Dr. Brock Bernstein

4. Predation of the sea urchin (*Strongylocentrotus droebachiensis*) by the american lobster (*Homarus americanus*) and the rock crab (*Cancer irroratus*)
   - Dr. Robert W. Elner

5. The distribution of sea urchin-dominated barren grounds along the south shore of Nova Scotia
   - Mr. W. Gary Wharton

6. The food of lobsters
   - Dr. David J. Scarratt

Session II: Urchin/Algal Associations in Other Geographical Areas
- Chairman - Mr. Glyn J. Sharp

7. Observations on algal-grazer interactions in Newfoundland and Labrador
   - Mr. Robert Hooper

8. The role of the green sea urchin, *Strongylocentrotus droebachiensis*, in the rocky subtidal region of Newfoundland
   - Dr. John H. Himmelman

9. Urchin/algal interactions off coastal Washington and Maine
   - Dr. Bob Vadas

10. A preliminary assessment of the *Laminaria* resources near Lower Woods Harbour, Nova Scotia, During July 1977
    - Mr. Ron H. McPeak

11. Multispecies considerations of resource management in southern California kelp beds
    - Dr. Mia J. Tegner

12. Benthic community recovery following intensive sea urchin grazing
    - Dr. Ron Foreman

Session III: The Ecology and Commercial Harvest of Important Benthic Species off Coastal Southwestern Nova Scotia
- Chairman - Dr. Robert Vadas

13. An overview of lobster life history and fishery in southwestern Nova Scotia
    - Dr. Alan Campbell and Dr. Aivars B. Stasko

14. Sea urchin (*Strongylocentrotus droebachiensis*) distribution around western Nova Scotia
    - Drs. Aivars B. Stasko, Alan Campbell and Mr. Donald E. Graham

15. The benthic algal biomass, commercial harvesting, and *Chondrus* growth and colonization off southwestern Nova Scotia
    - Dr. John D. Pringle and Mr. Robert E. Semple

16. Environmental control of kelp growth in St. Margaret's Bay and on the southwest shore of Nova Scotia
    - Dr. Tony Chapman and Mr. Jacque Gagne

17. A preliminary assessment of the *Laminaria* resource near Lower Woods Harbour, Nova Scotia, during July 1977
    - Mr. Ron H. McPeak

18. The history of kelp harvesting in southwestern Nova Scotia
    - Mr. Glyn J. Sharp

Session IV: Formal Discussion
- Chairman - Dr. John F. Caddy

APPENDIX III

The Agenda Followed In Session IV - The Round Table Discussion

AGENDA OF SESSION IV

March 7, 1979

13:00 hours:

1. Discussion of hypotheses on past and present status of the *Laminaria* ecosystem along the Nova Scotia Atlantic coast - its importance and the major factors affecting it.

A. *Laminaria*

1. There has been a significant decline in *Laminaria* in recent years.

2. Changes in density of *Laminaria* are a consequence of:

   a) abiotic environmental factors
   b) biotic factors (sea urchins)

B. *Urchins*

3. Increases in urchin abundance have occurred in recent years.

4. Control of urchin abundance is principally by (rank in order):

   a) lobsters
   b) crabs
   c) fish
   d) other
   e) abundance is limited by food availability

5. Abundance of sea urchins and *Laminaria* is

   a) cyclic
   b) permanent changes have occurred

C. *Predators*

6. Declines in lobster and inshore fish abundance have occurred in recent years. This is due (for the lobsters) to:

   a) changes in environmental factors
   b) overfishing or other predation
   c) food shortage
   d) lack of cover (*Laminaria*)
   e) lack of recruitment

7. Changes in crab abundance are controlled by (rank in order):

   a) lobsters
   b) fish
   c) urchin abundance

16:00 hours:

2. Areas that need further study

17:00 hours:

3. Manipulation of the system

   a) herbivore control (expected recovery
   b) predator control extent, timing)
   c) harvesting - kelp resource: 1. extent
                                 2. methods

18:00 hours:

