

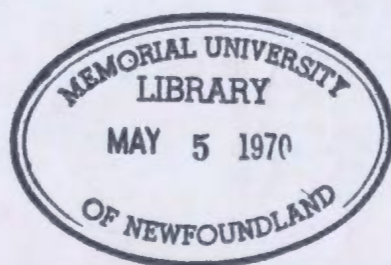
SOME ASPECTS OF THE ECOLOGY OF
STRONGYLOCENTROTUS DROEBACHIENSIS
IN EASTERN NEWFOUNDLAND

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THE ECOLOGY OF STRONGYLOCENTROTUS DROKRACHIENSIS
IN EASTERN NEWFOUNDLAND**

by

© John H. Himmelman, B.Sc. (Hons.)

**A thesis submitted in partial fulfilment
of the requirements for the degree of
MASTER OF SCIENCE**

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ABSTRACT

Strongylocentrotus droebachiensis is the dominant macroscopic benthic animal along the exposed coasts of Newfoundland. The gonads ripen during the fall, reach a peak in size and maturity in February or March, and spawnout occurs by April. In exposed areas the density is very high (up to 350 urchins/m²) and small urchins are abundant. In sheltered areas the density is much lower but most of the individuals are large. The urchin populations are concentrated in shallow water where macrophytes, their main food, grow abundantly. Urchins have variable preferences for and abilities to consume different algae. Feeding is least in the winter, when the gonads are near their peak, and greatest following spawnout. The potential grazing rate is sufficient to restrict noncalcareous macrophytes to the sublittoral fringe where the abrasion of the gonads, as they are washed back and forth by waves, keeps the urchins from advancing and devouring them. Only Agarum cribrosum and Ptilota serrata, which are undesirable urchin foods, grow at greater depths in urchin dominated areas. Sea stars, other urchins, lobsters, crabs, a number of fishes, and birds are common predators of S. droebachiensis but are not very effective in limiting their numbers.

ACKNOWLEDGEMENTS

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INTRODUCTION

The green sea urchin, Strongylocentrotus droebachiensis (O. F. Müller, 1776) is circumpolar in distribution in the seas around the Arctic Ocean. It is found as far north as Discovery Bay, northwest Greenland, around Spitsbergen, and north of Russia, Alaska and Canada (Danielssen 1892, Grainger 1955, Hyman 1955). In the North Atlantic it extends southward beyond the English Channel on the European side and to New Jersey on the American side (Mortensen 1907). It also extends into the North Pacific and is the dominant member of the subtidal fauna as far south as the state of Washington (Weese 1926, Shelford et al. 1935).

In 1854 Stimpson marvelled at the great numbers of S. droebachiensis on the shores on Grand Manan and wondered what must be the food of such a multitude of animals. Newcombe (1935) and Dexter (1944) in ecological studies in the St. Andrews region, New Brunswick, and at Ipswich, Massachusetts, respectively, found this urchin to be of such abundance that they used its generic name in designating the sublittoral biome. Dexter considered the Ipswich Bay Strongylocentrotus-Buccinum biome analagous to the Strongylocentrotus-Argobuccinum biome as described on the Pacific Coast of North America by Shelford and his associates (Shelford et al. 1935). The same urchin, S. droebachiensis, is a dominant in the latter.

I was repeatedly impressed by the abundance of this animal in the sublittoral rocky shore environment during a seaweed survey of Newfoundland in the summer of 1967. This situation I readily learned to associate with a scarcity of macrophytes. It is obvious that so dominant an organism must

exert a great biotic influence on the other organisms in its environment; and a great deal of the energy within its community must be within such a species. However, in spite of the prevalence of this situation throughout much of the range of S. droebachiensis, it is strange that so little effort has been made to more precisely understand the importance of this species. I hope that this study will contribute to our knowledge of this animal and its effects on other species.

There is considerable confusion about variation within S. droebachiensis. Swan (1962) has indicated that the closely related species, S. pallidus (G. O. Sars, 1871) is also probably present in the Northwest Atlantic. In Norway, Vasseur (1952) described differences in the colour of the spines and test, arrangement of the ocular plates, number of pore-pairs in each arc, weight of the Aristotle's lantern, depth preference, and time of spawning between these two species. However, there is considerable overlap in these characters and hybrids are apparently common. At Grande-Rivière, Quebec, Swan (1962) found that the two urchins could be distinguished when they were preserved in 5 percent formalin — urchins whose oral spines turn violet appeared to be S. droebachiensis and those the spines of which remain light-coloured appeared to be S. pallidus. Swan also found that the latter animal was very rare in depths of less than 120 feet. The formalin test was made on 100 urchins from each of the three areas studied in detail. In all but 8 of the animals from Logy Bay the oral spines turned violet or dark purple (a few darkened only slightly). No collections were made from deeper than 80 feet. Thus, it is concluded that most of the Newfoundland specimens studied were Strongylocentrotus droebachiensis.

It should, however, be mentioned that white or cream-coloured long-spined urchins have been observed in all of the areas investigated. Similar specimens have also been reported by Jackson (1912) from St. Pierre, by Prince (1913) at St. Andrews, New Brunswick, and by Swan (1958) from San Juan Islands, Washington; but the actual identity of these urchins is unknown. Six of my specimens were preserved in formalin, and all of their primary spines turned violet within 10 minutes.

The literature concerning the growth rate of S. droebachiensis was reviewed by Swan (1967). Soot-Ryen (1924) and Grieg (1928) examined the size frequency distributions of collections from Ramfjorde and Folden and Bals Fjords in Norway and suggested size ranges for the first five year classes. It appears, however, that they were dealing with both S. droebachiensis and S. pallidus and that their collecting methods were not very reliable. In June 1957 Swan (1958) carefully collected all the urchins from a low intertidal ledge at York, Maine. From the size-frequency distribution of the 1305 specimens obtained, he estimated the modal diameters of the first four year classes. In a subsequent study, he (1961) kept caged for a year at New Castle, Maine, a group of urchins from each of the 4 modal size groups. The results generally supported his previous interpretation of the modal diameters of the age classes. His concluding estimates were as follows: 8-10 mm, one year; 24-26 mm, two years; 40-42 mm, three years; and 46-52 mm (?), four years. Although no very small individuals were found during the 1957 collection, urchins ranging from 0.5 to 1.5 mm were abundant in June of 1953. These he considered to be the young of that year (Swan 1961).

Swan (1958, 1961) repeatedly noted the problems associated with the interpretation of size-frequency modes. The length of the spawning season; and the variable growth rates, which may be due to the quantity and types of food available or to other environmental or possibly genetic factors, tend to confuse these modes especially in the larger size classes. The question of adequate sampling, particularly of larger urchins which are usually sparse, and that it is not known whether these animals grow continually or cease to grow after reaching a certain size are also problems. Swan's (1961) growth experiments at New Castle indicated that urchins initially 5 mm in diameter grew to 15.4 mm on Ascophyllum nodosum and to 22.1 mm on Laminaria digitata over a year. He also found that the growth rate of S. droebachiensis on a diet of Nereocystis luetkeana at Friday Harbor, Washington, was even greater than on L. digitata at New Castle.

In Washington State, Vadas (1968) fed S. droebachiensis species of algae. After 15 months, the urchins eating Nereocystis luetkeana and Laminaria saccharina were 2 to 3 times heavier than those fed Agarum cribrosum and A. fimbriatum. The animals feeding on the former two algae grew logarithmically until the end of this period, but those feeding on Agarum spp. reached an asymptote after about 7 months. After 20 months, Vadas dissected these animals. He found that the mean gonad index (expressed as the ratio of the gonad volume to the wet weight of the urchin) was 27.16 for N. luetkeana, 20.64 for L. saccharina, 8.66 for A. fimbriatum and 7.18 for A. cribrosum. This suggests that the type of food available may effect the reproductive potential of an urchin population as well as the growth rate. Ebert (1966, 1967, 1968) studied growth in S. purpuratus and demonstrated that a scarcity of food and spine breakage due to weathering could inhibit or even cause negative growth in adult urchins.

Prior to 1926, numerous reports were made on the foods of S. droebachiensis. These were usually based on gut analyses (Dawson 1868, Verrill, 1874, Packard 1893, Scott 1901, Eickelbaum 1910, Awerinzew 1911, Blegvad 1915, Jansen 1915, Mielch 1922, and Weese 1926). From them it is apparent that the animal is omnivorous, feeding on whatever materials are available in its immediate environment. Only two more recent papers make quantitative observations on the feeding habits of this urchin. Kuznetsov (1946) working in the eastern Murman showed that the feeding intensity (ratio of the food eaten per day — measured over several days — to the weight of the urchin) was 27 times greater for 8.9 mm urchins than for 65.5 mm urchins, when the food was Laminaria saccharina. In 1940, there were three sharp peaks in the feeding intensity of 50-55 mm urchins eating the same food; one in March, which was followed by the lowest feeding intensity value in April and May, a slightly higher peak in June and July and the highest peak in November.

Vadas (1968), in studying the urchin and algal populations in the vicinity of Friday Harbor, Washington, conducted numerous experiments on the food preferences of S. droebachiensis, S. franciscanus and S. purpuratus. He found that Agarum cribrosum and A. fimbriatum consistently ranked low. The feeding rates, assimilation efficiencies, growth rates and gonadal development were also low when Agarum spp. were the food material. He showed that there is a correlation between the preferences of the urchin and the quality of the food, postulating that the urchin has so evolved that its food preferences are for the more nutritious algae. Agarum spp. have low reproductive capacities, lower growth rates, and smaller holdfasts than other

phaeophytes in that area. They are therefore inferior competitors in the upper sublittoral. However, the preferential feeding habits of the urchins allow Agarum spp. to become the dominant vegetation in deeper water.

STUDY AREAS

Logy Bay

Logy Bay (Figure 1) faces northeasterly towards the North Atlantic and is generally representative of extremely exposed Newfoundland shorelines. High cliffs of red conglomerate, which have a north north east strike and dip steeply, border the Bay.

Dyer's Gulch (Figure 2), a narrow inlet below the Marine Sciences Research Laboratory (MSRL), is the specific area in which detailed studies were made. Due to its narrowness, the Gulch usually receives diagonally the impact of heavy swells. A small brook drains over the steep walls into the bottom of the Gulch. However, any appreciable effect this may have on the salinity of this area is confined to the surface waters within the trench. The first 150 feet of the inner Gulch is about 80 feet wide and is bordered by very steep bedrock walls. The depth of this portion slowly increases to about 20 feet (near the slipway used by the MSRL and by local fishermen). This area, which will henceforth be referred to as the Bottom of the Gulch, is only subjected to turbulent water during storms. In the next 100 feet the depth increased to 50 feet. This is the maximum depth in the Gulch, and almost vertical submerged walls close in so that the trench is only about 40 feet wide at its deepest point. This portion will be referred to as the Narrows. So far the bottom is bedrock strewn with large boulders. Beyond this the wall on the west side of the trench slopes gently to about 15 feet and then drops off — the opposing wall retains its steepness to the surface but gives way to a smaller inlet which is about

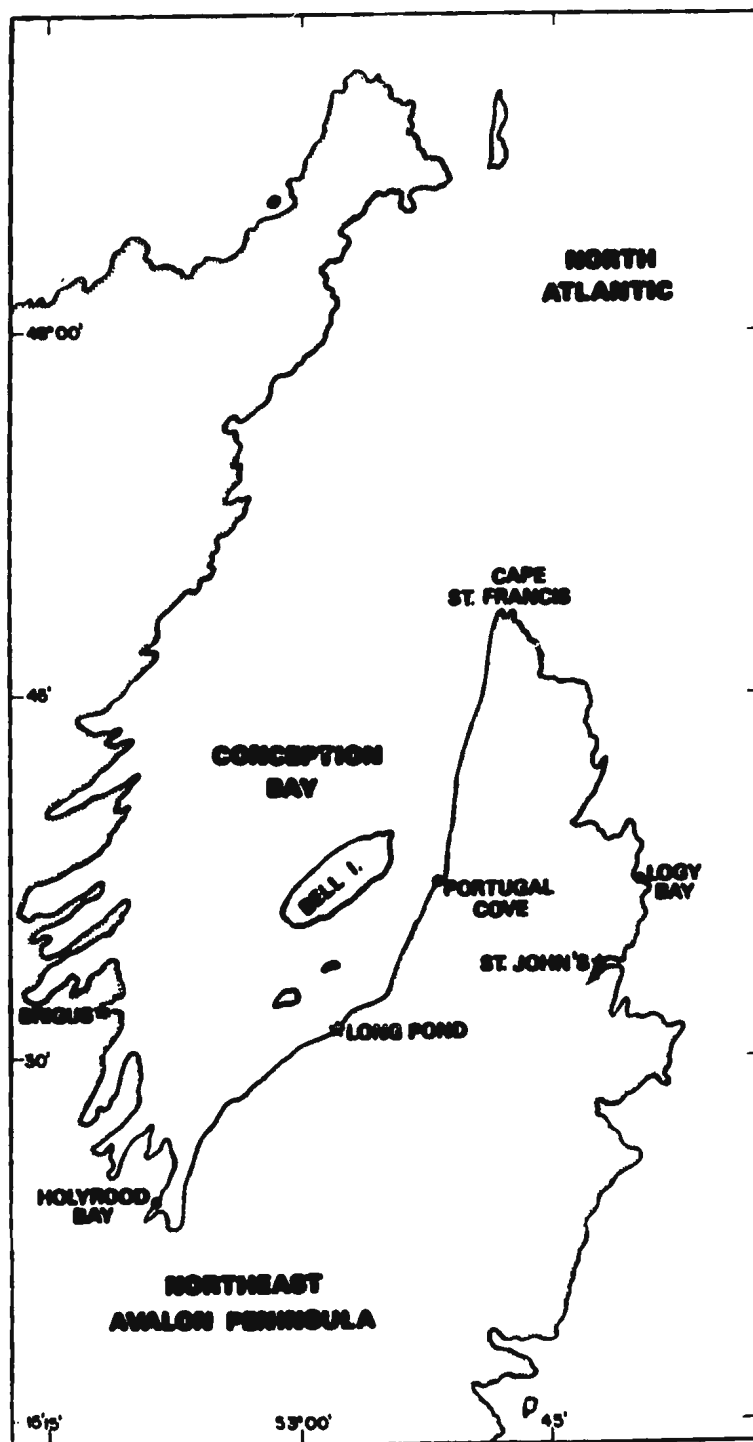


FIGURE I: Location of the Three Main Study Areas and Other Areas Referred to on the Northeast Avalon Peninsula.

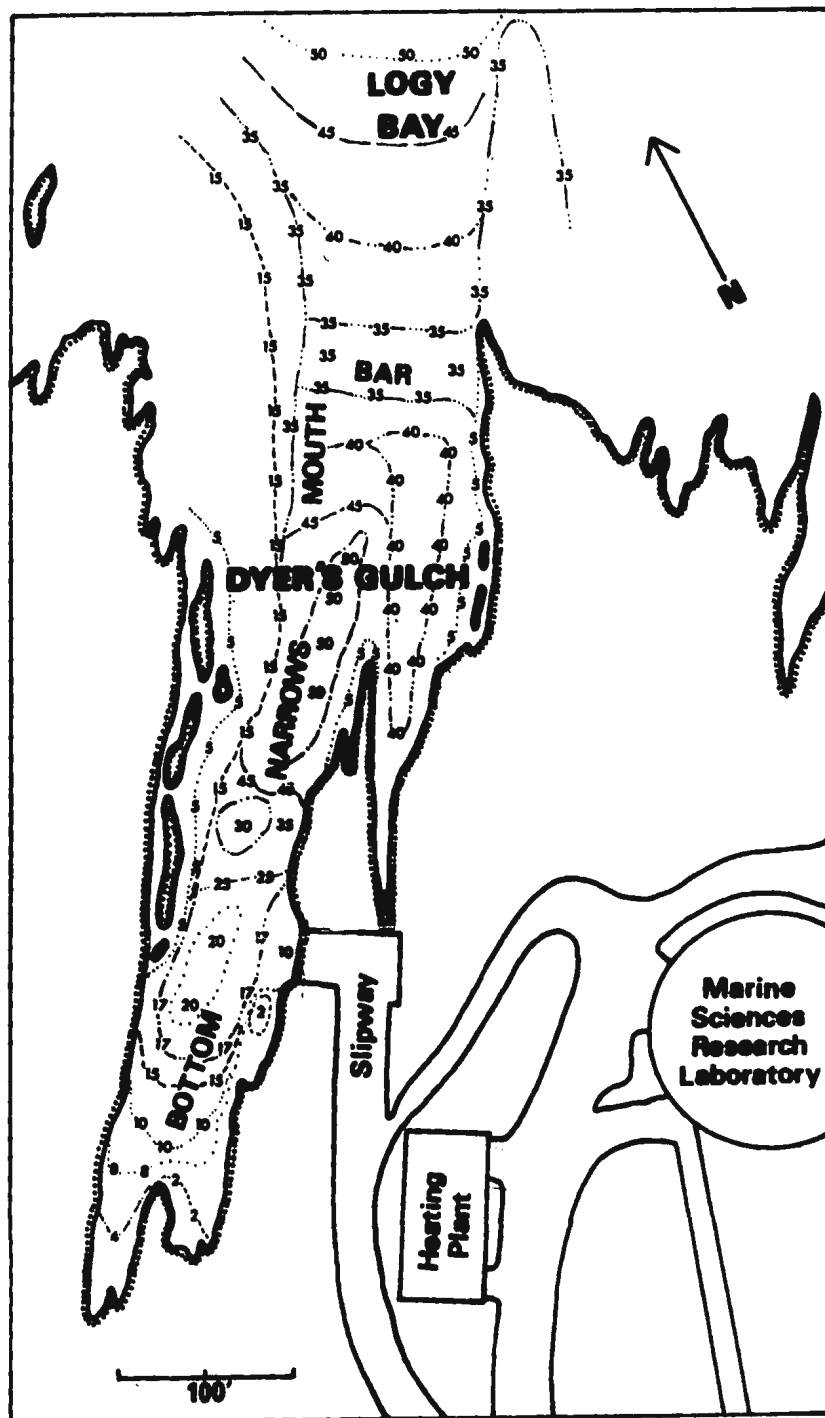


FIGURE 2: Dyer's Gulch Region Showing the Approximate Depths in Feet.

40 feet deep. Near the entrance of the trench an accumulation of boulders and cobble forms a bar at a depth of 35 feet. On the seaward side of this bar loose material extends down to a depth of 125 feet where the bottom becomes almost flat. The sediments decrease in size with depth and below 110 feet the bottom material is sand. However, scattered boulders are present between 60 and 85 feet. On the west side of the Gulch bedrock ridges extend down to about 70 feet. Bedrock outcrops are common throughout the area.

The perennial Fucus vesiculosus occurs commonly on the less vertical intertidal surfaces inside the Gulch, but only small fronds of this alga are scattered on the more vertical and exposed faces. F. disticus var. edentatus is less common and appears to be confined to the low intertidal inside the Gulch. Pilayella littoralis is a common epiphyte on these Fucus spp., particularly near the Bottom of the Gulch. Alaria esculenta usually grows in dense beds and forms a band about 2 feet wide just below low water level in the Bottom. The width of this zone increases towards the Mouth of the Gulch, at the Narrows it extends down to a depth of 8 feet (sporlings to 10 feet in June 1969) and further out (on the submerged bedrock wall on the west side of the Gulch) it forms a dense growth to a depth of 18 feet. On the east side A. esculenta, in association with Laminaria digitata, Agarum cribrosum and Desmarestia viridis, covers the tops of the bedrock ridges down as far as 35 feet. This Alaria zone is also uplifted in very exposed localities and at the entrance to the Gulch it extends up to about 2 feet above low tide level. Rhodomenia palmata commonly grows epiphytic on the stipes of older Alaria plants and Laminaria digitata is common subtidally throughout the Alaria beds except inside the slipway. Scattered plants of

Agarum cribrosum occur along the vertical walls of the Gulch below the Alaria zone. Around the Mouth of the Gulch, an extensive area of Halosaccion ramantaceum extends down through the Alaria to about 6 feet. Most of the submerged rock surfaces are encrusted with a smooth type of crustose coralline alga, although the upright branched type exists on some of the vertical walls of the Narrows. Outside the Gulch from 60 to at least 110 feet Ptilota serrata is the only conspicuous alga. It grows in small tufts on most of the bedrock outcrops.

During the winter months, when the cliffs receive much spray, a conspicuous green covering of Urospora panicilliformis forms over the immersed rock surfaces to a height of 30 feet above low water level. As spring approaches, Bangia fuscopurpurea forms a dense brown mat which extends up about 15 feet at the entrance to the Gulch. These zones are much lower at the Bottom of the Gulch because the spray zone is not usually very high. Ultimately, these algae are destroyed because of desiccation and as a result of the grazing activities of Littorina saxatilis. Another annual species, Petalonia fascia, which covers the low intertidal area during the winter, is rare by summer. Porphyra umbilicalis f. linearis sometimes occurs on the intertidal rock surfaces in the spring. It was not observed in 1969, though.

Enteromorpha sp. commonly grows in pools where fresh water collects. Spongomorpha arcta and S. hystrix are common in low intertidal pools or in shallow crevices during the spring and summer. Chordaria flagelliformis, frequently bearing the epiphyte Dictyosiphon foeniculaceus, also occurs in the latter habitat during the summer. The rhodophytes Ceramium spp.,

Polysiphonia spp. and Rhodomalia confervoides can usually be found in tidal pools and in shallow depths to about 20 feet. Monostroma sp. is common during early spring in depths up to 15 feet. Following sporulation it rapidly disappears, and is rare by the end of June.

Chorda tomentosa forms a dense growth near low water level inside the Gulch during the spring months and it may persist nearly till August. In June 1969 it was also observed covering many of the boulders on the Bar at depths of 35 feet and greater; but it was not seen here in 1968.

Desmarestia aculeata occurs throughout the year in the Gulch on the vertical cliff walls and the tops of boulders from 5 to 30 feet. It is quite worn by late September. In the spring of 1969 a luxuriant new growth was present, which in some areas formed a dense mat below the Alaria. Desmarestia viridis was not observed in the Gulch in 1968, but was scattered throughout the trench down to a depth of 40 feet in 1969.

The most conspicuous intertidal animal at Logy Bay is Balanus balanoides which forms a narrow white band in the mid-intertidal just above or extending down into Fucus spp. In the low intertidal and often extending down to 15 feet the small blue mussel, Mytilus edulis, frequently occurs in dense beds. The horse mussel Volvella modiolus is scattered along the walls of the Gulch and usually grows below M. edulis. Inside the trench, small Metridium dianthus commonly grow in the vertical range of M. edulis and may extend deeper. The scale worm, Lepidonotus squamatus, is common and Hiatella arctica and Nereis palagica are very common amongst the byssal fibers and detritus around the mussels and around the entangled stipes of the kelps. Obelia geniculata commonly occurs on Agarum cribrosum.

Subtidally to a depth of about 20 feet, the hydroid, Abietenaria turgida, forms small tufts on exposed ridges. The scarlet alcyonarian, Gersemia rubiformis, is common below 20 feet attached to the vertical walls of the Narrows. Yellow encrusting sponges frequently occur in shaded crevices and the upright growths of the eyed finger sponge, Chalina oculata, are scattered on the bedrock surfaces below 60 feet.

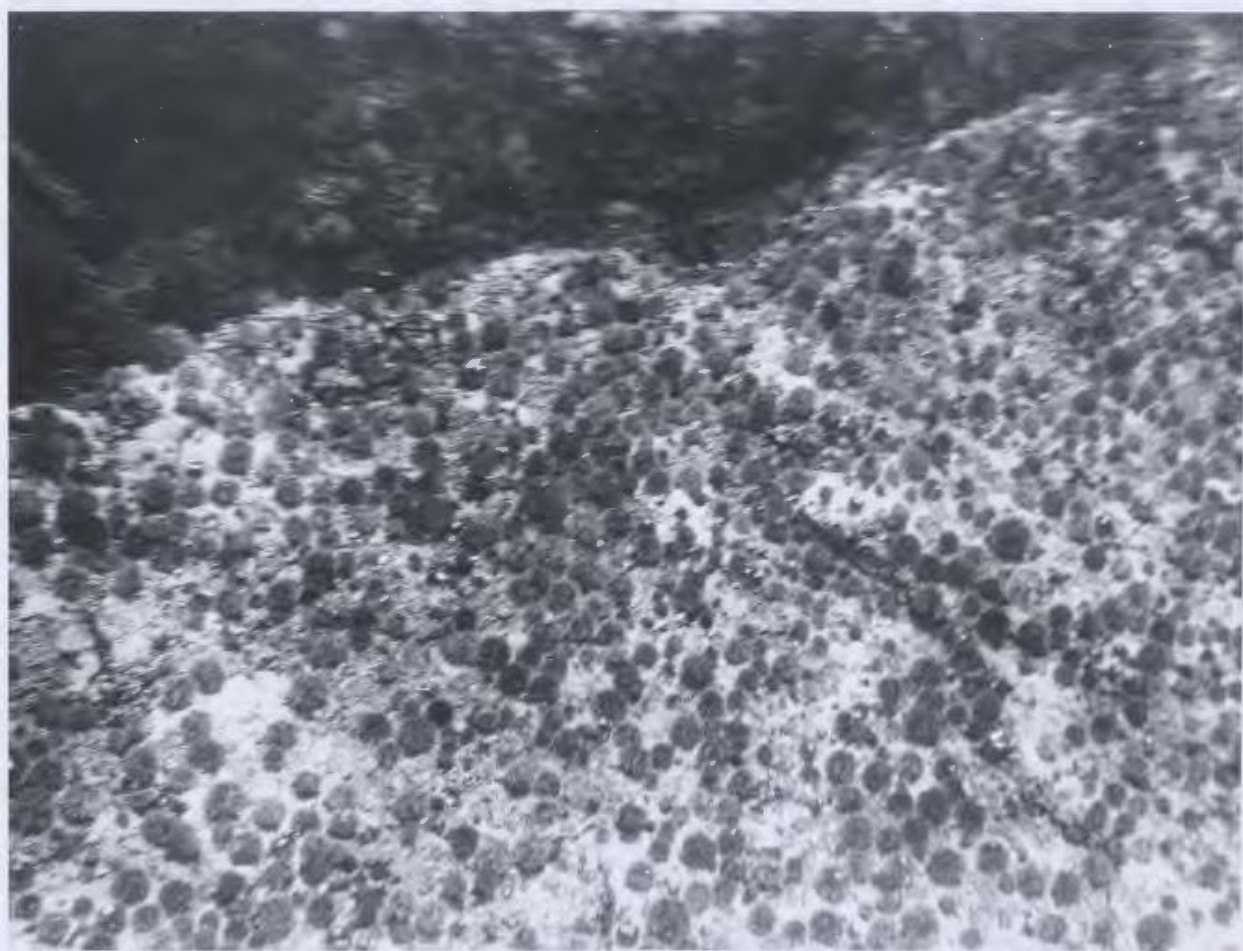
Intertidally Littorina saxatilis is very abundant and in the spring grazing lines of Bangia fuscopurpurea can be seen extending out from the moist crevices where this animal congregates for protection against desiccation. L. littorea is present but not very common. The chink shell, Lacuna vincta, is particularly abundant on Chorda tomentosa during the late spring and early summer, and also occurs on Chordaria flagelliformis when this alga is present. The Atlantic dogwinkle, Thais lapillis, and the limpet, Acmaea testudinalis, are common under Fucus spp. and Alaria esculenta. The latter is also very common throughout the Bottom of the Gulch. The sublittoral northern wulk, Buccinum undatum, is scattered only in the Gulch. The chiton, Tonicella marmorea, has been found subtidally, although rather infrequently, under Alaria.

The spider crab, Hyas araneus, particularly small individuals, is common in crevices throughout the area; the lobster, Homarus americanus, has only been observed on a few occasions; and a shrimp, Pandalas montagui, is abundant during the summer, hovering over the gravel outside the Bar.

Echinoderms are well represented at Logy Bay: Strongylocentrotus droebachiensis is by far the most conspicuous subtidal animal (Plate I);

Plate I

The southeast vertical wall of the Narrows, Dyer's Gulch, at a depth of 20 feet showing the dense population of S. droebachiensis. Note that many of the urchins are "capped" with shell fragments. (May 22, 1969).



Asterias vulgaris is common in the Gulch but is infrequent outside; Henricia sp. is common on the bedrock walls in the Gulch; Leptasterias polaris is common within the Gulch as far as the slipway. It is also outside the Gulch; Psolus fabricii, the scarlet sea cucumber, is only common in the Narrows, where its vertical distribution is similar to that of Gersemia rubiformis; Crossaster papposus occur occasionally in deeper water outside the trench, and a few Solaster endeca have been collected from the same area. The brittle star, Ophiopholia aculeata, is common in rock crevices, amongst kelp holdfasts and under branched Lithothamnion; the brown sea cucumber, Cucumaria frondosa, is scattered along the bedrock surfaces, usually below 20 feet, inside the Gulch and at greater depths outside the Gulch; and a number of small whitish sea cucumbers, Chiridota laevis, have been found in the gravel outside the Bar.

The most conspicuous fishes at Logy Bay are the longhorn sculpin (Myoxocephalus octodecemspinosus) and the winter flounder (Pseudopleuronectes americanus). The shorthorn sculpin (M. scorpius) and the yellow flounder (Limanda ferruginea) usually occur outside Dyer's Gulch. The rock gunnel (Pholis gunnellus), the radiated shanny (Ulvaria subbifurcata), and the arctic shanny (Stichaeus punctatus) are found scattered amongst the cobble and boulders in the Gulch during the summer months. Schools of Atlantic tomcod (Microgadus tomcod) are sometimes seen around the Mouth of the Gulch. During June and July, almost endless schools of caplin (Mallotus villosus) follow the coast. The lumpfish (Cyclopterus lumpus) and the Atlantic seasnail, Liparis atlanticus, also come to shallow water during the spring months to spawn. The Atlantic cod (Gadus morhua) and the Atlantic salmon (Salmo salar) are caught in gill nets just outside the Gulch by the local fishermen.

Portugal Cove

Portugal Cove (Figure 1) is a small indentation on the east shore of Conception Bay about 13 miles inside of Cape St. Francis. The area is only faced by a long fetch in a northerly direction, since excessive wave action from across the Bay is precluded by Bell Island, lying three miles west of the Cove.

Detailed studies were made around a small point at the southern side of the entrance to Portugal Cove (Figure 3). The strike of the bedrock outcrops is east northeast and the dip is quite steep. The elevation is much less than at Logy Bay, though, and the rock material is volcanic. Bedrock forms the Point and an Outer Ridge which encloses shallow flats, small inlets and pools. Northeast of the point the bedrock surface drops in a step-like fashion to a depth of about 50 feet over a horizontal distance of about 150 feet. In the same direction the bottom continues to drop, but at greater depths bedrock is only present as scattered outcrops.

Inside the Point there is a shallow Basin with a cobble beach at the bottom. The substrate of the Basin is primarily cobble and pebbles. However, there are scattered boulders, and bedrock flats emerge at low tide level. In a northeast direction from the Basin the bottom drops much more gradually and a depth of 70 feet is only reached nearly 500 feet from shore. The rock material in the Basin is well rounded by the abrasive action of the swell. Just outside the Point from 30 to 45 feet the bottom is more inclined and much of the loose rock material is larger and more jagged. At greater depths the bottom slopes very little and the substrate is composed of gravel and shell fragments overlaid by small cobble and pebbles. (Plate II).

