INVESTIGATIONS OF THE MARINE ALGAE OF NOVA SCOTIA XVII: VERTICAL AND GEOGRAPHIC DISTRIBUTION OF MARINE ALGAE ON ROCKY SHORES OF THE MARITIME PROVINCES¹

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A review is given of the physical features of three coastal environments of eastern Canada: the Gulf of St. Lawrence, the open Atlantic coast, and the Bay of Fundy. Intertidal and sublittoral regions of these environments were surveyed. Vertical limits of common macrophytic algae and their relative abundances were documented and a species list compiled for sectors of each coastal environment. Differences among the three coastal enviornments in terms of species composition and vertical distributions could be related to differences in ice scour, tidal amplitude, wave exposure, intertidal slope, water temperature and geology. Sites on the outer Atlantic coast generally showed patterns of zonation corresponding with the typical pattern for the North Atlantic Ocean, whereas both Fundy and Gulf shores deviated from this pattern. The vegetation belts dominated by fucoids, red turf algae and kelp were found at progressively lower intertidal or sublittoral levels moving from the Bay of Fundy to the Atlantic and from Atlantic to Gulf shores. The changing pattern from the Fundy to Atlantic shores was correlated mainly with changing tidal amplitudes and intertidal slopes. The difference between Atlantic and Gulf shores was primarily owing to the effects of ice scour. Certain species found sublittorally in other areas occurred intertidally in the Bay of Fundy. For some species, variations in physical factors accounted for a high proportion of the variability in vertical limits. Whether this is the result of direct effects of physical factors or a consequence of changing biotic interactions requires experimental analysis. Nutrient enrichment of southwest Atlantic shores may have produced a slight increase in species diversity of this environment. Differences in the temperature regimes of the three coastal environments were clearly reflected in species compositions. Some cold-temperate to Arctic species were absent from the warmest environment, the Gulf, while certain warm-temperate species were restricted to Gulf waters.

Une revue est presentée des traits physiques de trois environnements côtiers de l'est du Canada: le Golfe du St. Laurent, la côte de l'Atlantique, et la Baie de Fundy. On a fait un relève des lieux entre les limites des marées ainsi que de ceux audessous du littoral. Les limites verticales des algues macrophytiques ordinaires ainsi que leurs abondances comparatives, ont été examinées et une liste des espèces a été préparée ayant trait aux secteurs de chaque environnement côtier. Les différences en ce qui concerne la composition d'espèces et leurs distributions verticales s'apparentent aux différences en sillonage dù à la glace, à l'ampleur des marées, à l'exposition aux vagues, à la pente entre les limites des marées, à la température de l'eau, et à la géologie. Les sites de la côte atlantique extérieure ont demontré une distribution de zones ressemblant à ceux de l'Océan Atlantique du Nord, tandis que la Fundy et le Golfe s'écartent de ce modèle. Les zones de plantes composées pour la plupart de fucus, de la varech, et des algues rouges se trouvent à de plus grandes profondeurs près de la côte en passant de la Baie de Fundy à l'Atlantique, et de l'Atlantique au Golfe. Le changement de distribution entre la Fundy et l'Atlantique se place en corrélation avec les variations d'ampleur de la marée, et des pentes entre les mers hautes et basses. La différence entre l'Atlantique et le Golfe se refère surtout aux effets du sillonage causé par la glace. Certaines espèces sont restreintes entre les limites des marées dans la Baie de Fundy, mais elles se trouvent audessous du littoral dans les autres cas. Quant à quelques autres espèces, la variation des facteurs physiques est responsable d'une haute proportion des écarts des limites verticaux. Une analyse expérimentale devrait être faite afin de comprendre si les faits ci-dessus se rattachent directement à des facteurs physiques ou à la suite d'actions réciproques biotiques inconstantes. L'enrichissement nutritif des côtes sud-ouest de l'Atlantique peut être responsable d'un petit accroissement de la diversité d'espèces de cet environnement. Les différences des régimes de température des trois environnements côtiers ont une influence sensible sur la composition des espèces. Certaines espèces situées dans les eaux froides-tempérées et arctiques sont absentes des environnements les plus chauds, e.g., le Golfe, tandis que certaines espèces des eaux chaudes-tempérées se trouvent exclusivement dans les eaux du Golfe.

