Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia

Robert Scheibling

Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 4J1

Summary. Recurrent outbreaks of disease between 1980 and 1983 caused catastrophic mortality of sea urchins (>260,000 t fresh weight) along 280 km (straight line distance) of the Atlantic coast of Nova Scotia. The complete elimination of sea urchins and concomitant development of fleshy macroalgal communities have occurred along different parts of this coast in different years. Macroalgal communities in areas where sea urchins died off 1, 3 and 4 years previously are compared to existing sea urchin-dominated barren grounds and to a mature kelp bed without sea urchins. Changes in macroalgal cover and species composition, and increases in biomass, density and size of kelp (*Laminaria*) species, characterize the succession from barren grounds to 3- and 4-year-old kelp beds. The greatest change occurred between one and three years following sea urchin mass mortality. Within 3 years, kelp beds attained a level of biomass (7.6 kg m^{-2}) comparable to that of mature beds. Recovery of sea urchin populations via recruitment of planktonic larvae has been slow and spatially variable. Large-scale reciprocal fluctuations in kelp and sea urchin biomass may characterize the trajectory of a dynamic system which cycles between two alternate community states: kelp beds and sea urchin-dominated barren grounds. Periodic decimation of sea urchin populations by disease may be an important mechanism underlying this cyclicity.

The importance of herbivorous sea urchins in structuring marine macrophyte communities is well known (see reviews by Lawrence 1975; Lawrence and Sammarco 1982; Chapman in press). At moderate population densities, sea urchins may alter plant species composition through selective feeding and promote species diversity. However, at high densities they can destructively graze all fleshy macrophytes resulting in the formation of "sea urchin-dominated barren grounds" (Lawrence 1975). In this situation, the rocky substratum is encrusted with coralline red algae, resilient to sea urchin grazing. When sea urchin abundance is reduced, either by artificial or natural means, a plant community dominated by fleshy macrophytes generally develops.

Predation by high level carnivores may be an important biological factor regulating sea urchin populations and thereby influencing community structure. In kelp bed communities, sea otters and lobsters have been identified as "keystone predators" (Paine 1966) in this context (Estes

and Palmisano 1974; Breen and Mann 1976b; Mann 1977; Estes et al. 1978; Simenstad et al. 1978; Duggins 1980). In many areas, destructive grazing of macrophytes by expanding sea urchin populations has been related to a reduction in sea urchin predators due to overfishing (Estes et al. 1978; Duggins 1980; Wharton and Mann 1981).

Recently mass mortalities of sea urchins, attributed to outbreaks of disease, have occurred in widespread geographical areas (Johnson 1971; Pearse et al. 1977; Pearse and Hines 1979; Bourdouresque et al. 1981; Hobaus et al. 1981; Miller and Colodey 1983; Moore and Miller 1983; Bak et al. 1984; Lessios et al. 1984; Maes and Jangoux 1984; Scheibling 1984a; Scheibling and Stephenson 1984). An increase in the abundance of fleshy macrophytes has been reported in these areas following the depopulation of sea urchins (Pearse and Hines 1979; Ballantine 1984; Bak et al. 1984; Moore and Miller 1983). These events indicate that disease also may be an important regulatory agent in sea urchin-macrophyte communities (Scheibling 1984a).

Off Nova Scotia, outbreaks of disease and mass mortality of the green sea urchin, *Strongylocentrotus droebachiensis*, have occurred each fall between 1980 and 1983. The extent of sea urchin mass mortalities along the entire Atlantic coast of Nova Scotia between 1980 and 1982 has been well documented (Miller and Colodey 1983; Moore and Miller 1983; Scheibling 1984a). This study extends these observations to include 1983 and examines the extent of macroalgal growth and sea urchin recruitment in areas where sea urchins were eliminated by disease one, three and four years previously. These areas are compared to existing sea urchin-dominated barren grounds, and to a mature kelp bed where sea urchins have been rare or absent for decades. Differences in the abundance, species composition and size structure of macroalgae in these various areas provide insight into biological interactions among macroalgal species and the process of succession. The importance of disease and other perturbations in regulating the large-scale dynamics of the subtidal community off Nova Scotia is discussed.

Materials and methods

Nine sites along the Atlantic coast of Nova Scotia were surveyed using SCUBA in October and November 1983, to record the range of sea urchin mass mortalities. These were in areas where sea urchins had not been completely eliminated in previous years: Dover Island, Cape Moco-
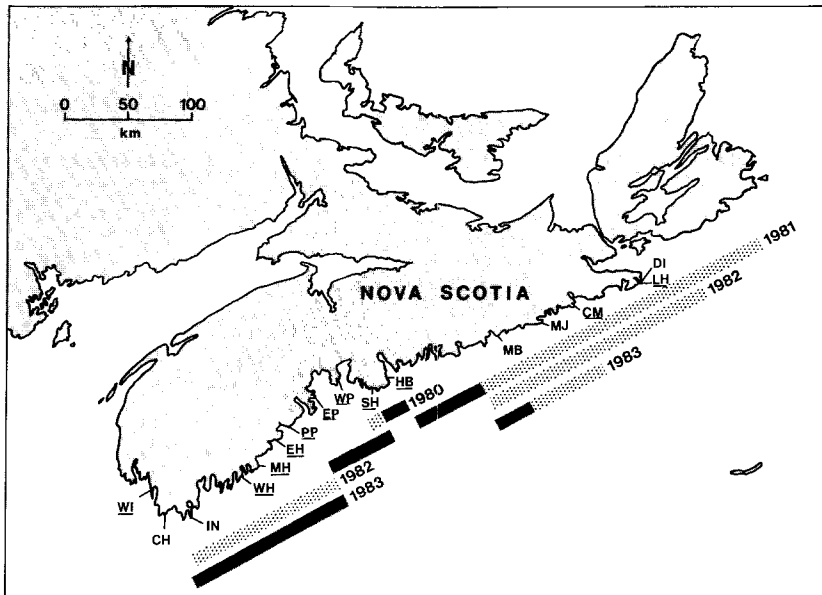
Fig. 1. Map of Nova Scotia showing study sites: *WI* Whitehead Island; *CH* Clarke's Harbour; *IN* Ingomar; *WH* Western Head; *MH* Mouton Head; *EH* Eagle Head; *PP* Pollock Point; *EP* East Point; *WP* White Point; *SH* Shipley Head; *HB* Halibut Bay; *MB* Mushaboom; *MJ* Marie Joseph; *CM* Cape Mocodome; *LH* Louse Head; *DI* Dover Island. Underlining designates sites where macroalgal communities were sampled. Solid bars indicate the range of complete die-off of *Strongylocentrotus droebachiensis*, stippled bars indicate the range of partial die-off, from 1980 to 1983. (Ranges from 1980 to 1982 are from Miller and Colodey 1983 and Moore and Miller 1983)

Table 1. Description of sites where macroalgal communities were surveyed in this study (1984) and reference to previous surveys at these sites

Site	Sample date	Location	Exposure[a]	Substratum type	Previous surveys
Louse Head	Aug. 8	45° 15.2′ N, 61° 01.6′ W	SSW-E, 117°	bedrock pavement, large boulders	Wharton 1980: Dover, Station 7
Cape Mocodome	Aug. 7	45° 05.5′ N, 61° 38.7′ W	WSW-E, 176°	small boulders, cobble	Wharton 1980: Drumhead, Station 12
Eagle Head	July 27	44° 03.6′ N, 64° 36.3′ W	SSW-E, 112°	bedrock pavement, large boulders	Scheibling unpubl.: Eagle Head, Station 3, Sept. 1982
Mouton Head	July 14	43° 52.2′ N, 64° 46.9′ W	SSW-NE, 166°	bedrock pavement, small-large boulders	Wharton 1980: Port Mouton, Station 9
Western Head	Aug. 3	40° 00.3′ N, 65° 07.2′ W	S-ENE, 126°	bedrock ridges, small-large boulders	Johnson unpub.: Lockeport, Station 3
White Point	July 18	44° 30.4′ N, 64° 00.2′ W	WSW-ESE, 121°	bedrock ridges	Wharton 1980: Northwest Cove, Station 5
East Point	July 11	44° 20.5′ N, 64° 12.3′ W	SSW-NE, 130°	bedrock ridges	Wharton 1980; Blue Rocks, Station 7
Pollock Point	July 20	44° 08.4′ N, 64° 29.0′ W	SW-ENE, 151°	bedrock ridges	Moore and Miller 1983: Apple Cove, Transect 57
Halibut Bay	July 25	44° 33.0′ N, 63° 33.3′ W	SSE-ENE, 91°	large boulders	Moore and Miller 1983: Halibut Bay, Transect 16
Shipley Head	July 31	44° 27.3′ N, 63° 42.4′ W	SSW-ESE, 92°	bedrock ridges	Moore and Miller 1983: Terrence Bay, Transect 19
Whitehead Island	Aug. 10	43° 39.7′ N, 65° 52.0′ W	W-SSW, 111°	bedrock pavement, large boulders	Wharton 1980: Pubnico, Station 6

[a] Direction and range of exposure to the open ocean

dome, Marie Joseph, Mushaboom, Eagle Head, Port Mouton, Western Head, Ingomar and Clarke's Harbour (Fig. 1). Live sea urchins were collected in 20 randomly-tossed 0.25 m² quadrats.