End

APPENDIX IV

Conclusions and Recommendations From the Workshop on Lobster/Sea Urchin/Algal Interactions as Submitted to CAFSAC

Studies by Mann et al., beginning in 1968 on the algal biomass in St. Margaret's Bay and herbivore energetics (Miller et al., 1971), found benthic macrophyte production greatly exceeded ingestion by herbivores. However, destructive grazing in St. Margaret's Bay was recognized at the same time (Mann and Breen, 1972). See Conclusion 3. Overfishing of a sea urchin predator, lobster, and resultant low predation were identified as the causes of sea urchin overabundance. See Conclusion 10. The abundance of sea urchins and lack of macrophytes ("barren ground") was viewed as a permanent condition (Mann, 1977). See Conclusion 6. Kelp beds were hypothesized to have recently disappeared along hundreds of kilometers of Atlantic coastline (Evans and Mann, 1977). See Conclusions 2 and 5. The correlation between reduced lobster landings and the existence of urchin-dominated barren grounds for eastern and southern shores of Nova Scotia was supported by Wharton (1979). See Conclusion 9. A multispecies approach which was lacking in early fisheries management may have prevented the decline in macrophyte beds (Mann, 1977). See Conclusion 8. Southwestern Nova Scotia is an area of extremently good inshore production which appeared to be threatened by sea urchin overgrazing.

A workshop was held in March, 1979, to provide information and guide fisheries action on Mann's hypothesis. Sixty-five delegates with expertise on this particular topic attended the workshop. Eighteen papers were presented and a five-hour formal discussion was held, chaired by Dr. J.F. Caddy. Discussion centered around seven prepared statements and a conclusion was arrived at for each statement. The discussion session was tape recorded; and by using the original discussions, papers presented, and pertinent published works, a review paper was written (Pringle, Sharp, and Caddy). The conculsions and recommendations that follow include original conclusions:

1. Little baseline data are available on the qualitative and quantitative aspects of Maritime marine, benthic communities.

2. For some areas, a significant decline was observed in macrophyte biomass over the last decade; for many other areas, baseline data are not available but circumstantial evidence (mainly anecdotal) suggests there has been a general decline on the Nova Scotia shore east of Cape Sable Island.*

3. In areas where destructive grazing of macrophytes by sea urchins has been observed, they are the direct cause of macrophyte biomass decline. The data available are insufficient, however, to claim they are the sole cause as there have been environmental changes.*

*Workshop conclusions

4. There has been an increase in the biomass of sea urchins at specific sites on Nova Scotia's coast where data are available, but data are insufficient to claim an increase in the density of urchins along vast stretches of Nova Scotia's coast.*

5. The south and west coasts of Newfoundland have not had extensive Laminaria populations for many years - possibly hundreds of years.

6. Based on anecdotal evidence only, there appears to be a degree of cyclicity between high sea urchin densities and high kelp densities in certain areas of the Maritime coast. The length of the period of the "urchin-dominated barren" mode in St. Margaret's Bay is longer than others cited, but this does not imply permanency.*

7. Little is known about the biology and ecology of many of the commercially important nearshore marine species. As well, little is known about those factors which control sea urchin densities.

8. A number of species prey on sea urchins in the northwest Atlantic, not just lobster; many have been subjected to heavy fishing pressure. Urchin densities were shown to increase in southern California due to overharvesting of numerous commercial species.

9. Overfishing appears to have been a major factor in the decline in lobster landings along Nova Scotia's eastern shore. There is little evidence environmental factors, lack of food, or lack of plant cover were important factors in this decline.*

10. Evidence at present is insufficient to claim lobsters are the primary predator of sea urchins and that urchin populations in St. Margaret's Bay exploded due to the release from predation by lobsters.*

11. The benthic community of St. Margaret's Bay has changed from a productive macrophyte community to a less-productive, "barren" mode.

RECOMMENDATIONS

1. That wherever possible, the multispecies ecosystem approach be considered in the management of inshore marine resources.

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*Workshop conclusions

2. That quantitative baseline studies and long-term monitoring of benthic communities throughout the Maritime waters be encouraged and that a more thorough assessment of ocean climate of inshore Maritime waters be made.