Introduction

The Maritime Provinces (Nova Scotia, New Brunswick and Prince Edward Island) have three coastal environments: the southern Gulf of St. Lawrence (hereafter the Gulf), the Atlantic coast, and the Bay of Fundy (Owens and Bowen, 1977). The algal flora is cold-temperate with warm-temperate algae occurring in some shallow embayments (Novaczek et al., 1987). The first comprehensive survey of algae in these environments was performed by Bell and MacFarlane (1933a, 1933b). Since then, algal distributions in the Bay of Fundy (Wilson et al., 1979) and Gulf of St. Lawrence (Cardinal, 1968) have been documented. There are major differences among these environments, for instance in hydrography (especially tidal amplitude), water temperature, geology, wave energy and ice scour. Differences in the vertical and geographical distributions of intertidal and sublittoral algae are therefore to be expected among the three coastal environments, either owing to physiological limitations of the algae or through the influence of physical factors on competitive interactions among algae, herbivores and predators.

Table I Abbreviations for shore levels

CD	chart datum, the level of lowest normal tides
LLWS	lower low water of spring tides
LLWM	lower low water of mean tides
MWL	mean of all hourly observations of tidal height
HHWN	higher high water of neap tides
HHWM	higher high water of mean tides
HHWS	higher high water of spring tides

The intertidal region of rocky shores in the North Atlantic (i.e. from LLWS to HHWS, see Table I for abbreviations) can in general be divided (Fig 1) into three biotic zones (Lewis, 1964; Stephenson and Stephenson, 1972). The uppermost zone, the littoral fringe, lies between the uppermost marine organisms and the upper limit of barnacles. Except for special cases, such as in severe wave exposure, this zone spans the level of HHWS. In the North Atlantic the midlittoral zone is typically occupied by dominant stands of fucoid algae, and reaches from the upper barnacle line down to the upper limit of kelp. The lowest zone, the sublittoral fringe, runs from the upper limit of kelp down to the level of LLWS and may blend indistinguishably into the shallow sublittoral region. On British shores this general pattern is known to be

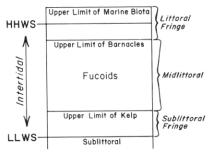


Fig 1 Schematic representation of the general pattern of zonation on rocky shores of the North Atlantic Ocean (adapted from Lewis, 1964; Stephenson and Stephenson, 1972).

sensitive to differences in wave exposure, slope, and degrees of sun and shade, any of which may alter the level of the boundaries of the zones or their species compositions.

With respect to vertical distributions of macroalgae, Stephenson and Stephenson (1954) reported that the Atlantic shores they observed conformed to the typical North Atlantic pattern, having a dominant kelp canopy defining the sublittoral fringe. In contrast, they found that the lowest intertidal level in the Gulf of St. Lawrence was either bare or dominated by *Chondrus crispus*, by fucoid algae, or by small annual brown algae. The occurrence of ice scour and the friable nature of the sandstone substratum were considered responsible for the absence of large kelp. Colinvaux (1966, 1970) found that shores of the Bay of Fundy also deviated from the expected pattern in that normally sublittoral species occurred in the intertidal region.

A few sites have recently been examined in more detail. Zonation of intertidal algae in the Gulf of St. Lawrence has been described by Lobban and Hanic (1984), and in the outer Bay of Fundy by Thomas et al. (1983). The sublittoral flora has been described in detail for one area in the lower Gulf (Bird et al., 1983), three Atlantic coastal sites (Edelstein et al., 1969; Mann, 1972; Novaczek and McLachlan, 1986); and Passamaquoddy Bay in the outer Bay of Fundy (Logan et al., 1983). A number of surveys have been conducted to determine the extent of sublittoral laminarian cover (Wharton, 1980; Moore and Miller, 1983), the distribution of large macrophytes relative to sea urchins (Moore et al., 1986), and the extent of commercially important Chondrus and fucoid beds (MacFarlane, 1952, 1965; Moseley and MacFarlane, 1969; Neish and Dunn, 1971; Taylor, 1973).

In this paper we review and update the comparison of the physical features of the three coastal environments of the Maritimes and look for correlations between the changing physical features and the vertical and geographical distributions of common macroalgae in 89 study sites (Fig 2). As limits of vertical distribution can vary between adjacent transects (Southward, 1958), from year to year (Hartnoll and Hawkins, 1980), and from season to season (Druehl and Green, 1982), we concentrate on general trends in dominant species rather than describing single sites in detail.