Macroalgal communities were surveyed using SCUBA at eleven sites in July and August, 1984 (Fig. 1, Table 1). These sites were located in areas where (1) sea urchins were abundant (Louse Head, Cape Mocodome), (2) sea urchins were eliminated by disease about 1 year previously (Eagle Head, Mouton Head, Western Head), (3) sea urchins were eliminated by disease about 3 years previously (White Point, East Point, Pollock Point), (4) sea urchins were elimi-

nated by disease about 4 years previously (Halibut Bay, Shipley Head), or (4) sea urchins have been rare for decades and mature kelp beds exist (Whitehead Island). Sites were selected in or near (within 500 m) areas where macroalgae and sea urchins were surveyed between 1978 and 1982 (Table 1). To facilitate comparisons of sites within this survey, and between this and previous surveys, sites were selected off headlands or large islands exposed to the open ocean and at 8–10 m depth.

Sites were located by boat using hydrographic charts and a depth sounding line. The mature kelp bed site and the two sites where sea urchins were abundant were located

Table 2. Mean ± S.E. numerical and biomass density and size for *Stronglyocentrotus droebachiensis* at sites along the Atlantic coast of Nova Scotia

Population parameters	Survey Sites											
	Barren ground		1 year post-die-off			3 years post-die-off			4 years post-die-off		Kelp bed
	Louse Head	Cape Mocodome	Eagle Head	Mouton Head	Western Head	White Point	East Point	Pollock Point	Halibut Bay	Shipley Head	White-head Island
Density (ind m^{-2})	89.3 ± 22.0	49.8 ± 6.0	56.0 ± 19.2	3.3 ± 1.9	5.8 ± 2.3	1.7 ± 1.1	0	0	0	0	0
Biomass (g m^{-2})	1,271.0 ± 367.6	1,145.8 ± 131.6	4.4 ± 1.4	0.3 ± 0.2	0.8 ± 0.3	0.3 ± 0.2	0	0	0	0	0
Size (mm)	26.5 ± 0.5	33.1 ± 0.7	5.1 ± 0.2	5.0 ± 0.5	6.1 ± 0.6	6.5 ± 0.5	–	–	–	–	–

after a preliminary survey of these areas by divers. One end of a weighted 50 m transect line, graduated at 1 m intervals, was anchored to the bottom and the remaining line played out from the boat in an alongshore direction. A diver with a depth gauge ensured that the line fell within the 8–10 m depth range and secured the free end of the line on the bottom.

Twelve 1 m² quadrats were randomly located within a 4 m × 50 m (200 m²) belt transect delineated by the transect line. The quadrats were delineated by a 1 m square iron rod frame with a 0.32 m square frame (0.1 m²) inset at one corner.

Quadrats in which macroalgae (excluding crustose coralline algae) did not completely cover the rocky substratum were photographed on color slide film from a point 2 m above the center of the quadrat. The developed slides were projected onto an array of 50 randomly-located dots on a square field aligned with the frame of the 1 m² quadrat. The percentage cover of macroalgae was estimated as the percentage of dots on macroalgae.

Large brown algae (*Laminaria* and *Desmarestia* species) were collected by hand from 1 m² quadrats. Smaller foliose and filamentous algae, and juvenile sea urchins, were scraped from 0.1 m² quadrats and aspirated into 1 mm mesh bags using an air-lift connected to a compressed air cylinder.

The large brown algae were sorted and drained for 5–10 min on the shore. The total wet weight of each species was measured on a spring balance (25 g accuracy for weight > 500 g) or a triple beam balance (1 g accuracy for weight < 500 g) for each 1 m² quadrat. Stipe length (holdfast to meristem) and total length (holdfast to tip of longest blade) were measured for kelp species with a plastic measuring tape (1 cm accuracy). Density of each kelp species was estimated from counts of individuals in each quadrat. Juvenile *Laminaria* (total length < 20 cm) were not identifiable to species in the field.

The smaller algae and juvenile sea urchins were transferred to plastic bags with seawater and transported to the laboratory in a cooler. They were refrigerated at 3° C for no more than 48 h before processing. Algal species were sorted, blotted on paper towelling and wet weighed on an electronic top loader balance (0.1 g accuracy). Some species of filamentous red algae (primarily *Polysiphonia*, *Antithamnionella*, and *Bonnemaisonia*) could not be effectively sepa-
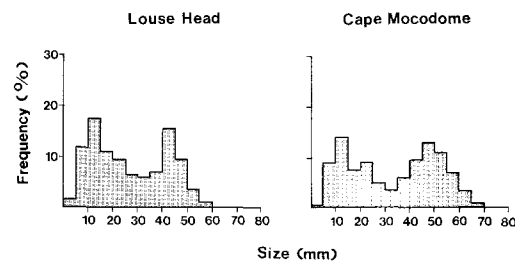
Fig. 2. Size frequency distributions of *Strongylocentrotus droebachiensis* at Louse Head and Cape Mocodome Nova Scotia, August 1984
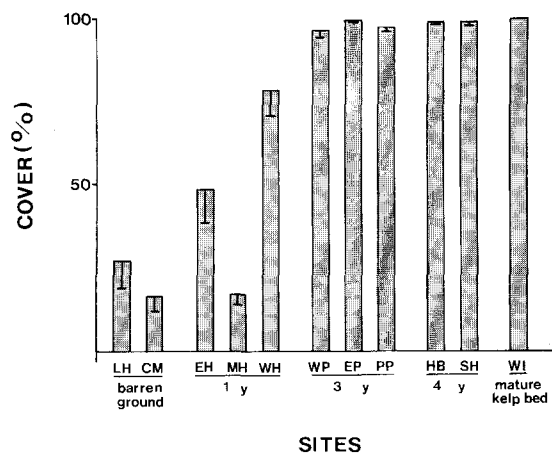
Fig. 3. Percentage cover of all macroalgae (excluding crustose coralline algae) at sites along the Atlantic coast of Nova Scotia (see Fig. 1). Data are $\bar{X} \pm$ SE; $N = 12$

rated and were weighed together. The biomass of each species (or species group) in 0.1 m² quadrats was standardized to 1 m² by multiplying by 10.

Sea urchins were measured with vernier calipers (horizontal test diameter, 1 mm accuracy). Density of juvenile sea urchins was estimated from counts of individuals in 0.1 m² quadrats. At two sites (Louse Head and Cape Mocodome) where adult sea urchins were abundant, all sea urchins were collected by hand from the entire 1 m² quadrat. The total wet weight of sea urchins was measured on a spring balance or electronic balance for each quadrat.

Fig. 5. Percentage composition of major algal groups at sites along the Atlantic coast of Nova Scotia (see Fig. 1)
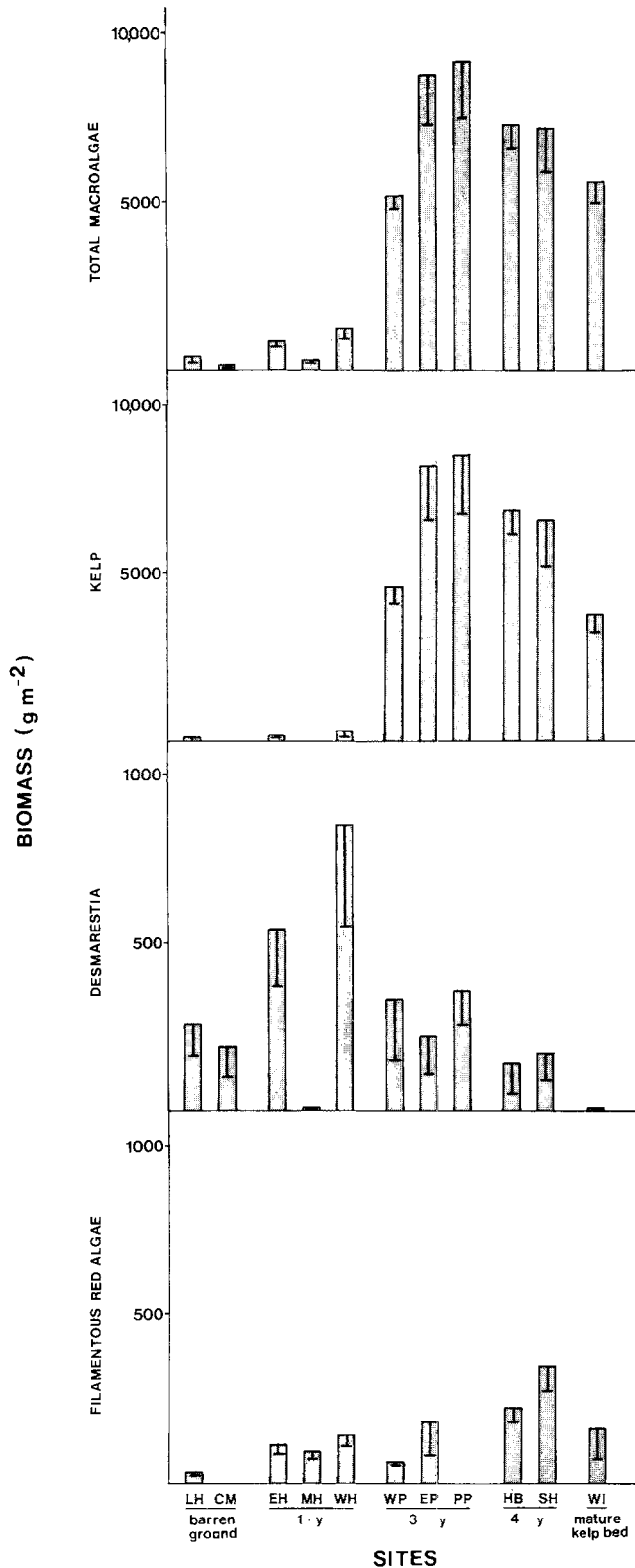