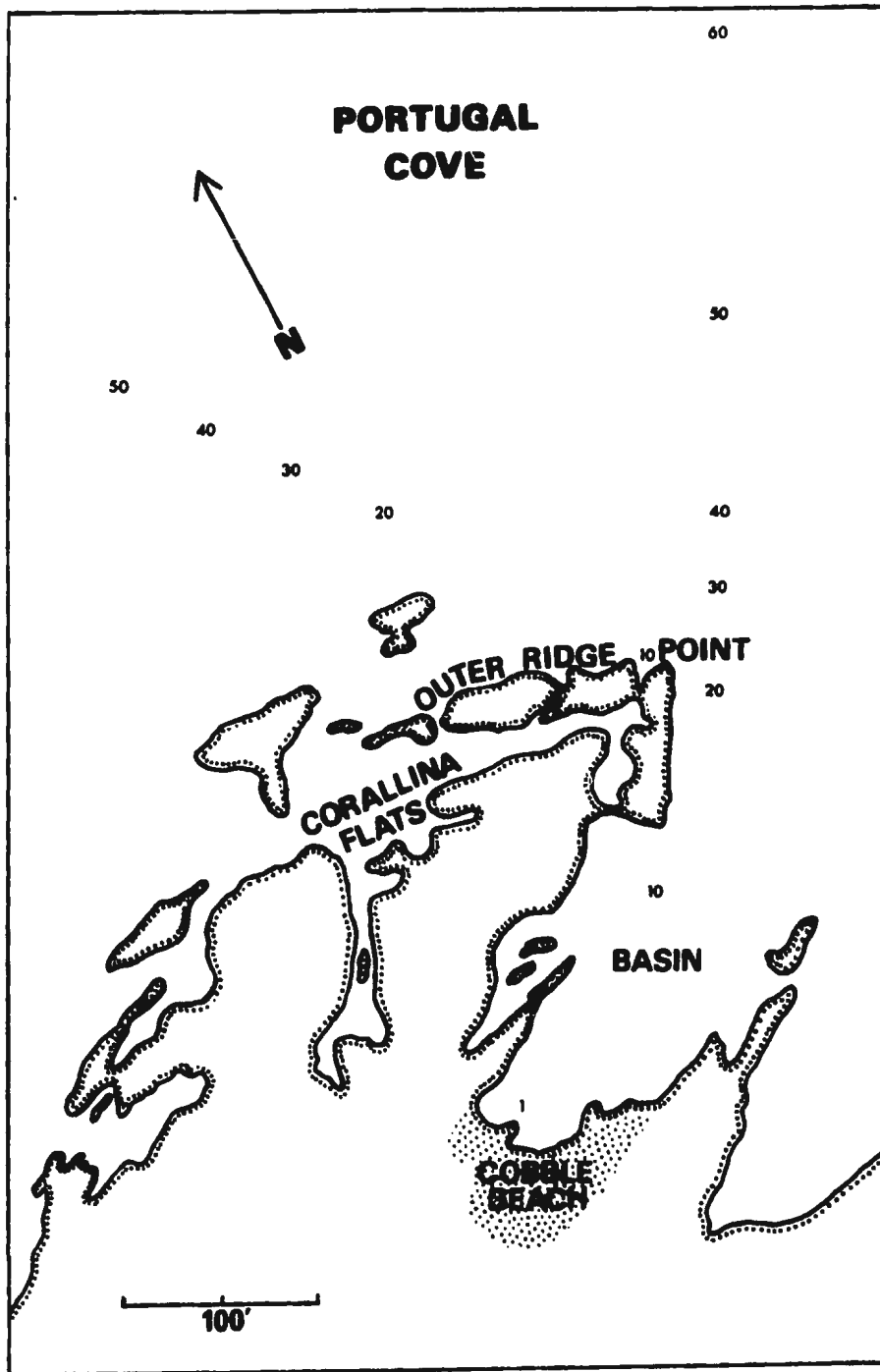
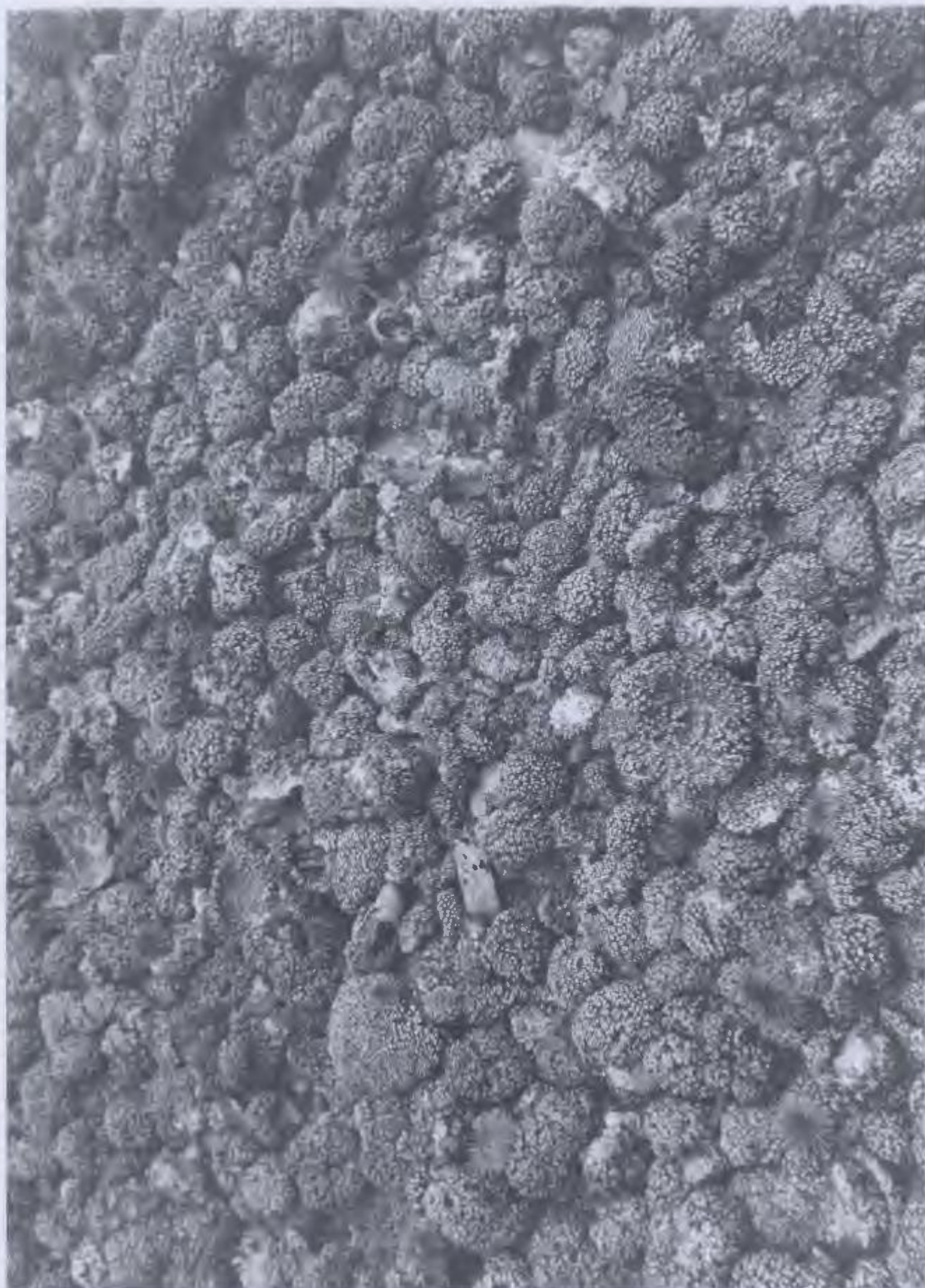


FIGURE 3: Portugal Cove Study Area Showing the Locations where the Various Depths were Sampled.

Plate II

The heavily coralline-encrusted loose substrate at 50 feet at Portugal Cove. There are nearly 200 urchins/m² on this material, but more than 90 percent of these are less than 20 mm in test diameter. Soft macrophytes are absent in this area.





Fucus vesiculosus and Ascophyllum nodosum are very abundant at Portugal Cove, where they grow intertidally attached to bedrock and large boulders. The former is less prevalent and the latter is absent on the exposed side of the Point and Outer Ridge. Both species grow very luxuriantly along the more protected inlets and bordering the Basin. Although not as prevalent, Fucus disticus v. edentatus is common in the low intertidal bordering the pools inside the Outer Ridge and at the bottom of the Basin. Pilayella littoralis is a common epiphyte on these fucoids, and Polysiphonia lanosa often occurs on A. nodosum. Fucus disticus v. disticus grows in many of the high tide pools, and it can be found in pools which are as much as five feet above high tide level. These are only reached by spray.

Chondrus crispus occurs commonly under the intertidal fucoids and in a few localities it forms patches by itself near low tide level. Ahnfeltia plicata is rare but has a similar distribution. In partially protected areas Corallina officinalis forms dense mats which are exposed during very low tides. Such mats are very extensive on the bedrock flats inside the Outer Ridge. Small rounded tufts of this alga also occur as deep as 40 feet on exposed bedrock surfaces. Halosaccion ramentaceum is generally only scattered subtidally, but at the bottom of one small gulch, into which the swell is usually funnelled, it was abundant.

On the seaward side of the Point and Outer Ridge, where the water is usually turbulent, Alaria esculenta beds cover the bedrock surfaces from near low tide level to about 8 feet. On some of the very exposed surfaces, Alaria follows the substrate down to as deep as 15 feet. Inside the Point the Alaria zone narrows, and disappears over a short distance. Agarum

cribrosum is scattered on the seaward bedrock surfaces from 20 to 40 feet, where it is the most conspicuous seaweed. Small rhodophytes, Euthora cristata, Phycodrys rubens, and Ptilota serrata can also be found in small quantities associated with Agarum.

Crustose corallines cover bedrock surfaces, starting near low tide level. In shallow water the covering is usually smooth and patchy but with increasing depth it becomes thicker and covers most of the rock surfaces. At 30 feet the covering is about 2 inches in thickness, and is made up of many upright projections. Sheets of this material commonly blister from the bedrock surfaces and can easily be pried loose with a diving knife.

Crustose corallines are not present on the smaller rocks in the Basin because of abrasion. At 30 feet, though, there is less water movement, and the cobble starts to become encrusted. The covering on loose rock material increases with depth and below 45 feet most of the hard surfaces, including pebbles, horse mussel shells, and glass are heavily encrusted with the beautiful branched kind of Lithothamnion. The fact that all sides of most of the cobbles are covered is evidence that at times there is enough turbulence to rotate these objects.

Very small fronds of Ptilota serrata are present on the encrusted cobble. This alga is only abundant on the bedrock outcrops below 50 feet east of the Point.

Urospora penicilliformis and Bangia fuscopurpurea cover the rock surfaces in the spray zone during the winter and spring months and disappear

with the approach of summer. During the same period Petalonia fascia is prevalent intertidally and in shallow water. In April, 1969, a luxuriant growth of P. fascia var. zosterifolia, over a foot in length, was present in the Basin. In March, 1969, very long filaments of Urospora wormskjoldii were present near the Cobble Beach and also subtidally on boulder tops and on rock surfaces where there is much water movement. At the same time Monostroma sp. was very abundant in pools inside the Outer Ridge and along the Beach. Colonial diatoms formed a very conspicuous covering on all the subtidal rock surfaces during February through April, but this material rapidly disappeared in May. Ulva sp. is present but uncommon near low tide level during the summer and Enteromorpha sp. is present during much of the year in fresh water drainage.

Scytosiphon lomentaria grows on the low intertidal shore and is very abundant during the spring months. Saccorhiza dermatodea first appears in the spring and the plants become very large in moderately protected pools and inlets during the summer. Chordaria flagelliformis is first present in about June and is usually very common intertidally, particularly in the Basin. The latter almost always bears epiphytic Dictyosiphon foeniculaceus. D. viridis is the only species of Desmarestia present at Portugal Cove. It is usually attached to stable rock surfaces, from low tide level to about 25 feet. It grows rapidly during the spring and is most abundant in June and July, particularly where there is almost continual water movement.

The distribution of Balanus balanoides and Mytilus edulis at Portugal Cove is similar to that at Logy Bay. The former usually forms a white zone above the furoids and the latter occurs in dense beds in the low

intertidal shore and extends down to 10 to 15 feet in smaller numbers. The horse mussel, Volseella modiolus, is more abundant than in Dyer's Gulch and often forms large clusters between 20 and 40 feet. Metridium dianthus is also abundant and forms large congregations on several vertical bedrock faces. Large M. dianthus are more common than at Logy Bay. The Arctic saxicave, Hiatella arctica, is very common in the low intertidal where it is frequently matted amongst Corallina officinalis and it is also found to at least 50 feet in crevices produced by branched crustose corallines and in byssal fibers of V. modiolus. Spirobis borealis grows on fucoids and Obelia geniculata grows luxuriantly on Agarum cribrosum. Tubularia larynx, another common hydroid at Portugal Cove, is usually attached to vertical bedrock surfaces. It also occurs on V. modiolus. The segmented worm, Myxicola infundibulum, which secretes a thick gelatinous sheath around itself, is commonly found inhabiting small crevices in the bedrock, around V. modiolus, in crustose corallines, and in gravel.

A number of gastropods are grazers in the intertidal area. The edible periwinkle, Littorina littorea, and the northern rough periwinkle, L. saxatilis, are very common; the smooth periwinkle, L. obtusata, and the pale chink, Lacuna pallidula neritoidea, are also present. The common Atlantic chink shell, Lacuna vineta, is present on algae intertidally and down to 50 feet; the grazing limpet, Acmaea testudinalis, is common both in the low intertidal and subtidal shore; the predaceous Atlantic dogwinkle, Thais lapillis, is common intertidally; and the northern welk, Buccinum undatum, is scattered in shallow water.

The white northern chiton, Ishnochiton albus, is very abundant on the branched crustose corallines between 30 and 70 feet. The larger mottled red chiton, Tonicella marmorea, the little Puncturella noachina, the velvet shell, Velutina laevigata, Nereis pelagica (abundant), and a nemertean worm are also present in this environment. The jingle shell, Anomia aculeata, is common on V. modiolus between 30 and 45 feet and the scale worm, Lepidonatus squamatus, the terabellidian worm, Amphitrite figulus, and the trumpet worm, Cistenides gouldii, are common amongst the tangled byssal fibers, shell fragments and other debris from 30 to 45 feet. The Island scallop, Chlamys islandicus, was sometimes found under blistering layers of Lithothamnion.

The rock crab, Cancer irroratus, was scattered in shallow water; the spider crab, Hyas araneus, was present but not common, usually in bedrock areas; and the American lobster, Homarus americanus, was sometimes observed in large crevices in the bedrock or in cavities burrowed in the gravel under boulders. The shrimp, Pandalus montagui, is common during the summer below 15 feet, where it hovers over the coralline encrusted bedrock and cobble surfaces.

Strongylocentrotus droebachiensis is again the dominant subtidal animal. It frequently congregates around submerged algae which are not being washed around excessively by wave action. The purple starfish, Asterias vulgaris, is also very abundant, especially in small pockets at the base of the bedrock cliffs (30-40) where M. edulis or other food materials have washed down and collected. Very often one can observe two or three A. vulgaris feeding together on individual V. modiolus. Blood stars, Henricia

sp. are scattered throughout the area but are more common on the bedrock surfaces. The brittle star, Ophiopholis aculeata, is extremely abundant amongst the Lithothamnion-covered cobble between 30 and 60 feet, where their density may exceed that of S. droebachiensis. The sunstar, Crossaster papposus, and the sea cucumbers, Psolus fabricii, and Cucumaria frondosa, are very rare. However, the small white sea cucumber, Chiridota laevis, was commonly observed in the gravel from 20 to 50 feet.

During the summer months, cunners (Tautoglabrus adspersus) were abundant at Portugal Cove, but they were not observed during the winter. The longhorn sculpin (Myoxocephalus octodecemspinosus) and the winter flounder (Pseudopleuronectes americanus) were commonly seen; the shorthorn sculpin, (M. scorpius), the yellow flounder (Limanda ferruginea), the Atlantic cod (Gadus morhua), the lumpfish (Cyclopterus lumpus), and the ocean pout (Macrozoarces americanus) were less frequently observed; and shannys (Ulvaria subbifurcata and Stichaeus punctatus), and the rock gunnel (Pholis gunnellus) were usually common amongst the cobble in shallow water. The threespine stickleback (Gasterosteus aculeatus) is very common in very shallow water including tide pools; multitudes of caplin (Mallotus villosus) visit the area during their spawning period. A skate, probably Raja senta was observed on one occasion on a gravel bottom.

Holyrood

A brief study was made of the urchin population on the west shore of Holyrood Bay, Conception Bay (Figure 1), at the entrance to the northeasterly facing North Arm. This area receives little wave action from Conception Bay and the maximum fetch within Holyrood Bay is about 1.5 miles. The shoreline is very regular, and is only interrupted in a few places by bedrock outcrops.

The area where the water meets the land lies near the base of a steep gravel embankment. It consists of cobble and small boulders, interspersed amongst large boulders. The smaller rocks extend seaward for a distance of about 25 feet and to a depth of 4 feet. They then drop off more abruptly, to a depth of about 10 feet. The depth gradually increases from 10 to 35 feet, and the substrate over this level is mainly fine gravel and mud. Coarser gravel extends down from the shallower depths in places, and scattered cobbles are present. Below 35 feet gravel and cobble become predominant, but a thin mud film usually covers this material. The slope below the latter depth decreases, and at 60 feet the bottom is almost flat. Most of the rock material of this area is jagged, not having undergone much abrasion, since there is little wave action.

In August a very marked thermocline was apparent. The water temperature near the surface was 13.5°C but at 50 feet was 6.3°C. This situation is also a result of the sheltered conditions within Holyrood Bay.

Two species of Fucus, F. vesiculosus and F. disticus var. edentatus are present intertidally on the boulders in this area. The former is very

abundant and the latter is only common on the low intertidal shore.

Ascophyllum nodosum is less prevalent than F. vesiculosus but it occupies a similar range on the shore. Pilayella littoralis commonly occurs epiphytic on these fucoids.

Near low tide level Scytosiphon lomentaria, Chordaria flagelliformis and Dictyosiphon foeniculaceus are common. The first mentioned is a winter species persisting to the summer, and the latter two are summer species. D. foeniculaceus is usually an epiphyte growing on Fucus spp., S. lomentaria and C. flagelliformis. The latter is sometimes epiphytic on Fucus spp. Desmarestia viridis is the only other conspicuous alga, apart from the encrusting corallines, and it is uncommon growing only on larger rocks to a depth of about 30 feet.

Smooth encrusting corallines are present in patches on the rocks in shallow water. Thicker encrustations cover the rock surfaces below 35 feet. It is notable that at greater depths these corallines only encrust the upper exposed surfaces of the cobble. This indicates that the wave action is not strong enough to rotate the rock material.

Balanus balanoides occurs abundantly with the fucoids and Mytilus edulis often occurs in dense beds in the low intertidal shore. Although the density of M. edulis in shallow water is not as great as in the former two areas, the individuals present are usually very large. Matridium dianthus, which is common on larger rocks and bedrock, is also very large. One Halocynthia pyriformis was observed on a bedrock outcrop at about 15 feet.

Large Littorina littorea are very conspicuous intertidally and on rock surfaces to a depth of about 25 feet. L. obtusata and the chink shell,

Lacuna vineta occur near low water level on algae and the tortoise shell limpet, Acmaea testudinalis, and the common northern welk, Buccinium undatum, are scattered in shallow water on rocks. The prickly jingle shell, Anomia aculeata, the arctic saxicave, Hiatella arctica, and the mottled red chiton, Tonicella marmorea are also present on the rock surface as deep as 65 feet. The filter-feeding annelid worm, Myxicola infundibulum, is present in gravel and mud areas. The horse mussel, Velosella modiolus, only occurs in cobble areas below 35 feet.

Below 10 feet the shell remains of the razor clam, Ensis directus, the soft-shell clam, Mya arenaria, and the giant scallop, Placopecten magellanicus, are present (a few living but very old specimens of the two latter bivalves were obtained). Shells of the Atlantic surf clam, Spisula polynya, are common from 50 to 65 feet, but no living animals were encountered.

The rock crab, Cancer irroratus, was very abundant (approximately 2-5/m²) around the rocks in shallow water in August 1968. Two months later, on November 2, only a few larger individuals were observed, partially buried under the mud below 10 feet. A number of lobsters, Homarus americanus, and spider crabs, Hyas araneus, were found in the rocky embankment between 4 and 10 feet.

Strongylocentrotus droebachiensis is the dominating subtidal invertebrate. The relative abundance of large urchins is a striking feature of this area. Sand dollars (Echinarachnius parma) are scattered on the mud-gravel substrate, where they are frequently partially buried. The tests of

this animal are quite common at the same level. The purple starfish (Asterias vulgaris) is widely scattered throughout the area, but the polar starfish (Leptasterias polaris) is less common. During two dives below 30 feet, only three sunstars, one Crossaster papposus and two Solaster endeca, were encountered. The brittle star, Ophiopholis aculeata, is relatively common amongst more thickly coralline encrusted cobble below 35 feet.

During the few dives made at Holyrood, sculpins (probably Myoxocephalus octodecemspinosus), flounders (probably Pseudopleuronectes americanus), cunners (Tautoglabrus adspersus), and one skate (Raja santa) were observed.

METHODS

Measurements

Dimensions were measured with a vernier caliper to the nearest 0.1 mm. Wet weights were measured on a Mettler (type P120) balance, and recorded to the nearest 0.01 gm. The following measurements and observations were made:

Test diameter - One reading was made of the distance from the outer surface of the ambulacrum on one side of the test, across the mid-periproct, to the outer surface of the interambulacrum on the opposite side of the test.

Test height - One reading was made of the distance between the anus and the lowermost surface of the test.

Urchin weight - The urchin was removed from the water, excess water was shaken from it, and its weight was recorded after drying for about 15 minutes on three layers of paper towel.

Weight of gut plus contents - The gut plus its contents were weighed after excess water was drained from them.

Gonad weight - The gonad was weighed after it had been on three layers of paper towel for about 8 minutes.

Sex - Sex was determined by visual examination of the gonads for ova or sperm. If neither could be seen a squash of some of the tissue was examined under the microscope at 10-40 X. In a few instances the gonads were undifferentiated and it was only possible to sex the animal by the presence of old sperm and ova.

Gonad colour - Prior to 1969, except for November 1969, the colour

of the gonad was classified by the author without comparison to a standard, however, in November 1968 and during 1969 the colour was described with reference to the Reinhold Colour Guide (Kornerup and Wanscher 1961).

State of development of the gonads - Squashes were made of material preserved in 5 percent formalin. They were classified into four categories, which are defined in Table I.

Reproductive Cycle

Monthly samples of at least 20 urchins were taken from the Portugal Cove area, for gonad and gut analyses. The first collection was made on February 2, 1968. Thereafter, samples were collected near the end of each month until June 27, 1969. These samples were usually collected from the shallow pools and ledges inside of the Point by means of a scoop net. However, on several occasions during the winter collections were made by snorkeling to about 10 feet in the Basin. These samples were taken to the lab where the above measurements were made within 12 hours of the collecting time. The weight of the gut plus its contents was only recorded as from March 1968. At the end of April, 1968, difficulties were encountered in identifying the sex. Thereafter, the gonads were preserved in formalin and sea water. Later, unstained squashes of these tissues were made to verify the sex of the urchin and to determine the state of development of its gonads. In the February 2, 1968 sample, 6 out of 41; in the February 29, 1968 sample, 2 out of 21; and in the March 28, 1968 sample, 1 out of the 20 urchins were less than 30 mm in diameter; thereafter all urchins were larger than 30 mm in diameter. All of the urchins in these analyses had reached sexual maturity. The surface water temperature at the Point was recorded at the time of sampling (Figure 3).

A gonad index and an index of the gut plus its contents were derived for each urchin by the following formulae:

$$\text{Gonad Index} = \frac{\text{gonad weight}}{\text{urchin weight}} \times 100 \quad \text{Index of Gut} = \frac{\text{Weight of gut plus contents}}{\text{urchin weight}} \times 100$$

Data are also presented from 14 collections, of 10 urchins each, made by Acreman (1966) in 1965. Eleven of these collections were made at Bellevue, Trinity Bay, from May 22 to October 2; 1 was made at Brigus, Conception Bay on June 22; and 2 were from Long Pond, Conception Bay, on July 7 and 13. She weighed the empty gut, after allowing it to drain for 5 minutes on three layers of paper towel, and calculated a gut index as follows:

$$\text{Gut Index} = \frac{\text{Gut Weight}}{\text{Urchin Weight}} \times 100$$

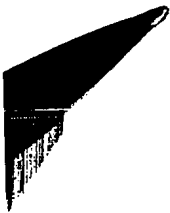
Both this gut index and the gonad index were used by Lawrence et al. (1965) in a study of Strongylocentrotus purpuratus.

Sampling

Sampling was done by two SCUBA divers equipped with fine mesh collecting bags, wire grids and a Voit sondic depth gauge (Plate III). At each depth sampled, the first grid was placed randomly by blindly swimming towards or sinking to the substrate. Usually 5 additional grids were placed horizontally along the bottom, one grid width away from the preceeding grid. Each quadrat was carefully examined. All visible urchins were transferred by hand into a collecting bag, and observations were made on the associated flora and fauna. Small urchins were sometimes very difficult to collect, since the cold waters of the Newfoundland coast almost always necessitated the wearing of neoprene mits. Also, susceptibility to chilling was greatly

Plate III

Two divers sampling the urchin population at 16 feet on the steep northwest wall of the Narrows, Dyer's Gulch. Congregations of urchins around blades of Alaria esculenta can be seen at the right. (May 22, 1969).





increased since one had to remain relatively inactive while examining a grid. The urchins from each grid were brought to the lab where the test height and diameter and total weight of each animal were measured.

During the summer of 1968 four vertical transects were made at the three study areas on the Avalon Peninsula. Specific information on the number and size of the grids and the depth and time at which the sampling was done is given in Figures 6 and 7 and Appendices III and IV.

(1) At Logy Bay the urchin population was sampled at 16, 27, 30 and 40 feet on the nearly vertical walls of the west side of the Narrows. Deeper samples were taken from 50, 60, 70 and 80 feet on the more moderately inclined bedrock surfaces outside of and to the east of Dyer's Gulch. The same area at 16 feet was sampled again in May and September, 1969. Swell action was often a problem at Logy Bay, and the shallow water quadrats could only be taken during infrequent calm periods.

(2) At Portugal Cove, one transect was made on the gently inclined bedrock surfaces in a line extending northwestward from the Point. Grids were taken at 10 foot intervals between 10 and 50 feet, and the same area at 10 feet was again sampled in May and September 1969. Bedrock is not a prominent part of the environment below 50 feet in this area. Below 30 feet the thick crust of corallines had to be pried loose and carefully examined to ensure that small urchins were not missed. Samples from bedrock were not collected near the surface at Logy Bay and Portugal Cove since dense beds of Alaria exist there. A number of short-spined larger urchins were commonly observed in protected crevices at this level.

(3) A second transect was made on loose substrate at Portugal Cove

in a northeasterly direction from the Cobble Beach. This area was sampled at 10 foot intervals from near the surface to 70 feet and the 50 foot level was sampled again in May and August, 1969. Crustose corallines, which occurred on the rocks below 30 feet, again presented a problem in that they provided small crevices in which young urchins frequently were found. From 40 to 60 feet this problem along with the great abundance of small urchins prohibited one diver from working over more than 2 quadrats on a cylinder of air. From 20 to 30 feet sampling was also a very slow process, since small urchins were commonly buried as deep as 6 to 8 inches under loose cobbles, pebbles, Volzella modiolus, shell fragments, and other detritus.

Usually 6 square grids, 0.2 m^2 in area, were used in the above three transects.

(4) Less detailed sampling was done on the west shore of Holyrood Bay at the entrance to North Arm. Grids were taken at 1, 10, 20, 40 and at 60 feet. It was necessary to increase the size of the grids owing to the scarcity of urchins in this area. The 1 foot level was sampled on two occasions, on August 16 and on November 2, 1968. Sampling could be done quite rapidly, since most of the urchins were large and the density was very low, except near low tide level. In the gravel-mud area along the transect urchins were entirely epibenthic. Further up the North Arm, though, a few small urchins were observed buried in the gravel.

Feeding Experiments

Four groups of experiments were conducted on the feeding abilities of urchins: (1) the feeding abilities of 10, 30 and 50 mm urchins on eight species of algae was investigated; (2) a more detailed study was made of

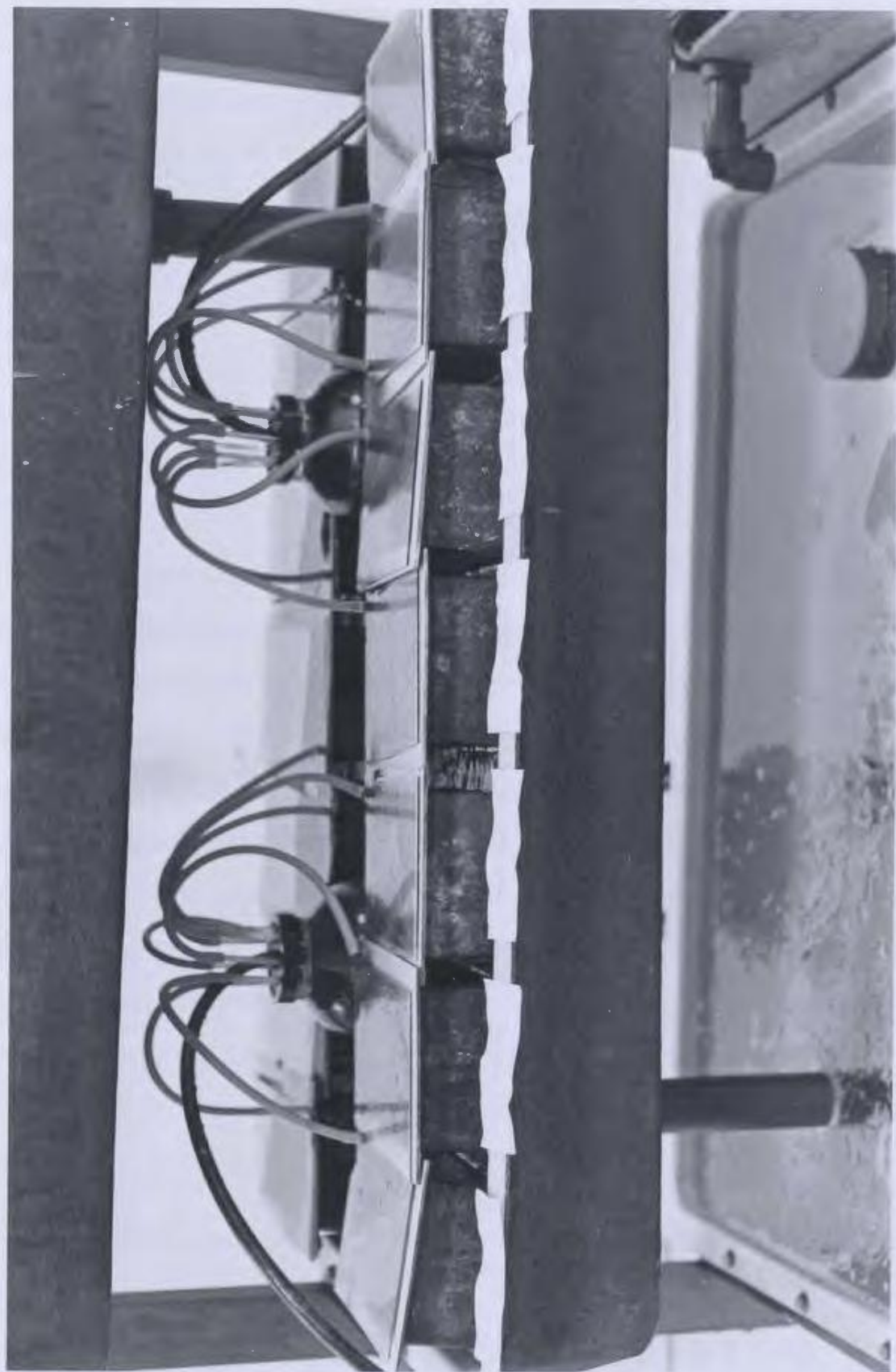
the feeding of seven size groups, 10, 20, ..., 70 mm, on Laminaria spp. (L. saccharina and, or L. longicrusis); (3) the feeding habits of 20 and 50 mm urchins on the same alga during alternating 12 hour dark: 12 hour light periods was measured; and (4) the algal preferences and feeding rate of 20 and 50 mm urchins on 13 algae was studied in May.

The urchins used in the feeding experiments were kept in the lab from the time when they were collected during the distribution studies. Tests on urchins less than 32 mm in diameter were carried on in tanks 24 x 13 x 17 cm in size and larger urchins were kept in tanks 34 x 23 x 23 cm in size. Sea water was slowly and continually supplied to each tank from the MBRL seawater system, which pumps water directly from Logy Bay, (Plate IV). The illumination reaching the tanks from the above fluorescent lights was 200-400 lux, except during the dark periods in the third experiment. For at least a week prior to each experiment the urchins were maintained under experimental conditions in respect to lighting and the type of food eaten.

The amount of food eaten and the faeces excreted were determined using methods adapted from Fujii (1962, 1967). Daily (or twice daily as in the light: dark period experiment) the algae in each tank were taken out, the surface water was removed with absorbent paper and the fronds were weighed to the nearest .01 g. The loss in weight between consecutive weighings represented the amount of food eaten (consumption) during that period of time. There was always an abundance of food available in each tank. At the same time the faecal material was siphoned from the bottom of the tank and filtered under suction onto preweighed filter papers. Sea

Plate IV

Tank setup for feeding experiments.



water without faeces was also poured through a sample of filter papers so that mean percent salt gain could be estimated. The amount of faeces excreted was determined by the following formula:

$$\begin{array}{ccccccc} \text{Dry weight} & & \text{Dry weight} & & \text{Weight of} & & \text{Estimated} \\ \text{of faeces} & = & \text{of faeces} & - & \text{preweighed} & - & \text{salt gain} \\ (\text{mg}) & & \text{with filter} & & \text{dry filter} & & \text{of filter} \\ & & \text{paper (mg)} & & \text{paper (mg)} & & \text{paper (mg)} \end{array}$$

where

$$\begin{array}{ccccccc} \text{Estimated} & & \text{Weight of} & & \text{Mean } \bar{x} \\ \text{salt gain} & = & \text{preweighed} & - & \text{salt gain} \\ \text{of filter} & & \text{dry filter} & & \text{of filter} \\ \text{paper (mg)} & & \text{paper (mg)} & & \text{papers (mg)} \end{array}$$

Filter papers were always kept in an oven at 40°C for at least four days to insure uniform dryness and then the weight of each paper was recorded about 45 seconds after removal from the oven. Small fronds of each alga, which were used to determine the percent ratio of dry weight to wet weight, and the faeces with the filter papers were first dried at room temperature and then oven-dried and weighed as above. It was found that these objects did not continue to lose weight after three days in the oven. The percent ratio of dry weight to wet weight for the eight species of algae used in the feeding experiments are listed in Appendix V. The variability of these figures is attributed both to error in weighing wet plant material and to variation in the actual weight and water content of the different pieces of algae.

The feeding rates and assimilation efficiencies were calculated as follows:

$$\text{Feeding rate (\%)} = \frac{\text{Food eaten (gms wet weight)/urchin/day}}{\text{Mean weight of urchins (gms wet weight)}} \times 100$$

$$\text{Assimilation efficiency (\%)} = \frac{\text{Dry weight of food eaten (mg)} - \text{Dry weight of faeces excreted (mg)}}{\text{Dry weight of food eaten (mg)}} \times 100$$

These formulae were used by Fujii (1962, 1967) in studies on S. intermedius in Japan.

In May and June, 1969 a simple experiment was performed to better understand the food preferences of S. droebachiensis and to obtain an estimate of the post-spawning feeding abilities of urchins on algae species which are abundant at that time of year. The different algae were arranged along the sides of two shallow trays, 84 x 170 x 8 cm in size, one of these containing 42 urchins, 48-52 mm in diameter, and the other 110 urchins, 28-32 mm. Tray illumination was 200-600 lux; water temperature was 2-4°C. At the beginning of the experiment daily records were kept of (1) the number of urchins in contact with each species of alga and (2) the rate at which each species was devoured. After 10 days less frequent observations were made. (Appendix VIII).

The number of urchin days spent on an alga is here defined as the total number of urchins on an alga in the daily observation periods. By making many comparisons, two species at a time, of the number of urchin days spent on each alga over the period when they were both present, the order of preference the urchin has for the various species can be derived. The rate at which the various algae disappeared is thus the combined results of the urchin's ability to consume the various species with its attraction to the algae. For example, Alaria esculenta and Laminaria sp. both disappeared in four days in the tray with the 50 mm urchins. Over most of this period,

though, there were more urchins in contact with the former than with the latter. Based on the number of urchin days, Alaria esculenta is more preferred than Laminaria sp. even though the consumption rate of Laminaria sp. is higher.