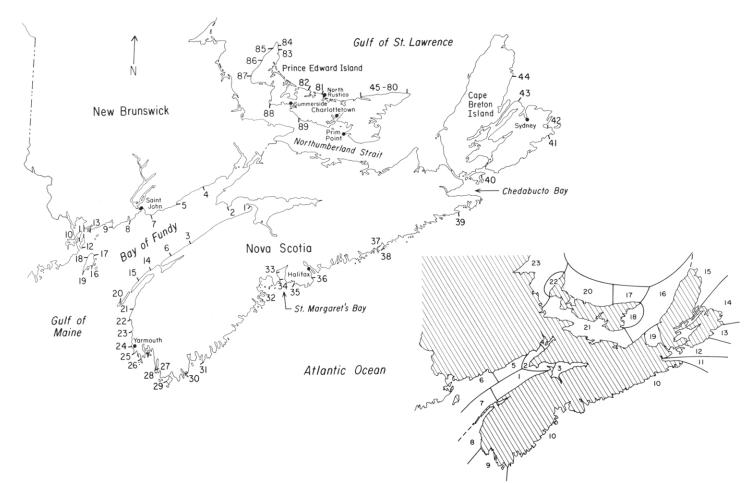
Review of Some Features of the Coastal Environments

Hydrography and climate. The southern Gulf of St. Lawrence is a wave-dominated, microtidal environment (Owens and Bowen, 1977). The spring-tidal range is generally around 1 m but reaches almost 3 m in parts of the more wave-sheltered and current-swept Northumberland Strait. Because the tides are of a mixed semi-diurnal type, the shores regularly experience long periods of emersion (Bell and McFarlane, 1933b). Low tide sometimes coincides with mid day in summer and protective fog cover is uncommon (Table II).

Tidal amplitudes (Fig 2b) along the Atlantic coast are 1 to 2 m in Cape Breton Island (shores 11-15), about 2 m along the eastern shore of Nova Scotia (shore 10), and 5-6 m along the Fundy approaches (shores 8 and 9). The Bay of Fundy is macrotidal with the tidal range increasing to 15 m at the head of the bay. Along the Fundy approaches and outer Bay of Fundy, spring low tides are rare at mid day and often occur in near-darkness during winter months. The intertidal algae are also protected from excessive irradiance and desiccation by frequent fog (Table II). Whereas most locations in the Maritimes have maximum monthly sunshine hours in mid-summer, shore 9 experiences the most sunshine in May (Canadian Climate Normals, 1982), when the water temperature (Fig 3) is still low. Owing to swift tidal currents (1-3 m s⁻¹) bearing sediment from marshes at the head of the bay, light penetration in the Bay of Fundy is limited compared to that of the Atlantic and Gulf coasts (Table III).

ment into shores (from Owens and Bowen 1977). Maps showing a) study sites and b) the division of each coastal environ-

Fig 2



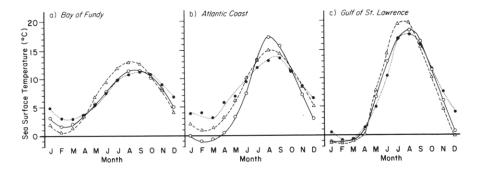


Fig 3 Representative (normal or mean) monthly sea surface temperatures in each coastal environment a) Fundy: shore 1 = ● shore 6 = ▽, mouth of Fundy = ○.b) Atlantic: shore 9 = ● shore 10 = ▽, shore 14 = ○.c) Gulf: shore 17 = ●, shore 20 = ▽, shore 21 = ○. (Lauzier and Hull, 1969; Dobson and Petrie, 1982; Weiler and Keeley, 1980).

Geology. The southern Gulf of St. Lawrence, except for shore 16 (northwestern Cape Breton Island), is composed of friable sandstone, commonly covered by patches of sand and gravel. On the Atlantic side of Cape Breton Island, resistant granites occur on shore 13, whereas sandstone and shale predominate on shores 12, 14, and 15. Glacial till is common over both types of bedrock (Roland, 1982).

The rocky Atlantic coast of mainland Nova Scotia consists predominantly of resistant granite and slate. In bays, on shoals and shoreward of islands, sublittoral bedrock is usually covered with glacial till.

In the Bay of Fundy, both resistant basalt and friable sandstone shores are present. Especially in the inner reaches, both the intertidal and the sublittoral regions are often covered by sand or mud.

Wind, waves and ice. In the Maritime provinces the prevailing winds are southwest and south from April to September, and north, northeast and northwest in winter

Table II Tide and fog patterns affecting desiccation in the intertidal regions of three coastal environments of eastern Canada (Canadian tide and current tables, 1984; Canadian climate normals, 1984).