Fig. 4. Biomass of all macroalgae (excluding crustose coralline algae), kelp, *Desmarestia* spp. and filamentous red algae at sites along the Atlantic coast of Nova Scotia (see Fig. 1). Data are $\bar{X} \pm$ SE; $N = 12$

Results

Sea urchin mass mortality and post-epizootic recruitment

Of the 9 sites surveyed in October and November 1983, live sea urchins were found only at Marie Joseph ($\bar{X} \pm$ SD =
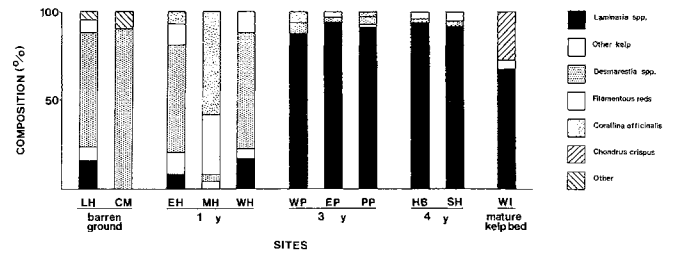
4 ± 1 individuals m^{-2}), Cape Mocodome (15 ± 4 individuals m^{-2}), and Dover Island (29 ± 5 individuals m^{-2}) (Fig. 1). Thirty percent of sea urchins at Marie Joseph had epidermal lesions and there were scattered sea urchin tests on the bottom. There were fewer tests at Cape Mocodome and none at Dover Island. Sea urchin tests were numerous at Mushaboom on the northeastern shore, and from Eagle Head to Clarke's Harbour on the southwestern shore. Aggregations of 147 and 309 tests m^{-2} were recorded at Western Head.

In August 1984, sea urchins in the barren ground sites (Cape Mocodome, Louse Head) occurred in dense aggregations (Table 2). Density at Cape Mocodome had increased significantly (Mann Whitney U test $P < 0.05$) since November 1983. The population size structure of sea urchins at both sites was bimodal (Fig. 2). Juvenile sea urchins (< 20 cm horizontal test diameter) were abundant accounting for 31% of the population at Cape Mocodome and 42% at Louse Head. They occurred in cryptic microhabitats: under cobble and small boulders at Cape Mocodome and in crevices in the bedrock pavement at Louse Head, often beneath aggregations of adults.

Juvenile sea urchins occurred at all sites where sea urchins were eliminated 1 year previously (Table 2). They were particularly abundant at Eagle Head (56 ± 19.2 individuals m^{-2}) where they occurred in small pockets and crevices in the coralline crust. Juvenile sea urchins were not found at sites where sea urchins were eliminated 3 or 4 years previously, with the exception of White Point where they occurred at low density (1.7 ± 1.1 individuals m^{-2}), nor were they found at the mature kelp bed site (Table 2).
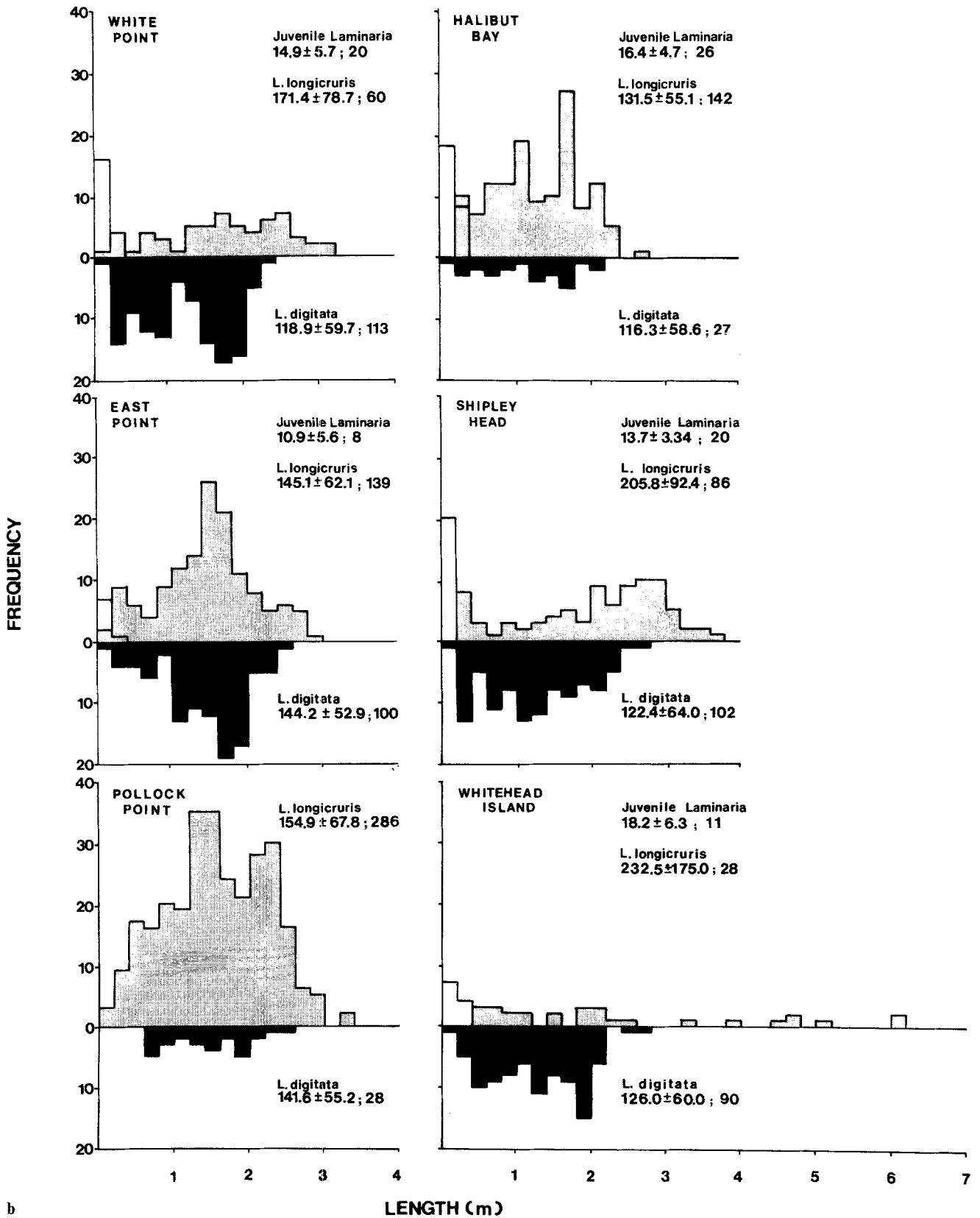
Macroalgal species composition and abundance

Macroalgal abundance was low at sites that were sea urchin-dominated barren grounds (Louse Head and Cape Mocodome) (Fig. 3 and 4, Table 3). (This does not include crustose coralline red algae (*Lithothamnium* sp., *Clathromorphum* sp. and *Phymatolithon* sp.) which almost entirely covered the rock bottom at all locations forming the secondary substratum.) Patches of plumose brown algae, *Desmarestia* spp., accounted for most of the macroalgal biomass (Fig. 5). Small kelps (*Laminaria longicruris*, *L. digitata*, *Alaria esculenta* and *Saccorhiza dermatodea*) occurred in patches at Louse Head often in association with *Desmarestia* spp. (Fig. 6, Tables 3 and 4). Juveniles of the fast growing annual kelp, *S. dermatodea* (mean length $\pm$ SE = 16.2 ± 10.2 cm, $N = 152$), were particularly abundant at Louse Head (Table 4). Small filamentous red algae, primarily *Polysiphonia* sp. and *Antithamnionella* sp., occurred among the patches of kelp and *Desmarestia* spp. (Table 3).