The consumption rates can be estimated in the same experiment by the following formula:

$$\begin{array}{lcl} \text{Food eaten} & & \text{Initial weight of the alga (mg wet weight)} \\ \text{(mg wet weight)} & = & \text{Total number of urchin days spent on the} \\ \text{/urchin/day} & & \text{alga until it was devoured.} \end{array}$$

For the more slowly consumed algae the number of urchin days was estimated for the days on which no observations were made. The feeding rate was calculated as before.

RESULTS

Reproductive Cycle

Gonad Cycle

Figure 4 (Appendix I) shows the mean male and female gonad indices from February 2, 1968 to June 29, 1969. The highest index was reached at the end of February, 1968. In the following month there was a sharp drop, due to spawning (see below). Consistently low values then existed until the end of June. A small peak was present in July and August, and a slightly higher one occurred in late November. During the intervening months, values similar to those of the post-spawning period were found. In 1969, the maximum peak occurred in March, and was followed by an abrupt decline until the end of April, when the lowest gonad index values were recorded. The latter peak was considerably lower than that of the pre-spawning peak in 1968. The male and female cycles were similar except during February and March when the mean index of the female gonads was notably higher than that of the male.

Microscopic examination of the gonads produced additional information on the reproductive cycle. Fuji (1960a, b, c) made thorough histological observations of the gametogenic cycle of S. nudus and S. intermedius in Japan and described and photographed six stages. The four stages used in this study are defined in Table I and the frequency of these stages between April, 1968 and June, 1969 are shown in Figure 4.

During the late spring and summer months, when the gonad indices were low, most of the samples were in the recovering stage. Only a few

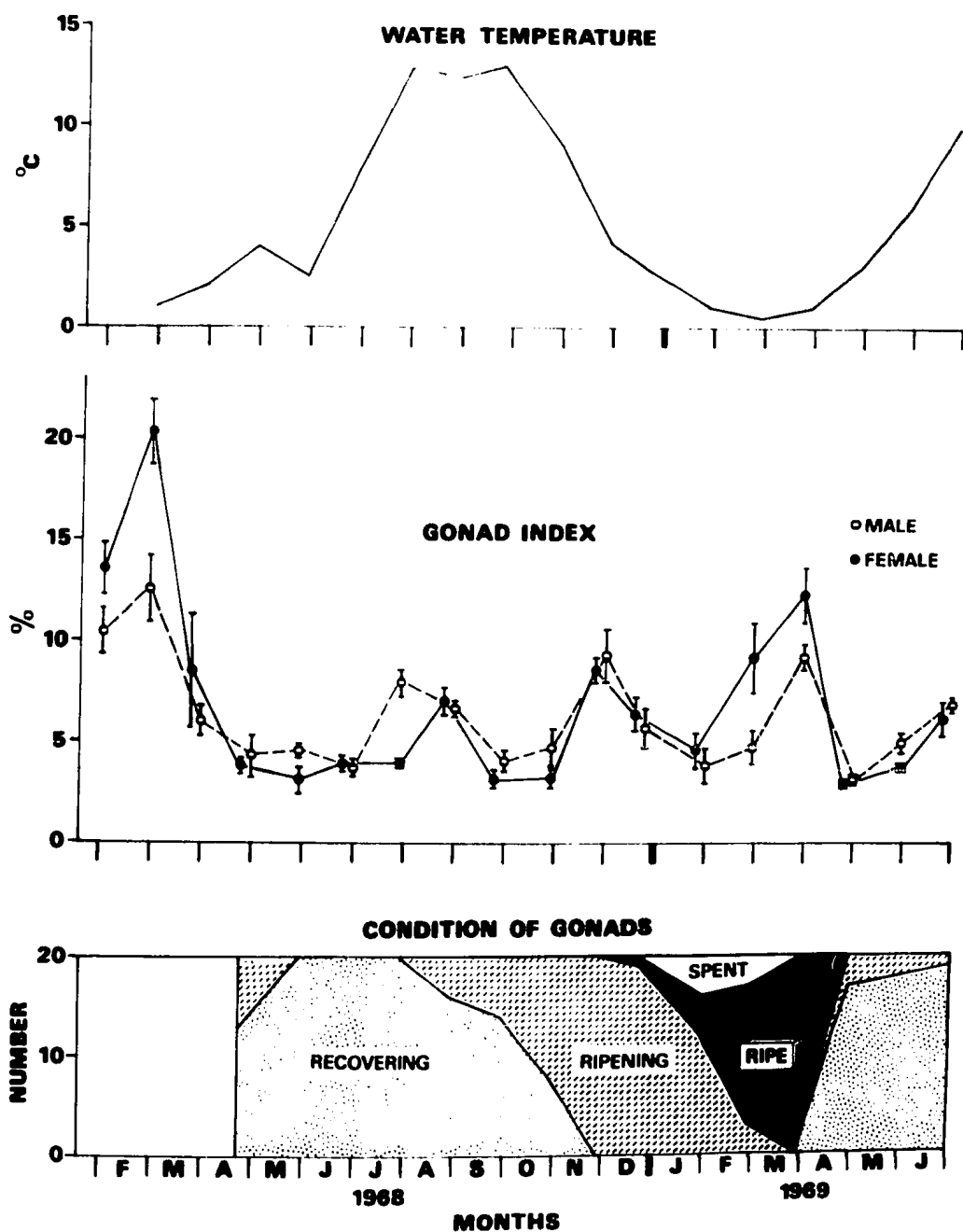


FIGURE 4 : Surface Water Temperatures, the Mean Male and Female Gonad Indices (Standard Error of the Means Represented by Vertical Lines) and the Number of Individuals in Spent, Recovering, Ripening and Rife Condition in the Monthly Samples at Portugal Cove.

males contained sufficient spermatozoa in their gonads to be classified as ripening. At the end of October, 13 of the sample of 20 were in the ripening stage and mature ova were present for the first time. The ripening condition predominated from November to January and then mature individuals became frequent. In late March when the highest mean gonad index in 1969 was recorded all of the samples were ripe and gametes were readily liberated when the gonads were handled. By the end of April, coinciding with low gonad index values, the recovering stage again predominated and only a few male individuals contained gametes in any quantity. Active sperm were present throughout most of the year; however, mature ova were only observed from late October to March or April.

There was some irregularity in early 1969 in that a few spent individuals occurred in January but not in March. This might possibly have been caused by a slight change in the collecting area. Owing to stormy conditions during December to March samples were obtained by snorkeling to about 10 feet inside the Point, rather than by scoop net in the outer pools as was the method in the other months. It is also possible that new tissues develop prior to the end of the spawning season so that no spent individuals were observed in April.

Throughout most of the year the colour of the gonads is variable and ranges from light yellow and grayish yellow to light orange, orange, grayish orange and brownish orange to light brown, brown and dark brown. The colour of the recovering and ripening gonads includes most of this range, but orange and the various shades of orange predominate. All individuals which were classified as ripe were orange or very near orange.

Table I - Definitions of the sexual stages used in this study.
The stages used by Fujii (1960a) which are similar are indicated in brackets following the names used here.

MALE	FEMALE
RECOVERING (O-II)	
Spermatozoa are rare to common, and not in dense patches	Various stages of developing oocytes are embedded in the germinal matrix but mature ova are absent.
RIPENING (III)	
Spermatozoa are very common and occur in dense patches amongst the germinal matrix; white sperm suspension oozes from the tissue when it is teased.	The ovaries contain both developing oocytes and mature ova, the latter, however, are not prevalent; ova are sometimes visible when the tissue is teased.
RIPE (IV)	
Most of the sex tissue consisting of densely packed spermatozoa; the testes are easily ruptured extruding sperm suspension.	The bulk of the ovary consists of mature ova; oocyte stages are also present but not common; this tissue is easily fractured and ova ranging 140 to 220 μ in size are released.
SPENT (V)	
Testes are very small and only a few sperm are present; gonad indices are less than 2.0; and the colour of the gonads is brown or yellowish brown.	Ovary is very small, usually containing a few ova and sometimes young oocytes; gonad indices are less than 2.0 and the colour of the gonads is brown or yellowish brown.

In March, 1969, when the entire sample was mature, nearly all of the urchins had orange gonads. However, the tone of orange differed between the sexes. All of the females were a yellowish tone of orange (orange, Plate 5; Kornerup and Wanscher 1961). Two of the male samples were this colour but the other 8 were a reddish tone of orange (Plate 6). The same difference was also apparent in February, 1968. During the other months there appeared to be little relationship between colour and sex and it must be stated that the colour of the gonads is never a reliable characteristic for sex determination. In January and February, 7 spent individuals were encountered and their gonads were brown or yellowish brown.

Acreman's data, Figure 5 (Appendix II), on collections from Bellevue, Trinity Bay, in 1965 showed that the gonad index was low by May 22, likely because spawning had occurred by this time, and then the indices rose during the summer much more rapidly than was the case at Portugal Cove in 1968. On June 22, 1965, she found the gonad index at Brigus, Conception Bay, was about the same as at Bellevue. However, two samples collected from Long Pond, Conception Bay, on July 7 and 13, 1965, had much higher indices. Water temperatures at Long Pond were 4-5°C higher than at Bellevue during July, 1966. Also the foods available at Long Pond were probably different from those at Bellevue and Brigus. The great influence of type of food eaten upon gonadal development was well demonstrated by Vadas (1968) as was previously mentioned. At Port Erin, Isle of Man, Moore (1934) studied the gonad cycles of Echinus esculentus populations in two areas; in shallow water near the ruined Breakwater, where there was a heavy growth of laminarians, and in 100-120 feet of water at the Breast, where the bottom

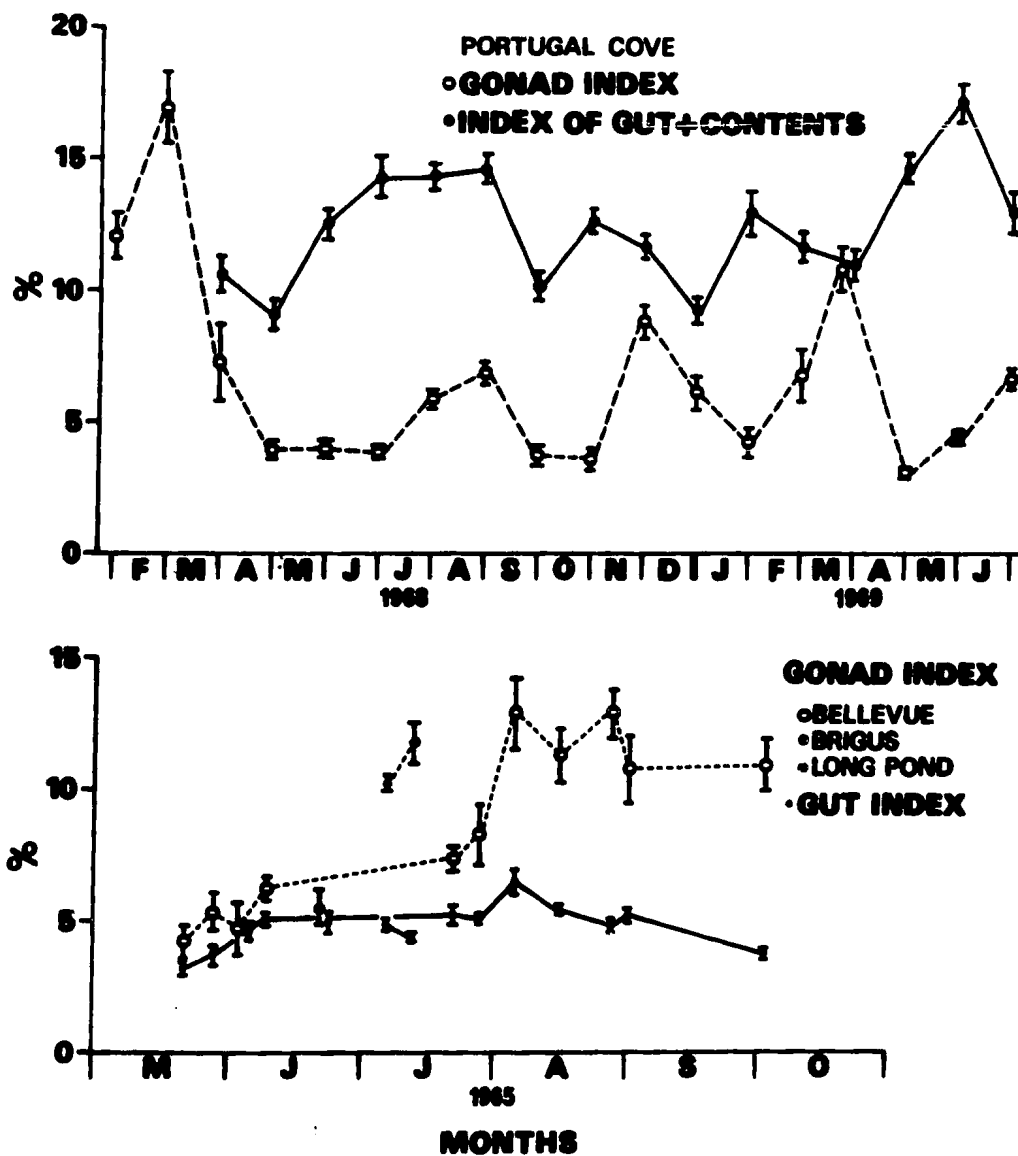


FIGURE 5: Above - The Mean Gonad Indices and Indices of the Gut Plus Contents for the Samples Collected at Portugal Cove.
 Below - The Mean Gonad and Gut Indices of the Samples Studied by Acreman (1966) for Other Areas on the Avalon Peninsula.
 The Vertical Lines Represent the Standard Error of the Means.

was shell and sand. The mean male and female gonad indices, expressed as the ratio of the gonad volume to urchin volume times 10, varied from 0.35 to 1.90 at the Breakwater but from only 0.05 to 0.36 at the Breast. The time of ripening at the Breast lagged behind that at the Breakwater and although spawning occurred over a two month period near April in both areas, spawning took place about two weeks later at the Breast. Food undoubtedly is largely responsible for the differences in the reproductive cycles in these areas.

In Lamoine, Maine, Cocanour and Allen (1967) made a study on the gonad cycle of S. droebachiensis from January, 1965 to January, 1966. A distinct annual cycle was evident. The gonad index, expressed as the ratio of the gonad volume to the total wet weight of the animal, reached its highest values in February and March. They noted that this period coincided with the lowest water temperatures in the year. This was also the situation in Newfoundland. The gonad index dropped sharply from March through June during which time spawning occurred. From records Agassiz (1864, 1872-74) made in the 1800's in Maine, spawning generally reached a peak in late winter to early spring. In my study spawning appeared to be completed by the end of April in both 1968 and 1969; and Turner and Boolootian (Boolootian 1967) in a study of this species from June, 1964 to June, 1965 found that spawnout was in March. Vasseur (1952) reported that spawning in S. droebachiensis in three widely separated areas in Norway, at Dröbak in the Oslo Fjord, at Trondheim and at Tromsø, occurred at about the same time, usually in February and March. Boolootian (1967), in The Physiology of Echinodermata, gives an extensive review of reproduction in echinoids and shows that an annual reproductive cycle is present in most members of this

class. The above reports would certainly indicate that this is true of Strongylocentrotus droebachiensis and that the breeding season appears to have its peak in February and March throughout its range.

The higher female gonad index during the prespawning peak of the gonad cycle is not unique to S. droebachiensis. This is reported to be characteristic of the irregular echinoids Echinarachnius parma (Cocanour and Allen, 1967) and Echinocardium cordatum (Moore, 1935) as well as the sea urchin Echinus esculentus (as is suggested by the diagrams of Moore 1934, 1937). However, Bennett and Giese (1955) working on S. purpuratus and S. franciscanus, and Fuji (1960b, c) studying S. nudus and S. intermedius state that the relative gonad volumes of male and female urchins are similar throughout the year in these species.

Secondary peaks, such as those which occur in July and August and in November of this study and in August of Acreman's records, are very common in echinoid gonad cycles. The 1965-66 study of S. droebachiensis by Cocanour and Allen (1967) shows a slight peak in July, however, the low post-spawning levels are not resumed in September as is the case in the 1968 gonad cycle. Irregular non-annual peaks are very common in S. purpuratus (as is apparent in the many Figures of Boolootian 1967, Lasker and Giese 1954, and Bennett and Giese 1959, and Leighton and Jones 1968) and are also reported in S. franciscanus (Greenfield et al. 1958, Leighton and Jones 1968), Tripneustes esculentus (Lewis 1958), Echinus esculentus (Moore 1935, 1937) and in Echinarachnius parma (Cocanour and Allen 1967). Whether this is attributed to (1) absorption of the germinal tissue or (2) to sampling errors due to local variations over a very short distance or (3) to secondary spawning periods is not certain. However, there is some evidence suggesting

the latter possibility. In September and October following the slight peak in gonad index values in August a number of individuals with low gonad indices and with gonads which were brownish in colour were encountered. Mature gametes were uncommon in these and they were classified as recovering. This could not explain the drop in the mean female index in September, however, since mature ova were not present until October. The presence of spent individuals in January and February following the December peak certainly suggests that spawning was the cause of that drop. This early spawning activity is very likely the reason for the lower prespawning peak at the end of March, 1969. This study would indicate that the gonad index is useful in assessing the reproductive cycle of an echinoid, but a much more thorough understanding is achieved when this is accompanied by microscopic examinations.

During February, 1968 and 1969, limited data were obtained on the size at which S. droebachiensis reaches maturity. All of seven individuals less than 20 mm in diameter were immature; one male urchin 22 mm in diameter was mature; and all of five urchins between 25 and 28 mm contained ripe gametes.

Gut Index and Index of the Gut Plus Contents

Lawrence et al. (1965), using a gut index, expressed as the ratio of the wet weight of the gut to the wet weight of the animal, found that there was an annual cycle in the weight of the gut of S. purpuratus. However, the amplitude of the cycle was much lower than that of the gonad cycle. The indices were low in the winter, increased during the summer and reached a peak in October. Figure 5 shows the mean gut indices from May 22 to

October 2, 1965, at Bellevue (Acreman, 1966). A low amplitude cycle which reached a peak in August seems to be apparent.

Figure 5 shows the relative weight of the gut plus its contents in the Portugal Cove samples from May, 1968, through June, 1969. Using the Bellevue gut index data as a baseline, it can be seen that there is always food in the gut. However, the amount varies greatly from time to time. There was much material in the gut from June through August, less from September to March and much again in the post spawning period. Fujii (1967) showed that the relative gut contents of large S. intermedius in three areas in Japan exhibited a regular annual cycle. The guts contained the least material during July through September when the gonads were large but following spawning gut content increased markedly.

Urchin Populations in Study Areas

Size Frequency Distributions

The urchins were grouped into 2 mm size classes, and size frequency distributions, calculated per square metre, were constructed for each of the levels sampled in the 4 transects. A mean distribution (\bar{X}) was also constructed for each transect by averaging the samples collected on the first dates at the various levels. (Figure 6, Appendix IV).

Logy Bay (Figure 6a)

Logy Bay urchins ranged from 3.2 to 56.8 mm in diameter. The mean size distribution rises abruptly to its first and highest peak in the 8 - 10 mm size class and then gradually descends towards the 52-54 mm size class. Four lower peaks occur in the 14 - 16, 22 - 24, 26 - 28, and 30 - 32 mm size classes. These peaks descend in an almost linear manner, and are spaced at intervals of 6, 8, 4 and 4 mm respectively.

Examination of the separate diagrams of the various depths shows that the first peak is recognizable at the 27, 50 and 80 foot depths, and are also suggested to be 2 mm behind at 16 and 60 feet. The first and second peaks can be distinguished at 40 and 70 feet, but the third peak is not present.

The 16 foot samples, collected in the early summer of 1968, have a well defined mode of small urchins at 6 - 8 mm. Resampling of the same area in May, 1969, almost 11 months later, indicates that this mode has shifted to the 10 - 12 mm size class. This represents a progression of 4 mm. A third sample in September shows that this mode is still at the same position.

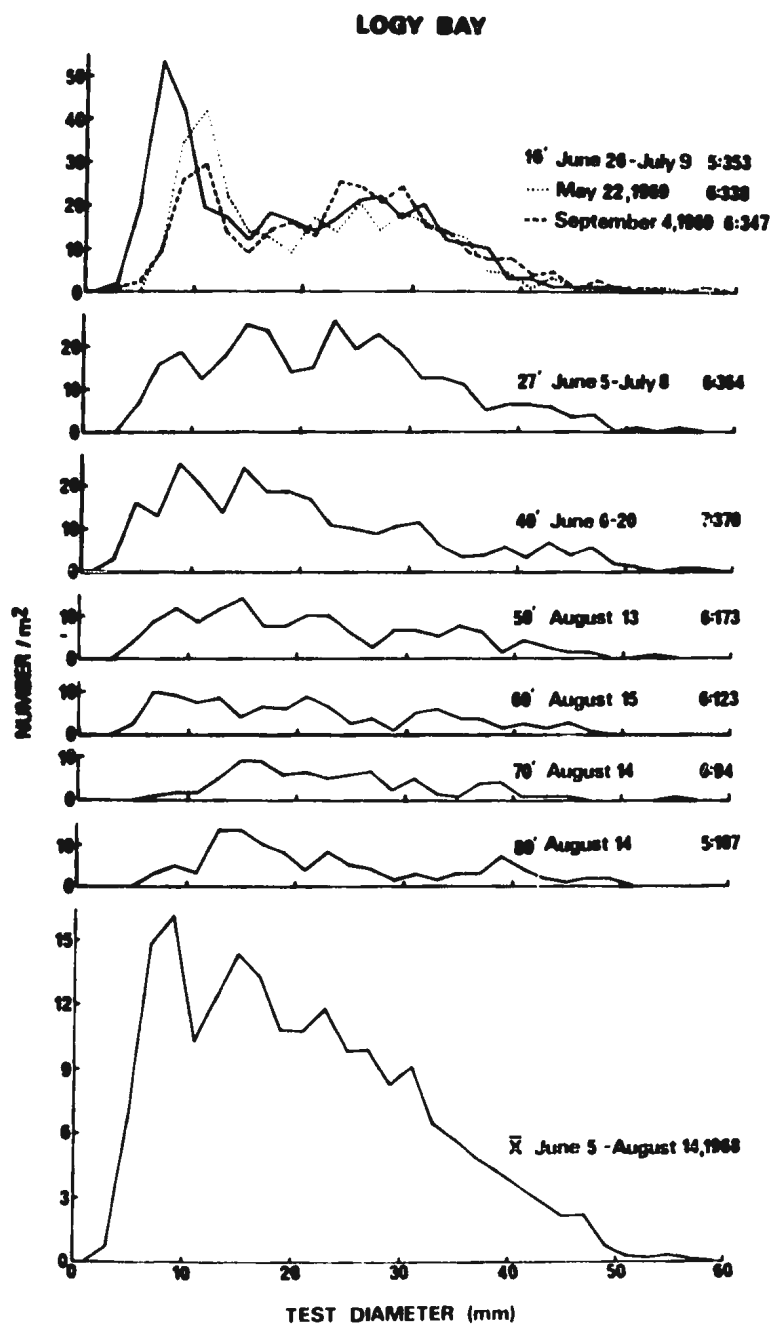


FIGURE 6 a: Size Frequency Distributions for (1) the Various Depths Sampled, (2) the Average (\bar{X}) of the Samples Collected on the First Dates at the Various Levels, and (3) the Resampled Levels. (The Number of Samples and Total Number of Urchins on which the Diagrams are Based are Indicated after the Sampling Dates).

PORTUGAL COVE - BEDROCK

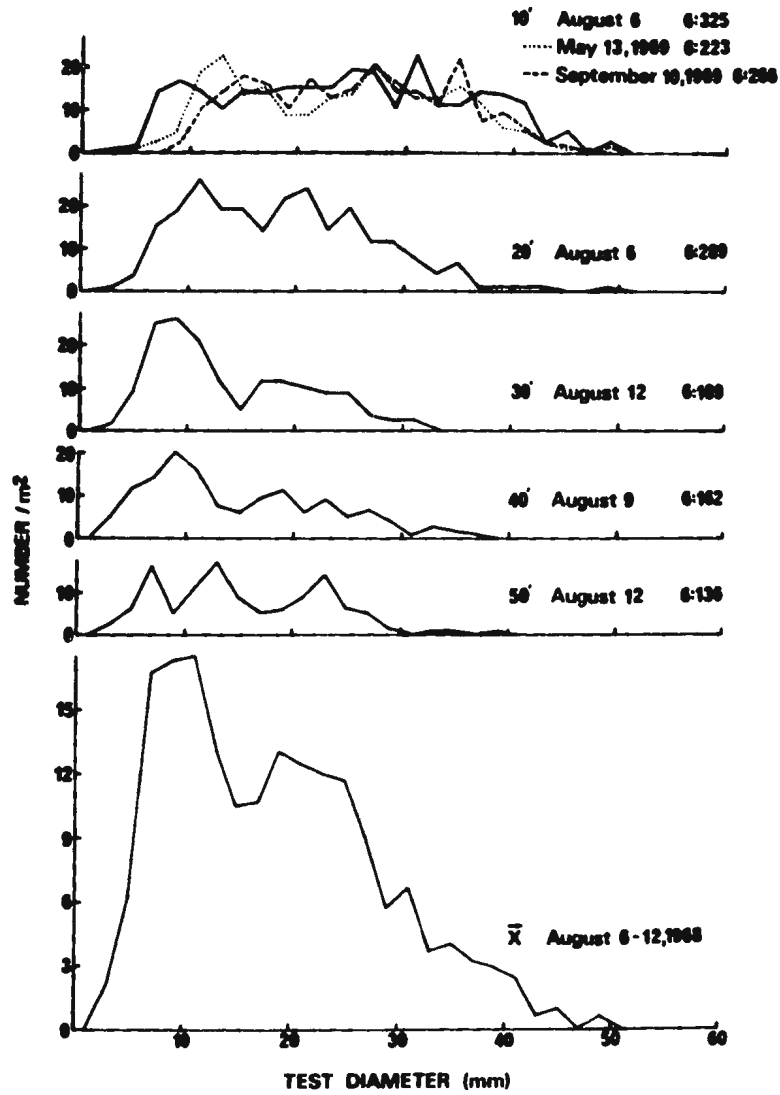


FIGURE 6b .

PORTUGAL COVE - LOOSE SUBSTRATE

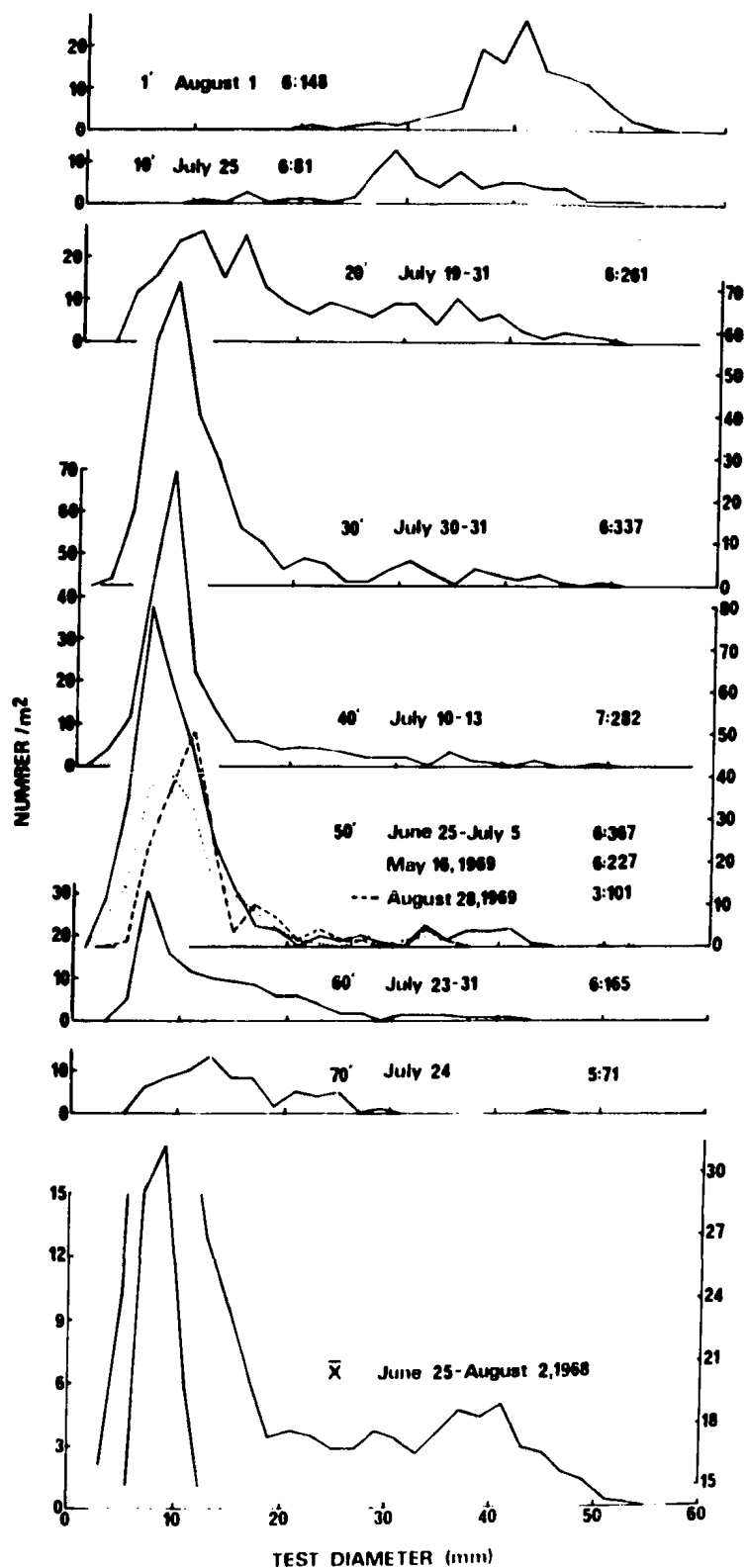


FIGURE 6c.

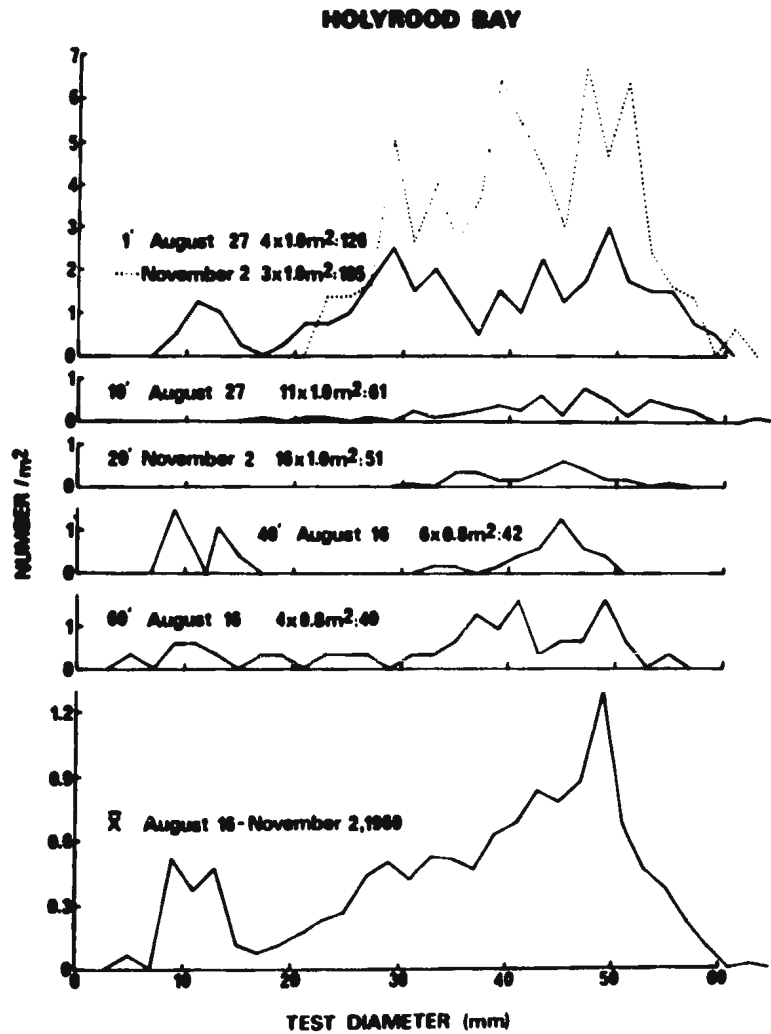


FIGURE 6d.

Portugal Cove - Bedrock (Figure 6b)

The largest urchin on bedrock at Portugal Cove measured 49.5 mm in diameter and was collected at 10 feet but at depths greater than 20 feet all urchins collected were less than 40 mm. There is a strong mode at about 10 mm in the mean size distribution and then a gradual decrease in frequencies.

Several modes are evident. The first one has its apex in the 8 - 10 mm size class at 10, 30 and 40 feet, is advanced one size class at 20 feet, and is retarded one size class at 50 feet. At 20, 30 and 40 a second peak seems evident 10 mm ahead on the first mode. At 50 feet the second mode is only advanced by 6 mm as is the second mode in most of the Logy Bay samples. Additional peaks are difficult to identify, however, they are suggested at 24 - 26 mm and 30 - 32 mm.

Resampling at 10 feet 9 months later in May, 1969 shows that the first mode has progressed 4 mm and during the following 4 summer months the peak appears to have advanced an additional 4 mm. Although the latter does not show up in the size distributions which are based on 2 mm size classes, it appears when the samples are analyzed using 1 mm size classes.

Portugal Cove - Loose Substrate (Figure 6c)

The urchins collected on loose substrate at Portugal Cove ranged from 2.1 to 52.8 mm in diameter, which is similar to the size variation encountered in the previous two transects, however, the mean size-frequency distribution is very different. The first mode is nearly twice as high as the corresponding modes in the mean distributions on bedrock at Logy Bay

and Portugal Cove and urchins larger than 20 mm are relatively uncommon, except in shallow water. The mode of young urchins rises abruptly to a peak at 8 - 10 mm, which is nearly twice as high as the corresponding modes in the mean distributions on bedrock at Logy Bay and Portugal Cove - and then drops sharply until it nears 20 mm. There are only 2.5 - 3.8 urchins/m² in the size classes from 18 to 36 mm, a few more around 40 mm and finally a decrease in frequencies to 52 mm. Most of the larger urchins are in the first 20 feet.