		Fog	(30 yr mean)
	Noon low* tides yr ⁻¹ (Reference port)	da yr ⁻¹ (Refe	Max da mo ⁻¹ erence town)
FUNDY			
shore 6	0 (St. John)	106	> 10, June-Sept. (St. John)
ATLANTIC			
shore 9	0 (Yarmouth)	118	> 10, May-Sept. (Yarmouth)
shores 10, 14	12, SeptJune (Halifax)	80-84	> 10, May-Aug. (Halifax, Sydney)
GULF			
shores 20-21	9, AprAug. (Rustico)	47	< 10, JanDec. (Charlottetown)

^{*} Below LLWM between 1000 h and 1300 h.

Table III Light attenuation coefficients (Kd) measured in the surface water layer (< 30 m depth) of three coastal environments (Platt and Irwin, 1970; Marine Ecology Lab, 1980; Thomas et al., 1983; Logan et al., 1983; Prouse, 1983; C. Hudon, unpubl. data).

	$Kd (m^{-1})$	Month
FUNDY		
shore 2	0.6-2.4	Feb., Mar., Aug.
shore 6	0.3-0.45	Aug., Oct.
shore 7	0.3-0.6	Feb., May, Aug.
	0.5-1.4	July, Aug.
ATLANTIC		
shore 10	0.1-0.25	JanDec.
	0.2-0.4	Jul., Aug.
GULF		
shore 17	0.1-0.6	June-Aug.
shore 19	0.1-0.4	April-Nov.

(Owens and Bowen, 1977). Parts of the Atlantic and Fundy coasts facing south and southwest are consequently most wave-exposed during summer. In winter the prevailing northwest winds blow offshore over most of the coastline. The maximum wave heights (>7 m) are nevertheless recorded in winter on the outer Atlantic shores (shores 10-13) because the winter winds of maximum velocity are from the east and northeast (Owens and Bowen, 1977) across the Atlantic Ocean. Waves reach 6 m high on the Fundy approaches, can be 5.8 m on shore 17 in the Gulf and rarely exceed 4 m within the Bay of Fundy (Owens and Bowen, 1977).

Sea ice moderates wave energy in winter but by its motion it can denude intertidal and upper sublittoral regions. In the southern Gulf of St. Lawrence, ice is present for three to five months (Owens, 1976). Atlantic shores 12 and 15 have onshore ice for two to four months. Except for sheltered bays, the remainder of the Atlantic and Fundy coasts is virtually ice-free (Stephenson and Stephenson, 1954), experiencing only sporadic damage from moving floes.

Another factor moderating wave energy is the presence of shoals and offshore islands. Along most of the outer Atlantic and Fundy shores, the 18m depth contour is less than 2 km offshore (Canadian Hydrographic Service Charts, Marine Science Branch, Ottawa). Exceptions are found at the head of the Bay of Fundy and round southwestern Nova Scotia (shore 9) where shoals less than 18 m deep extend outward 6-12 km. Offshore islands shelter much of the northern half of shore 10. In the southern Gulf, shoals less than 18 m deep extend at least 2 km, and often 4-6 km offshore.

Wave shock in intertidal regions is also related to slope, with less stress-tolerant species being confined to gentle slopes on wave-exposed shores (Lewis, 1964). Our survey sites in the Bay of Fundy had significantly steeper intertidal slopes (tested by analysis of variance, p = 0.003) than the Atlantic sites.

Water temperature, salinity and nutrients. Minimum average monthly sea surface temperatures vary from -1.8°C on Gulf and ice-bound Atlantic shores to 3°C in parts of the Bay of Fundy and Fundy approaches (Fig 3). Because of upwelling at the mouth of the bay, Fundy surface-water temperature reaches only 12-15°C in summer, compared to maxima of 17-18°C on the Atlantic coast and over 20°C (26°C in bays) in the Gulf. The Gulf is strongly stratified in summer (Steven, 1974): at 20 m depth the temperature remains 5-8°C below that at the surface (Marine Ecology Laboratory,

1980; Bird et al., 1983), and incursions of cold water may reach upwards to 10 m depth. Atlantic waters are also stratified in summer, temperatures at 20 m remaining below 10°C (Drinkwater and Taylor, 1982). In contrast, Fundy waters are well mixed, with only a 1-3°C decrease in the top 20-40 m in summer (Gran and Braarud, 1935; Bailey, 1954).