190
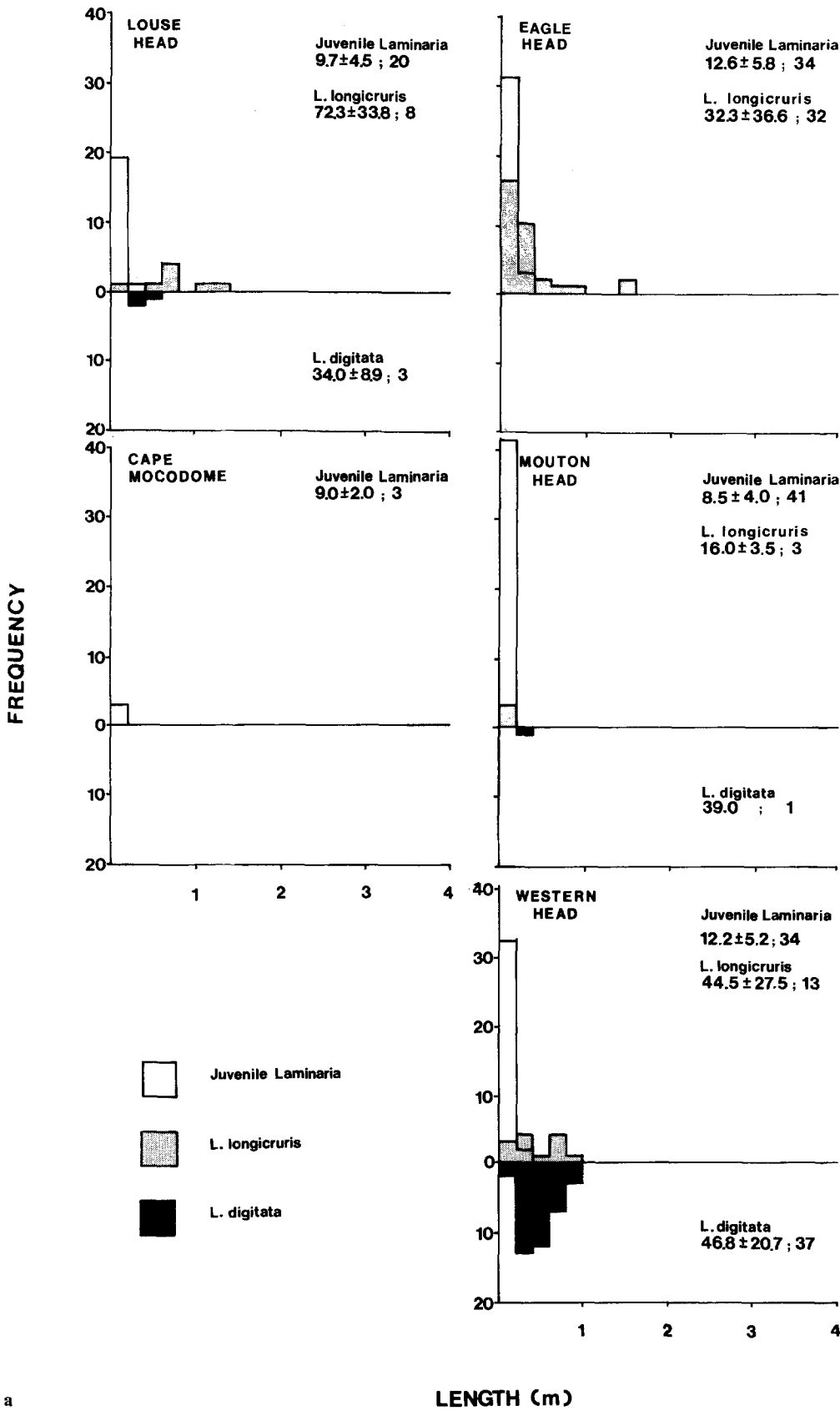
Fig. 6a, b. Size-frequency distributions of *Laminaria longicruris* and *L. digitata* at sites along the Atlantic coast of Nova Scotia. Data are $\bar{X} \pm SD$; N

WHITE POINT
Juvenile Laminaria 14.9±5.7; 20
L. longicruris 171.4±78.7; 60
L. digitata 118.9±59.7; 113

HALIBUT BAY
Juvenile Laminaria 16.4±4.7; 26
L. longicruris 131.5±55.1; 142
L. digitata 116.3±58.6; 27

EAST POINT
Juvenile Laminaria 10.9±5.6; 8
L. longicruris 145.1±62.1; 139
L. digitata 144.2 ± 52.9; 100

SHIPLEY HEAD
Juvenile Laminaria 13.7±3.34; 20
L. longicruris 205.8±92.4; 86
L. digitata 122.4±64.0; 102

POLLOCK POINT
L. longicruris 154.9 ± 67.8; 286
L. digitata 141.6 ±55.2; 28

WHITEHEAD ISLAND
Juvenile Laminaria 18.2±6.3; 11
L. longicruris 232.5±175.0; 28
L. digitata 126.0±60.0; 90

FREQUENCY

LENGTH (m)

b

Kelps were virtually absent in the transect at Cape Moco-dome (Tables 3 and 4). However, diving surveys along adjacent tracts of coast indicated areas of extensive macrophyte cover (including large patches of *Desmarestia* spp. or dense beds of *Laminaria* spp.) where sea urchins were absent.

The sites where sea urchins were eliminated about 1 year previously (Eagle Head, Mouton Head, Western Head) showed the greatest variation in macroalgal abundance and species composition (Fig. 3, 4 and 5; Tables 3 and 4). *Desmarestia* spp. were the dominant macroalgae at Eagle Head

Table 3. Mean ± S.E. biomass (g m^{-2}) macroalgal species at sites along the Atlantic coast of Nova Scotia. Sample size is 12

Macroalgal species	Barren ground		1 year post-die-off			3 years post-die-off			4 years post-die-off		Kelp bed
	Louse Head	Cape Mocodome	Eagle Head	Mouton Head	Western Head	White Point	East Point	Pollock Point	Halibut Bay	Shipley Head	Whitehead Island
Phaeophyceae											
Laminaria digitata	7±7	0	63±58	1±1	147±73	2,900±419	5,076±1,085	798±264	1,106±247	3,483±1,226	2,752±435
Laminaria longicruris	57±56	0	0	0	78±44	1,633±235	3,135±672	7,513±1,612	5,769±799	3,096±752	1,002±367
Juvenile *Laminaria* spp.	1±1	0	4±1	2±0	4±2	1±1	0	0	3±1	1±1	1±1
Agarum cribrosum	0	0	26±25	8±8	73±35	0	0	1±1	4±4	0	0
Alaria esculenta	5±5	0	6±4	0	6±6	52±35	0	171±69	6±8	48±21	0
Saccorhiza dermatodea	29±7	1±1	84±144	2±1	2±1	0	0	0	0	3±3	0
Desmarestia aculeata	98±61	129±92	196±138	0	568±233	323±180	214±105	335±94	142±85	146±80	8±8
Desmarestia viridis	162±49	60±18	341±149	10±4	286±248	8±5	2±1	0	1±1	27±19	0
Chordaria flagelliformis	8±5	21±15	0	0	1±1	0	0	0	2±1	0	0
Eudesme virescens	13±8	0	0	0	0	0	0	0	0	0	0
Rhodophyceae											
Ceramium rubrum	0	0	6±5	1±1	6±6	0	4±3	0	5±2	2±2	14±8
Ptilota plumosa	0	0	1±1	1±1	5±4	4±3	1±1	0	1±0	0	4±3
Rhodomela conteroides	0	0	0	1±1	1±1	20±10	0	0	40±42	190±35	0
Cystoclonium purpureum	2±1	0	0	0	0	0	24±11	1±1	0	21±14	0
Mixed filamentous spp.	25±8	0	101±29	88±20	123±39	37±7	146±85	0	176±44	131±40	139±85
Porphyra spp.	0	0	0	0	0	0	0	0	0	0	0
Phycodrys rubens	0	0	2±2	0	2±1	4±3	0	0	0	3±2	103±25
Chondrus crispus	0	0	0	0	0	0	0	0	13±6	30±18	1,486±246
Palmaria palmata	0	0	0	0	13±8	0	5±4	0	18±7	0	2±2
Corallina officinalis	0	0	61±40	158±59	0	178±86	85±45	237±147	1±1	17±8	33±10
Total macroalgae	407±161	211±88	891±238	272±57	1,315±376	5,160±388	8,692±1,445	9,076±1,601	7,287±669	7,198±1,340	5,544±582