At 20 feet the first peak is reached at 10 - 12 mm, at 30 and 40 feet at 8 - 10 mm and at 50 and 60 feet at 6 - 8 mm. No corresponding mode of small urchins is present at 1 and 10 feet. A second mode may be present at about 21 mm.

Resampling in May, 1969, revealed that there was a decrease in the numbers of small urchins over the winter and that the first mode had progressed to the next size class. The third sample in August, 1969, indicated that this mode had advanced one more size class. Only when the samples were analyzed using 1 mm size classes was it apparent that greater growth had occurred during the summer than in the previous period. The peak of the class of young urchins was at 7 mm in the summer of 1968, at 8 mm eleven months later in May, 1969, and at 10 mm in late August, 1969.

Holyrood Bay (Figure 6d)

The low density of urchins and relative abundance of very large urchins are striking features of the urchin population at Holyrood Bay. Urchins larger than 40 mm were predominant at all depths and three urchins

larger than 60 mm were collected in samples. One of these measured 62.5 x 29.4 mm and is the largest individual encountered during sampling. The low density of urchins and the limited sampling makes interpretation of modes more difficult than in the previous transects. Apart from a small mode which rises between 2 and 18 mm, the mean size distribution gradually rises to about 49 mm and then drops to 60 mm. In spite of a very great change in the density of urchins at 1 foot from August 27 to November 2, 1968 similar modes of larger urchins can be identified.

Density and Biomass

The total density and biomass and the contribution of each of the less than 20.0, 20.0 - 39.9, and more than 39.9 mm size groupings were displayed for the various levels sampled in the 4 transects in the form of histograms (Figure 7). These 3 groupings will be referred to as the small, medium-size, and large urchins respectively. (Figure 7, Appendix IV).

Logy Bay

The density of urchins dropped progressively from 353.0 urchins/m² at 16 feet to 78.3/m² at 70 feet. An increase to 107.0/m² at 80 feet may be related to an increase in the abundance of Ptilota serrata at this depth. This was the main food material observed during gut analyses of urchins from 80 feet. The proportion of large urchins increased from 2.0 to 9.5 percent from 16 to 40 feet and then decreased to 4.3 percent at 70 feet. The former increase in samples along the walls of the Narrows, and the latter decrease occurred in the samples from outside the Gulch. Resampling at 20 feet on May 22, 1969, indicated that the density of the

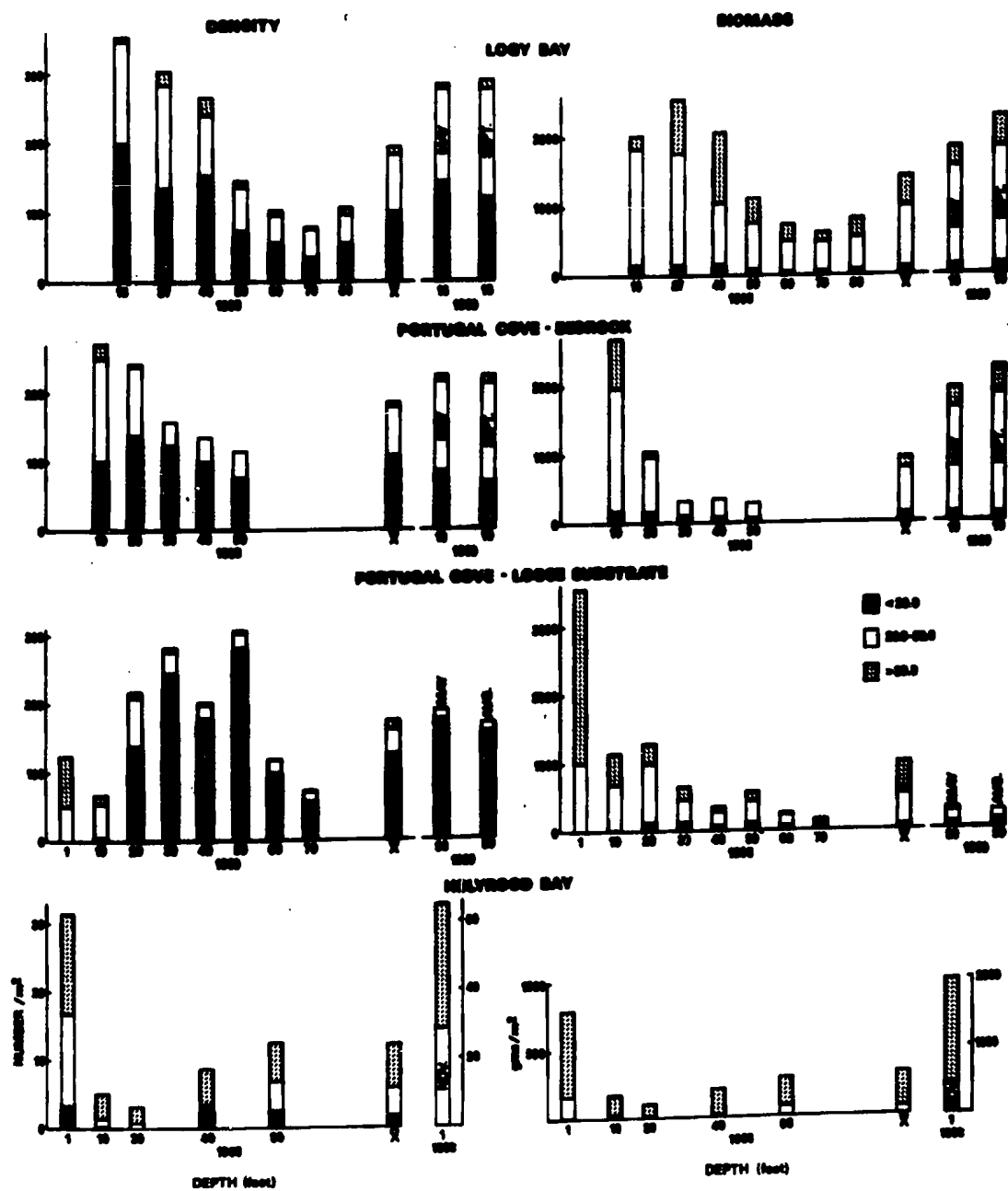


FIGURE 7 : The Density and Biomass of Small, Medium-size and Large Urchins for (1) the Various Depths Sampled in the Three Study Areas, (2) the Average of the Samples Collected on the First Dates at the Various Levels, and (3) the Resampled Levels.

urchin population at this level dropped by 71.3 urchins/m² over the winter. This drop is attributed to a drop in the numbers of smaller urchins (199.0 - 141.7/m²). The third sample on September 4, 1969, showed a further decrease in small urchins (to 120.0/m²) but an increase in larger urchins.

The greatest biomass of 2544.5 gms/m² occurred at 27 feet and at greater depths there was a progressive drop to 610.4 gms/m² at 70 feet. The small percentage of large urchins at 16 feet accounted for the greatest biomass not occurring at this level. The biomass of small urchins followed the total pattern but contributed little to the total biomass; the biomass of medium-size urchins decreased steadily from 16 feet to 70 feet and contributed most to the total biomass; the biomass of large urchins increased to 40 feet and then decreased to 70 feet.

The highest densities obtained in the 0.2 m² grids were 560 and 530 urchins/m² and these occurred in the July 6, 1968, sample at 40 feet and in the May 22, 1969, sample at 16 feet, respectively. The corresponding biomasses were over 4500 gms/m².

Portugal Cove - Bedrock

On bedrock at Portugal Cove, there was a regular decrease in the density from 270.8 urchins/m² at 10 feet to 113.3/m² at 50 feet. The density of small urchins was greatest at 20 feet and then gradually decreased with depth; medium-size urchins decreased from 10 to 30 feet and then remained about the same to 50 feet; and the large urchins decreased from 10 to 20 feet and were not present at greater depths. Biomass dropped very sharply from 2689.3 gms/m² at 10 feet to 311.4 gms at 30 feet and

remained about the same to 50 feet. The abrupt decrease was primarily due to the decline in numbers of larger urchins to 30 feet.

In May, 1969, the same area at 10 feet showed little change apart from a slight decrease which was proportionally equal for small and medium-size urchins but greater for larger urchins. In September the total density was about the same as in May, however, there was a further reduction in the number of small urchins and an increase in larger urchins.

Portugal Cove - Loose Substrate

On the loose substrate at Portugal Cove, the total numbers increased from about 100 urchins/m² in shallow water to a maximum of 305.8/m² at 50 feet and then dropped to 71.0/m² at 70 feet. This pattern is primarily attributed to changes in the density of small urchins. They were absent at 1 foot, sharply increased to 30 feet, reached a maximum of 280.0/m² at 50 feet and then dropped to 55.0/m² at 70 feet. The percentage of small urchins increased steadily from 6.1 at 10 feet to 91.6 at 50 feet and then decreased to 71.8 percent at 70 feet. The proportion of large and medium-size urchins generally decreased with decreasing depth.

There was a very high biomass of 3561.8 gms/m² on the mixed cobble and bedrock substrate below the Cobble Beach corresponding to the high density of larger urchins at that level. In two of the grids the biomass even exceeded 5000 gms/m². These values represent the highest biomass encountered during this study. An abrupt drop in biomass occurred from 1 to 10 feet and then there was a more gradual decline to 70 feet. The proportion which small urchins contribute to the total biomass increases steadily from 0.0 percent at 1 foot to 37.7 percent at 70 feet.

The resampled area at 50 feet in May, 1969, showed that over the winter both the density and biomass decreased in all three size groups. The number of small urchins was reduced by $105/\text{m}^2$. In September, only three grids were taken. However, little change appears to have occurred, except that large urchins were no longer present.

Holyrood Bay

The very low densities of urchins and relative abundance of large urchins were striking features of Holyrood Bay. The density dropped relatively sharply from $31.5 \text{ urchins}/\text{m}^2$ at 1 foot on August 27, 1968, to $5.1/\text{m}^2$ at 10 feet and then increased from its minimum of $3.2/\text{m}^2$ at 20 feet to $12.5/\text{m}^2$ at 60 feet. Since large urchins made the greatest contribution to total density at all depths, the biomass histograms present essentially the same pattern. The biomass was $794.7 \text{ gms}/\text{m}^2$ at 1 foot on August 27 and from 103.1 to $286.8 \text{ gms}/\text{m}^2$ at greater depths. Small urchins were not present on the mud substratum at 20 feet and did not occur in the grids at 10 feet where the bottom material was slightly coarser. However, they were observed on some gravel patches which projected down beyond the 10 foot level but which were outside the area of the transect. At these levels larger urchins usually congregated on scattered rocks. At 40 and 60 feet the bottom sediments consisted of gravel and coralline encrusted cobble and urchins were more common, especially smaller individuals.

The second sample at 1 foot, which was made two months later on November 2, 1968, shows that during that period the density and biomass more than doubled but small urchins were no longer present. Apparently the larger urchins, which formerly must have been more equally distributed over the

small boulders and cobbles to a depth of about 10 feet, had migrated to the very shallow water. The area was visited again on July 5, 1969, and although no samples were taken, the urchin density appeared to be slightly less than on August 27, 1968. On July 20, 1969, only about 4 urchins were found in the first 3 feet depth along 100 feet of the shore and notable growth of Chordaria, Dictyosiphon and Chorda filum had occurred since July 5. It appears that a shoreward migration may take place in the fall and that an offshore migration may occur during the summer.

Discussion

In all the study areas there was generally a decrease in the urchin biomass with increasing depth. At Portugal Cove this trend was most pronounced in the first 20 feet. An exception to this occurred at Hailyrood where the mud substrate between 10 and 35 feet was particularly unsuitable and more suitable rocky bottom was present at greater depths. Density also generally decreased with depth, except on loose substrate at Portugal Cove where the highest density was at 50 feet. This was primarily attributed to small urchins which were absent near shore but extremely abundant (about $200/m^2$) on the coralline encrusted material at 30-50 feet. Medium-size and large urchins generally decreased with depth in the usual manner. In both bedrock and loose substrate transects at Portugal Cove there was a decrease in larger urchins at greater depths. This suggests that larger urchins move from greater depths towards the shore. Certainly the abundance of readily eaten macrophytes near the surface must exert a major influence in maintaining or attracting urchins to shallower depths, so that the highest density and biomass is found near low water level.

In the eastern Murman, Propp (1964a, 1966) studied the fauna on Lithothamnion substrate at depths from 10 - 108 feet (3 to 32 m), and also found that S. droebachiensis generally decreased in both density and biomass with increasing depth. The mean density dropped from 35.7 urchins/m² and a biomass of 172 gms/m² at 10 - 20 feet (3-6 m) to 24.2/m² (824 gms/m²) at 33 - 39 feet (10 - 12 m). These values were derived from samples in two areas in the mouth of the Dalnisaia Zelenckaja River, but the densities at the same depths in the two areas did not vary significantly, however, the values for 10 - 20 feet (3-6 m) in both areas were significantly different from those at 33 - 39 feet (10 - 12 m). At greater depths the density decreased steadily to 16.2 urchins/m² (490 gms/m²) at 59 - 66 feet (18 - 20 m) and 4.0/m² (98 gms/m²) at 105 feet (32 m). These density values seem very low compared to those on Lithothamnion substrate at Logy Bay and Portugal Cove, but his biomass estimates compare more favourably. Large urchins were apparently relatively common at all depths as at Logy Bay. It may be that Propp did not bother to sample very small urchins since they are difficult to collect and their contribution to total biomass is small. Propp (1964a) also recorded much higher densities of urchins (up to 170 - 250 /m²) which completely covered the bottom where the Lithothamnion substrate bordered Laminaria beds. Strongylocentrotus droebachiensis was the most prevalent animal at all depths.

In an earlier study in the eastern Murman, Kusnetzov (1946) noted that S. droebachiensis was most abundant near the shore. He suggested that this was related to the presence of the macrophytes in shallow water, since they are the main food source of this species. Sometimes densities of 180-220 urchins/m² and biomasses of 6.0-61.5 kg/m² were reached in depths of up

to 26 feet (8 m). The latter represents the highest biomass ever reported for S. droebachiensis.

In a sheltered bay in Greenland, where there was little ice because of strong currents, Madsen (1940) also observed that this species was abundant in the upper sublittoral and especially near low water level.

The differences in the size compositions, densities and biomasses in the three study areas can be related to the effects of waves and exposure, and substrate on settlement, survival and growth.

The greatest quantities of urchins occurred at Logy Bay where the exposure was greatest and where bedrock predominates to 60 feet or more. The highest density (353 urchins/m²) occurred at 16 feet on the steep bedrock walls just below the Alaria zone, and densities of over 250/m² were present to 40 feet, near the bottom of the Narrows. Outside Dyer's Gulch densities of about 100 urchins/m² were present to 80 feet. Such high densities suggest that settlement in this area is normally very high. Nevertheless, the relative scarcity of large urchins (6.39 %) indicates that survival is not great. Similarly, very high biomasses of over 2,000 gms/m² occurred along the walls of the Narrows and of 1112 - 610 gms/m² were present outside the Gulch to 80 feet. S. droebachiensis is very well adapted to clinging to the bedrock surfaces as it takes considerable force to remove an urchin from its substrate when turbulent water is flowing over it. Although large urchins were common on the boulders and cobble lining the Gulch, they were uncommon on the Bar and on the loose substrate which gently slopes out from the Gulch. Here urchins are likely to be crushed by stones which are thrown around by high waves which surge upon this area during winter storms. The turbulent

conditions at Logy Bay frequently break off pieces of macrophytes from the intertidal and sublittoral fringe and distribute them to greater depths. For example, pieces of Alaria were commonly found at all depths along the walls of the Narrows and during the summer great quantities of this alga collect in the deeper parts of the Gulch. This may explain the increasing numbers of large urchins at greater depths within the Gulch (as shown in the samples from 16 to 40 feet).

At Portugal Cove, exposure is more moderate and bedrock and loose substrates are both common along the shore. The urchin population on bedrock showed a marked similarity to that at Logy Bay but densities and biomasses at similar levels were less and large urchins were concentrated in shallow water. The density decreased from 271 urchins/m² at 10 feet to 113/m² at 50 feet and the biomass dropped from 2689 gms/m² at 10 feet to 1044 gms/m² at 20 feet and was about 300 gms/m² at 30-50 feet. The lower densities suggest that settlement is not quite as great as at Logy Bay.

There also appears to be a downward displacement with increasing depth in the bedrock populations of S. droebachiensis which Propp (1964b, 1966) studied in the eastern Murman. In the mouth of Dalniaia Zelenckaja there were 22.7 urchins/m² or 703 gms of urchins/m² on Lithothamnion substrate at 29.5 feet (Propp 1966) but on the same substrate and at the same depth in a more exposed area near Great Ainov Island there were 34 urchins/m² of 1080 gms/m² (Propp 1964b). The latter density and biomass were similar to those at 13.1 feet at Dalniaia Zelenckaja.

A very dense urchin population was also present on loose substrate at Portugal Cove. However, the absence of small urchins and abundance of

large urchins near the shore, and the abundance of large urchins at greater depths, are notable. The rock material in shallow water was well rounded by abrasion. It is likely that movements of this loose material during storms have crushed, and thus eliminated small urchins. Larger urchins which are not as easily crushed occurred near the shore in densities of $123/\text{m}^2$. At greater depths, where wave action has less effect, the substrate showed no signs of abrasion since it was heavily encrusted with crustose corallines. Very high densities of over $200 \text{ urchins}/\text{m}^2$, mostly small urchins, occurred between 20 and 50 feet. Biomasses on the loose substrate abruptly dropped from $3562 \text{ gms}/\text{m}^2$ at 1 foot to about $1200 \text{ gms}/\text{m}^2$ at 10 and 20 feet and then varied from 663 to $153 \text{ gms}/\text{m}^2$ to 70 feet. Apparently settlement and early development have been very successful in this area, except near the shore.

Holyrood is a sheltered area and substrates varied from loose rock material to mud. Urchin densities were very low, but the percentage of large urchins was very high at all depths which is in marked contrast to the other areas. The highest density occurred at 1 foot in November, 1968, ($65/\text{m}^2$), but this is less than the lowest densities at any of the levels sampled in the other areas. However, the biomass of large urchins in this sample was $1537 \text{ gms}/\text{m}^2$, which is only surpassed at 1 foot below the Cobble Beach at Portugal Cove where large urchins also predominated. The relatively very low densities at Holyrood indicate that settlement must be very poor in this area, however, there must be very high survival since very large urchins are relatively abundant.

In Florida McPherson (1969) found that the tropical sea urchin, Echinometra lucunter, was larger on offshore areas than on highly exposed

water reefs and suggests that this is due to either a faster growth rate or greater longevity on the former.

A tendency of echinoids to aggregate during the breeding season has been recorded for Echinocardium cordatum (Orton 1914, Buchanan 1966), Psammachinus miliaris (Orton 1914), Tripneustes esculentus (Lewis 1958) and Lytechinus variegatus (Moore et al. 1963) and a shoreward migration has been indicated in Echinus esculentus (Elmhurst 1922, Scott 1931, and by the data of Kain and Jones 1967). It is very possible that the congregating of urchins in shallow water at Holyrood during the winter is a result of a similar phenomena in S. droebachiensis.

Mitchell's Brook, Salmonier Arm, St. Mary's Bay is a very sheltered inlet and both the types of substrate and urchin population were notably similar to those at Holyrood. The area was only visited on two occasions, and samples were not collected. Cobble and small boulders bordered the shore, sand predominated at depths of 15 to 40 feet, and jagged cobbles were present at greater depths. The largest urchins I have seen, 50-72 mm in diameter, were very conspicuous near the rocks along the shore and were scattered over the sand zone where Echinarachnius parma were common. At 40-60 feet the urchin population appeared very similar to that level at Holyrood.

Thus the urchin populations in sheltered areas appear to be characterized by light settlement, low densities and very high survival. On the other hand where wave exposure is more severe, densities (especially of smaller urchins) and biomasses are very high, but survival is relatively low.

Dexter (1944) reported that S. droebachiensis was a dominant in the bottom community of Ipswich Bay, Massachusetts, however, his highest density was only about $0.4/m^2$. In a similar community of the Pacific Coast, between Victoria, British Columbia, and the mainland, Shelford et al. (1935) recorded densities of $4.0 - 20.0$ S. droebachiensis/ m^2 . Wismer and Swanson (1935) made a more detailed study near Brown Island in San Juan Strait and found that the highest density of 10 S. droebachiensis/ m^2 occurred at $6.6 - 19.6$ feet on a shell-sand bottom near eel grass and kelp. From 26.2 to 108.3 feet the bottom was mud and densities varied from 2.2 to $5.2/m^2$. The latter estimates were obtained from dredge hauls, however, they are very low compared to the densities in Newfoundland and in the eastern Murman. Undoubtedly the soft substrate in these areas must be an important factor. In an exposed area at York, Maine, Swan found 1305 urchins in an area about $3 m^2$ on a low intertidal ledge. Small urchins made up 59.2 percent of these, medium-size urchins 35.5 percent and large urchins 5.4 percent. Both the high density and high mortality in this sample compares very favourably with the bedrock populations at Logy Bay and Portugal Cove.

In 1968 and 1969, spawning in the urchin population at Portugal Cove was concentrated from about February through April. Urchin recruitment was apparently very poor in all the study areas, since very small urchins (less than 3 mm in diameter) were very rare. In Norway, Greig (1928) found small urchins, $0.5 - 2.5$ mm in diameter, during the summer of 1923, and at York, Maine, Swan observed that $0.5 - 1.5$ mm urchins were common in June, 1953, but not in June, 1957. Both Greig and Swan agree that these very small individuals represent newly settled urchins from the early spring spawning.

A strong mode of small urchins occurred in the mean size frequency distributions for the 4 transects. At 16 feet at Logy Bay, this mode occurred at 6 mm in June-July, 1968; advanced to 10 mm by May 22, 1969; but remained stationary during the summer until September 4, 1969. At 10 feet on bedrock at Portugal Cove the corresponding mode was at about 8 mm on August 6, 1968; had shifted to 12 mm by May 13, 1969; and to 15-16 mm by September 10, 1969. The increase of this mode suggests that it and the following modes represent successive year classes. The fact that the advancement was nearly twice as great at Portugal Cove (8 mm) as at Logy Bay (4 mm), in a period of slightly more than a year, indicates that growth is greater at Portugal Cove, where the exposure is not as great. The latter was further indicated by the wider spacing of the following modes, which probably are successive year classes, at Portugal Cove (see below). The above modes of small urchins likely represent urchins from a very successful recruitment in 1967.

A very distinct class of 1 year old urchins between 3-16 mm, which reached a peak at the same position as in the mean size distributions (8 - 10 mm) was also present in the population studied by Swan (1958) in 1957 in Maine. At 16 feet at Logy Bay, at 50 feet on bedrock and at 40 to 60 and perhaps 70 feet on loose substrate at Portugal Cove the 1 year mode of urchins was at 6 - 8 mm. This closely corresponds to the 1 year old mode of urchins at 5-6 mm which Grieg (1928) found in samples from 0 - 49 feet in the Folden Fjord, Norway. The size ranges indicated by Soot-Ryen (1924) and Schorygin (1928) for the corresponding year class are 6 - 10 mm in Ramfjorde, Norway, and 7 - 11 mm in the Barents Sea, respectively. However, it should be noted that Swan (1961, 1967) has indicated that Grieg and

Soot-Ryen may have been dealing with S. pallidus as well as S. droebachiensis and that Schorygin's collections were S. pallidus. I would support Swan's suggestion that the latter two workers have listed their year class estimates a year too young. They considered that the above mode, which occurred in summer collections, represented urchins from the same year's spawning. However, my observations indicate that this mode is already present in the spring when urchins from the early spring spawning are barely visible.

The mean size distribution on bedrock at Logy Bay and Portugal Cove decreased in a regular manner from peak frequencies of near 17 urchins/m² in the 8 - 10 mm size class to very low frequencies at 50 mm. At Logy Bay succeeding modes fell in the 14 - 16, 22 - 24, 26 - 28, and 30 - 32 mm size classes and at Portugal Cove peaks are suggested at 18 - 20, 24 - 26 and 30 - 32 mm. These modes most closely correspond with those at 15, 23, and 30 mm in Grieg's data (1928). Soot-Ryen (1924) reported wider spaced yearly modes at 18, 23, 37 - 38, and 48 mm and although Schorygin (1928) was probably dealing with S. pallidus it is notable that the size ranges he records for older year classes agree with the estimates of Soot-Ryen. Swan's (1961) estimated modal diameters at 24 - 26, 40 - 42 and 46 - 54 (?) mm for 2, 3 and 4 year old urchins are comparatively high, however, his studies were made in the southern part of the range of S. droebachiensis and warmer water temperatures may contribute towards faster growth rates. Also Laminaria spp. was fed to the urchins in growth experiments he conducted which supported these modes. His own data demonstrated that growth was much greater on this alga than on Ascophyllum nodosum and a more recent study by Vadas (1968) showed that S. droebachiensis grew much faster on Laminaria saccharina than

on Agarum cribrosum and A. fimbriatum. At Logy Bay Laminaria digitata was only scattered amongst the Alaria. At Portugal Cove it was absent in the study area but Ascophyllum was abundant intertidally. Agarum cribrosum was scattered in both areas.

The size distributions at various depths differed from the mean distribution for each transect. The mode of small urchins at 10 feet at Portugal Cove was not nearly so prominent as at 16 feet at Logy Bay and urchins larger than 40 mm were absent below 20 feet at Portugal Cove but not at Logy Bay. The resemblance of the size distribution, density and biomass patterns at 10 and 20 feet at Portugal Cove to those at 27 and 40 feet respectively at Logy Bay probably indicates that there is a downward displacement of Portugal Cove conditions at Logy Bay due to the greater exposure.

The mean size distribution from loose substrate at Portugal Cove was unlike that from bedrock. The mode of small urchins occurs in the same position, but was about twice as high. There is a sharp drop in urchin diameter frequencies to about 19 mm, and then no further drop until after 40 mm. The very pronounced mode probably represents 1 year old urchins, from the 1967 spawning. If so, settlement and early survival were apparently much more successful on loose substrate than on bedrock, except in shallow water, where smaller urchins are probably destroyed by wave action as previously suggested. The explanation for the drop in frequencies to 19 mm is not yet known. This may have been an unusually successful year class, or it is possible that urchins after reaching a size of about 15 mm tend to move away, perhaps to shallower water where they could easily be crushed by moving rocks and thus eliminated.

At Holyrood, while there is some suggestion of a similarly positioned but very small mode of small urchins, the relative increase in the frequencies of urchins with increasing size is a much more striking feature. As previously indicated, the low densities but increasing frequencies of larger urchins in this area indicate that although settlement is poor, survival is great.

Both at 10 feet on bedrock and at 50 feet on loose substrate at Portugal Cove, the first mode advanced considerably more during the 4 summer months of 1969 than during the 9 - 10 months previous to May, 1969. At Portugal Cove, there is also a trend towards decreased growth with increasing depth. This is indicated by the modal advancement, which was more than twice as great at 10 feet than at 50 feet, and by the position of the first mode at the various levels in the samples from the summer of 1968. The mode of young urchins was at 6 - 8 mm at 60 and 50 feet, 8 - 10 mm at 40 and 30 feet and at 10 - 12 mm at 20 feet. The only exception in this trend appeared at 10 feet where it was back one size class at 8 - 10 mm. Buchanan (1966) also observed slower growth rates at greater depths in Echinocardium cordatum. A strong mode from a heavy settlement in 1968 progressed 8 mm/year in a littoral population and only 2 mm/year in an offshore population at 98-131 feet. The offshore population was on a silty substrate which was rich in organic content and the littoral population lived on clean sand, however, Buchanan suggested that E. cordatum may be morphologically better suited to extracting food from coarser material or that the organic material at greater depths may not be a suitable food. If young S. droebachiensis feed more on macrophytes than on decaying detritus certainly their food would be more abundant near the surface and growth would be limited at greater depths.

In both the shallow water bedrock samples at 10 feet at Portugal Cove and at 16 feet at Logy Bay the first mode was not as far advanced (by one size class) as at the next level sampled. Ebert (1966, 1968) has shown that growth of S. purpuratus may be reduced by excessive spine breakage, since the urchin must utilize some of its total energy budget, which would otherwise be used for growth, in repairing spines. Heavy wave action near the surface likely causes spine breakage, so that this factor may explain the above situation. It was frequently noted that larger urchins in shallow water at Logy Bay and Portugal Cove, especially those in crevices amongst the Alaria beds, has short thick spines, whereas, urchins from greater depths had long slender spines. This could contribute towards the slower growth rate at Logy Bay as indicated by the slower progression of the mode at 16 feet and by the closer spacing of succeeding modes.

Ebert (1966, 1967, 1968) studied 3 subpopulations of S. purpuratus at Sunset Bay, Oregon, and found that in each population the growth rate varied and that the yearly modes of small urchins could be identified for 2 or 3 years and then were obliterated when they fused with the more static group of adult urchins. He also found that in some instances that urchins could resorb calcite and shrink in size (Ebert 1967). The food supply appeared to be the main governing factor and he hypothesized that the growth rate and ultimate size, but not the numbers, of urchins is limited by the availability of food. Leighton (1967) found that the same situation existed in Southern California in areas where food was limited, and suggested that the size of the urchins in the stationary mode of adult urchins reflects the food conditions. In the very dense bedrock populations at Portugal Cove and

Logy Bay there is no indication of such a buildup of adult urchins of similar size. Instead there is a steady decline in the numbers with size which probably represents a natural mortality rate. Food limitation could possibly contribute towards the slow growth rate of these populations. Ebert's hypothesis may have value in interpreting the very strong mode of large urchins at 49 mm at Holyrood and the slight buildup at 40 mm on loose substrate at Portugal Cove.

The diameter: age relationship of S. nudus and S. intermedius as reported by Kawamura (1966) and Fuji (1967), respectively, indicates that growth is much faster in these species to the size of about 35 mm test diameter, but similar to S. droebachiensis in larger urchins. Studies by Swan (1961), North (1967) and Ebert (1968) suggest that S. purpuratus and S. franciscanus grow at a similar rate, or sometimes faster in the first 2 or 3 years.

Feeding

Field Observations

During the course of this study many field observations were made on the grazing behaviour of urchins. In the winter months of 1968-69, there was a heavy settlement of Alaria esculenta at Portugal Cove. On the west side of the Basin a dense growth covered the bedrock surfaces to a depth of 3 - 5 feet from the Point to about half way up the Basin. During April and May urchin browsing raised the lower limit of Alaria by about 2 feet. On numerous occasions, particularly on calm days, there was an almost continuous band of urchins, 6 - 14 inches in width, crowded along the bottom of the Alaria zone (Plate V). By June or July the entire area inside the Point was completely cleared of Alaria and other macrophytes to slightly above low water level. Alaria was also removed from the pools inside the Outer Ridge and by the end of August only the stipes of Alaria and Fucus plants remained. Stipes of grazed-off Alaria were also common in deeper more exposed areas at the end of the summer (Plate VII).

A similar situation occurred at Logy Bay where a solid zone of larger urchins was frequently seen destroying the young Alaria plants which had settled at greater depths further inside the Gulch during the winter. Also, whenever it was calm, the blades of older plants would hang down along the walls of the Gulch where they would be anchored and devoured by aggregations of urchins. The stipes seem to be more resistant to grazing and are the last portion of the plant to be utilized.

During periods when there was swell action, these aggregations were usually dispersed downwards so that no distinct band of urchins was

evident. The part water movement plays in protecting the macrophytes from urchins was displayed on several occasions on the walls of the Narrows. Plants of Desmarestia viridis and Agarum cribrum rotated from their points of attachment, and within the circular areas over which they moved no urchins were apparent; but the normal dense urchin cover (as shown in Plate I) existed outside these areas.

Bands of urchins have also been observed around Monostroma sp. in the spring. In 1968, there was a luxuriant growth of Desmarestia viridis on the bedrock ridges and outcrops off the Point at Portugal Cove. In August, though, when it was frequently calm, the urchins weighed down and consumed this alga (Plate VI). At various times, Portugal Cove congregations of urchins, with pieces of fucoids wrapped around them, were commonly seen in the shallow crevices around the Basin. During the summer, there were masses of urchins gorging on Alaria which had collected at the bottom of the Gulch at Logy Bay. Kuznetsov (1946) also reported that feeding on torn-off algae is a dominating phenomenon during certain times of the year.

At Portugal Cove, whenever pieces of macrophytes drifted to greater depths (which were generally devoid of such material) urchins would quickly devour them (Plate VIII). In July, 1968, a large clump of Ascophyllum nodosum and another of Fucus vesiculosus were anchored on the cobble substrate at 50 feet. After a few days larger urchins completely covered this material and after 6 days only a few fragments remained. The ability of urchins to detect and locate food has been seen in the lab. Starving urchins are usually stationary, but when a piece of Laminaria is added their podia soon become active and the alga is quickly found. On July 5, 1968, a galvanized

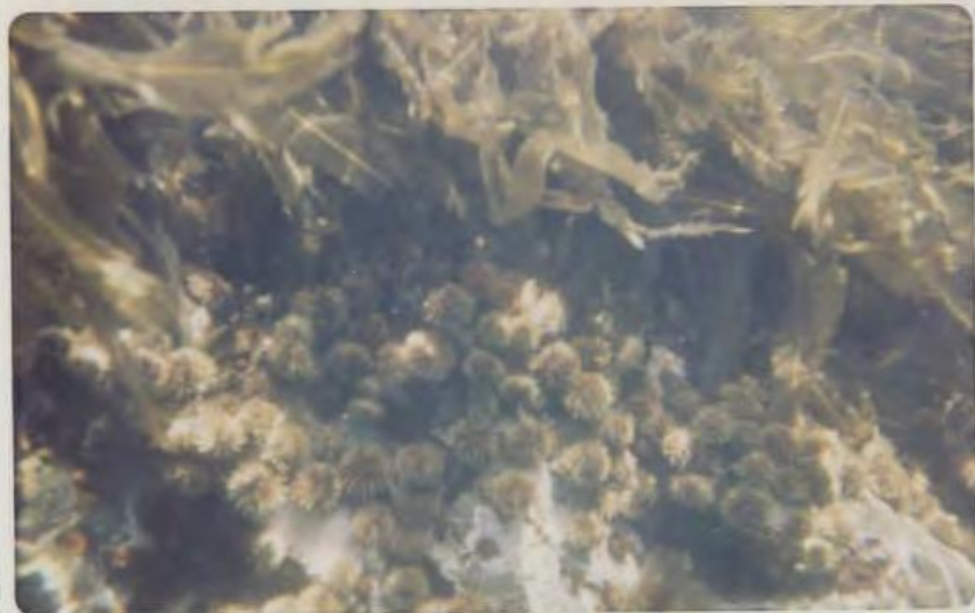


Plate V: Herds of larger urchins grazing at the bottom of the zone of young *Alaria esculenta* inside the Point at Portugal Cove. (May 13, 1969). One month later *Alaria* was absent in this area. (Depth 3')



Plate VI: A congregation of larger urchins holding down and devouring *Demarestia viridis* at Portugal Cove during a calm period in August, 1968. (Depth 10')

Plate VII

High density of larger urchins at about 12 feet near the bottom of the Alaria zone on the seaward side of the Outer Ridge, Portugal Cove in September, 1969. The stipes are the last part of A. esculenta to be eaten and grazed-off plants are common at the end of the summer. Note the grazing scars on the stipes. Most of the bedrock surfaces at this depth are covered with crustose corallines and clumps of Cerallina officinalis are common.