3. That ecological and biological studies of all commercially important marine inshore species be encouraged and that a study be undertaken to determine the importance of benthic macroalgae to the ecology and production of these species in comparison to the trophic relationships in barren mode communities.

4. That a program be developed and implemented to return commercially fished populations such as lobster, haddock, etc. in certain Maritime waters (initially, the eastern Nova Scotian shore) to densities which would permit optimum sustainable yield.

5. That until the mechanism of sea urchin invasion of macrophyte beds is better understood, the commercial harvesting of kelp be tightly controlled, and that clear cutting practices be banned.

6. That studies be initiated on the population biology and ecology of sea urchins off Atlantic Nova Scotia and the Bay of Fundy.

APPENDIX V

Areas of Further Study as Recommended by Workshop Participants in Session IV

AREAS OF FURTHER STUDY

During Session IV, delegates were asked to suggest topics of study in relation to the workshop theme. As shown below, a wide range of projects were recommended:

1. habitat preference experiments for lobster larvae;

2. large-scale predator/prey studies in ecological reserves (it was unanimously felt that underwater ecological reserves are required for this type of study and many others. Tegner (pers. comm.) noted that this technique is employed in California but with some problems. First, fishermen ring the reserve with traps, nets, etc. Second, with a highly motile study species there is little to prevent the population from migrating);

3. larval and juvenile urchin distribution studies in relation to kelp beds;

4. a comprehensive study of existing kelp beds;

5. monitoring of urchin fronts;

6. trophic modelling of both "urchin-dominated barren grounds" and areas of heavy macrophyte cover;

7. development of methods for dating "urchin-dominated barren grounds"; and

8. baseline surveys noting distribution and abundance of species along the coastal zone.

APPENDIX VI

Comments on Urchin Eradication by Workshop Delegates

URCHIN ERADICATION

Some time was spent discussing the eradication of sea urchins along the Atlantic shore of Nova Scotia. Kelco Co. of California harvests Macrocystis for the production of algin. Over the years, large portions of this resource have been heavily grazed by local urchins. The company, under the direction of Ron McPeak, have tried various methods of urchin control, including dredging, hammering, and liming (CaO). Despite the high cost of the latter ($750/acre), the company uses this method only. It is employed at the "urchin front" where the density is high and the reproductive potential of the population is located.

Sea urchins are of commercial value if their gonads are of marketable size. Urchins at the "front" are of commercial value; however, those on "barren grounds" are not (J. Himmelman, pers. comm.). Consequently, where urchins are a severe problem, such as off Atlantic Nova Scotia, a commercial industry cannot be considered.

Predator control of urchins would require a sound knowledge of the trophic relationships (R. Miller, pers. comm.). Increasing the population density of lobsters off the counties of Guysborough, Halifax, Lunenburg, and Queens was considered a top priority. It was also suggested that fishermen be encouraged not to destroy crabs when harvesting lobsters.

APPENDIX VII

Comments on *Laminaria* Harvesting by Workshop Delegates

LAMINARIA HARVESTING

Scotia Marine Products of Lower Woods Harbour is seriously considering the commercial harvest of *Laminaria longicruris* off western Shelburne County and Yarmouth County. It would be employed as the raw material for algin production. Rarely are urchins found in these kelp beds (R. Miller, pers. comm.). It is feared that were clear cutting of kelp permitted, the latter areas would then be conducive to urchin settlement and possibly the initiation of fronts. It was hypothesized that a threshold density of kelp may exist which would prevent sea urchin invasion; this hypothesis should be tested (R. McPeak, pers. comm). Also, it was recommended that kelp harvesting not be permitted at an urchin front for fear of extending the latter (G. Sharp, pers. comm.).

Methods presently employed for harvesting *Laminaria* spp. either remove the entire plant or cut below the meristematic zone. Two to three years would be required for plant replacement. Emphasis should be placed on developing a kelp harvester that would cut the lamina above the meristematic zone. Only three to four months would then be required for replacement (T. Chapman, pers. comm.).