Table 4. Mean ± S.E. density (individuals m^{-2}) of kelp species at sites along the Atlantic coast of Nova Scotia. Sample size is 12

| Kelp species	Barren ground		1 year post-die-off			3 years post-die-off			4 years post-die-off		Kelp bed
	Louse Head	Cape Mocodome	Eagle Head	Mouton Head	Western Head	White Point	East Point	Pollock Point	Halibut Bay	Shipley Head	Whitehead Island
Laminaria digitata	0.5±0.4	0	0	0.1±0.1	3.2±1.3	9.7±1.4	9.6±1.2	2.4±0.6	2.9±0.5	12.2±3.0	8.2±0.8
Laminaria longicruris	0.8±0.7	0	2.4±1.1	0.3±0.2	1.1±0.7	5.0±0.8	13.0±2.3	33.4±5.6	24.2±2.7	9.2±1.5	2.7±0.7
Juvenile *Laminaria* spp.	1.8±1.1	0.4±0.3	4.1±1.3	4.6±0.9	3.5±1.3	1.8±0.6	0	0	3.0±0.7	1.8±0.4	0.9±0.5
Agarum cribrosum	0	0	1.4±3.5	0.8±0.8	3.6±1.3	0	0	0.1±0.1	0.1±0.1	0	0
Alaria esculenta	0.3±0.2	0	2.5±1.2	0.5±0.3	0.3±0.3	0.4±0.3	0	1.9±0.9	0.1±0.1	0.9±0.5	0
Saccorhiza dermatodea	16.4±4.8	0.6±0.3	3.8±1.7	1.3±0.5	0.7±0.4	0	0	0	0	0.2±0.2	0
Total kelp	19.8±5.8	1.0±0.4	14.3±4.6	7.6±1.2	12.3±3.8	16.8±2.5	22.6±3.2	37.8±6.0	30.3±2.7	24.2±3.9	11.8±1.4
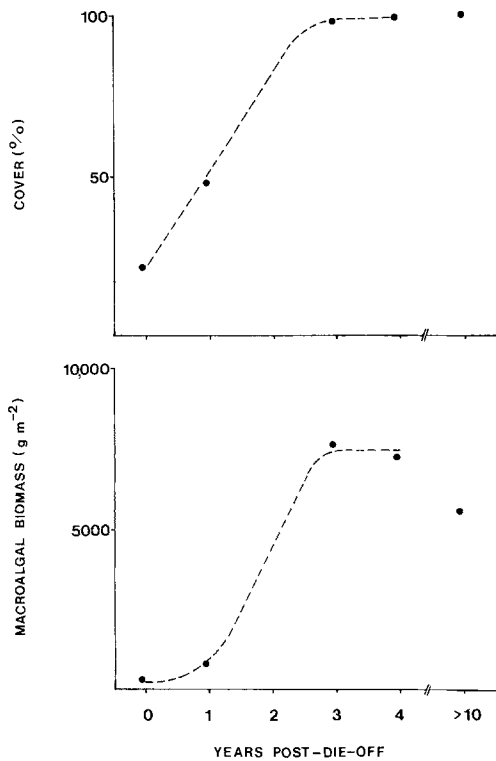
Fig. 7. Mean percentage cover and macroalgal biomass for groups of sites along the Atlantic coast of Nova Scotia where *Strongylocentrotus droebachiensis* died off at different times in the past. Sites that are sea urchin-dominated barren grounds are denoted as 0 years post-die-off. The mature kelp bed site is denoted as >10 years post-die-off

and Western Head but rare at Mouton Head where *Corallina officinalis* was dominant. *Saccorhiza dermatodea* was the most abundant kelp at Eagle Head; *Laminaria digitata* was the most abundant kelp at Western Head. *Agarum cribosum* occurred at each of the three sites. Kelp species generally were <100 cm total length (Fig. 6). The biomass of filamentous red algae was similar among the three sites.

The sites where sea urchins were eliminated about 3 years (White Point, East Point, Pollock Point) and 4 years (Halibut Bay, Shipley Head) previously were dominated by *Laminaria digitata* and *L. longicruris*. The relative abundance of these two species varied among sites, but together they accounted for about 90% of the total macroalgal biomass and formed a dense canopy covering >95% of the bottom at each site (Fig. 3, 4 and 5; Tables 3 and 4). Size distributions of *Laminaria* spp. were bimodal or polymodal at each site (Fig. 6). The small size (total length) of *L. longicruris* at Halibut Bay was due to extensive erosion of the blades. *Desmarestia* spp. typically occurred in patches where kelps were sparse. Filamentous and foliose red algae and/or *Corallina officinalis* formed the understory.

At the mature kelp bed site (Whitehead Island), *Laminaria digitata* and *L. longicruris* were the only kelp species (Tables 3 and 4). *Laminaria longicruris* attained large size (up to 620 cm total length) (Fig. 6) but *L. digitata* was more abundant in terms of density and biomass (Tables 3 and 4). The leafy red alga, *Chondrus crispus*, was the dominant component of the understory which also included filamentous red algae, *Phycodrys rubens* and *Ceramium rubrum* (Fig. 5, Table 3).

Comparisons among sites indicate significant differences in macroalgal cover and biomass (Kruskal Wallis Test, $P < 0.001$). The barren ground and 1 year sites represent one non-significantly heterogeneous set ($P < 0.05$), and the 3 and 4 year sites and the mature kelp bed site represent another (Mann-Whitney U test, simultaneous test procedure, Sokal and Rohlf 1969). Percentage cover of macroalgae increased from an average of 22% at barren ground sites to 45% at 1 year sites and 98% at 3 and 4 year sites, and was 100% at the mature kelp bed site (Fig. 7). Total macroalgal biomass increased from an average of 0.3 kg m^{-2} for barren ground sites to 0.8 kg m^{-2} in 1 year sites to 7.6 kg m^{-2} at 3 year sites and 7.2 kg m^{-2} at 4 year sites, and was 5.6 kg m^{-2} at the mature bed site (Fig. 7). The high biomass at 3 and 4 year sites and at the mature kelp bed site is due primarily to *Laminaria* spp.

Discussion

Sea urchin mass mortality

Total mortality of *Strongylocentrotus droebachiensis* at 5 sites between Clarke's Harbour and Eagle Head suggests that sea urchins were eliminated over ~108 km (straight line distance) along the southwestern shore in the summer or fall of 1983. Total mortality of sea urchins at Mushaboom and evidence of extensive mortality at Marie Joseph suggest that the epizootic spread in a northeasterly direction along the northeastern shore, and that sea urchins were completely eliminated over at least 25 km of shoreline. Previous surveys (Miller and Colodey 1983; Moore and Miller 1983) indicated that sea urchin mortality was virtually complete (>99% of biomass) over widespread areas during a former epizootic of comparable severity in 1981. Therefore, although survey sites in the present study represent only point observations along extensive tracts of shoreline, it is unlikely that pockets of surviving sea urchins occurred within the range of these sites, at least within the shallow rocky subtidal zone (<25 m).

Scheibling and Stephenson (1984) showed that epizootics of *Strongylocentrotus droebachiensis* between 1980 and 1982 were associated with anomalously warm summer/fall seawater temperatures and that the extent of mortality varied directly with temperature. The widespread mass mortality of sea urchins observed in 1983 was consistent with this pattern: mean seawater temperature near Halifax in August was a record high relative to a 40 year period of monthly means (1927–1967), and the number of degrees and degree days above 12° or 15° C were highest in 1983 relative to the previous 4 years (Halifax Research Laboratory, Department of Fisheries and Oceans, and Sandy Cove Research Station, National Research Council, unpub. data). At Eagle Head, mass mortality of sea urchins occurred in late August or early September 1983 (Scheibling 1984b) when local sea water temperatures were 16–18° C. Histopathological studies and laboratory infection experiments have identified an amoeba (*Paramoeba* sp.) as the probable causative agent of this disease (Jones et al. in press, Jones and Scheibling unpub. ms.). The pathogen may be associated with warm water masses originating to the south (e.g. Gulf Stream eddies).

To estimate the mortality of *Strongylocentrotus droebachiensis* between 1980 and 1983, sea urchins are assumed to have been completely eliminated between eastern Cape

Sable Island (Clarke's Harbor) and Mushaboom (280 km straight-line distance) (Fig. 1). The area affected by mass mortality is estimated as 541 km^2 using the following approximations based on a survey of this coast by Moore and Miller (1983): (1) the ratio of coastline distance to straight-line distance $= 11:1$, (2) the percentage of coastline with suitable habitat for sea urchins/macroalgae $= 48\%$, and (3) the average width of suitable habitat $= 366$ m. The average biomass of *S. droebachiensis* prior to mass mortalities is estimated as 480 g fresh weight m^{-2} (Miller and Colodey 1983). Therefore, the estimated loss of sea urchin biomass in the area of complete die-off is 260 thousand metric tons fresh weight. This extends (by 2 to 3 fold) previous estimates of sea urchin mortality: 80 thousand metric tons (Miller and Colodey 1983) and 109 thousand metric tons (Moore and Miller 1983) in areas of complete die-off in 1981 and 1982 respectively.

The extent of sea urchin mortality in areas of partial die-off is unknown. Diving surveys along the southwestern shore in 1982 indicated that sea urchin density and mortality were highest in shallow, nearshore areas and decreased offshore (Moore and Miller 1983; Scheibling and Stephenson 1984). Accumulations of sea urchin tests were observed on exposed beaches as far north as Cape Breton Island following epizootics in 1981 and 1982 (Miller and Colodey 1983; Moore and Miller 1983).

High densities of *Strongylocentrotus droebachiensis* occurred in the two barren ground sites in August 1984, despite recurrent outbreaks of disease in these areas. At Cape Mocodome, sea urchin density at the study site increased markedly since the epizootic in 1983, although sea urchins were absent in surrounding areas. This suggests that sea urchins which survive an epizootic, actively aggregate to regain former levels of population density and consequently become more localized in distribution.

Sea urchin recruitment

The occurrence of juvenile *Strongylocentrotus droebachiensis* at sites where former sea urchin populations died off 1 year previously, and the paucity or absence of juveniles at sites where the die-off occurred 3 or 4 years previously and at the mature kelp bed site, suggests that larval recruitment and/or post-metamorphic survival of sea urchins is low in kelp beds. This may be due to predation by a variety of fish and invertebrates associated with the kelp. Low rates of recruitment of *S. franciscanus* inside kelp beds (*Macrocystis pyrifera*) in California have been attributed to predation (Pearse et al. 1970; Bernstein and Jung 1981; Tegner and Dayton 1981).