Plate VIII

The loose substrate at 35 - 40 feet at Portugal Cove which is devoid of macrophytes other than crustose corallines which cover the rock surfaces and Volsella medialis. A piece of Desmarestia viridis has washed down and is being eaten by urchins which have been attracted to it.



wire mesh cage, which excluded larger urchins from a 1 square meter area, was set out at 50 feet. Half the area was lined with the heavily coralline encrusted cobble from that level and the rest with clean cobbles from the Cobble Beach. On September 10, 1969, one small Agarum plant, 18 cm in length, was present in the cage. This alga did not occur below 40 feet outside the cage at Portugal Cove. Ptilota grows poorly on the cobble substrate but a slightly greater growth occurred on the Lithothamnion covered surfaces in the cage. Small spots of crustose algae, a few millimeters in diameter, were scattered on the surfaces of the clean cobbles.

Thus the field observations make it clear that grazing, both upon attached and living macrophytes and upon algal detritus, is an important activity of S. droebachiensis.

Food of S. droebachiensis

Gut analyses made on urchins, collected between February 2 and November 29, 1968, in shallow water at Portugal Cove for gonad samples, provided information on the diet of this animal (Table II). It was found that the gut materials reflected the foods available where the urchins were collected. Throughout most of the year, small green and yellow-brown pieces of phaeophytes (mostly fucoids and Alaria esculenta) constituted the bulk of the gut contents. In March, though, Monostroma sp. was very abundant in the collecting pools. It was in fact the most common material. Small quantities of Pilayella littoralis (a very common epiphyte on the fucoids) also occurred frequently. Corallina officinalis, which was abundant in the pools inside of the Outer Ridge, was scattered and occasionally abundant in the viscera of 20 - 65 percent of the samples.

TABLE II: The incidence (%) of the materials most commonly found in the gut of S. droebachiensis in shallow water at Portugal Cove in 1968.

DATE	February 2	March 28	May 29	June 29	July 29	August 29	September 29	October 30	November 29
Phaeophytes (fucoids and <u>Alaria esculenta</u>)	65.85	66.67	95.00	100.00	100.00	100.00	100.00	90.00	100.00
Brown globules of sand, diatoms, detritus, etc.	12.20	33.33	00.00	10.00	40.00	30.00	30.00	30.00	10.00
<u>Coralina officinalis</u>	48.78	38.10	65.00	20.00	30.00	40.00	20.00	30.00	60.00
<u>Pilayella littoralis</u> , <u>Urospora</u> spp. etc.	21.95	9.52	10.00	80.00	95.00	50.00	15.00	30.00	0.00
<u>Monostroma</u> sp.	0.00	90.49	5.00	15.00	0.00	0.00	0.00	0.00	0.00
<u>Ulva</u> sp.	0.00	0.00	0.00	0.00	0.00	0.00	10.00	20.00	10.00
<u>Ptilota serrata</u>	17.07	38.10	10.00	0.00	0.00	0.00	0.00	0.00	0.00
Fragile white calcareous globules	70.17	66.67	100.00	75.00	65.00	65.00	75.00	0.00	90.00
Hard calcareous chips	2.44	0.00	30.00	20.00	5.00	25.00	5.00	0.00	0.00
<u>Balanus balanoides</u>	0.00	0.00	5.00	20.00	0.00	5.00	70.00	10.00	0.00
<u>Mytilus edulis</u>	46.34	38.10	45.00	55.00	20.00	60.00	80.00	80.00	60.00
Small gastropods	12.00	9.52	5.00	0.00	5.00	0.00	15.00	10.00	50.00
NUMBER	41	21	20	20	20	20	20	10	10

Fragile globules of white calcareous material, which may originate from Corallina or from crustose corallines, were scattered to abundant in 65 - 100 percent of the urchins and hard calcareous chips, which likely came from the latter, were present in some urchins. The guts of 6 urchins, which had been kept in a tank for about half a year with Lithothamnion as the only food, contained little other than the fragile white globules, which often contained some harder material, and the chips of Lithothamnion. It is interesting that two of these urchins contained some blue material, apparently scraped from the sides of the fiberglass tank. In a similar situation starving urchins grazed tracks through the painted wood partitions which separated them in a holding tank. Soft brown globules, consisting of such materials as sand, diatoms and detritus, were common in up to 40 percent of the Portugal Cove samples.

Ptilota serrata was only present in February through March, when it was commonly washed in from greater depths. Urospora spp. were scattered in a few individuals during the spring months and Ulva sp. was present in the fall.

The incidence of small Mytilus edulis, mussel fragments and the shiny byssal fibers was 20 - 60 percent in the samples from the pools, but 60 - 80 percent in urchins from along the east side of the Point. Small Balanus balanoides, and fragments of the same, usually occurred in only a few individuals, however, they were present in 70 percent of the September sample. Mussels and barnacles were usually present in small quantities but in a few instances they predominated. A few small gastropods (Lacuna vineta and littorinids) usually occurred in a few individuals each month, and in November were present in 50 percent of the sample.

Fragments of ambulacral plates, Polysiphonia spp., wood and other vascular plant tissues, feathers, bryozoans and nudibranchs were only observed infrequently.

On July 5, 1968, 3 urchins from 50 feet at Portugal Cove contained mostly hard white or pinkish calcareous chips, undoubtedly from Lithothamnion nodules. Fragile white globules and Ptilota were common in all 3 and soft detritus globules and a filamentous green each occurred in only one individual. Seven urchins, collected from 30 feet at Logy Bay on July 8, contained pieces of Alaria in abundance and smaller amounts of fragile white globules. Shiny fibers, probably from mussels, were found in 2 individuals and Ptilota was present in 1 urchin. Ptilota was the main material in 4 urchins from 80 feet on bedrock where this alga was growing.

When urchins and sand dollars, Echinarachnius parma, were put in the same tank in the laboratory the latter were readily preyed upon by the urchins. The spines were first grazed from the sand dollar test, particularly along the edge of the test, and eventually a hole was eaten through the apical region (Plate XB). This situation may occur in areas, for example Salmonier Arm, St. Mary's Bay, where these species are found together on sand.

Dawson (1868), Scott (1901) and Wease (1926), have examined the gut contents of S. droebachiensis in North America and they agree that this animal is principally a plant eater. It is interesting that they, but not the European workers (below), have indicated that the urchin forms its food into small globular pellets as was observed in the Newfoundland examinations.

Weese (1926) studied the urchins at Friday Harbor, Washington, and found the digestive tracts of the urchins there contained mostly Ulva, Zostera and Fucus. Urchins as deep as 250 m also contained plant material from shallow water and thus he noted that the vertical distribution of urchins was not limited by where their foods grow, as is the case with terrestrial animals, since water movements distribute their foods.

Macrophytes must have been absent where Dawson (1868) collected his urchins at Tadoussac, Quebec, since epibenthic microphytes were the main food material in his observations.

Scott (1901) made extensive examinations of urchins from several habitats in the St. Andrews Region, N.B. and ascertained that this urchin's diet depends on the foods available in the specific environment in which it is found. Urchins near fucoids and laminarians were filled with small, 1 - 2 mm, pieces of these seaweeds and urchins not near macrophytes contained globular masses chiefly made up of sand, diatoms and other microphytes.

Although fish are not commonly part of the urchin's diet, Packard (1893) and Scott (1901) record that they are readily devoured when present, i.e. around fishermen's wharfs. I have also observed this in Newfoundland and in such instances urchins usually show a preference for fish over seaweeds. Large quantities of capelin (Mallotus villosus) may be consumed by urchins when they come to the coast to spawn in June and July.

In Danish waters, Blegvad (1915) and Jensen (1915) found that plant material (particularly Zostera) was the principal material in the gut of S. droebachiensis and that epiphytic bryozoans, sponges and hydroids were

also common. Small gastropods, aphrodites, gammarids, small barnacles, Ophioglypha spp., and ascidians were present only in small quantities. In Norway, Awerinzew (1911) tried (unsuccessfully) to relate the reddish or purplish colouration of some urchins to the Lithothamnion substrate on which they were found. Similar colour variation has also been seen at Friday Harbor (Weese 1926) and in Newfoundland. Kuznetsov (1946) made gut analyses of urchins from the shallow water in the eastern Murman and found that the littoral and sublittoral algae were predominant. He also recognized seasonal variation related to the foods available in the different seasons. In the summer Laminaria saccharina was very abundant and urchins fed mainly on this alga, but in the fall when Laminaria became less common along the coast Desmarestia aculeata, Fucus and Urospora became important constituents in the urchin's diet.

Richelbaum (1910) and Mielch (1922) found that hydroids, polychaetes and sponges were predominant (macrophytes were rare) and concluded that S. droebachiensis was primarily a predator. It is likely that the specimens they examined were some distance from large algae, perhaps in deeper water.

These numerous observations make it clear that plant material, particularly macrophytes, are the principal food of S. droebachiensis. However, smaller quantities of slow moving or sessile animals and carrion are regularly ingested along with plant material or when algae are not available.

Feeding Experiments

Feeding Under Light : Dark Periods

From April 20 to 30, 1969, 20 and 50 mm urchins were studied under alternating 12 hour light (200-400 lux): 12 hour dark periods. The water temperature varied from 1.2 to 2.0°C. There is little difference in the amount of food eaten in the light and dark periods (Table III), but the mean amount of faeces excreted is greater during the light intervals. The latter difference is not significant ($P = < 0.05$).

Effect of Size on Feeding

Feeding abilities of 7 size groups of urchins on Laminaria spp. were investigated from February 10 to 22, 1969, when the water temperature was 1.0 - 1.5°C. The results of this study are in Appendix VI. The relation of the amount of food eaten (c), the amount of faeces excreted (f), and the feeding rate to test diameter (d) are shown in Figure 8. When the values are plotted against test diameter on log-log graph paper these relationships are linear, with the exception of the consumption rate (c) of 10 mm urchins. However, this is likely an error since the method employed is only capable of giving a rough estimate of the amount of food eaten by such small urchins. The equations of these lines, which are shown in the figures, as derived by the method of least squares from the data on 20 to 70 mm groups, are as follows:

$$\text{Food eaten (mg wet weight)/urchin/day } c = 0.2323 \times d^{2.0970}$$

$$\text{Faeces excreted (mg dry weight)/urchin/day } f = 0.0022 \times d^{2.5831}$$

$$\text{Feeding rate (Z)} \quad r = 30.87 \times d^{-0.7528}$$

TABLE III: Feeding abilities of two size groups of urchins under alternating light : dark periods during April 20-30, 1969. (Water temperature 1.2 - 2.0°C).

Size Group	12 HOUR LIGHT PERIOD (200 - 400 lux)						12 HOUR DARK PERIOD					
	<u>\bar{X} FOOD EATEN</u>	<u>SE</u>	<u>N</u>	<u>\bar{X} FAECES EXCRETED</u>	<u>SE</u>	<u>N</u>	<u>\bar{X} FOOD EATEN</u>	<u>SE</u>	<u>N</u>	<u>\bar{X} FAECES EXCRETED</u>	<u>SE</u>	<u>N</u>
19.0 - 20.9	59.71	5.02	8	5.14	0.45	9	67.75	10.64	10	3.66	0.23	9
49.0 - 50.9	324.99	30.19	9	21.00	1.66	9	320.24	29.11	10	13.45	2.01	10

	FOOD EATEN mgs (WET WEIGHT) URCHIN/DAY			FAECES EXCRETED mgs (DRY WEIGHT) /URCHIN/DAY			FOOD EATEN URCHIN WEIGHT (gms %)		ASSIMILATION EFFICIENCY (%)
	<u>\bar{X}</u>	<u>SE</u>	<u>N</u>	<u>\bar{X}</u>	<u>SE</u>	<u>N</u>	<u>(gms %)</u>		<u>(%)</u>
19.0 - 20.9	119.90	8.61	8	8.76	0.51	9	3.19		23.80
49.0 - 50.9	651.39	49.46	9	35.34	3.26	9	1.29		43.39

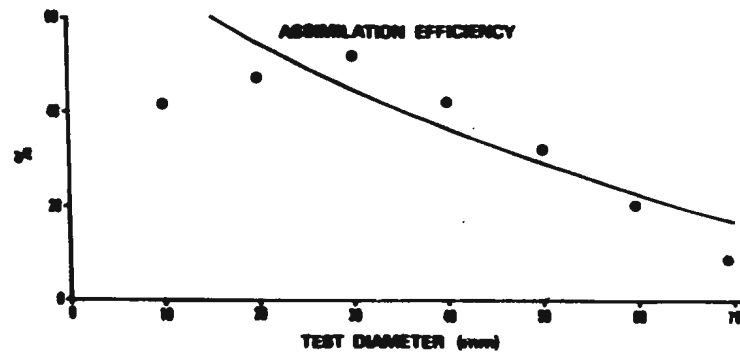
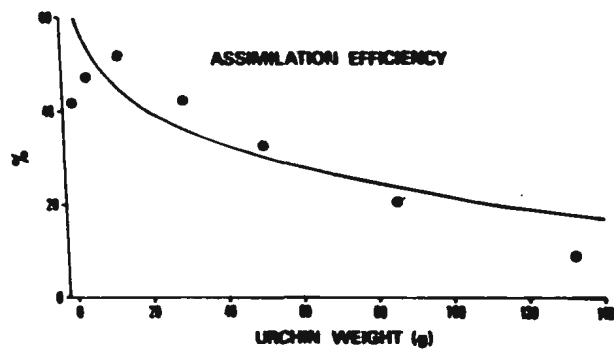
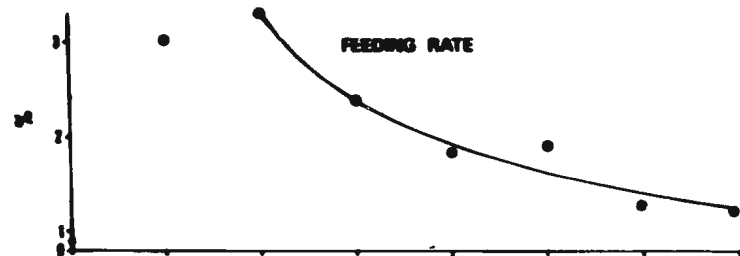
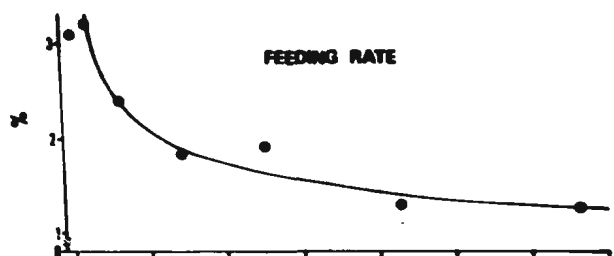
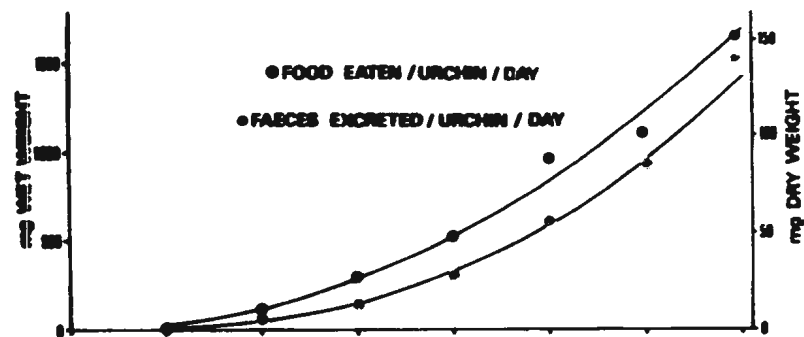
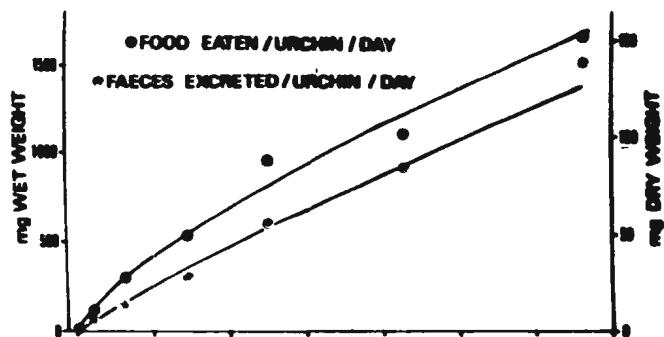


FIGURE 8 : The Feeding Abilities of Various Sizes of S. droebachiensis on Laminaria spp. during February.

The amount of food eaten increases from 124 mg (wet weight)/urchin/day for 20 mm urchins to 1718 mg/day for 70 mm urchins. The amount of faeces excreted is 5 mg (dry weight)/urchin/day for 20 mm urchins and 130 mg/day for 70 mm urchins. The latter increase is proportionally slightly greater, as is indicated by the greater slope in the equation for f. The feeding rate decreases as the urchin becomes larger. For example, a 20 mm urchin eats about 3.5 percent of its weight/day and a 70 mm urchin consumes 1.3 percent of its weight daily.

The assimilation efficiencies, as derived from the experimental data, increased from 42 percent for 10 mm urchins to 52 percent for 30 mm urchins and then steadily decreased to 9 percent for 70 mm urchins. This is not linearly related to the test diameter and the line shown in Figure 10 was interpolated from values from the equations for food eaten and faeces excreted.

The relationships of the amount of food eaten, the amount of faeces excreted, the feeding rate and the assimilation efficiency to the weight (w) of the urchin are also shown in Figure 8 and the equations of the first three are as follows:

Food eaten (mg wet weight)/urchin/day	$c = 46.28 \times w^{0.7352}$
Faeces excreted (mg dry weight)/urchin/day	$f = 1.535 \times w^{0.9023}$
Feeding Rate (%)	$r = 4.630 \times w^{-0.2649}$

The greatest changes in the consumption, faecal production, feeding rate and assimilation efficiency occur in the smaller urchins up to about 20 gms body weight.

September Feeding Rates

The results of the experiments of the feeding abilities of 10, 30 and 50 mm urchins on eight species of algae between September 20 and October 3, 1968, are shown in Figure 9 and in Appendix VII. The water temperature over this period ranged from 11.0 - 13.0°C. It must first be stated that the difficulties in measuring the wet weight of algae and in measuring very small amounts of dry faecal material present a serious problem, especially when dealing with small urchins. The filamentous algae, Ptilota serrata, and Desmarestia viridis are also problems, since small fragments easily break off and settle to the bottom without being ingested. Also calcareous animals are commonly attached to P. serrata.

Laminaria spp. and Alaria esculenta are eaten most rapidly. The rate is less for Ulva sp.*, Desmarestia viridis, Fucus vesiculosus, Ascophyllum nodosum, Agarum cribrosum and Ptilota serrata. The slow consumption of the latter two algae is in agreement with the observation that small quantities of these algae have been observed to persist with urchins for months in the lab.

The expected decrease of the feeding rate with an increase in urchin size occurred with all the algae except Laminaria spp. and Ascophyllum nodosum. The latter exceptions and the relatively small differences in the feeding rate of the two smaller groups of urchins on Agarum cribrosum and Fucus vesiculosus may to some extent be attributed to physical difficulty small urchins have in eating these thicker and leathery phaeophytes. Small urchins are probably

*The Ulva sp. referred to in the feeding experiments is neither U. lactuca or U. rigida (- U. lactuca var. rigida), the only species so far known for Newfoundland, and appears to be an undescribed species (personal communication to Dr. G. R. South by Dr. Carl Bliding in Sweden).

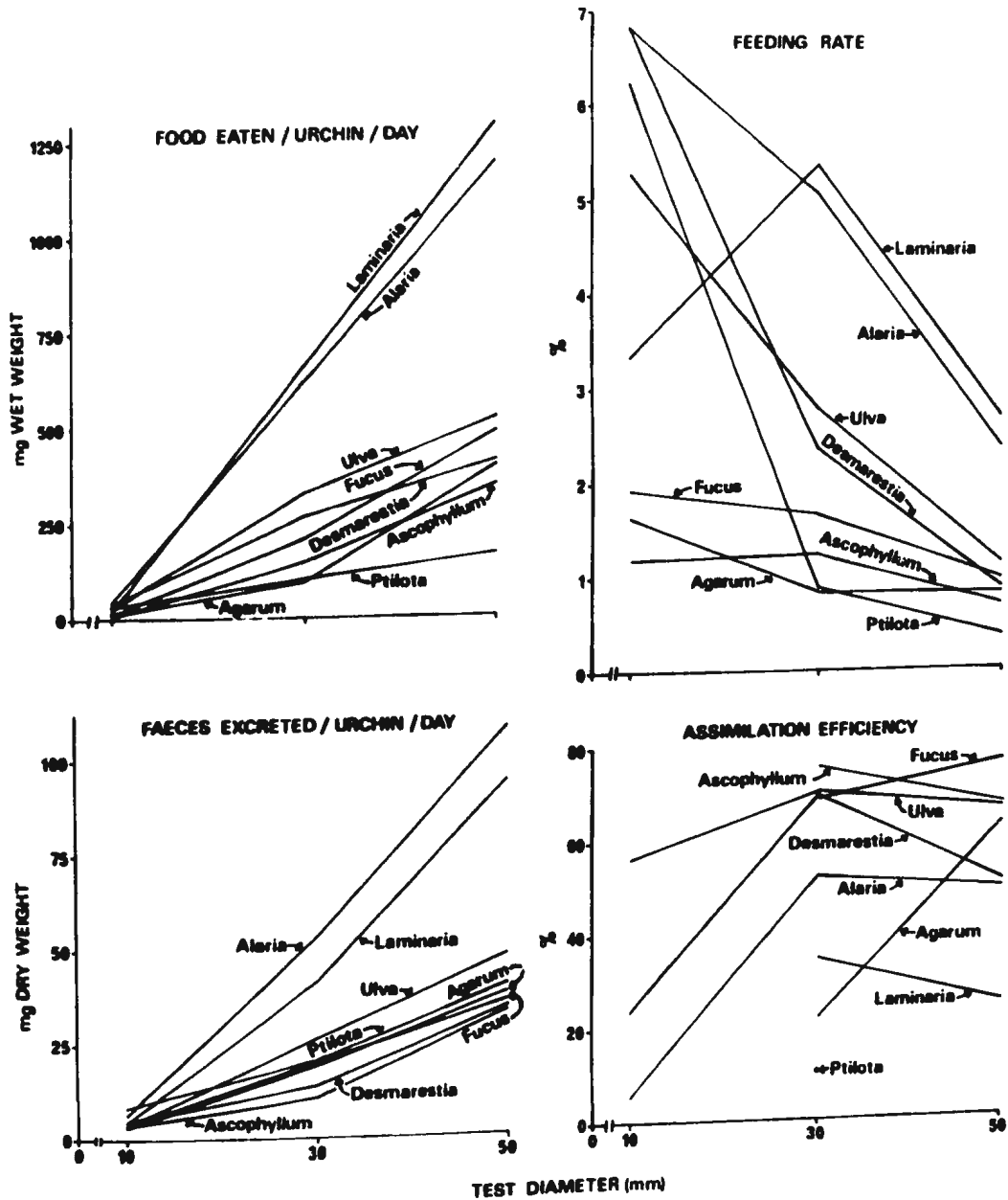


FIGURE 9: The Feeding Abilities of 10, 30 and 50 mm S. droebachiensis on Eight Species of Algae during September.

detritus feeders since they are usually found in the protection of small crevices or under cobble and coarse gravel, where detritus collects. Also, Fuji (1967), who analyzed the guts of various sizes of S. intermedius found that small specimens feed on detritus. The feeding rates of small urchins on Alaria esculenta and Ulva sp., which are more thin-bladed, were much higher than for 30 mm urchins. The problem of small fragments of undigested algae being lost undoubtedly accounts for the very high feeding rates of 10 mm urchins on Ptilota serrata and Desmarestia viridis. The maximum feeding rates of about 5 percent for 30 mm urchins and about 2.5 percent for 50 mm urchins occurred when Laminaria spp. and Alaria esculenta were the foods. The feeding rate was slightly more than half this for these size groups feeding on Ulva sp. The feeding rate of 30 mm urchins was 2.3 percent for Agarum cribrosum and Ptilota serrata. Large urchins ate less than 1 percent of their weight per day of Fucus vesiculosus, Ascophyllum nodosum, Desmarestia viridis, Agarum cribrosum and Ptilota serrata.

Thirty millimeter urchins assimilated about 70 percent of Ulva sp., Fucus vesiculosus, Ascophyllum nodosum and Desmarestia viridis, 52 percent of Alaria esculenta and 35 percent of Laminaria spp. These algae are usually assimilated slightly less efficiently by 50 mm urchins, but in Agarum cribrosum the values increased abruptly from 22 percent for 30 mm urchins to 63 percent for 50 mm urchins. The assimilation efficiency appears to be very low for Ptilota serrata, but this could partly be due to the small fragments and calcareous animals which are attached to it and which settle to the bottom, and could not completely be separated from the faeces. The data suggest that small urchins assimilate these algae inefficiently. However, much of this inefficiency is obviously a result of the relative inaccuracy of the

measurements. The values for Ulva sp. may closely indicate the true situation.

May Feeding Rates

During the May-June food preference experiments, the urchins were in the post spawning condition. The amount of food eaten per urchin per day and the feeding rates of 20 and 50 mm urchins on twelve species of algae are shown in Table IV. It must be remembered that these urchins were prestarved for two weeks and that these figures were obtained in a different manner. The feeding rates on Alaria esculenta and Ulva sp. are practically the same as in September. Laminaria sp. was most rapidly eaten at about 2200 mg per 50 mm urchin per day and 460 mg per 30 mm urchin per day; Chorda tomentosa and Halosaccion ramentaceum were consumed at a slightly slower rate; and Chondrus crispus, Alaria esculenta, Petalonia fascia and Rhodymenia palmata were ingested about half as quickly as Laminaria spp. Fucus vesiculosus and Ascophyllum nodosum were eaten at about one third the rate and Ptilota serrata and Agarum cribrosum were very slowly eaten. It is likely that the values for 20 mm urchins eating Ascophyllum nodosum, Ptilota serrata and Agarum cribrosum are too high. They were the only food material in the tray with the 110 small urchins for the last month of the experiment and it is probable that the infrequent observations of the number of urchins on these algae did not provide a reliable estimate of the number of urchins feeding on these algae.

Seasonal Aspect of Feeding

The consumption and feeding rates of urchins feeding on Laminaria spp. are shown for September, February and May in Figure 10. In February,

TABLE IV: Consumption and feeding rates of 20 and 50 mm urchins in May, 1969.
(Water temperature 1.3 - 3.4°C).

	18 - 22 mm SIZE GROUP		48 - 52 mm SIZE GROUP	
	FOOD EATEN (mgs wet wt.) /URCHIN/DAY	FEEDING RATE (%)	FOOD EATEN (mgs wet wt.) /URCHIN/DAY	FEEDING RATE (%)
<u>Laminaria</u> sp.	468.5	12.3	2229.4	4.6
<u>Halosaccion ramentaceum</u>	357.4	9.4	1621.6	3.3
<u>Chorda tomentosa</u>	342.2	9.0	2049.4	4.2
<u>Chondrus crispus</u>	275.3	7.3	1214.5	2.5
<u>Alaria esculenta</u>	217.2	5.7	1190.3	2.5
<u>Petalonia fascia</u>	239.8	6.8	1065.8	2.2
<u>Rhodomenia palmata</u>	240.2	6.3	1156.8	2.4
<u>Fucus vesiculosus</u>	176.0	4.6	896.8	1.9
<u>Desmarestia viridis</u>	---	---	871.9	1.8
<u>Ascophyllum nodosum</u>	225.0#	5.9#	758.9	1.5
<u>Ulva</u> sp.	169.0#	4.4	504.6	1.0
<u>Ptilota serrata</u> *	149.0#	3.9#	---	---
<u>Agarum cribrosum</u> *	101.4#	2.7#	401.3	0.8

* These algae persisted into June and the water temperature reached as high as 9°C while P. serrata was present.

These estimates are likely high since the infrequent observations of the number of urchins feeding on them in the latter part of the experiment, when they were the only foods present, is probably an underestimate of the actual number of urchins feeding on this material.

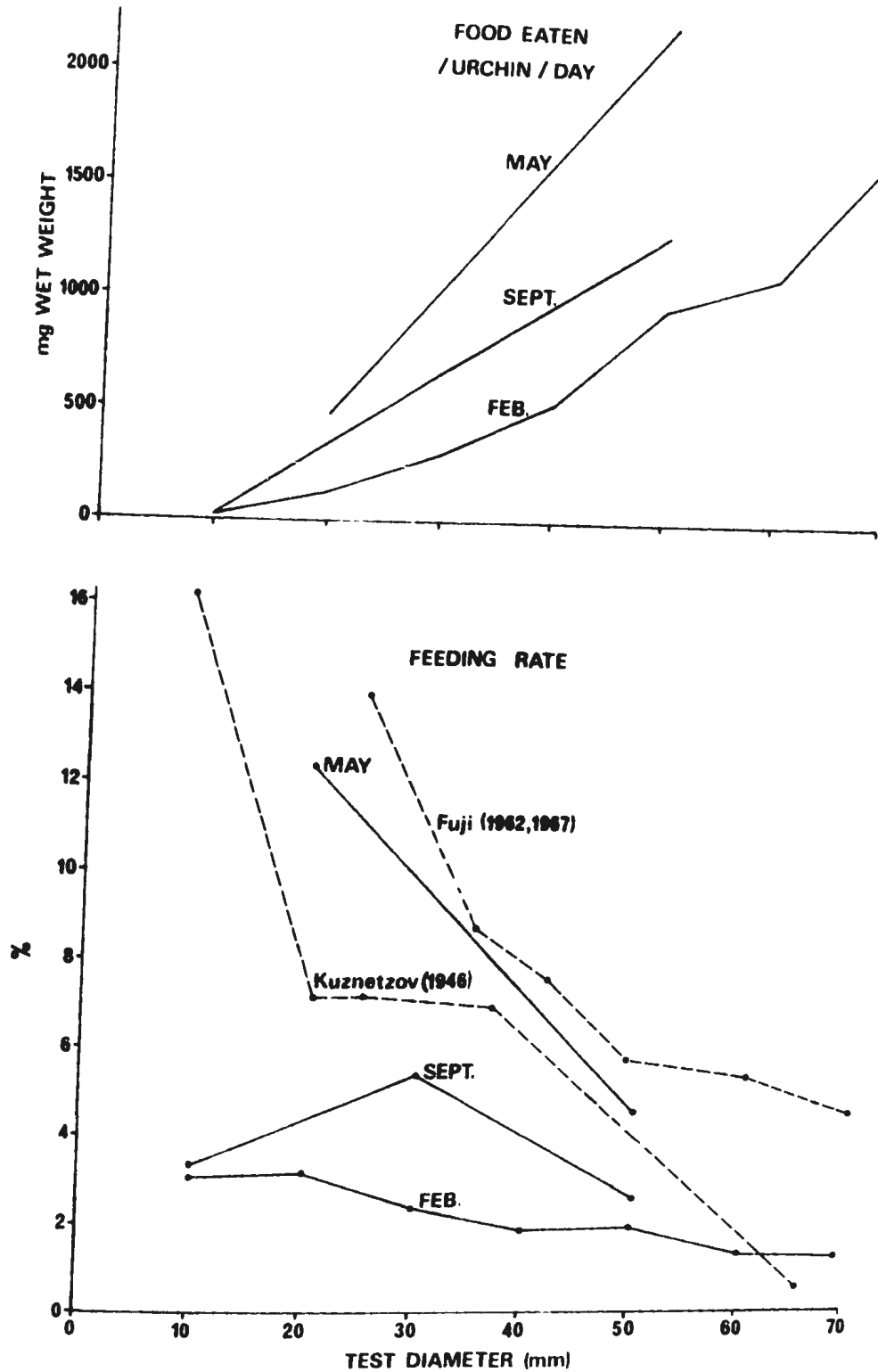


FIGURE 10: The Consumption and Feeding Rates of Various Sizes of *S. droebachiensis* on *Laminaria* spp. during Different Seasons in this Study, the Equivalent Feeding Rates of *S. droebachiensis* on *L. saccharina* as Determined by Kuznetsov (1946) and the Feeding Rates of *S. intermedius* on *L. japonica* as recorded by Fuji (1962, 1967).

the water temperature was about 10°C lower than in September, and the amount of Laminaria eaten dropped 55 percent for 30 mm urchins and 26 percent for 50 mm urchins. The feeding rates decreased in the same manner, although, the assimilation efficiency (Appendix VI and VII) increased from 35.0 to 51.9 for 30 mm urchins and from 25.1 to 32.5 percent for 50 mm urchins. The actual amount of Laminaria assimilated was 324 mg wet weight in September and 349 mg in February for 50 mm urchins, and 230 mg in September and 155 mg in February for 30 mm urchins. This indicates that urchins assimilate more efficiently when they eat less, even though the water may be colder. The gonad index of urchins in September was very low, but in February the gonads were large and urchins were about ready to spawn. The highest feeding rates were recorded in May, when the water temperature was only slightly higher than in February, but the urchins were in post spawning condition. This suggests that the amount of feeding depends on the condition of the gonads more than on the water temperature. However, the feeding rate and amount eaten were almost fourfold from February to May for 20 mm urchins, which have probably not reached maturity, and only about 2.5 times for 50 mm urchins which were mature. This indicates that seasonal fluctuations are greater in smaller urchins.