The mean size of juvenile *Strongylocentrotus droebachiensis* at 1 year sites was 5–6 mm dia in July, 1984. *Strongylocentrotus droebachiensis* has a major spawning peak around April/May (Himmelman 1978; Scheibling unpub. data) and the duration of the planktonic larval stage varies from 7–22 wk (Strathman 1978). Assuming larval settlement occurred shortly after the sea urchin die-off in August/September 1983, the average growth rate of juvenile sea urchins would be about 6–7 mm y^{-1}. This is similar to the growth rate of juveniles which settled along the western shore of St. Margaret's Bay following the sea urchin die-off in 1981 (Raymond and Scheibling unpub. data). However, Himmelman et al. (1983a) report initial growth rates of *S. droebachiensis* of 2–5 mm y^{-1} in barren grounds in the

St. Lawrence estuary. Increased growth of juvenile sea urchins in areas where adults have been eliminated by disease may be due to increased availability of algal resources (Himmelman et al. 1983b).

Macroalgal succession

Numerous studies have shown that reduction or elimination of sea urchins, either by experimental removal (Kitching and Ebling 1961; Leighton et al. 1966; Jones and Kain 1967; Vadas 1968; Paine and Vadas 1969; Sammarco et al. 1974; Breen and Mann 1976a; Vance 1979; Cowen et al. 1982; Himmelman et al. 1983; Dayton et al. 1984; Dean et al. 1984) or by natural processes such as emigration (Foreman 1977; Duggins 1983), disease (Pearse and Hines 1977; Bak et al. 1984) or predation (Estes et al. 1978; Duggins 1980; Breen et al. 1982), results in a rapid colonization of the substratum by macroalgae. Initial colonists are diatoms and fast-growing opportunistic species. In temperate subtidal areas, macroalgal succession eventually leads to the establishment of canopy-forming kelps. The rate of succession and patterns of species distribution and abundance are influenced by various environmental factors, including light, temperature, exposure to wave action, and nutrient availability (Foster 1975; Luning 1979; Dean and Jacobsen 1984). In this study, macroalgal sampling was restricted in depth (8–10 m), degree of exposure to oceanic waves (high), and time of year (July/August) to limit environmental variability among sites. Assuming that structurally similar macroalgal communities will develop at each site over similar time periods, those sites where sea urchins died off about 1 year previously represent early successional stages, and those where urchins died off about 3 or 4 years previously, late successional stages.

Early successional stage sites showed marked differences in macroalgal cover, biomass and species composition. Some of the variability among these sites may be related to differences in abundance and composition of macroalgal species that occurred in the former barren grounds. *Desmarestia* spp., the most abundant macroalgae at the barren ground sites, also were the dominant species in two of the three early successional stage sites (Eagle Head and Western Head). (*Desmarestia* contains chemical compounds that make it unpalatable to sea urchins (Anderson and Velimerov 1982) which may account for its abundance in barren grounds.) Macroalgal abundance in July/August may approximate seasonal maxima in barren ground and early successional stage sites due to the prevalence of summer annual species, such as *D. viridis* and *Saccorhiza dermatodea*, which degenerate in the fall and winter.

The similarities in macroalgal biomass and species composition among sites where sea urchins died off about 3 and 4 years previously suggest that the respective communities are in late successional stages and approaching equilibrium. The macroalgal assemblage at 8–10 m at these sites is similar to that described in areas near Halifax (Edelstein et al. 1969; Gerard and Mann 1979) and in St. Margaret's Bay (Mann 1972a) prior to sea urchin population outbreaks and destructive grazing. The kelps, *Laminaria longicruris* and *L. digitata*, dominate the late successional stage sites, forming a dense canopy. Average macroalgal biomass (5.2–9.1 kg m^{-2} fresh weight) was comparable to that recorded in former kelp beds. Gerard and Mann (1979) estimated average *Laminaria* biomass as 4.4 and 5.5 kg m^{-2}

in sheltered and exposed sites respectively. Mann's (1972a) estimates in St. Margaret's Bay were higher: 16.0 and 12.7 kg m^{-2} in mixed *Laminaria* and *L. longicruris* zones respectively. However, he sampled only in areas of complete plant cover. Chapman (1981) reported an average macroalgal biomass of 3.6 kg m^{-2} in a refugial kelp bed in St. Margaret's Bay.

Although *Laminaria longicruris* and *L. digitata* coexisted at all late successional stage sites, the relative proportion of each species varied markedly among sites. Other kelps, such as *Agarum cribosum* and *Saccorhiza dermatodea*, present in early successional stages, were rare or absent among the *Laminaria* canopy, suggesting competitive exclusion. The kelp canopy also may limit recruitment of juvenile *Laminaria*. Juveniles were more abundant in early successional stage sites than in late stage sites. Johnson (1984) showed that experimental removal of the *Laminaria* canopy increased juvenile recruitment. A similar canopy effect on recruitment has been reported in other kelps (Santelices et al. 1980; Reed and Foster 1984; Santelices and Ojeda 1984).

Desmarestia aculeata, a perennial brown alga, generally occurred in patches within the *Laminaria* beds in late successional stage sites. The greater abundance of *D. aculeata* and the congeneric annual species, *D. viridis*, in early successional stage sites (except Mouton Head) suggests that *Desmarestia* is competitively displaced by *Laminaria* during development of the kelp canopy. Johnson (1984) reported a progressive reduction of *D. aculeata* in a *Laminaria* bed in eastern St. Margaret's Bay between 2 and 3 years after a die-off of sea urchins. *Desmarestia* also occurred in association with *Laminaria* in former kelp beds near Halifax prior to destructive grazing by sea urchins (Edelstein et al. 1969).

The sequence of macroalgal recolonization, inferred by contrasting sites where sea urchins died off in different years, is similar to that recorded by Breen and Mann (1976) when they experimentally removed sea urchins from a barren area in St. Margaret's Bay. They found that *Desmarestia viridis* and *Saccorhiza dermatodea* grew rapidly in the first year and then were displaced by a dense canopy of *Laminaria longicruris* and an understory of filamentous red algae and *D. aculeata*. After 18 months, the biomass of kelp in the experimental area was equivalent to that in an adjacent established bed. The rapid recolonization of available space, initially by fast growing emphemeral or opportunistic species and followed by perennial kelps, has been documented in a number of similar studies (Jones and Kain 1967; Paine and Vadas 1968; Kain 1975; Foreman 1977; Pearse and Hines 1979; Himmelman et al. 1983b).

The rate of recolonization of kelp beds off Nova Scotia probably varies markedly with depth and exposure to water movement. Within the limited depth and exposure range of the present study, kelp beds attained a biomass level comparable to former, established beds within 3 years. Unfortunately, the extent of recolonization after 2 years is unknown since sea urchins were not completely eliminated by disease along large tracts of coastline in 1982 (Moore and Miller 1983). However, Moore and Miller (1983) noted that macroalgal cover exceeded 80%, and was dominated by *Laminaria* spp., at two sites where sea urchins died-off 20–22 months previously (these were proximal to the Halibut Bay and Shipley Head sites in the present study). Johnson (1984) correlated differences in the rate of recovery of kelp beds at two sites in St. Margaret's Bay to water

movements and distance from reproductive kelp populations. At the more exposed site, which was proximal to an established kelp bed, a dense *Laminaria* canopy was present 18–20 months after sea urchin mortality. At the more sheltered site without a nearby kelp refugium, the extent of *Laminaria* cover was about an order of magnitude lower after an equivalent period. Foreman (1977) showed that the rate of recovery of kelp beds off British Columbia decreased with depth, and that 2 or 3 years were required to regain or exceed the biomass present before destructive grazing. Himmelman et al. (1983 b) found that the kelp recolonization following sea urchin removal in the St. Lawrence estuary also decreased with depth due to low light penetration.

It is not known whether the kelp beds recolonizing the Atlantic Coast will approach a climax state similar to the mature kelp beds along the southwestern tip of Nova Scotia. These mature beds, as exemplified by the Whitehead Island site, are characterized by a dense turf of *Chondrus crispus* which forms the dominant macroalgal component in many areas (A.R.O. Chapman pers. comm.). Kelp density was much lower in the mature bed and *Laminaria longicruris* attained a much larger size than in the late successional stage sites. These differences may be associated with differing environmental conditions. Kelp beds along the southwestern tip are exposed to less wave action, greater tidal ranges and different nutrient regimes than those along the rest of the Atlantic coast of Nova Scotia (Pringle et al. 1982).