In May, the feeding rates on Fucus vesiculosus, Ascophyllum nodosum and Desmarestia viridis had about doubled the September rates, however, the rates on Alaria esculenta and Ulva sp. were about the same. There may be an increase in the amounts of Agarum cribrosum and Ptilota serrata eaten, however, these values are probably too high, as previously indicated.

Food Preferences

The May-June experiments indicate that the urchin's preferences decrease in the order shown in Table V. It is apparent that Halosaccion ramentaceum, Petalonia fascia, Chorda tomentosa, Alaria esculenta and Desmarestia viridis are desirable to the urchin; Laminaria sp., Chondrus crispus, Fucus vesiculosus and Rhodomenia palmata are intermediate and Ascophyllum nodosum has little attraction. Agarum cribrosum and Ptilota serrata are by far the least desirable and are only resorted to in the absence of other food materials. Ulva sp. appears to be very attractive to large urchins but was only intermediate in the likes of small urchins. The higher score for larger urchins may result because consumption time is greater as the alga is very membranous.

There was considerable variation in the numbers of urchins in contact with the various species during the September experiments where only one type of food was available to each group of urchins (Appendix VIII). This may also be indicative of the food preferences of the urchin. The daily records indicate that at least 93 percent of the 30 and 50 mm urchins in the tanks with Ulva sp. and Alaria esculenta were in contact with these algae. Fucus vesiculosus, Desmarestia viridis, and Laminaria sp. are intermediate, Ptilota serrata and Ascophyllum nodosum are less desirable and Agarum cribrosum is least desirable.

The more desirable foods appear to be fed upon almost continually until they are devoured and the less desirable foods are only eaten for short periods when other more desirable algae are not present.

TABLE V: Food preferences of S. droebachiensis in descending order of attractiveness.

<u>18 - 22 mm Size Group</u>	<u>48 - 52 mm Size Group</u>
<u>Halosaccion ramentaceum</u>	<u>Ulva sp.</u>
<u>Petalonia fascia</u>	<u>Petalonia fascia</u>
<u>Alaria esculenta</u>	<u>Halosaccion ramentaceum</u>
<u>Chorda tomentosa</u>	<u>Chorda tomentosa</u>
<u>Rhodomenia palmata</u>	<u>Alaria esculenta</u>
<u>Laminaria sp.</u>	<u>Desmarestia viridis</u>
<u>Chondrus crispus</u>	<u>Fucus vesiculosus</u>
<u>Ulva sp.</u>	<u>Chondrus crispus</u>
<u>Fucus vesiculosus</u>	<u>Rhodomenia palmata</u>
<u>Ascophyllum nodosum</u>	<u>Laminaria sp.</u>
<u>Agarum cribrosum</u>	<u>Ascophyllum nodosum</u>
<u>Ptilota serrata</u>	<u>Agarum cribrosum</u>

Discussion

There was no significant difference in the consumption rates of urchins feeding under light and dark conditions. However, this does not necessarily indicate that the consumption rate is the same in the night as in the day in shallow water, since the lighting intensity during the light periods (200 -400 lux) is considerably less than daytime light intensities. Furthermore, Fuji (1967) has shown that in S. intermedius feeding was significantly less during light periods of 6000 lux or more, than during dark periods.

In all the feeding experiments, the feeding rate decreased with increasing size. This was especially pronounced during peak feeding periods. A few exceptions occurred where the rate for 10 mm urchins was less than for the next larger group, but these were probably due to the difficulty in measuring very small amounts eaten by this size group. In Japan, Fuji (1962, 1967) also found that the feeding rate of S. intermedius on Laminaria japonica decreased greatly with size. The rates he records (Figure 10) are slightly greater than the May rates for S. droebachiensis in this study. At the time of his experiment the gonad indices were at an intermediate level and water temperatures were low for that area. In contrast to my results, Fuji found that the assimilation efficiency did not vary significantly in the different size groups. Kuznetsov (1946) studied the "feeding intensity" of S. droebachiensis in the eastern Murman and found that small urchins consumed a much greater percentage of their weight than large urchins, however, his results showed that urchins 20.5, 25.2 and 36.5 mm in diameter all consumed 7 percent of their weight per day, which is not consistent with trend of decreasing rate with increasing size as shown in this study and by

Fuji. His term "feeding intensity" is equivalent to the amount of food eaten/urchin/day over the average urchin weight, but the amount of food eaten was measured in periods longer than a day. Thus his "feeding intensity" of 0.162 for 8.9 mm urchins is equivalent to a feeding rate of 16.2 percent. The equivalent feeding rates for the various size groups he tested are shown in Figure 10. The time during which he conducted his experiment was not indicated, but the equivalent feeding rates are intermediate between that September and May feeding rates in this study.

My results indicate that there is much variation in the feeding rates of S. droebachiensis during different seasons. In February, when the gonads were at their peak and water temperatures were near minimal values, the feeding rates were very low; in May, when spawning was over and water temperatures had increased slightly, the highest feeding rates occurred; and in September, when the temperatures were near a maximum for this area and the gonads were beginning to ripen, the feeding rates were intermediate.

The seasonal pattern of consumption rates reported by Fuji (1962, 1967) for 50 mm S. intermedius feeding on L. japonica compare very closely with those of 50 mm S. droebachiensis feeding on Laminaria spp. The gonad index in S. intermedius reaches a peak in August and September when the water temperatures are beginning to drop, and the lowest values are in October and November. S. intermedius consumed over 2500 mg/urchin/day from January to June, when the gonads were enlarging, and then the amount gradually decreased to a minimum of 500 mg in September, corresponding to the gonad peak and spawning. Adult S. droebachiensis consumed 2229 mg in May, and higher values may exist during the late spring or early summer when tests were not conducted.

The September value of 1292 mg was about the same as Fuji's prespawning July and August rates and the February rate of 962 mg eaten/urchin/day was not as low as Fuji's minimal September value, however, lower values may exist near this time of year. The consumption rate of immature S. intermedius, 20 mm in diameter, fluctuated little from the high value of 1000 mg/urchin/day throughout the year, however, 20 mm S. droebachiensis only consumed 120 mg in February and 469 mg in May. Fuji (1962) examined the consumption rates of S. intermedius in two different seasons, March and September, at a temperature range from 5-23°C and found that at the same temperatures much more was eaten in March, when the gonads were recovering, than in September when the gonads were mature. Since there was great seasonal fluctuation in adult urchins but not in immature urchins and since similar temperatures did not induce similar feeding rates at different seasons, he concluded that the amount eaten by S. intermedius is regulated by some physiological pathway related to the condition of the gonads. This may also be true of S. droebachiensis, however, the notable fluctuation in the amount eaten by 20 mm S. droebachiensis, which are likely immatures, suggests that other factors may also be involved. Ebert (1967) suggested that the amount eaten may be directly related to the size of the gonads, because of physical crowding inside the test when the gonads are large.

Kurnetsov (1946) studied the seasonal aspect of the feeding of 50 - 55 mm S. droebachiensis and found that 3 sharp peaks in the "feeding intensity" occurred during 1940. The lowest peak of 0.013 (= feeding rate of 1.3%) occurred in March; practically nothing was eaten in April and May; a second peak of 0.016 occurred in June and the highest peak of 0.019 was in November.

Apart from the generally lower rates which occurred in the early part of the year, which may correspond to the advanced state of gonadal development at this time, this pattern is very unusual. It is also notable that his highest value in November, which is equivalent to a feeding rate of 1.9 percent, is as high as the lowest value of 1.29 percent for 50 mm S. droebachiensis in this study.

Fifty millimeter S. droebachiensis assimilated 324 mg wet weight of Laminaria spp. daily in September and about the same amount, 349 mg, in February, even though the temperature and gonad size were at opposite extremes in these periods. However, Fuji (1962, 1967) found an annual cycle in the amount of L. japonica assimilated by 50 mm S. intermedius. From about 230 to 270 mg were assimilated from February to June; the amount gradually decreased to 50 mg in September and then steadily increased to the former values. However, the amount assimilated by 30 mm S. droebachiensis increased from 14 mg in September to 22 mg in February.

In S. droebachiensis, the assimilation efficiency increased by 17 percent for 30 mm urchins and by 7 percent for 50 mm urchins from September to February. Associated with this was a decrease in the amount eaten, which was proportionally greater in 30 mm urchins, and a drop of about 10°C in water temperatures. Conversely, Fuji (1962, 1967) observed that the assimilation efficiency was very closely related to water temperature. In both S. droebachiensis and S. intermedius the highest assimilation efficiencies occurred when the gonads were at peak size and in S. intermedius the lowest values correspond to the lowest gonad indices as closely as they do to the minimal temperatures. Thus, I suggest that the condition of the gonads may

in some way regulate the assimilation efficiency, and this is very likely associated with its effect on the amount eaten. Generally the assimilation efficiency is greater when less is eaten and vice versa.

In September, when the gonads of S. droebachiensis were beginning to ripen, the feeding rates for 50 mm urchins ranged from 0.4 percent on Ptilota serrata to 2.7 percent of Laminaria spp. The rates were notably higher in May, when spawning was over, and compare favourably with the rates Fuji (1962, 1967) records for S. intermedius in January and June (Appendix IV), when the latter urchin is feeding at near maximal rates on Laminaria. Unfortunately I have only tested the assimilation efficiencies on a range of algae in September. It appears that S. intermedius assimilates its foods more efficiently and this may be related to the higher range of water temperatures in Japan. S. intermedius consumed about 5.8 percent of its weight of Laminaria japonica which compares quite favourably with the May rate of 4.6 percent for S. droebachiensis on Laminaria spp. The seasonal experiment he conducted on Laminaria shows that the assimilation efficiency varied from about 55 percent in November to about 73 percent in July and August, which is well above the values of S. droebachiensis feeding on Laminaria. Alaria esculenta was consumed at about the same rate in both September and May (2.4% and 2.5% respectively) and these values are very close to the rate of 2.3 for S. intermedius on A. crassifolia, however the assimilation efficiency was about 30 percent greater for S. intermedius in June than for S. droebachiensis in September. The feeding rate on Agarum cribrosum was 1.4 for S. intermedius and 0.8 percent for S. droebachiensis and the assimilation efficiency was only about 10 percent higher for S.

intermedius. The feeding rate of S. intermedius on Scytosiphon lomentaria was 3.8 percent (1930 mg eaten/urchin/day) and this value may be some indication of the rate of S. droebachiensis on this important element in the Newfoundland marine flora. Both the feeding rate and assimilation efficiency of S. droebachiensis on Ulva sp. compares very favourably with the values for S. intermedius feeding on Ulva pertusa. Also the May feeding rates of S. droebachiensis on Chondrus crispus (2.5%) and Rhodomenia palmata (2.4%) are only slightly higher than the rates of S. intermedius on C. ocellatus (2.0%) and R. palmata (1.8%), respectively.

The consumption rates reported by Vadas (1968) for S. franciscanus, S. droebachiensis and S. purpuratus on 7 species of algae were notably higher when they were compared to corresponding rates for S. droebachiensis in this study and S. intermedius as studied by Fuji (1962, 1967). He measured the amount eaten by individual urchins, in similar or different seasons, over periods of usually 24 hours and expressed his results in terms of gms/hour/animal. Assimilation efficiencies were estimated in the same experiments by feeding the urchins a marker material (the rhodophytes Rhodomenia pertusa or Callophyllis flabellulata) prior to and following the feeding of the test alga. A summary of his consumption rates, interpolated in terms of mg/urchin/day, and assimilation efficiencies are presented in Appendix K. Unfortunately, he does not indicate the size of his animals, however, the very high rates would imply they are adult urchins. He does compare his data to Fuji's results for urchins averaging 50 mm so perhaps his animals are of similar size.

He made one set of tests on Agarum cribrosum in July, and the feeding rates at this time were much higher than in a second trial in January. The

gonads of the Strongylocentrotus spp. he studied are usually very large and approaching maturity during the winter months and recovering in the summer (Bennett and Giese 1955, Boolootian 1967, Cocanour and Allen 1967, Leighton and Jones 1968, and this paper), so it appears that this may be another instance where the feeding rate is regulated by the gonad cycle. It is, however, unusual that the assimilation efficiency was similar at both times. Vadas states that the mean consumption values of S. droebachiensis and S. purpuratus feeding on Agarum cribrosum agree with Fuji's June rate for S. intermedius on the same alga, however, it is likely that only his July values are comparable since the latter values are from a maximal feeding period in S. intermedius. In this case, Vadas's rate for S. droebachiensis is 5.4 times that for S. intermedius and the rate for S. purpuratus is less than for S. intermedius. Also, Vadas's consumption rate for S. droebachiensis on Laminaria saccharina is similar to the May rates for S. droebachiensis in this study and the January rates for S. intermedius. However, his tests were conducted in the winter, when one would expect minimal rates, and the latter are near maximal seasonal values. Since his urchins were fed marker algae, which may not be as desirable to the urchins as the test algae, the consumption rates derived from his short term experiments may be greater than if the experiments were conducted for longer periods. His assimilation values closely correspond in the three species he tested and the values on L. saccharina in the winter agree with the peak values for S. intermedius on L. japonica in July and August. This may support my observation that the assimilation efficiency is higher when the gonads are near their peak, even if water temperatures are lower.

Moore and McPherson (1965) and Ebert (1968) studied the feeding rates

of Lytechinus variegatus and S. purpuratus respectively, in the field and their results suggest that when food is not limited urchins may eat more in the field, where there is water movement, than in the lab.

In California, during the early 1960's, three papers were published on the efficiency at which S. purpuratus digests various macrophytes. Lasker and Boolootian (1960, 1964) estimated this by measuring the food eaten, faeces excreted and material in the gut of prestarved urchins for a period of 9 - 19 days. Their first experiment (1960) reported that a 63 mm urchin assimilated 76 percent of one meal of Macrocystis pyrifera. In numerous following experiments (Boolootian and Lasker 1964), they found that large urchins assimilated an average of 81 percent of M. pyrifera, 62 percent of Egria laevigata, 51 percent of Petalonia fascia and 45 percent of Halidrys dioica. It appeared that urchins continually did not waste much of their food since the assimilation efficiency of urchins fed daily was about the same as for urchins fed one meal. Farmanfarmaian and Phillips (1962) estimated the assimilation efficiency of prestarved S. purpuratus eating Iridaea flaccidum by labelling the food with C^{14} and then comparing the specific activity of this material before it is eaten and when in the digestive tract. The assimilation efficiency remained at about 91 percent for 1 to 9 days. Since the food material had not passed the stomach in two days he suggested that the esophagus and stomach are the main sites of digestion. The above authors have indicated that M. pyrifera and I. flaccidum are common foods of S. purpuratus in California.

Thus S. droebachiensis and other Strongylocentrotidae, which have been studied, show distinct preferences for and varying abilities to consume and assimilate different species of algae. Consumption and assimilation

efficiency also vary seasonally. Least is eaten when the gonads are large and mature, the highest rates occur following spawning, and the assimilation efficiency generally varies inversely with the consumption rates.

PREDATION

A wide variety of urchin predators has been recorded. Some of the literature dealing with this topic has been reviewed by Harvey (1956) and by Moore (1963, 1967).

Predation by Sea Stars

I have seen two or three purple starfish, Asterias vulgaris, wrapped around single S. droebachiensis at Portugal Cove many times and once in the laboratory. In the latter attack Asterias first digested the tissues on the outside of the test, so that the spines fell off, and then consumed the soft tissues around the Aristotle's lantern and inside the test. The test remained completely intact (Plate XA). This very likely explains the presence of well cleaned, unbroken tests which are commonly encountered underwater at Portugal Cove (Plate IX). The initial attack has never been observed, and it may be that only urchins which are somehow weakened are vulnerable to predation by Asterias. The reverse situation in which starved urchins prey on Asterias, Solaster endeca and Crossaster papposus has also been seen in the laboratory.

Asteroids are well-known predators of urchins in other areas. On the Atlantic Coast of North America, Harvey (1956) reported that Arbacia punctulata is consumed by starfish. On the Pacific Coast, Leighton et al. (1966) record that S. purpuratus, S. franciscanus and Lytechinus anamesus are preyed upon by the sunstar, Pycnopodia helianthoides, and the agile sea-star, Astrometris sertulifera. In Lough Ine, Ireland, Ebling et al. (1966) have indicated that the seastar, Marthasterias glacialis, may be a predator of Paracentrotus lividus, although, in the natural environment these two animals tend to be separated since they migrate diurnally in opposite directions. In Norway, Jensen (1966) studied the defence responses of

Psammechinus lividus and S. droebachiensis to Marthasterias and found that when touched by this seastar these urchins would bend their spines down towards the test in the stimulated area and extend their globiferous pedicellaria. Unlike Psammechinus, S. droebachiensis can move faster than Marthasterias (up to 17.6 cm/minute) and whenever possible it displays the escape response of moving away by its spines (when on a horizontal surface) rather than by its tube feet. No response is evident when these two urchins are touched by Solaster endica, Crossaster papposus and Asterias rubens.

Cannibalism in Urchins

Cannibalism in S. droebachiensis was frequently observed in tanks in which there was insufficient food. The preying urchin usually climbed on top of its victim, removed the spines and ate through the weaker plates in the apical region. Further plates were devoured in tracts which radiated outward (Plate XC). Cannibalism in S. droebachiensis has previously been reported by Beers (1948) and in other species by Agassiz (1872-1874) and Harvey (1956). A few specimens found at Portugal Cove were probably victims of cannibalism. Mr. Ray Cote (personal communication) observed urchins with holes in the apical region in a dense urchin population near low water level at Bellevue, Trinity Bay.

Predation by Decapod Crustacea

Two experiments were conducted on the ability of two common decapods to destroy S. droebachiensis. Two male lobsters, Homarus americanus, one measuring 95 mm and the other measuring 88 mm from the eye cavity to the most posterior mid-dorsal part of the carapace, were maintained from November 22, 1968 to June 23, 1969 in a large tank 125 x 78 x 28 cm in size. Usually 10-20 urchins, most of which were 30-50 mm in diameter, were kept in the tank. The urchins usually climbed to the top of the tank out of reach of

the lobsters, but they were placed on the bottom of the tank whenever the lab was visited, which during certain intervals was twice daily and during other periods was as infrequently as once in 2 weeks. Lighting conditions were irregular and sometimes were on or off for intervals of several weeks and the water temperature usually a few degrees higher than in Logy Bay. A total of 131 urchins with a gross weight of 3423.2 gms were destroyed. This averages out to 0.3 urchins or 7.0 gms of urchins destroyed/lobster/day. The greatest quantity of urchins were destroyed from December 3 to 5 when the rate was 1.2 urchins or 28.0 gms of urchins/lobster/day. Since the urchins were often not accessible and since much higher densities of urchins are present in nature, it may be that lobsters are more destructive in the natural environment.

Lobsters usually hide when disturbed by the presence of people in the lab, however, in September, following over 2 months starvation, the 95 mm lobster was observed attacking an urchin, 38.5 x 20.0 mm in size. The lobster pried the urchin from the tank using both its chelae and its walking legs, and then manipulated it primarily by the walking legs. Large urchins are invulnerable as long as they can remain attached to the substrate. When the urchin was held in a suitable position on its side the more awkward crushing chela attempted to grasp and crush the test. After numerous attempts it managed to force one jaw of the crushing chela through the soft tissues around the Aristotle's lantern. Eventually plates were crushed and the hole was enlarged. On other occasions a hole was pierced in the upper edge of the test (Plate XG). During the attack, which lasted for about an hour, the urchin was frequently released from the crushing chela and brought into reach of the maxillipeds and mandibles and as the

inner tissues became exposed these were eaten. In this manner the lobster apparently continues to crush the test until it is reduced to fragments and all of the soft tissues are devoured. The largest urchin eaten was 72 mm in diameter and 43 mm in height which was not within the grasp of the crushing chelae of these animals.

A similar experiment was conducted with two rock crabs, Cancer irroratus, measuring 91 and 88 mm in carapace width, in a tank 45 x 30 x 9 cm in size from December 6, 1969 to July 9, 1969. Unfortunately the 88 mm crab was dropped and killed on November 22. An average of 0.56 urchins or 1.24 gms of urchins were destroyed/crab/day and the highest rate of 2.19 urchins or 8.18 gms of urchins/crab/day was recorded from May 10 to 20. Most of these urchins were 15-30 mm in diameter.

In September the 91 mm crab was also observed preying on an urchin. The urchin, 22 mm in height, was larger than the grasp of the crab's chelae. The chelae of the crab are much more agile than those of the lobster and both the chelae and walking legs were used in manoeuvring the urchin. The crab first turned the urchin over and held it under itself. Within 10-15 minutes it succeeded in making a hole in the lower edge of the test (but not starting at the edge of the peristomium) (Plate XF). Urchins are also reduced to fragments by crabs.

Both the crabs and lobsters appeared healthy throughout these experiments and until September, 1969 in spite of their uniform diet. However, moulting has not occurred in these animals since they were collected in late August, 1968.

At Lough Ine, Muntz et al. (1965) have studied the ability of

three crabs, Carcinus maenas, Portunus ruber and Cancer pagurus, to destroy Paracentrotus lividus, and found that Carcinus could only open small urchins but the latter two crabs could open much larger ones, even larger than their grasp, by puncturing the ventral side of the urchin with the points of their chelae. These crabs probably affect the distribution at the Lough. The lobster, Homarus vulgaris, and three less common crabs, Maia squinado, Xantho incisus and Portunus corrugatus also destroyed Paracentrotus, but only the latter two proved capable of opening smaller urchins.

Predation by Fish

Mr. Chandra Sekhar kindly made his records of gut analyses on cunners (Tautogolabrus adspersus) from Newfoundland available to me. The incidence of urchins at various locations is shown in Appendix XI. It is evident that in areas where sediments are not too fine and in which urchins are likely abundant, S. droebachiensis are a regular part of the diet of this fish. The highest incidences of 50-60 percent occurred at St. Phillips and Portugal Cove where urchins are known to be extremely abundant. At Holyrood, where the urchin density is lower and urchins are generally very large, the incidence was 21 percent. Urchins were common in the stomachs of cunners 10-20 cm in length, as well as in larger animals, however, they were not present in the 3.1-4.5 cm specimens from Cod All Islands, Notre Dame Bay, in spite of the probable abundance of urchins in this area. Johansen (1925) found urchins to be uncommon in the stomachs of cunners from the Gulf of St. Lawrence and the coast of Nova Scotia.

In a recent study, Kennedy (1964) found that the frequency of urchins in the stomachs of winter flounder (Pseudopleuronectes americanus) was 64 percent (mean volume 1.5%) at Horse Cove, which is very near Portugal

Cove. In Long Pond, where the substrate is sand and urchins are less abundant, a lower incidence of 2.7 percent (mean volume 0.4%) was found. Mostly small urchins were consumed whole. Mr. Bevin LeDrew (personal communication) informed me that he has found the tube feet of urchins in the stomachs of the radiated shanny (Ulvaria subbifurcata).

Other fish, too, are known to eat S. droebachiensis. Mortensen (1943) recorded that it is a food of cod, Greenland shark and the wolf fish (Anarhichas). In 1874 Verrill stated that "it is swallowed whole in large quantities by the wolf fish and by other large fishes". Cornish (1907), Bigelow and Schroeder (1953) also reported that urchins were a regular part of the diet of the Atlantic wolf fish (A. lupus): Huntsman (1918) recorded that the urchins are eaten by larger specimens of the American plaice (Hippoglossoides platessoides) and Leim and Scott (1966) reported that they are eaten by the Atlantic sea raven (Hemitripterus americanus), the shorthorn sculpin (Myoxocephalus scorpius), and the ocean pout (Macrozoarces americanus). The latter two fishes are also common in the study areas.

Predation by Birds

I have commonly found the empty tests of S. droebachiensis, with the spines still on and a jagged hole in the peristomial region (Plate XE), on the upper shore to the tops of cliffs and embankments along the coast of Newfoundland and also in Nova Scotia. Dr. Wm. Threlfall (personal communication) has told me that he has observed Herring Gulls (Larus argentatus) carrying urchins from the lower shore, and pecking them open and leaving them as above. Threlfall (1968a) has examined the stomach contents and pellets of Herring Gulls and two other gulls, the Great Black-backed Gull (L. marinus) and the Kittiwake (Rissa tridactyla) from the bird islands south of St. John's. S. droebachiensis occurred commonly in

the diet of gulls except during the summer months, when other foods were plentiful. "In May 1967, 165 pellets composed entirely of small pieces of green sea urchins (Strongylocentrotus droebachiensis) were found on Gull Island, and in one case two whole sea urchins (3.7 cm and 3.6 cm in diameter) were recovered from the crop of an adult Herring Gull."

Mr. Claude Bishop (personal communication) has recently examined 53 Common Eiders, (Somateria mollissima) from eastern Newfoundland and S. droebachiensis were present in 10 of the 43 birds which contained food. Seven of these were from one collection on January 14, 1969, from Tors Cove, south of St. John's, and several of the latter birds contained up to 5 whole urchins. The largest urchin measured 24.8 x 12.0 mm. In 1939, Cottam recorded that S. droebachiensis was a common item in the diet of the Northern Common Eider (S. mollissima borealis), the American Common Eider (S. mollissima dresseri), the King Eider (S. spectabilis), the Harlequin Duck (Histrionicus histrionicus) and the Scurf Scoter (Melanitta perspicillata). Urchins only occasionally occurred in the White-winged Scoter (M. deplandi), the American Scoter (Idemia americana) and the Great Scaup (Nyroca marila).

In the low littoral at Lough Ine, Ireland, Ebling et al. (1966) found empty Paracentrotus lividus with a jagged hole in the top of each animal. They attributed these to birds and this is confirmed by observations by Moore et al. (1963) of Herring Gulls pecking open Echinus esculentus on the English seashore. In Miami, Moore et al. have also frequently see Herring Gulls picking up Lytechinus variegatus, which are exposed at low tide, and dropping them until they broke open. Urchins with a hole in the apical region were also commonly found, but the predators have not been observed

opening Lytechinus in this manner. On one occasion they reported that the Herring Gull was very likely responsible for a patch of about 100 opened urchins near low water level. They indicate that the Herring Gull may have recently acquired this habit in the Miami area and that predation by this bird now plays an important role in setting the upper limit of Lytechinus. Threlfall (1968b) has found Echinus in the stomach of both old and young Herring Gulls in Wales and on a number of occasions has seen predation in the same manner as he observed in Newfoundland (personal communication). It is interesting that the apical region of the urchin is pecked open by Herring Gulls in some regions while the peristomial region is opened in other areas.

Predation by Mammals

Mortenson (1943) recorded that S. droebachiensis was a major part of the diet of the arctic fox, and in areas of California where the sea otter, Enhydra lutris, exists it is known to be a very effective predator of urchins, particularly S. franciscanus (McLean 1962, North 1965, Leighton et al. 1966). Shidlovakaya (1962) found that urchins were a dietary essential to otters in captivity, and that on an urchin diet about 35 kg of urchins were consumed daily per animal.

Consumption by Humans

In Newfoundland the gonads of S. droebachiensis are infrequently eaten by visiting Portuguese fishermen. The local residents of St. Lawrence, on the Burin Peninsula, eat urchins, baked in the shell, during Lent (when the gonads are near peak size). Fishermen usually refer to S. droebachiensis as the "whore's egg" since it is a nuisance when it covers their lobster traps; in some villages this is pronounced "ore's egg". The name has become

modified to the more polite terms of "hozey egg, oze egg, ozey egg, and ozey hegg" in many areas. S. droebachiensis is reported to be eaten by Italians in New York City and by people in the Aleutian Islands of Alaska. Other urchin species are used for human consumption in British Columbia, California, the West Indies, Peru, Ecuador, the Mediterranean and New Zealand (Harvey 1957, Hyman 1955). In Japan, commercial fishing for S. intermedius has developed to the extent that limiting the catches or artificial propagation may soon be necessary (Fuji 1967).

Plate IX

Piles of cleaned Mytilus edulis shells and unbroken urchin tests, which are probably the result of predation by Asterias vulgaris, collect in pockets where the bedrock meets the loose substrate at a depth of 35 feet at Portugal Cove. The cunner, Tautoglabrus adspersus (bottom) is also an urchin predator.



Plate X

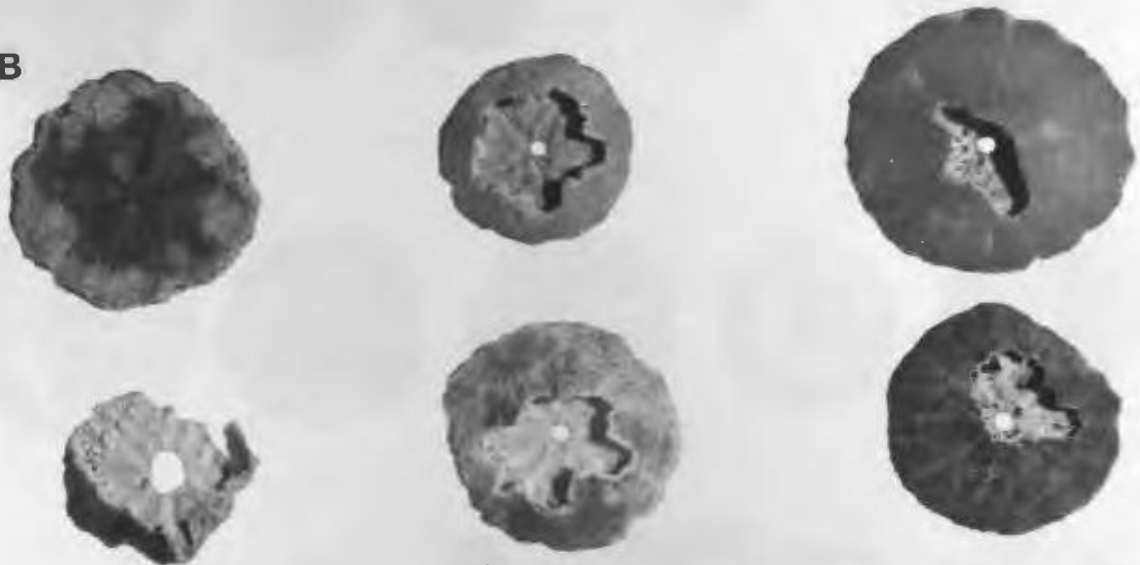
Predation

- A. Asterias vulgaris predation on S. droebachiensis. The spines and soft tissues are removed leaving an unbroken test.
- B. Urchin predation on Echinarachnius parma. Spines are first browsed off (upper left), the edge of the test is usually eaten, a hole is eaten through the apical region, and tracts are grazed radially.
- C. Cannibalism in S. droebacheinsis. Spines are removed and a hole is usually eaten through the apical region (lower right - initial attack) and then tracts are grazed radially as above. The two specimens on upper right are from Portugal Cove..
- D. Unknown predator. Freshly opened tests with the bottom portions removed were found in high tide pools at Portugal Cove on September 14, 1969. This may result from urchin or bird predation.
- E. Herring Gull predation. A hole is pecked through the apical region and the soft tissues in the test are removed. Such specimens are common on cliffs and embankments along the coast.
- F. Fragments left after predation by Cancer irroratus. The specimen on the left, which has a small hole through its lower edge, resulted after 10-15 minutes.
- G. Fragments left after predation by Homarus americanus. The two specimens at the left were removed before they were reduced to fragments and show that the initial hole may or may not be through the peristomial region.

A



B



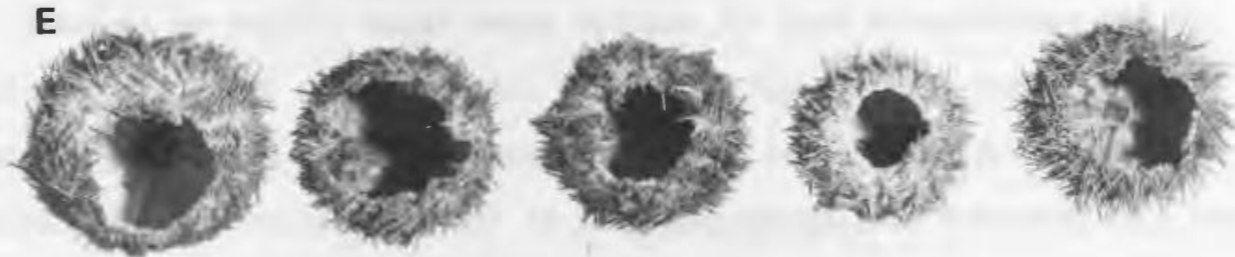
C



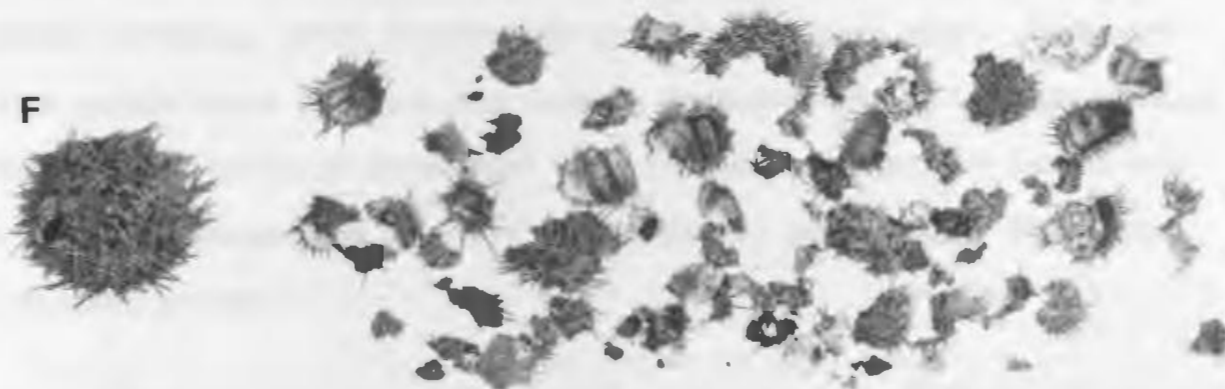
D



E



F



G



GENERAL DISCUSSION

From the data on the abundance of the urchins in the field and their feeding abilities as determined in the laboratory it is apparent that urchins must be an important influence on the algal vegetation of Newfoundland. The amount of algae eaten by the various size classes of urchins can be estimated from the laboratory data and this can be applied to the population data in order to estimate the grazing potential. This is greatest in shallow water where urchins are most concentrated and decreases with depth and decreasing exposure. However, the survival of large specimens in sheltered locations partly compensates for the smaller numbers. The grazing potential of S. droebachiensis is comparatively low in February, when the gonads are very large and mostly ripe, but in May, following spawning, their consumption potential is very high. In September the gonads begin to ripen and feeding decreases again. Although large urchins can eat more per individual than smaller urchins, the latter consume a greater percentage of their weight daily, particularly during the peak feeding period.

The most rapidly eaten alga is Laminaria. L. digitata is present at Logy Bay and grows scattered in the more exposed regions of the Alaria zone. During a kelp survey of Newfoundland I observed that this alga is typical of exposed areas and on very exposed prominences it often forms dense beds near low water level. On bedrock at 16 feet at Logy Bay and at 10 feet at Portugal Cove the urchins could potentially consume about 60 gms/ m^2 of Laminaria daily in February, over 160 gms in May and 100 gms in September. This very high grazing pressure plus the urchin's preference for

Laminaria, probably prevents its establishment except where exposure is very great and urchins are kept away because of abrasion by the fronds. L. digitata was not present at Portugal Cove where exposure is less severe. L. saccharina and L. longicruris grew luxuriantly on the pier further in the Cove but not in the study area. This can be attributed to the heavier grazing pressure in the study area. On the mud and gravel substrate around the pier there is a low density of large urchins and few individuals have been seen climbing the wood pilings. Also the Laminaria blades usually float free from the pier and the bottom and are out of the reach of the urchins. Although no Laminaria appeared in the wire cage at 50 feet, where urchins were excluded, this is probably because no adult plants existed near enough to provide a source of spores. In areas of Newfoundland where I have observed L. saccharina and L. longicruris, strong tidal currents or substrate barriers of mud or sand protected the plants from the urchins.

Alaria esculenta is the most prevalent macrophyte in the sublittoral fringe along all exposed bedrock shores in Newfoundland. It forms a very distinct zone at Logy Bay which is shallow in the Bottom of the Gulch but deepens with increasing exposure to a depth of 35 feet outside the Gulch. At Portugal Cove the Alaria zone is primarily limited to the outer exposed bedrock faces and normally extends down to about 8 feet but is present to 15 feet on a few more exposed prominences. It is not present at Holyrood and other sheltered areas. The lower limit of Alaria is primarily set by urchin grazing which in turn is limited by abrasion by the fronds when there is wave action. This explains the downward displacement of Alaria with increasing exposure since wave action provides pro-

tection to greater depths where the exposure is more severe. The tougher stipes of older plants, which are more resistant to grazing also offer some protection, but whenever it is calm the urchins attack from the blade end, which sinks to the substrate. In a few instances they climb the stipes.

Alaria sporlings appear and grow very rapidly in the winter when the minimal feeding condition of S. droebachiensis and the most severe swell conditions exist. This may represent an evolutionary adaptation of Alaria. The Alaria recruitment was very heavy in the spring of 1969 and young plants colonized the bedrock surfaces at greater depths and in the less exposed areas of Dyer's Gulch and the Basin at Portugal Cove. Where sampling was done on bedrock at 16 feet at Logy Bay and at 10 Feet at Portugal Cove the urchins could potentially consume about 100 gms of Alaria daily/m² and this likely explains why this alga did not become established here. The ability of Alaria to grow at greater depths at Portugal Cove was demonstrated by the observation of sporlings epiphytic on Agarum blades at 30 feet. As soon as there were calm conditions, following April, the new growth was rapidly devoured by grazing fronts of larger urchins which must consume considerably more than 100 gms/day/m². By midsummer the Alaria zone was reduced to the area it occupied the previous autumn, and in September only the stipes, which were usually scarred, remained near the bottom of the zone.

Chorda tomentosa first appeared in early April and grew very rapidly for a few months. At both Logy Bay and Portugal Cove it was

most prevalent on bedrock surfaces near low water level. S. droebachiensis shows both a high preference and a great ability to consume this alga. In May the population at 16 feet along the Narrows at Logy Bay could potentially eat 140 gms of Chorda daily/m² and this undoubtedly accounts for its absence here. The herds of urchins which gorged at the bottom of the dense shallow water growth must consume considerably more. In 1969 Chorda also grew on the Bar at Logy Bay. The urchin population was not nearly as dense here, probably because of destruction in this area by moving cobbles during winter storms. The congregations of larger urchins below the Cobble Beach at Portugal Cove could possibly consume nearly 220 gms of this alga/day/m².

The fucoids are usually limited to the intertidal shore, but I have observed Ascophyllum nodosum growing subtidally on a number of occasions. For example in the region of Governor's Island, Bay of Islands, huge plants of Ascophyllum extend several feet below low water level. Urchins are uncommon in this region. The urchins at 1 foot at Portugal Cove could eat Fucus vesiculosus at a rate of 44 gms/day/m² in September and about twice that in May. The stipes of chewed-off Fucus plants were common at the end of the summer around the Basin and bordering the Coralline Flats. About 40 gms of Ascophyllum could be consumed at the same level.

When large clumps of Fucus vesiculosus and Ascophyllum nodosum were anchored at 50 feet, they were attacked by masses of larger urchins and devoured in about a week. At Holyrood the population at 1 foot could consume about 10 gms of Fucus and 7 gms of Ascophyllum daily/

2
m in September and the greater concentration of urchins which was present in November could potentially consume more than twice as much.

Petalonia fascia, Scytosiphon lomentaria, Halosaccion rementaceum, Urospora wormskjoldii and Monostroma sp. are annual species which were common on the low intertidal and subtidal in the spring but rapidly disappeared with the approach of summer. Chordaria flagelliformis, Dictyosiphon foeniculaceus, Chorda filix, Saccorhiza dermatodea and Ulva sp. grew at similar levels and were common in some areas during the summer. Rhodymenia palmata most commonly occurred on Alaria stipes. The food preference experiment demonstrated that Halosaccion and Petalonia were highly preferred and readily consumed foods. During May and June grazing on Monostroma was commonly observed and was also evidenced by gut analyses. Urchin grazing may well limit the distribution of many of these species.

At Holyrood, perennials were absent below low water level. Scytosiphon lomentaria occurred near low water level in the late winter and Chordaria flagelliformis and Dictyosiphon foeniculaceus became quite common near shore in July when the urchins had migrated to greater depths.

In the spring Desmarestia viridis appears at depths of up to 40 feet on bedrock and on boulders where there is usually water movement from swell action. It grows very rapidly and its delicate structure allows it to be washed over the surrounding rock surfaces even

when there is very little water movement. The effectiveness of this abrasion in keeping urchins away from the plants was observed several times in the field. This alga is readily weighed down and eaten in calm periods during the summer. Rapid growth and abrasion may similarly be factors which enable D. aculeata to become established at greater depths. The latter species is typical of very exposed environments but D. viridis occurs in a wide range of exposures.

Agarum cribrosum and Ptilota serrata are the only perennial noncalcareous macrophytes which are common at greater depths in urchin dominated areas in Newfoundland and it is notable that both are highly unpreferred foods which are consumed at very slow rates.

Agarum grows on bedrock and boulders below the sublittoral fringe and most often occurs in exposed areas but is also usually present as an understory species in beds of Laminaria saccharina and L. longicruris.

Agarum was scattered along the walls of the Narrows at Logy Bay and it was observed that urchins stayed outside the area which was abraded by the fronds as they washed back and forth. At 27 feet 22 gms/day/m² could possibly be consumed. However, the lab studies demonstrated that it would be eaten only if no other foods were available. At Portugal Cove Agarum also occurred on vertical bedrock faces which were diagonal to the direction of the exposure. At 30 feet only 5 gms/day/m² could be consumed compared to 27 gms of Alaria at the same level. At Portugal Cove Agarum was not usually present on the loose substrate or below 40 feet on bedrock, however, one plant, about 18 cm in length, did occur in the cage, which excluded larger urchins from one square meter

of loose substrate at 50 feet.

Ptilota serrata occurs on bedrock, boulder and cobble substrates and is common from 40-100 feet in exposed areas. At Logy Bay it was common at 80 feet and the urchin population at this depth could consume 8 gms/day/m². On bedrock at Portugal Cove Ptilota became common at about 50 feet where the urchin population could only consume about 5 gms daily. Only very small fronds of this alga existed on the cobbles at this depth where the grazing potential was slightly higher, but a slightly greater growth occurred in this habitat in the wire cage where urchins were excluded for over a year. Water movement offers little protection to this low growing alga and this may explain why it is generally absent in shallower water where the grazing potential is high. Ptilota grows well at greater depths where light conditions are diminished and as this alga is not a desirable food of urchins they therefore do not congregate at greater depths and thus the Ptilota is not destroyed there.

Vadas (1968) found a very similar situation with the distribution of Agarum cribrosum and A. fimbriatum in the San Juan Islands. He demonstrated that although Agarum grows better in shallow water it is excluded from the sublittoral fringe because it is competitively inferior to the other kelps. He suggested that the chemical nature of Agarum makes it undesirable to urchins. It is nutritionally an unsuitable food for urchin growth and reproduction so urchins may have evolved their lack of preference for this species. The discriminant feeding

behavior of urchins has made it possible for Agarum to become established in deeper water where urchins are prevalent. The results of this study support his hypothesis, and a similar situation probably applies to Ptilota. In a number of exposed areas along the south coast of Newfoundland I have found extensive beds of Agarum between 40-65 feet and Ptilota is usually present as an understory. In other areas only Ptilota is present as is the case at 50-70 feet on bed-rock outcrops north of the Portugal Cove study area.

Urchins may control the faunal distribution by direct predation of sessile and slow moving forms as well as indirectly by destroying the habitats which are provided by algal growth. In the three study areas, urchins were commonly found on beds of small mussels (Mytilis edulis), and the gut analyses proved that both mussels and barnacles (Balanus balanoides), were eaten by S. droebachiensis. Newcombe (1935) gives evidence that predation by urchins and Asterias spp. is important in limiting the downward distribution of both these animals.

In the eastern Murman, Propp (1966) found that the grazing of S. droebachiensis was particularly important in shallow water where this animal is concentrated and of less importance at greater depths. His approach was to estimate the rate at which the bottom was grazed over from the urchin density, average urchin speed and feeding intensity. At 49-82 feet (15-25 m) the bottom would be grazed over in 30-60 or more days but below 164 feet (50 m) the effect of grazing on the

epiflora was no longer significant. He also records that new growth of Chaetomorpha melanogonium, Monostroma grevillei, M. fuscum and Enteromorpha compressa occurs in March and April in the transition zone between the laminarians and the Lithothamnion community but rapidly disappears as a result of urchin grazing during June and July.

A number of studies have also been made on the influence of grazing by other echinoids on algae. On the sea bed at Plymouth, England, Forster (1959) found that the mean density of Echinus esculentus was $0.2/m^2$ and estimated the Echinus grazed over about one-third of the rock surface annually removing algae, diatoms, and associated organisms. At the ruined Breakwater at Port Erin, Isle of Man, Kain and Jones (1966, Jones and Kain 1967) found that the mean density of Echinus in the bare rock area from 8 to 11 m, below a dense growth of Laminaria hyperborea, was $3.6/m^2$ and up to $5/m^2$ on the boulders just above the sand at 11 m. When urchins were removed at monthly intervals for 3 years the Laminaria and also Saccorhiza polyschides became established at greater depths in the cleared area. The above densities apparently had limited the Laminaria to about 7 m depth. However, reduced light at greater depths may also have been a contributing factor.

At Lough Ine, Ireland, Kitching and Ebling (1961) found that algae were absent in the Paracentrotus lividus zone near the shore but a dense growth of algae, mainly Enteromorpha, was present in slightly

deeper water. In July 1959 nearly all the urchins, except for small ones, were cleared from an area of nearly 300 m^2 in the shallow water Paracentrotus zone where the urchin density was $6.6/\text{m}^2$. In September there was a 50 percent algal cover in this area and in July of the following year a thick growth covered the entire area. Conversely when 1326 Paracentrotus were transferred to an Enteromorpha covered area the urchins first cleared a central area and then formed a grazing front which in 2 months had extended outward exposing an area of 21 m^2 .

In Miami, the importance of Lytechinus variagatus in the Thalassia community was indicated by Moore and McPherson (1965) who estimated that mean densities of 1.9 large and 42.8 small Lytechinus/ m^2 would consume an average of 1.6 kg and a maximum of 9.1 kg of Thalassia per year and that the annual production of Thalassia was about $8.8 \text{ kg}/\text{m}^2$.

In southern California, Leighton, Jones and North (1966) intensively studied certain large beds of giant kelp, Macrocystis pyrifera, which have drastically dwindled since 1940 as a result of excessive grazing, primarily by sea urchins, S. franciscanus, S. purpuratus and Lytechinus anamesus. Distinct fronts of grazing urchins were sometimes seen advancing through beds of kelp and when the vegetation was removed from one area the animals usually moved on. Urchins were particularly destructive since they typically attacked the base of the plant so that the remainder drifted away. The larger

urchin populations, which caused the imbalance of urchin consumption over plant production, appeared to be a result of additional nutrients provided for the urchins by discharged sewage. Three forms of control were suggested: (1) Predation by the sea otter, Enhydra lutris, however, this species was exploited by overhunting and the present herd is very small ; (2) Treatments with quicklime (CaO) in quantities which will eliminate the urchins, which are especially sensitive to it, and have little effect on other life ; (3) Manually killing the urchins in low density areas by puncturing them to prevent them from invading vegetated areas. Urchin removal by quicklime treatments has proven very successful. They found that algae did not become established unless there were less than 1 S. franciscanus/m², 10 S. purpuratus/m² or 10 Lytechinus anamesus/m². Since S. droebachiensis feeds at a slightly greater rate than S. purpuratus (Vadas 1968) probably less than 10 S. droebachiensis/m² would be necessary to keep an area bare of algae.

In 1962 McLean suggested that the luxuriant development of the Nereocystis - Pterygophora association on the open coast at Carmel, California, was made possible by the predation of S. franciscanus by the sea otter. In Monterey Bay, where the otters had not reached, there were high densities of urchins and scrubby algal growth. Soon after McLean's observation, sea otters extended their range into the Monterey area and in 1964 North (1965) found that urchin concentrations were low and that there had been "massive development of Macrocystis".

The mounting interest in feeding habits of urchins during the past decade has well demonstrated the importance of these animals as grazers in shallow water coastal communities. When urchins are insufficiently controlled by predators they sharply limit many important macrophytes and their associated fauna to a narrow wave-beaten zone near the shore. Kelp species are highly preferred foods of urchins and in deeper water kelp communities are eliminated when urchin densities are too high. Thus the urchin may be of great commercial importance to industries interested in harvesting algae. Urchins also may be of positive value as a source of food for lobsters and many fishes.

Hairston et al. (1960) have stated that in terrestrial communities primary production is usually limited by light or essential materials and not by herbivores; herbivores are limited by predation rather than by food supply; and predators control their own numbers by their effect on the herbivores. Exceptions sometimes occur because of unusual meteorological events or as a result of human activities.

In the marine environment the vegetation is commonly limited and sometimes eliminated by overgrazing. Randall (1961, 1965) has shown that in tropical areas herbivorous reef fishes have caused such situations. The depletion of the kelp beds in California has ultimately resulted from over hunting of sea otters, which formerly regulated the grazers, primarily urchins, and the discharge of wastes which provided additional nutrients for and thus increased the urchin population (McLean 1962, Leighton et al. 1966).

In Newfoundland overgrazing in the sublittoral community is almost entirely the result of one herbivore, S. droebachiensis. This urchin may well be an important food to lobsters, crabs and many fishes but these predators are not very effective in controlling the numbers of urchins. In areas where urchins are highly concentrated and where food is not available cannibalism may also exist. Ebert (1968) has shown that food limitation may limit the size of adult urchins in a population (of S. purpuratus) but does not reduce the density. However, Moore (1934), Buchanan (1966) and Vadas (1968) have shown that the type and quantity of food available may also limit the amount of spawn produced by echinoids and thus food may ultimately affect the density of urchins. In the steady areas normal gonadal development of the urchins which gorge on the algae of the sublittoral fringe and on foods washed down from the littoral zone probably ensure that there is sufficient recruitment to maintain the populations.

The monotony of the fauna and flora below the sublittoral fringe in exposed areas is probably largely attributed to the predominance of S. droebachiensis. Crustose corallines do not appear to be restricted by urchins and are greatly developed. Ptilota serrata and Agarum cribrosum are the only perennial macrophytes which can establish themselves in this urchin-dominated community and this is only possible because they are undesirable food materials for the urchin. The fauna is also limited. A few star fish, Cucumaria frondosa, and Volseella modiolus are the only common epibenthic forms

and Hiatella arcta, Ophiopholis aculeata, Ishnochitin albus, Nereis
plagica and a few other small organisms live in protected crevices
in and under the Lithothamnion. Propp (1966) also mentioned the
limited species diversity in the same S. droebachiensis dominated
community in the eastern Murman. Undoubtedly many more forms could
exist if urchin grazing were not so severe as to prevent the devel-
opment of kelp communities.

SUMMARY

An annual reproductive cycle is present in the green sea urchin, Strongylocentrotus droebachiensis (O.F. Müller 1776). The gonads are small and in recovering condition during the late spring and summer, ripening occurs in the fall, a peak in size and maturity occurs in February and March, and spawnout usually occurs by the end of April. The extent of gonadal development varies in different localities and from year to year, and irregular spawning may occur when the gonads are in ripening condition.

In the three study areas, as well as along most of the coast of Newfoundland, this urchin is conspicuously the dominant epibenthic animal. Generally the size composition and density of the urchin populations in the study areas can be related to the effect of wave exposure and substrate on settlement, survival and growth. There were very high densities on the exposed bedrock surfaces at Portugal Cove and even greater densities (up to $350/m^2$) occurred at Logy Bay where exposure is more severe. Urchin populations, similar to those at Portugal Cove were found at greater depths at Logy Bay suggesting that there is a downward displacement at Portugal Cove. This is also evident in the greater downward expansion of the Alaria zone at Logy Bay. The high density on these exposed bedrock faces suggests that settlement is normally high. Settlement and early survival may be even higher on the cobble substrate below 20 feet, but near shore smaller urchins may have been crushed and thus destroyed. The wider spacing of successive modes and the greater progression of the mode of small urchins in shallow water at Portugal Cove than at Logy Bay suggests that faster growth occurs at Portugal Cove.

On the other hand in the sheltered Holyrood Bay and Salmonier Arm areas the urchin density was low but there was a very high percentage of large individuals. Settlement must be poor here but the chances of survival are exceedingly great.

In all the areas studied the biomass and density of S. droebachiensis generally decreased with depth. One notable exception was on the loose substrate at Portugal Cove because small urchins were absent in shallow water and very abundant at 30 to 50 feet. However, even here the density and biomass of larger urchins were consistent with the usual trend.

On many occasions masses of urchins were observed covering the bottom near low water level, or along the lower border of the sublittoral fringe or around scattered patches of macrophytes in deeper water. Gut analyses have clearly indicated the predominance of algae in the diet of S. droebachiensis whenever it is available and certainly the distribution of this food source must greatly influence the distribution of larger urchins.

The laboratory studies demonstrated that there is great seasonal variation in the amount of algae consumed by S. droebachiensis and this is mostly closely related to the gonad cycle. Very little is eaten in February when the gonads are very large and mostly ripe, but in May, when spawning is completed and the gonads are small, the consumption is very high. By September the gonads begin to ripen and the feeding rate again decreases. Although large urchins consume more than smaller urchins the latter consume a greater percentage of their weight daily, particularly during peak feeding periods. Assimilation efficiency also varied on different algae. Laminaria

was more efficiently assimilated in February, when less was eaten, than in September.

The grazing potential of the urchin populations in the field indicates that S. droebachiensis may exert a great influence on the distribution of macrophytes. Most of the species of the sublittoral fringe are desirable foods and concentrations of urchins in shallow water probably is a major factor in setting their lower limit. Wave action may provide some protection for these plants since urchins will not enter areas where algal fronds are washing back and forth over the rock surface. This is well demonstrated by the extent of the Alaria esculenta zone which is shallow or absent in protected areas but reaches depths of up to 35 feet on exposed ridges. Sporlings appear and grow very rapidly in the winter, when swell conditions are most severe and the urchins are in minimal feeding condition, but they are rapidly devoured during calm periods following April. Apart from calcareous algae, Agarum cribrosum and Ptilota serrata are the only perennial macrophytes which exist below the sublittoral fringe in urchin dominated areas. This is possible because these species are highly undesirable foods for the urchins. Also S. droebachiensis likely limits the distribution of the fauna both directly by grazing and indirectly by preventing the establishment of kelp communities at greater depths.

Lobsters, crabs, starfish, birds, a number of fishes, and other S. droebachiensis are probably frequent predators of the green sea urchin, but they are not effective in limiting the numbers of this species. Food supply and space availability are probably important controls of urchin density and biomass.

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* When the original reference was not available the secondary source is indicated in brackets.

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APPENDIX I: Data on gonad indices and indices of gut plus contents of urchins from Portugal Cove.

<u>Date</u>		GONAD INDEX			INDEX OF GUT PLUS CONTENTS		
		<u>\bar{X}</u>	<u>N</u>	<u>SE</u>	<u>\bar{X}</u>	<u>N</u>	<u>SE</u>
February 2, 1968	male	10.42	19	1.13	----		
	female	13.51	22	1.31			
	\bar{X}	12.08	41	0.90			
February 29, 1968	male	12.53	9	1.65	----		
	female	20.28	12	1.61			
	\bar{X}	16.96	21	1.42			
March 28, 1968	male	6.01	10	0.72	10.67	20	0.70
	female	8.48	10	2.86			
	\bar{X}	7.24	20	1.47			
April 28, 1968	male	4.28	6	1.07	9.15	20	0.48
	female	3.77	14	0.33			
	\bar{X}	3.92	20	0.38			
May 29, 1968	male	4.53	12	0.34	12.53	20	0.56
	female	3.07	8	0.64			
	\bar{X}	3.94	20	0.36			
June 27, 1968	male	3.71	9	0.36	14.33	20	0.75
	female	3.88	11	0.40			
	\bar{X}	3.81	20	0.27			
July 29, 1968	male	7.90	7	0.67	14.36	20	0.57
	female	4.90	13	0.23			
	\bar{X}	5.90	20	0.41			
August 29, 1968	male	6.62	9	0.39	14.64	20	0.60
	female	7.04	11	0.68			
	\bar{X}	6.85	20	0.41			
September 29, 1968	male	4.05	13	0.52	10.18	20	0.55
	female	3.14	7	0.44			
	\bar{X}	3.73	20	0.38			
October 30, 1968	male	4.70	5	0.93	12.68	20	0.50
	female	3.17	15	0.47			
	\bar{X}	3.56	20	0.44			
November 29, 1968	male	9.34	7	1.36	11.72	20	0.45
	female	8.57	13	0.67			
	\bar{X}	8.84	20	0.63			
December 20, 1968	male	5.68	8	0.98	9.26	20	0.54
	female	6.43	12	0.90			
	\bar{X}	6.13	20	0.66			

APPENDIX I (Cont'd).

<u>Date</u>		GONAD INDEX			INDEX OF GUT PLUS GONADS		
		<u>\bar{X}</u>	<u>N</u>	<u>SE</u>	<u>\bar{X}</u>	<u>N</u>	<u>SE</u>
January 29, 1969	male	3.85	10	0.88			
	female	4.59	10	0.92			
	\bar{X}	4.22	20	0.62	13.00	20	0.92
February 26, 1969	male	4.77	11	0.80			
	female	9.24	9	1.76			
	\bar{X}	6.78	20	1.02	11.70	20	0.62
March 28, 1969	male	9.31	10	0.66			
	female	12.39	10	1.37			
	\bar{X}	10.85	20	0.82	11.02	20	0.58
April 27, 1969	male	3.16	12	0.30			
	female	2.98	8	0.23			
	\bar{X}	3.09	20	0.20	14.69	20	0.59
May 28, 1969	male	4.98	11	0.52			
	female	3.76	9	0.23			
	\bar{X}	4.43	20	0.33	17.21	20	0.76
June 27, 1969	male	6.91	14	0.40			
	female	6.20	6	0.84			
	\bar{X}	6.69	20	0.37	13.03	20	0.81

APPENDIX II: Data from Acreman's study (1966) on the gonad and gut indices of urchins from Bellevue, Brigus and Long Pond in 1965.

<u>Date</u>	<u>GONAD INDEX</u>			<u>GUT INDEX</u>		
	<u>\bar{X}</u>	<u>N</u>	<u>SE</u>	<u>\bar{X}</u>	<u>N</u>	<u>SE</u>
BELLEVUE, TRINITY BAY						
May 20	4.15	10	0.64	3.19	10	0.27
May 27	5.32	10	0.76	4.68	10	0.37
June 3	4.66	10	1.05	4.63	10	0.36
June 8	6.16	10	0.47	5.03	10	0.22
July 21	7.34	10	0.49	5.19	10	0.38
July 27	8.23	10	1.21	5.01	10	0.15
August 5	12.81	10	1.35	6.43	10	0.52
August 18	11.26	10	1.10	5.36	10	0.17
August 27	12.82	10	0.96	4.77	10	0.27
September 1	10.75	10	1.35	5.16	10	0.27
October 2	11.87	10	0.99	3.70	10	0.21
BRIGUS, CONCEPTION BAY						
June 22	5.45	10	0.64	4.88	10	0.46
LONG POND, CONCEPTION BAY						
July 7	10.20	10	0.30	4.78	10	0.24
July 13	11.68	10	0.80	4.29	10	0.20

APPENDIX III: Time of sampling, grid size, the number of grids, and the mean number of urchins in the samples collected from various depths at Logy Bay, Portugal Cove and Holyrood.

<u>DEPTH</u>	<u>TIME OF SAMPLING</u>	<u>NUMBER OF SAMPLES</u>	<u>GRID SIZE</u>	<u>\bar{X}</u>	<u>SE</u>
<u>LOGY BAY</u>					
16' (5m)	June 26 - July 9, 1968	5	0.2 m ²	70.60	5.00
27' (8m)	June 5 - July 8, 1968	6	0.2 m ²	60.67	4.03
40' (12m)	June 6 - June 20, 1968	7	0.2 m ²	52.86	11.09
50' (15m)	August 13, 1968	6	0.2 m ²	28.83	3.44
60' (18m)	August 15, 1968	6	0.2 m ²	20.50	3.05
70' (21m)	August 14, 1968	6	0.2 m ²	15.67	2.32
80' (24m)	August 14, 1968	5	0.2 m ²	21.40	4.11
16' (5m)	May 22, 1969	6	0.2 m ²	56.33	10.51
16' (5m)	Sept. 4, 1969	6	0.2 m ²	57.83	2.41
<u>PORTUGAL COVE - BEDROCK</u>					
10' (3m)	August 6, 1968	6	0.2 m ²	54.17	10.04
20' (6m)	August 6, 1968	6	0.2 m ²	48.17	6.71
30' (9m)	August 12, 1968	6	0.2 m ²	31.50	4.13
40' (12m)	August 9, 1968	6	0.2 m ²	27.00	5.44
50' (15m)	August 12, 1968	6	0.2 m ²	22.67	2.30
10' (3m)	May 13, 1969	6	0.2 m ²	44.67	11.41
10' (3m)	Sept. 10, 1969	6	0.2 m ²	44.33	6.12
<u>PORTUGAL COVE - LOOSE SUBSTRATE</u>					
1' (0m)	August 2, 1968	6	0.2 m ²	24.67	4.14
10' (3m)	July 25, 1968	6	0.2 m ²	13.50	1.28
20' (6m)	July 19 - July 31, 1968	6	0.2 m ²	43.50	4.22
30' (9m)	July 30 - July 31, 1968	6	0.2 m ²	56.17	2.73
40' (12m)	July 10 - July 13, 1968	7	0.2 m ²	40.29	1.85
50' (15m)	July 10 - July 13, 1968	7	0.2 m ²	61.17	5.38
60' (18m)	June 25 - July 5, 1968	6	0.2 m ²	23.57	4.90
70' (21m)	July 23 - July 31, 1968	7	0.2 m ²	14.20	1.32
50' (15m)	July 24, 1968	5	0.2 m ²	37.83	5.61
50' (15m)	May 16, 1969	6	0.2 m ²	33.67	3.93
50' (15m)	August 28, 1969	3	0.2 m ²		
<u>HOLYROOD BAY</u>					
1' (0m)	August 27, 1968	4	1.0 m ²	31.50	9.79
10' (3m)	August 27, 1968	12	1.0 m ²	5.08	2.46
20' (6m)	November 2, 1968	16	1.0 m ²	3.19	0.50
40' (12m)	August 16, 1968	6	0.8 m ²	7.00	1.93
60' (18m)	August 16, 1968	4	0.8 m ²	10.00	0.91
1' (0m)	November 2, 1968	3	1.0 m ²	65.00	5.03

APPENDIX IVa: Density and biomass/m² at various depths -- Logy Bay.