Community stability

Large-scale fluctuations in kelp and sea urchin biomass off Nova Scotia may characterize the trajectory of a dynamic subtidal system which cycles between two alternative community states: kelp beds and sea urchin-dominated barren grounds (Scheibling 1984a). Destructive grazing of kelp beds by expanding sea urchin populations was well documented in St. Margaret's Bay in the early 1970's (Breen and Mann 1976a; Mann 1977). The occurrence of sea urchin-dominated barren grounds along more than 400 km of coastline (from Clarke's Harbour to Dover) by 1980 was attributed to large-scale outbreaks of destructive grazing in the previous 1–2 decades (Wharton and Mann 1981). Mass mortalities of sea urchins since late 1980 have enabled kelp beds to regenerate along most of that coastline. There is anecdotal evidence from fishermen that mass mortalities of sea urchins, and reciprocal fluctuations in kelp and sea urchin abundance, have occurred off the Nova Scotian coast since the turn of the century (Breen 1980; Wharton and Mann 1981; Pringle et al. 1982; Scheibling and Stephenson 1984).

Recent reviews have emphasized the importance of temporal and spatial scales, and type or level of perturbation, in assessing community stability (Sutherland 1981; Connell and Sousa 1983). Barren ground and kelp bed communities off Nova Scotia exhibit a high degree of persistance stability: they extend in time well beyond the generation times of the respective dominant species, sea urchins and *Laminaria*, and in space over hundreds of km of coastline (Scheibling 1984a). These communities alternate in space as well as time. Along the southwest tip of Nova Scotia, kelp beds have persisted for many decades in the absence of sea urchins (MacFarlane 1950; A.R.O. Chapman pers. comm.),

whereas in Newfoundland, sea urchin-dominated barren grounds exhibit a similar degree of permanence (Hooper 1980; Himmelman 1980). The crustose coralline algae are a persistent component of both community types. In barren grounds they are the dominant macroalgae; in kelp beds they form the secondary substratum upon which kelps and other fleshy algae attach.

Barren ground and kelp beds both appear to be resistent or resilient to various biotic and abiotic perturbations (Type I and II perturbations, Sutherland 1981). Barren grounds are continually invaded by algal spores but intensive grazing by sea urchins precludes the establishment of most species and maintains the macroalgal community at an early successional state (Chapman 1981). Seasonal pulses of recruitment (e.g. summer annual species) result in some ephemeral algal growth and patchiness, as was observed at Louse Head. Localized mortality of sea urchins due to intrusions of low salinity water or outbreaks of disease (Hooper 1980; Himmelman 1980; Scheibling and Stephenson 1984) have a similar effect, although sea urchins can readily repopulate areas by immigration and destroy newly-recruited plants (Chapman 1981). In kelp beds, sea urchin recruitment may be limited by canopy effects and/or by predators associated with the kelp, such as fish, crabs and lobsters. Local infestations of a small gastropod, *Lacuna vincta*, can cause considerable damage to kelp blades, although this is rapidly regenerated (Johnson 1984). Storms may dislodge plants creating holes in the canopy and providing space for opportunistic species (Dayton et al. 1984). These types of perturbations, may create spatial and temporal mosaics in the species assemblages of both barren ground and kelp bed communities, although they are of insufficient intensity or duration to markedly alter the integral structure of these communities.

However, certain types or levels of perturbation (Type III, Sutherland 1981) may bring about catastrophic mortalities of dominant species and a shift to the alternative community state. Off Nova Scotia, infectious disease is the only type of perturbation known to effect the transition from barren grounds to kelp beds. Moreover, outbreaks of disease must be of sufficient severity or frequency so as to effectively eliminate sea urchins over widespread areas. Although localized mass mortalities of sea urchins occurred in nearshore areas along the southwestern coast in 1982 (Moore and Miller 1983; Scheibling and Stephenson 1984), extensive recolonization of these areas by kelp and other fleshy macroalgae did not take place until the surviving sea urchins were totally eliminated the following year (Scheibling, pers. obs.). However, along the northeastern coast, where sea urchin populations have been repeatedly decimated by disease over 2–3 years, barren grounds may have become progressively more localized, enabling macroalgal regeneration in peripheral areas. At Cape Mocodome, for example, sea urchin dominated barren grounds were adjacent to areas of extensive macroalgal cover resembling both early and late successional stage sites. In a previous survey in 1979, Wharton (1980) observed only barren grounds with little macroalgal cover at Cape Mocodome and 11 other sites in the vicinity.

The types of perturbation that may bring about the transition from kelp beds to sea urchin-dominated barren grounds are less clear. Mann and colleagues hypothesized that overfishing of sea urchin predators, such as lobsters and finfish, led to increases in sea urchin abundance and

destructive grazing of kelp beds in Nova Scotia (see reviews by Mann 1977, 1982). This hypothesis remains controversial (Pringle et al. 1982): it relies mainly on circumstantial evidence and feeding studies indicate that sea urchins are not a preferred prey of lobsters (Evans and Mann 1977; Hirtle and Mann 1978; Elner 1980). The basic premise of Mann's hypothesis is that predators control adult sea urchin abundance. However, predation may be more important in limiting recruitment to adult populations and juvenile sea urchins have a different suite of predators than adults (Hooper 1980).

An alternative and nonexclusive hypothesis is that sea urchin population outbreaks in kelp beds may be a consequence of periodic episodes of intensive recruitment which outstrip predatory controls. Such events may be contingent on large-scale oceanographic or climatic features, conducive to survival of the planktonic larvae (Foreman 1977; Birkeland 1982). After a major recruitment event, there probably would be a lag of several years before sea urchins attained a size at which they could effectively graze kelp. Even then, destructive grazing would require the formation of dense aggregations of sea urchins within kelp beds (Breen and Mann 1976, Mann 1977; Bernstein et al. 1981, 1983). Therefore, it may be many years, even decades, before the newly established kelp beds off Nova Scotia are once again transformed to sea urchin-dominated barren grounds. Historical evidence, however, suggests that this change ultimately will occur, and that these alternative community states will continue to replace one another as they have in the past.

References

Anderson RJ, Velimerov B (1982) An experimental investigation of the palatability of kelp bed algae to the sea urchin *Parechinus angulosus* Leske. Mar Ecol 3:357–373

Bak RPM, Carpay MJE, de Ruyter van Steveninck ED (1984) Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curacao. Mar Ecol Prog Ser 17:105–108

Ballantine DL (1984) Hurricane-induced mass mortalities to a tropical subtidal algal community and subsequent recoveries. Mar Ecol Prog Ser 20:75–83

Bernstein BB, Jung N (1979) Selective pressures and coevolution in a kelp canopy community in southern California. Ecol Monog 49:335–355

Bernstein BB, Williams BE, Mann KH (1981) The role of behavioural responses to predators in modifying urchins' (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. Mar Biol 63:39–49

Bernstein BB, Schroeter SC, Mann KH (1983) Sea urchin (*Strongylocentrotus droebachiensis*) aggregating behaviour investigated by a subtidal multifactorial experiment. Can J Fish Aquat Sci 40:1975–1986

Birkeland C (1982) Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). Mar Biol 69:175–185

Boudouresque CF, Nedelec N, Shepard SA (1981) The decline

of population of the sea urchin *Paracentrotus lividus* in the bay of Port-Cros (Var, France). Rapp P-v Reun Commn int Explor Scient Mer Mediterr 27:233–244

Breen PA (1980) Relations among lobsters, sea urchins and kelp in Nova Scotia. In: Pringle JD, Sharp GJ, Caddy JF (eds) Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can Tech Rept Fish Aquat Sci 954, pp 24–32

Breen PA, Mann KH (1976a) Destructive grazing of kelp by sea urchins in eastern Canada. J Fish Res Bd Can 33:1278–1283

Breen PA, Mann KH (1976b) Changing lobster abundance and the destruction of kelp beds by sea urchins. Mar Biol 34:137–142

Breen PA, Carson TA, Foster JB, Stewart EA (1982) Changes in subtidal community structure associated with British Columbia sea otter transplants. Mar Ecol Prog Ser 7:13–20

Chapman ARO (1981) Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, eastern Canada. Mar Biol 62:307–311

Chapman ARO (1985) Population and community ecology of seaweeds. Ann Rev Oceanog Mar Biol (in press)

Connell JH, Sousa WP (1983) On the evidence needed to judge ecological stability or persistence. Am Nat 121:789–824

Cowen RK, Agegian CR, Foster MS (1982) The maintenance of community structure in a central California giant kelp forest. J Exp Mar Biol Ecol 64:189–201

Dayton PK, Currie V, Gerrodette T, Keller BD, Rosenthal R, Ven Tresca D (1984) Patch dynamics and stability of some California kelp communities. Ecol Monogr 54:253–289

Dean TA, Jacobsen FR (1984) Growth of juvenile *Macrocystis pyrifera* (Laminariales) in relation to environmental factors. Mar Biol 83:301–311

Dean TA, Schroeter SC, Dixon JD (1984) Effects of grazing by two species of sea urchins (*Strongylocentrotus franciscanus* and *Lytechinus anamesus*) on recruitment and survival of two species of kelp (*Macrocystis pyrifera* and *Pterygophora californica*). Mar Biol 78:301–313

Duggins DO (1980) Kelp beds and sea otters: an experimental approach. Ecology 61:447–453

Duggins DO (1983) Starfish predation and the creation of mosaic patterns in a kelp-dominated community. Ecology 64:1610–1619

Edelstein T, Craigie JS, McLachlan J (1969) Preliminary survey of the sublittoral flora of Halifax County. J Fish Res Board Can 26:2703–2713