DEPTH:	<u>16'</u>	<u>27'</u>	<u>40'</u>	<u>50'</u>	<u>60'</u>	<u>70'</u>
	NUMBERS / m ²					
<u>SIZE CLASS</u>						
2.0 - 3.9	2.00	0.00	2.86	0.00	0.00	0.00
4.0 - 5.9	20.00	6.67	15.71	3.33	2.50	0.00
6.0 - 7.9	53.00	15.83	12.86	8.33	10.00	0.83
8.0 - 9.9	42.00	18.33	25.00	11.67	9.17	1.67
10.0 - 11.9	19.00	12.50	20.00	8.33	7.50	1.67
12.0 - 13.9	17.00	17.50	13.57	11.67	8.33	5.00
14.0 - 15.9	12.00	25.00	23.57	13.33	4.17	9.17
16.0 - 17.9	18.00	23.33	18.57	7.50	6.67	9.17
18.0 - 19.9	<u>16.00</u>	<u>14.17</u>	<u>18.57</u>	<u>7.50</u>	<u>5.83</u>	<u>5.83</u>
	199.00	133.33	150.71	71.67	54.17	33.33
20.0 - 21.9	14.00	15.00	17.14	10.00	8.33	6.67
22.0 - 23.9	17.00	25.83	10.71	10.00	6.67	5.00
24.0 - 25.9	21.00	19.17	10.00	5.83	2.50	5.83
26.0 - 27.9	22.00	22.50	8.57	2.50	3.33	6.67
28.0 - 29.9	17.00	18.33	10.71	6.67	0.83	2.50
30.0 - 31.9	20.00	12.50	11.43	6.67	5.00	5.00
32.0 - 33.9	12.00	12.50	6.43	5.00	5.83	1.67
34.0 - 35.9	11.00	10.83	3.57	7.50	3.33	0.83
36.0 - 37.9	10.00	5.00	4.29	5.83	3.33	3.33
38.0 - 39.9	<u>3.00</u>	<u>6.67</u>	<u>5.71</u>	<u>1.67</u>	<u>1.67</u>	<u>4.17</u>
	147.00	148.33	88.57	61.67	40.83	41.67
40.0 - 41.9	3.00	6.67	3.57	4.17	2.50	0.83
42.0 - 43.9	1.00	5.83	6.43	2.50	1.67	0.83
44.0 - 45.9	1.00	3.33	4.29	1.67	2.50	0.83
46.0 - 47.9	1.00	4.17	5.71	1.67	0.83	0.00
48.0 - 49.9	1.00	0.00	2.14	0.00	0.00	0.00
50.0 - 51.9	0.00	0.83	1.43	0.00	0.00	0.00
52.0 - 53.9	0.00	0.00	0.00	0.83	0.00	0.00
54.0 - 55.9	0.00	0.83	0.71	0.00	0.00	0.00
56.0 - 57.9	0.00	0.00	0.71	0.00	0.00	0.00
58.0 - 59.9	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>
	7.00	21.67	25.00	10.83	7.50	3.33
	<u>353.00</u>	<u>303.33</u>	<u>264.29</u>	<u>144.17</u>	<u>102.50</u>	<u>78.33</u>

	BIOMASS (gms) / m ²					
< 19.9	149.05	159.39	153.29	79.54	53.18	54.38
20.0 - 39.9	1669.12	1598.75	885.27	674.61	439.31	429.23
> 40.0	<u>199.67</u>	<u>786.39</u>	<u>1037.84</u>	<u>357.62</u>	<u>235.03</u>	<u>126.77</u>
	2017.84	2544.53	2076.41	1111.77	727.53	610.38

ass/m² at various depths -- Logy Bay.

f'	40'	50'	60'	70'	80'	\bar{x}	May, 1969 16'	Sept., 1969 16'
NUMBERS / m ²								
10	2.86	0.00	0.00	0.00	0.00	0.69	0.00	0.83
17	15.71	3.33	2.50	0.00	0.00	6.89	0.00	2.50
13	12.86	8.33	10.00	0.83	3.00	14.84	10.00	9.17
13	25.00	11.67	9.17	1.67	5.00	16.12	34.17	25.83
10	20.00	8.33	7.50	1.67	3.00	10.29	41.67	29.17
10	13.57	11.67	8.33	5.00	13.00	12.30	21.67	13.33
10	23.57	13.33	4.17	9.17	13.00	14.32	13.33	9.17
13	18.57	7.50	6.67	9.17	10.00	13.32	12.50	14.17
7	18.57	7.50	5.83	5.83	8.00	10.84	8.33	15.83
3	150.71	71.67	54.17	33.33	55.00	99.60	141.67	120.00
10	17.14	10.00	8.33	6.67	4.00	10.73	16.67	12.50
13	10.71	10.00	6.67	5.00	8.00	11.89	13.33	25.00
7	10.00	5.83	2.50	5.83	5.00	9.90	20.00	23.33
0	8.57	2.50	3.33	6.67	4.00	9.94	14.17	20.00
3	10.71	6.67	0.83	2.50	2.00	8.29	17.50	23.33
0	11.43	6.67	5.00	5.00	3.00	9.09	15.83	15.00
0	6.43	5.00	5.83	1.67	2.00	6.49	13.33	13.33
3	3.57	7.50	3.33	0.83	3.00	5.72	12.50	9.17
0	4.29	5.83	3.33	3.33	3.00	4.97	5.00	7.50
7	5.71	1.67	1.67	4.17	7.00	4.27	4.17	7.50
3	88.57	61.67	40.83	41.67	41.00	81.30	132.50	156.67
7	3.57	4.17	2.50	0.83	4.00	3.53	0.83	3.33
3	6.43	2.50	1.67	0.83	2.00	2.89	3.33	4.17
3	4.29	1.67	2.50	0.83	1.00	2.09	0.83	0.83
7	5.71	1.67	0.83	0.00	2.00	2.20	0.83	2.50
0	2.14	0.00	0.00	0.00	2.00	0.73	0.83	0.00
3	1.43	0.00	0.00	0.00	0.00	0.32	0.00	0.83
0	0.00	0.83	0.00	0.00	0.00	0.12	0.83	0.00
3	0.71	0.00	0.00	0.83	0.00	0.34	0.00	0.00
0	0.71	0.00	0.00	0.00	0.00	0.10	0.00	0.83
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7	25.00	10.83	7.50	3.33	11.00	12.33	7.50	12.50
3	264.29	144.17	102.50	78.33	107.00	193.23	281.67	289.17
BIOMASS (gms) / m ²								
0	153.29	79.54	53.18	54.38	75.73	103.51	128.78	133.36
5	885.27	674.61	439.31	429.23	473.58	881.41	1414.29	1678.06
2	1037.84	357.62	235.03	126.77	262.84	429.45	290.89	477.88
3	2076.41	1111.77	727.53	610.38	812.15	1414.37	1833.96	2289.29

APPENDIX IVb: PORTUGAL COVE -

	<u>10'</u>	<u>20'</u>	<u>30'</u>	<u>40'</u>
<u>SIZE CLASS</u>	<u>NUMBERS / m²</u>			
2.0 - 3.9	0.83	0.83	1.67	5.00
4.0 - 5.9	1.67	3.33	9.17	11.67
6.0 - 7.9	14.17	15.00	25.00	13.33
8.0 - 9.9	16.67	19.17	25.83	20.00
10.0 -11.9	14.17	25.83	20.83	15.83
12.0 -13.9	10.00	19.17	11.67	7.50
14.0 -15.9	14.17	19.17	5.00	5.83
16.0 -17.9	13.33	14.17	11.67	9.17
18.0 -19.9	<u>15.00</u>	<u>21.67</u>	<u>11.67</u>	<u>10.83</u>
	100.00	138.33	122.50	99.17
20.0 -21.9	15.00	23.33	10.00	5.83
22.0 -23.9	15.00	14.17	8.33	9.17
24.0 -25.9	19.17	19.17	8.33	5.00
26.0 -27.9	18.33	11.67	3.33	6.67
28.0 -29.9	10.00	11.67	2.50	3.33
30.0 -31.9	22.50	7.50	2.50	0.83
32.0 -33.9	10.83	4.17	0.00	2.50
34.0 -35.9	10.83	6.67	0.00	1.67
36.0 -37.9	14.17	0.83	0.00	0.83
38.0 -39.9	<u>13.33</u>	<u>0.83</u>	<u>0.00</u>	<u>0.00</u>
	149.17	100.00	35.00	35.83
40.0 -41.9	11.67	0.83	0.00	0.00
42.0 -43.9	2.50	0.83	0.00	0.00
44.0 -45.9	5.00	0.00	0.00	0.00
46.0 -47.9	0.00	0.00	0.00	0.00
48.0 -49.9	<u>2.50</u>	<u>0.83</u>	<u>0.00</u>	<u>0.00</u>
	21.67	2.50	0.00	0.00
	<u>270.83</u>	<u>240.83</u>	<u>157.50</u>	<u>135.00</u>

	<u>BIOMASS (gms) / m²</u>			
< 19.9	178.32	157.86	97.66	78.47
20.0 -39.9	1793.20	797.29	213.70	274.04
> 40.0	<u>717.82</u>	<u>89.20</u>	<u>0.00</u>	<u>0.00</u>
	2689.33	1044.35	311.36	352.51

: PORTUGAL COVE - BEDROCK

	40'	50'	\bar{X}	May, 1969 10'	Sept., 1969 10'
0'	NUMBERS / m ²				
67	5.00	2.50	2.17	0.00	0.00
17	11.67	5.83	6.33	0.83	0.00
10	13.33	15.83	16.67	2.50	0.00
13	20.00	5.00	17.33	5.00	2.50
13	15.83	10.83	17.50	18.33	10.00
17	7.50	16.67	13.00	22.50	13.33
10	5.83	8.33	10.50	13.33	17.50
17	9.17	5.00	10.67	15.00	15.83
17	10.83	5.83	13.00	8.33	10.00
0	99.17	75.83	107.17	85.83	69.17
0	5.83	8.33	12.49	8.33	16.67
3	9.17	13.33	12.00	12.50	12.50
3	5.00	6.67	11.67	13.33	14.17
3	6.67	5.00	9.00	20.00	20.00
0	3.33	1.67	5.83	16.67	14.67
0	0.83	0.00	6.67	12.50	14.67
0	2.50	0.83	3.67	12.50	10.83
0	1.67	0.83	4.00	15.00	21.67
0	0.83	0.00	3.17	11.67	7.50
0	0.00	0.83	3.00	5.83	9.17
0	35.83	37.50	71.50	128.33	140.83
0	0.00	0.00	2.50	5.00	5.83
0	0.00	0.00	0.67	2.50	2.50
0	0.00	0.00	1.00	0.83	1.67
0	0.00	0.00	0.00	0.83	0.00
0	0.00	0.00	0.67	0.00	1.67
0	0.00	0.00	4.83	9.17	11.57
0	135.00	113.33	183.50	223.33	221.67

BIOMASS (gms) / m²

78.47	62.18	114.89	112.97	116.23
274.04	231.24	661.90	1549.36	1755.50
0.00	0.00	161.40	285.28	399.45
352.51	293.42	938.19	1947.61	2271.18

APPENDIX IVc: PORTUGAL COVE - LOOSE

	<u>1'</u>	<u>10'</u>	<u>20'</u>	<u>30'</u>	<u>40'</u>
	NUMBERS / m ²				
<u>SIZE CLASS</u>					
2.0 - 3.9	0.00	0.00	0.00	1.67	3.57
4.0 - 5.9	0.00	0.00	11.67	17.50	12.14
6.0 - 7.9	0.00	0.00	15.83	57.50	42.13
8.0 - 9.9	0.00	0.00	23.33	71.67	69.29
10.0 - 11.9	0.00	0.83	25.83	40.00	22.14
12.0 - 13.9	0.00	0.00	15.00	28.33	12.86
14.0 - 15.9	0.00	2.50	25.00	13.33	5.71
16.0 - 17.9	0.00	0.00	12.50	10.00	5.71
18.0 - 19.9	<u>0.00</u>	<u>0.83</u>	<u>8.33</u>	<u>3.33</u>	<u>3.57</u>
	0.00	4.17	137.50	243.33	177.14
20.0 - 21.9	0.83	0.83	6.67	6.67	4.29
22.0 - 23.9	0.00	0.00	9.17	5.00	3.57
24.0 - 25.9	0.83	1.67	7.50	0.83	2.86
26.0 - 27.9	1.67	7.50	5.83	0.83	2.14
28.0 - 29.9	0.83	12.50	8.33	3.33	2.14
30.0 - 31.9	2.50	6.67	8.33	5.83	2.14
32.0 - 33.9	3.33	4.17	4.17	2.50	0.00
34.0 - 35.9	5.00	7.50	10.00	0.00	2.86
36.0 - 37.9	19.17	3.33	5.00	4.17	1.43
38.0 - 39.9	<u>15.83</u>	<u>5.00</u>	<u>6.67</u>	<u>2.50</u>	<u>0.71</u>
	50.00	49.17	71.67	31.67	22.14
40.0 - 41.9	25.83	5.00	2.50	1.67	0.00
42.0 - 43.9	14.17	3.33	0.83	2.50	1.43
44.0 - 45.9	12.50	3.33	2.50	0.83	0.00
46.0 - 47.9	10.83	0.83	1.67	0.00	0.00
48.0 - 49.9	6.67	0.83	0.83	0.83	0.71
50.0 - 51.9	2.50	0.83	0.00	0.00	0.00
52.0 - 53.9	<u>0.83</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>
	73.33	14.17	8.33	5.83	2.14
	<u>123.33</u>	<u>67.50</u>	<u>217.50</u>	<u>280.83</u>	<u>201.43</u>
				BIOMASS (gms) / m ²	
< 19.9	0.00	5.23	123.06	121.33	73.96
20.0 - 39.9	1000.66	668.63	866.85	341.70	206.72
> 40.0	<u>2561.17</u>	<u>464.13</u>	<u>300.98</u>	<u>200.85</u>	<u>74.96</u>
	3561.83	1137.98	1290.88	663.88	355.64

COVE - LOOSE SUBSTRATE

						May, 1969	Aug., 1969
'	40'	50'	60'	70'	\bar{x}	50'	50'
3 / m ²							
7	3.57	10.83	0.00	0.00	2.01	6.67	0.00
0	12.14	35.00	5.00	0.00	10.16	14.17	1.67
0	42.13	80.00	30.71	6.00	29.02	37.50	23.33
7	69.29	60.83	16.43	8.00	31.19	40.83	36.67
0	22.14	46.67	12.14	10.00	19.70	34.17	50.00
3	12.86	24.17	10.00	13.00	12.92	15.83	23.33
3	5.71	13.33	9.29	8.00	9.65	12.50	3.33
0	5.71	5.00	8.57	8.00	6.22	8.33	10.00
3	<u>3.57</u>	<u>4.17</u>	<u>5.71</u>	<u>2.00</u>	<u>3.49</u>	<u>4.17</u>	<u>6.67</u>
3	177.14	280.00	97.86	85.00	124.38	174.17	155.00
7	4.29	0.00	5.71	5.00	3.75	1.67	1.67
0	3.57	2.50	3.57	4.00	3.48	0.83	3.33
3	2.86	1.67	2.14	5.00	2.81	0.00	1.67
3	2.14	2.50	2.14	0.00	2.83	0.00	1.67
3	2.14	0.83	0.00	1.00	3.62	1.67	0.00
3	2.14	0.00	1.43	0.00	3.36	3.33	0.00
0	0.00	5.00	1.43	0.00	2.58	1.67	3.33
0	2.86	1.67	1.43	0.00	3.56	2.50	1.67
7	1.43	3.33	0.71	0.00	4.64	1.67	0.00
0	<u>0.71</u>	<u>3.33</u>	<u>0.71</u>	<u>0.00</u>	<u>4.35</u>	<u>0.00</u>	<u>0.00</u>
7	22.14	20.83	19.29	15.00	34.97	13.33	13.33
7	0.00	4.17	0.71	0.00	4.99	0.00	0.00
0	1.43	0.83	0.00	0.00	2.89	0.00	0.00
3	0.00	0.00	0.00	1.00	2.52	0.00	0.00
0	0.00	0.00	0.00	0.00	1.67	0.00	0.00
3	0.71	0.00	0.00	0.00	1.24	0.00	0.00
0	0.00	0.00	0.00	0.00	0.42	0.83	0.00
0	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.10</u>	<u>0.00</u>	<u>0.00</u>
3	2.14	5.00	0.71	1.00	13.82	0.83	0.00
3	<u>201.43</u>	<u>305.83</u>	<u>117.86</u>	<u>71.00</u>	<u>173.16</u>	<u>188.83</u>	<u>168.33</u>
SS (gms) / m ²							
3	73.96	109.96	72.19	57.77	70.44	99.23	112.40
0	206.72	317.25	153.13	77.23	454.02	168.12	142.38
5	<u>74.96</u>	<u>147.87</u>	<u>18.70</u>	<u>18.37</u>	<u>473.38</u>	<u>43.96</u>	<u>0.00</u>
8	355.64	575.08	244.01	153.37	997.83	311.31	254.78

APPENDIX IVd:

HOLYROOD BAY

Nov., 1968

	<u>1'</u>	<u>10'</u>	<u>20'</u>	<u>40'</u>	<u>60'</u>	<u>\bar{x}</u>	<u>1'</u>
	NUMBERS/m ²						
SIZE CLASS							
2.0 - 3.9	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4.0 - 5.9	0.00	0.00	0.00	0.00	0.31	0.06	0.00
6.0 - 7.9	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8.0 - 9.9	0.50	0.00	0.00	1.46	0.63	0.52	0.00
10.0 - 11.9	1.25	0.00	0.00	0.00	0.63	0.38	0.00
12.0 - 13.9	1.00	0.00	0.00	1.04	0.31	0.47	0.00
14.0 - 15.9	0.25	0.00	0.00	0.42	0.00	0.13	0.00
16.0 - 17.9	0.00	0.08	0.00	0.00	0.31	0.08	0.00
18.0 - 19.9	<u>0.25</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.31</u>	<u>0.11</u>	<u>0.00</u>
	3.25	0.08	0.00	2.92	2.50	1.75	0.00
20.0 - 21.9	0.75	0.08	0.00	0.00	0.00	0.17	0.00
22.0 - 23.9	0.75	0.08	0.00	0.00	0.31	0.23	1.33
24.0 - 25.9	1.00	0.00	0.00	0.00	0.31	0.26	1.33
26.0 - 27.9	1.75	0.08	0.00	0.00	0.31	0.43	1.67
28.0 - 29.9	2.50	0.00	0.00	0.00	0.00	0.50	5.00
30.0 - 31.9	1.50	0.25	0.06	0.00	0.31	0.43	2.67
32.0 - 33.9	2.00	0.08	0.00	0.21	0.31	0.52	4.00
34.0 - 35.9	1.25	0.17	0.31	0.21	0.63	0.51	2.67
36.0 - 37.9	0.50	0.25	0.31	0.00	1.25	0.46	3.67
38.0 - 39.9	<u>1.50</u>	<u>0.33</u>	<u>0.19</u>	<u>0.21</u>	<u>0.94</u>	<u>0.63</u>	<u>6.33</u>
	13.50	1.33	0.88	0.63	4.38	4.14	28.67
40.0 - 41.9	1.00	0.25	0.19	0.42	1.56	0.68	5.33
42.0 - 43.9	2.25	0.67	0.31	0.63	0.31	0.83	4.33
44.0 - 45.9	1.25	0.17	0.63	1.25	0.63	0.78	3.00
46.0 - 47.9	1.75	0.75	0.38	0.83	0.63	0.87	6.67
48.0 - 49.9	3.00	0.50	0.38	1.04	1.56	1.30	4.67
50.0 - 51.9	1.75	0.17	0.19	0.63	0.63	0.67	6.33
52.0 - 53.9	1.25	0.50	0.19	0.42	0.00	0.47	2.33
54.0 - 55.9	1.25	0.33	0.00	0.00	0.31	0.38	1.67
56.0 - 57.9	0.75	0.25	0.06	0.00	0.00	0.21	1.33
58.0 - 59.9	0.50	0.00	0.00	0.00	0.00	0.10	0.00
60.0 - 61.9	0.00	0.00	0.00	0.00	0.00	0.00	0.67
62.0 - 63.9	<u>0.00</u>	<u>0.08</u>	<u>0.00</u>	<u>0.00</u>	<u>0.00</u>	<u>0.02</u>	<u>0.00</u>
	14.75	3.67	2.31	5.21	5.63	6.31	36.33
	<u>31.50</u>	<u>5.08</u>	<u>3.19</u>	<u>8.75</u>	<u>12.50</u>	<u>12.20</u>	<u>65.00</u>
	BIOMASS (gms)/m ²						
< 19.9	3.08	0.15	0.00	1.75	2.17	1.43	0.00
20.0 - 39.9	165.47	20.51	16.16	11.09	72.28	57.10	446.58
> 40.0	<u>626.17</u>	<u>153.41</u>	<u>86.96</u>	<u>197.99</u>	<u>212.39</u>	<u>255.38</u>	<u>1537.16</u>
	794.73	174.07	103.12	210.83	286.84	313.92	1983.74

APPENDIX V: Percent ratio of dry weight to wet weight for the eight algal species and percent salt gain of filter papers.

<u>September 1968</u>	<u>%</u>	<u>N</u>	<u>SE</u>
<u>Laminaria</u> sp. (not <u>L. digitata</u>)	9.75	6	0.63
<u>Alaria esculenta</u>	17.96	8	0.31
<u>Agarum cribrosum</u>	26.00	7	0.79
<u>Fucus vesiculosus</u>	31.82	7	0.91
<u>Ascophyllum nodosum</u>	28.93	6	0.74
<u>Desmarestia viridis</u>	16.88	7	0.21
<u>Ptilota serrata</u>	22.97	7	0.22
<u>Ulva rigida</u>	27.75	6	0.26
Mean Percent Salt Gain of Filter Papers	4.69	8	0.28

<u>February 1969</u>			
<u>Laminaria</u> sp.	9.11	10	0.47
Mean Percent Salt Gain of Filter Papers	4.63	13	0.12

APPENDIX VI: The feeding abilities of seven size groups of urchins on Laminaria spp. (L. saccharina and/or L. longicruris) during February 10-22, 1969. (Water temperature 1.0 - 1.5°C).

TEST DIAMETER (mm)	NUMBER OF URCHINS	URCHIN WEIGHT \bar{X} (gms)	FOOD EATEN gms (WET WEIGHT) /URCHIN/DAY			FAECES EXCRETED mg (DRY WEIGHT) /URCHIN/DAY			FEEDING RATE (gms %)	ASSIMILATION EFFICIENCY (%)
			\bar{X}	SE	N DAYS	\bar{X}	SE	N DAYS		
9.0 - 10.9	37	0.46	14.07*	1.62	9	0.75	0.12	9	3.09*	41.58*
19.0 - 20.9	31	3.76	120.35	6.61	12	5.80	0.38	10	3.20	47.09
29.0 - 30.9	22	12.48	298.50	24.74	11	13.09	1.43	10	2.39	51.86
39.0 - 40.9	12	28.51	523.25	33.91	11	27.50	1.82	9	1.84	42.33
49.0 - 50.9	10	50.52	962.35	96.21	11	55.92	6.37	9	1.91	32.53
58.3 - 60.9	6	86.21	1112.80	82.42	9	84.33	5.58	5	1.29	20.79
66.9 - 72.7	5	132.62	1668.67	207.21	9	138.45	14.74	9	1.26	8.95

* The value for the amount of food eaten is very likely too low since it is not in line with the values for the larger size groups when they are plotted on log-log graph paper. The experimental method can only roughly estimate the consumption rate of such small urchins and this inaccuracy is accentuated when it is expressed in ratio to the mean urchin weight.

APPENDIX VII: The feeding abilities of three size groups of urchins on eight species of algae during September 21 - October 3, 1969.

TEST DIAMETER (mm)	NUMBER OF URCHINS	URCHIN WEIGHT \bar{X} (gms)	FOOD EATEN gms (WET WEIGHT) /URCHIN/DAY			FAECES EXCRETED mg (DRY WEIGHT) /URCHIN/DAY			FEEDING RATE (gms %)	URCHINS IN CONTACT WITH THE ALGA	
			\bar{X}	SE	N DAYS	\bar{X}	SE	N DAYS		ASSIMILATION EFFICIENCY %	% (%)
<u>LAMINARIA SPP.</u>											
8.0 - 11.9	12	0.45	15.11	2.01	12	4.43	0.74	8	3.33	---	45.50
28.0 - 31.9	8	12.27	659.24	69.75	12	41.80	4.02	12	5.37	34.95	78.13
48.0 - 51.9	6	48.16	1291.98	65.80	10	94.31	10.54	9	2.68	25.10	88.88
<u>ALARIA ESCULENTA</u>											
8.0 - 11.9	12	0.56	38.89	2.46	9	6.43	1.16	12	6.82	5.50	72.92
28.0 - 31.9	8	12.23	621.45	16.25	9	53.18	5.07	11	5.08	52.38	93.75
48.0 - 51.9	6	50.41	1195.39	53.31	9	108.21	9.94	11	2.37	49.61	93.63
<u>ULVA SP.</u>											
8.0 - 11.9	12	0.49	26.03	2.69	12	3.15	0.71	9	5.29	56.35	92.98
28.0 - 31.9	8	11.71	325.37	11.45	12	26.68	2.08	11	2.78	70.45	95.00
48.0 - 51.9	6	46.53	523.27	30.17	12	48.08	6.15	12	1.12	66.89	98.48
<u>FUCUS VESICULOSUS</u>											
8.0 - 11.9	12	0.48	9.22	2.32	11	3.24	0.69	9	1.92	---	52.09
28.0 - 31.9	8	12.46	206.48	28.49	12	20.39	4.06	10	1.66	68.97	80.68
48.0 - 51.9	6	50.53	485.25	47.59	11	35.92	5.31	9	0.96	76.74	89.39
<u>ASCOPHYLLUM NODOSUM</u>											

8.0 - 11.9	12	0.49	26.03	2.69	12	3.15	0.71	9	5.29	56.35	92.98
28.0 - 31.9	8	11.71	325.37	11.45	12	26.68	2.08	11	2.78	70.45	95.00
48.0 - 51.9	6	46.53	523.27	30.17	12	48.08	6.15	12	1.12	66.89	98.48

FUCUS VESICULOSUS

8.0 - 11.9	12	0.48	9.22	2.32	11	3.24	0.69	9	1.92	---	52.09
28.0 - 31.9	8	12.46	206.48	28.49	12	20.39	4.06	10	1.66	68.97	80.68
48.0 - 51.9	6	50.53	485.25	47.59	11	35.92	5.31	9	0.96	76.74	89.39

ASCOPHYLLUM NODOSUM

8.0 - 11.9	12	0.44	5.24	1.44	7	3.10	0.66	8	1.19	---	51.52
28.0 - 31.9	8	11.80	143.70	7.06	11	10.08	2.43	10	1.22	75.76	71.59
48.0 - 51.9	6	51.13	347.27	40.94	10	32.76	3.69	10	0.68	67.40	76.38

DESMARESTIA VIRIDIS

8.0 - 11.9	12	0.53	35.97	6.16	12	4.63	1.35	10	6.82	23.75	71.75
28.0 - 31.9	8	11.44	267.39	29.74	12	13.80	2.63	11	2.34	69.43	88.51
48.0 - 51.9	6	47.54	412.95	52.50	12	34.11	3.70	12	0.87	51.08	80.30

AGARUM CRIBROSUM

8.0 - 11.9	12	0.56	9.17	2.91	8	2.87	0.88	8	1.63	---	34.85
28.0 - 31.9	8	11.78	96.51	21.66	8	19.58	2.89	7	0.82	21.98	42.05
48.0 - 51.9	6	48.69	397.42	79.31	9	37.84	6.30	11	0.82	63.38	60.60

PTILOTA SERRATA

8.0 - 11.9	12	0.51	32.00	7.43	11	8.32	1.34	11	6.24	---	62.88
28.0 - 31.9	8	11.46	100.19	29.71	11	20.57	2.56	11	0.87	10.60	81.82
48.0 - 51.9	6	45.73	166.09	41.14	10	40.33	5.94	9	0.36	---	73.62

APPENDIX VIIIa: Daily record of the numbers of urchins on each algal species and the rate at which the different species disappeared in tank with 110 20mm urchins.

[illegible]

<u>Agarum cribrosum</u> (14.8 g)	8	4	1	0	0	2	0	3	1	3	1	1	4	4	11	7	5	5	5	1	1	1	-	-	-
<u>Ptilota serrata</u> (7.6 g)	0	0	0	0	0	0	2	1	1	0	1	2	1	4	1	0	0	0	2	3	2	1	1	1	-
<u>Ascophyllum nodosum</u> (54.0 g)	8	8	10	8	7	5	5	2	2	4	14	19	13	10	5	5	-	-	-	-	-	-	-	-	-
<u>Fucus vesiculosus</u> (21.3 g)	3	3	4	7	10	13	12	10	9	7	7	9	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Ulva sp.</u> (22.6 g)	6	8	8	10	8	8	8	15	22	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Chondrus crispus</u> (41.3 g)	10	7	2	3	5	12	22	26	27	26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Rhodomenia palmata</u> (19.1 g)	11	9	9	9	11	11	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Chorda tomentosa</u> (31.8 g)	4	7	13	14	26	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Laminaria sp.</u> (27.1 g)	8	9	10	11	8	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Halosaccion ramentaceum</u> (38.2 g)	20	21	21	19	19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Alaria esculenta</u> (12.9 g)	14	15	15	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Petalonia fascia</u> (17.5 g)	16	16	16	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
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

APPENDIX VIIIb: Daily record of the number of urchins on each algal species and the rate at which the different species disappeared in tank with 42 50mm urchins.

	10:15pm May 6	11:15pm May 7	1:35pm May 8	5:15pm May 9	10:45am May 10	12:10am May 11	3:30pm May 12	1:55pm May 13*	5:00pm May 14	5:00pm May 15	12:15am May 16	4:30pm May 20	5:40pm May 21	2:30pm May 26	4:30pm May 27		11:15am May 29	4:30pm May 30	1:45pm June 3	3:00pm June 5	1:00pm June 9
<u>Agarum cribrorum</u> (16.1 g)		1	0	0	0	0	0	+	0	2	0	0	3	3	2	3	3	2	1	1	-
<u>Ascophyllum nodosum</u> (46.1 g)		3	2	1	0	0	7	+	8	7	7	3	2	-	-	-	-	-	-	-	-
<u>Fucus vesiculosus</u> (35.2 g)		3	3	4	4	4	5	+	6	3	3	-	-	-	-	-	-	-	-	-	-
<u>Ulva sp.</u> (35.7 g)		5	5	6	6	5	11	+	5	2	12	-	-	-	-	-	-	-	-	-	-
<u>Chondrus crispus</u> (37.7 g)		3	3	3	4	3	4	+	3	2	2	-	-	-	-	-	-	-	-	-	-
<u>Desmarestia viridis</u> (24.85 g)		5	4	5	2	3	3	+	3	2	-	-	-	-	-	-	-	-	-	-	-
<u>Rhodomenia palmata</u> (19.7 g)		2	2	3	4	3	2	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Halosaccion ramentaceum</u> (40.9 g)		5	6	4	4	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Chorda tomentosa</u> (47.3 g)		4	4	4	7	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Petalonia fascia</u> (29.3 g)		3	5	6	4	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

<u>Agarum cribrorum</u> (16.1 g)	1	0	0	0	0	0	+	0	2	0	0	3	3	2	3	3	2	1	1	-
<u>Ascophyllum nodosum</u> (46.1 g)	3	2	1	0	0	7	+	8	7	7	3	2	-	-	-	-	-	-	-	-
<u>Fucus vesiculosus</u> (35.2 g)	3	3	4	4	4	5	+	6	3	3	-	-	-	-	-	-	-	-	-	-
<u>Ulva sp.</u> (35.7 g)	5	5	6	6	5	11	+	5	2	12	-	-	-	-	-	-	-	-	-	-
<u>Chondrus crispus</u> (37.7 g)	3	3	3	4	3	4	+	3	2	2	-	-	-	-	-	-	-	-	-	-
<u>Desmarestia viridis</u> (24.85 g)	5	4	5	2	3	3	+	3	2	-	-	-	-	-	-	-	-	-	-	-
<u>Rhodomenia palmata</u> (19.7 g)	2	2	3	4	3	2	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Halosaccion ramentaceum</u> (40.9 g)	5	6	4	4	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Chorda tomentosa</u> (47.3 g)	4	4	4	7	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Petalonia fascia</u> (29.3 g)	3	5	6	4	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Alaria esculenta</u> (20.1 g)	5	5	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>Laminaria sp.</u> (24.9 g)	2	3	1	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

URCHINS NOT FEEDING	1	0	2	0	10	7	-	17	26	18	39	37	39	40	39	39	40	41	41	42
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* Water stopped and urchins discontinued feeding.



APPENDIX IX: Summary of the data on the feeding of Strongylocentrotus intermedius on 11 species of algae and surf grass, Phyllospadix iwatensis, from Fuji (1962, 1967).

FOOD	MONTH	(mm) \bar{X} TEST DIAMETER	(g) \bar{X} WEIGHT	FOOD EATEN mg (WET WEIGHT) /URCHIN/DAY	FEEDING RATE (gms %)	ASSIMILATION EFFICIENCY (%)
<u>Laminaria japonica</u>	January	50.4	47.4	2710	5.72	56.7
Ditto	June	50.2	29.6	2890	5.81	66.0
<u>Alaria crassifolia</u>	June	45.7	42.6	970	2.27	69.4
<u>Agarum cribrosum</u>	June	48.3	47.6	650	1.36	72.6
<u>Sargassum tortile</u>	January	48.1	45.1	600	1.33	62.8
<u>S. thunbergii</u>	January	50.6	48.1	1040	2.16	58.7
<u>Scytosiphon lomentaria</u>	January	51.0	50.8	1950	3.84	83.4
<u>Ulva pertusa</u>	January	48.0	46.7	450	0.96	74.4
Ditto	June	46.1	45.2	540	1.19	81.9
<u>Chondrus ocellatus</u>	January	49.3	48.9	960	1.96	56.8
Ditto	June	50.1	51.2	1130	2.21	61.5
<u>Packymeniopsis yendoii</u>	June	48.9	50.3	660	1.31	68.3
<u>Rhodymenia palmata</u>	January	51.2	50.8	930	1.83	74.4
<u>Rhodoglossum pulchrum</u>	January	52.0	50.3	720	1.43	76.3
<u>Phyllospadix iwatensis</u>	June	50.0	50.1	1020	2.03	32.4

APPENDIX X: Summary of the data on the feeding of Strongylocentrotus franciscanus, S. droebachiensis and S. purpuratus on 7 species of algae from Vadas (1968). His original data on the amount eaten in grams wet weight/hour/animal is in brackets following the equivalent values in milligrams eaten (wet weight)/urchin/day. Also the time of each experiment and the total number of individuals tested for each species of urchin is indicated under the name of each alga.

FOOD	<u>S. franciscanus</u>		<u>S. droebachiensis</u>		<u>S. purpuratus</u>	
	FOOD EATEN mg (WET WEIGHT) /URCHIN/DAY-	ASSIMILATION EFFICIENCY %	FOOD EATEN mg (WET WEIGHT) /URCHIN/DAY	ASSIMILATION EFFICIENCY %	FOOD EATEN mg (WET WEIGHT) /URCHIN/DAY	ASSIMILATION EFFICIENCY %
<u>Nereocystis luetkeana</u> 11/29/65, 2/25/66 (6)	19848 (0.827)	91.15	4968 (0.207)	83.64	4440 (0.185)	85.22
<u>Costaria costata</u> 11/5/65 (3)	8640 (0.360)	82.56	4872 (0.203)	77.39	5280 (0.220)	77.65
<u>Laminaria saccharina</u> 11/29/65, 2/25/66 (6)	7008 (0.292)	77.77	3432 (0.143)	76.75	1824 (0.076)	64.39
<u>Callophyllis flabellulata</u> 10/18/65 (3)	6720 (0.280)	70.75	3672 (0.153)	62.30	2640 (0.110)	67.86
<u>Agarum cribrosum</u> 7/6/65 (3)	7128 (0.297)	53.45	3531 (0.063)	35.32	408 (0.017)	43.34
1/15/66 (3)	552 (0.023)	58.16	264 (0.011)	44.77	240 (0.010)	45.29
\bar{x} (6)	3840 (0.160)	55.80	888 (0.037)	40.04	312 (0.013)	44.32
<u>Agarum fimbriatum</u> 10/13/65, 1/15/66 (6)	1752 (0.073)	51.45	888 (0.037)	45.45	744 (0.031)	36.41
<u>Monostroma fuscum</u> 1/31/66 (6)	1200 (0.050)	47.60	408 (0.017)	56.29	288 (0.012)	27.98

APPENDIX XI: Incidence of urchin fragments or very small urchins in the gut contents of cunner's, Tautogolabrus adspersus, in collections examined by Mr. Chandra Sekhar.

<u>LOCALITY</u>	<u>DATE</u>	<u>INCIDENCE</u> _____%____	<u>SAMPLE SIZE</u>	<u>SIZE RANGE</u> <u>OF FISH (cm)</u>
<u>Bay of Islands</u>				
Lark Harbour	July 21, 1968	8.33	48	9.1-25.9
Frenchman's Cove*	July 20, 1968	0.00	34	13.6-25.3
Benoit's Cove*	July 20, 1968	0.00	18	9.3-23.3
<u>Notre Dame Bay</u>				
Botwood*	July 6, 1968	0.00	4	17.0-24.6
Lewisporte*	July 16, 1968	2.00	50	13.7-24.7
Cod All Islands	July 19, 1968	0.00	17	3.1-4.5
Inspector Islands	July 12, 1968	23.25	83	8.6-33.4
<u>Bonavista Bay</u>				
St. Shad's	Nov. 5-20, 1967	27.27	77	11.1-23.6
Sandy Cove	July 26, 1968	26.00	50	17.6-28.2
<u>Trinity Bay</u>				
Norman's Cove	July 15, 1968	8.54	82	16.3-30.7
<u>Conception Bay</u>				
Lake View	July 30, 1968	26.32	38	14.5-24.8
Holyrood	Aug. 31, 1968	21.44	42	13.2-33.8
St. Phillips	Aug. 10-			
	Sept. 3, 1968	51.22	40	12.0-29.4
	Oct. 10, 1968	60.00	5	16.8-21.9
Portugal Cove	June 6, 1968	50.00	8	15.2-31.5
	Sept. 1, 1968 ⁺	18.11	11	17.8-31.4
<u>St. Mary's Bay</u>				
Mt. Carmel, Salmoneer	July 22, 1968	20.00	35	11.0-22.1
<u>Hermitage Bay</u>				
Gaultois	Oct. 10, 1968	23.19	138	17.6-28.2

*Sheltered area where urchins are not likely to be common.

⁺This collection was from near the wharf at Portugal Cove where the sediment is fine and dead fish are usually available.