Elner RW (1980) Predation on the sea urchin (*Stronglyocentrotus droebachiensis*) by the American lobster (*Homarus americanus*) and the rock crab (*Cancer irroratus*). In: Pringle JD, Sharpe GJ, Caddy JF (eds) Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can Tech Rept Fish Aquat Sci 954, pp 48–65

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1060

Estes JA, Smith NS, Palmisano JF (1978) Sea otter predation and community organization in the western Aleutian islands, Alaska. Ecology 59:822–833

Evans PD, Mann KH (1977) Selection of prey by American lobsters (*Homarus americanus*) when offered a choice between sea urchins and crabs. J Fish Res Board Can 34:2203–2207

Foreman RE (1977) Benthic community modification and recovery following intensive grazing by *Strongylocentrotus droebachiensis*. Helgo Wiss Meeresunters 30:468–484

Foster MS (1975) Algal succession in a *Macrocystis pyrifera* forest. Mar Biol 32:313–329

Gerard VA, Mann KH (1979) Growth and production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement. J Phycol 15:33–41

Himmelman JH (1978) Reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*. Can J Zool 56:1828–1836

Himmelman JH (1980) The role of the green sea urchin, *Strongylocentrotus droebachiensis*, in the rocky subtidal region of New-foundland. In: Pringle JD, Sharp GJ, Caddy JF (eds) Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can Tech Rep Fish Aquat Sci 954, pp 92–119

Himmelman JH, Lavergne Y, Axelsen F, Cardinal A, Bourget E (1983a) Sea urchins in the Saint Lawrence Estuary: their abundance, site structure, and suitability for commercial exploitation. Can J Fish Aquat Sci 40:476–486

Himmelman JH, Cardinal A, Bourget E (1983b) Community development following removal of urchins, *Strongylocentrotus droebachiensis*, from the rocky subtidal zone of the St. Lawrence Estuary, Eastern Canada. Oecologia (Berlin) 59:27–39

Hobaus E, Fenaux L, Hignette M (1981) Premières observations sur les lésions provoquées par une maladie affectant le test des oursins en Méditerranée occidentale. Rapp P-v Commn int Explor Scient Mer Mediterr 27:221–222

Hooper R (1980) Observations on algal-grazer interactions in New-foundland and Labrador. In: Pringle JD, Sharp GJ, Caddy JF (eds) Proceedings of the workshop on the relationships between sea urchin grazing and commercial plant/animal harvesting. Can Tech Dept Fish Aquat Sci 954, pp 120–124

Johnson CR (1984) Ecology of the kelp *Laminaria longicruris* and its principal grazers in the rocky subtidal of Nova Scotia. PhD Thesis, Dalhousie University, Halifax, p 280

Johnson PT (1971) Studies on diseased urchins from Point Loma. In: Kelp habitat improvement project annual report, 1970–71. Calif Inst Tech Pasadena, pp 82–90

Jones GM, Hebda AJ, Scheibling RE, Miller RJ (in press) Histopathology of the disease causing mass mortality of sea urchins (*Strongylocentrotus droebachiensis*) in Nova Scotia. J Invert Path

Jones NS, Kain JM (1967) Subtidal algal colonization following the removal of *Echinus*. Helgo Wiss Meeresunters 15:460–466

Kain JM (1975) Algal recolonization of some cleared subtidal areas. J Ecol 63:739–765

Kitching JA, Ebling FJ (1961) The ecology of Lough Ine XI. The control of algae by *Paracentrotus lividus* (Echinoidea). J Anim Ecol 30:373–383

Lawrence JM (1975) On the relationships between marine plants and sea urchins. Oceanogr Mar Biol Annu Rev 13:213–286

Lawrence JM, Sammarco PW (1982) Effects of feeding on the environment: Echinoidea. In: Jangoux M, Lawrence JM (eds) Echinoderm nutrition. Balkema, Rotterdam, pp 283–316

Leighton DL, Jones LG, North WJ (1966) Ecological relationships between giant kelp and sea urchins in southern California. Halifax, N.S. Int Seaweed Symp 5:141–153

Lessios HA, Robertson DR, Cubit JD (1984) Spread of *Diadema* mass mortality through the Caribbean. Science 226:335–337

Luning K (1979) Growth strategies of three *Laminaria* spp. (Phaeophyceae) inhabiting different depth zones in the sublittoral region of Helgoland (North Sea). Mar Ecol Prog Ser 1:195–207

MacFarlane C (1980) A survey of certain seaweeds of commercial importance in southwest Nova Scotia. Can J Bot 30:78–97

Maes P, Jangoux M (1984) The bald-sea-urchin disease: a biopathological approach. Helgo Wiss Meeresunters 37:217–224

Mann KH (1972) Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. I Zonation and biomass of seaweeds. Mar Biol 12:1–10

Mann KH (1977) Destruction of kelp-beds by sea urchins: A cyclical phenomenon or irreversible degradation? Helgo Wiss Meeresunters 30:455–467

Mann KH (1982) Kelp, sea urchins and predators: a review of strong interactions in rocky ecosystems of eastern Canada, 1970–1980. Neth J Sea Res 16:414–423

Miller RJ, Colodey AG (1983) Widespread mass mortalities of the green sea urchin in Nova Scotia, Canada. Mar Biol 73:263–267

Moore DS, Miller RJ (1983) Recovery of macroalgae following widespread sea urchin mass mortality with a description of the nearshore hardbottom habitat on the Atlantic coast of Nova Scotia. Can Tech Rep Aquat Sci 1230:vii-94

Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–75

Paine RT, Vadas RL (1969) The effects of grazing by sea urchins Strongylocentrotus spp on benthic algal populations. Limnol Oceanogr 14:710–719

Pearse JS, Hines AH (1979) Expansion of a central California kelp forest following the mass mortality of sea urchins. Mar Biol 51:83–91

Pearse JS, Clark ME, Leighton DL, Mitchell CT, North WJ (1970) Final Report. Marine waste disposal and sea urchin ecology. Appendix In: Kelp bed habitat improvement project, annual report (1 July 1969–30 June 1970). Calif Institute Technology, Pasadena

Pearse JS, Costa DP, Yellin MB, Agegian CR (1977) Localized mass mortality of red sea urchin, Strongylocentrotus franciscanus, near Santa Cruz, California. Fish Bull 75:645–648

Pringle JD, Sharp GJ, Caddy JF (1982) Interactions in kelp bed ecosystems in the northwest Atlantic: review of a workshop. In: Mercer MC (ed) Multispecies approaches to fisheries management advice. Can Spec Publ Fish Aquat Sci 59:108–115

Reed DC, Foster MS (1984) The effects of canopy shading on algal recruitment and growth in a giant kelp forest. Ecology 65:937–948

Sammarco PW, Levinton JS, Ogden JC (1974) Grazing and control of coral reef community structure by Diadema antillarum Philippi (Echinodermata: Echinoidea): A preliminary study. J Mar Res 32:47–53

Santelices B, Ojeda FP (1984) Population dynamics of coastal forests of Macrocystis pyrifera in Puerto Toro, Isla Navarino, Southern Chile. Mar Ecol Prog Ser 14:175–183

Scheibling RE (1984a) Echinoids, epizootics and ecological stability in the rocky subtidal off Nova Scotia, Canada. Helgoländer Meeresunters 37:233–242

Scheibling RE (1984b) Predation by rock crabs (Cancer irroratus) on diseased sea urchins (Strongylocentrotus droebachiensis) in Nova Scotia. Can J Fish Aquat Sci 41:1847–1851

Scheibling RE, Stephenson RL (1984) Mass mortality of Strongylocentrotus droebachiensis (Echinodermata: Echinoidea) off Nova Scotia, Canada. Mar Biol 78:153–164

Simenstad CA, Esters JA, Kenyon KW (1978) Aleuts, sea otters and alternate stable-state communities. Science 200:403–411

Strathman R (1978) Length of pelagic period in echinoderms with feeding larvae from the northeast Pacific. J Exp Mar Biol Ecol 34:23–27

Sutherland JP (1981) The fouling community at Beaufort, North Carolina: a study in stability. Am Nat 118:499–519

Tegner MJ, Dayton PK (1981) Population structure, recruitment and mortality of two sea urchins (Strongylocentrotus franciscanus and S. purpuratus) in a kelp forest. Mar Ecol Prog Ser 5:255–268

Vadas RL (1968) The ecology of Agarum and the kelp bed community. PhD Thesis, Univ Washington, Seattle, p 280

Vance RR (1979) Effects of grazing by the sea urchin, Centrostephanus coronatus, on prey community composition. Ecology 60:537–546

Wharton WG (1980) The relationship between destructive grazing by the sea urchin Strongylocentrotus droebachiensis and the abundance of American lobster Homarus americanus, on the Atlantic Coast of Nova Scotia. MSc Thesis, Dalhousie University, Halifax, p 79

Wharton WG, Mann KH (1981) Relationship between destructive grazing by the sea urchin, Strongylocentrotus droebachiensis, and the abundance of American lobster, Homarus americanus, on the Atlantic coast of Nova Scotia. Can J Fish Aquat Sci 38:1339–1349