Salinity varies little except in estuaries, but can be lower in the Gulf surface layer (26-32 °/••) than in the other coast waters (30-33 °/••) (Bailey, 1954; Loring and Nota, 1973; Taylor, 1975; Lobban and Hanic, 1984).

Whereas phosphate is always measurable and found in similar concentrations in all three coastal environments, the concentration of nitrate is greatest in winter-spring in both Gulf and eastern Atlantic waters, and drops to very low levels in summer (Platt and Irwin, 1970, 1972; Coote and Hiltz, 1975; Chapman and Craigie, 1977; Coote and Yeats, 1970; Chapman and Gagné, 1980; Gagné and Mann, 1981; Probyn and Chapman, 1983). Atlantic waters have a longer-term and more pronounced nitrogen minimum concentration than Gulf waters because the Gulf is relatively enriched by upwelling and by input from the St. Lawrence River (Garret and Loucks, 1976; El-Sabh, 1976; Sutcliffe et al., 1976). There is substantial upwelling along the Fundy approaches. Consequently, these shores and the Bay of Fundy have relatively high and stable nutrient levels, with summer nitrate concentrations being an order of magnitude higher than on other Atlantic and Gulf shores (Gran and Braarud, 1935; Lauzier, 1967).

Herbivory. Any discussion of algal distribution must take account of the importance of herbivores. The sea urchin Strongylocentrotus droebachiensis can denude the sublittoral and lower intertidal regions, leaving behind only crustose corallines and a few non-preferred food species such as Agarum cribrosum, Desmarestia viridis, D. aculeata and Ptilota serrata (Himmelman, 1980; Wharton, 1980; Chapman, 1981; Wharton and Mann, 1981; Johnson, 1984). Sea urchins may be excluded from shallow water by wave action, low salinity or soft sediment. During our survey period, dense concentrations of sea urchins were present inside the Bay of Fundy, along the east coast of Cape Breton Island and below 7-12 m depth in the Gulf (Appendix 1). Sea urchins were uncommon on the southwest Atlantic shore. In the past, sea urchin numbers have varied among and within the coastal environments (Stasko et al., 1977; Stasko et al., 1980; McPeak, 1980; Steele, 1983). In the early 1980's there was a well-documented transition on the Atlantic eastern shore (shore 10) from urchindominated barrens to macroalgal beds (Moore and Miller, 1983; Miller and Colodey, 1983; Schiebling, 1986; Miller, 1985; Novaczek and McLachlan, 1986; Moore et al., 1986). We surveyed shore 10 after this transition.

Smaller herbivores such as gastropods, amphipods, isopods, limpets and chitons are present (Steele, 1983; Logan et al., 1983) and no doubt affect the local distributions of certain algae (Lubchenco, 1980, 1983; Johnson and Mann, 1986), but the relative abundances of such animals in the various coastal environments have not been documented.

Survey Methods

Intertidal and sublittoral surveys were conducted in spring and summer between 1977 and 1985 (Appendix 1). Some of the Gulf survey data (sites 45-80) have previously been presented in part (Bird et al., 1983). These 35 transects were selected, on the basis of absence of widespread sand cover, from a set of 50 transects performed at 1 km intervals. All other study sites were at least 30 km apart (Fig 2a).

Intertidal surveys were undertaken during calm weather and spring tides. Surveys were restricted to unpolluted marine sites with hard substrata and road access. To

obtain data from shores of comparable wave exposure in all environments, most transects sere set on moderately wave-exposed shores. Each site was assigned a wave exposure index (Table IV).

Table IV Wave exposure index applied to survey sites

In	dex	Criteria
1	Sheltered	Not exposed to open ocean in any direction; maximum fetch \leq 10 km.
2	Semi-sheltered	No NW, SW or E exposure to open ocean except over shoals of $<$ 18 m depth and $>$ 5 km width; open to $>$ 10 km fetch in other directions.
3	Semi-exposed	In an enclosed bay or gulf, with a fetch of $>$ 10 km; open to the SW, E or NW over an angle of $<$ 20° or moderated by shoals 2-5 km wide.
4	Exposed	Exposed to the SW or NW over an angle of at least 20°; $18 \text{ m contour} < 2 \text{ km offshore}.$

For intertidal observations, a transect line marked at 1 m intervals was run on a compass bearing from the uppermost marine vegetation down to about 1 m below the level of low tide. Relative heights of the upper, and when possible the lower, limits of distribution of all common macroscopic algal species, major breaks in shore slope, and the low water mark were measured using a Geotec surveyor's level and stadia rod. Estimates were made of the total and relative abundances of macroalgae along the transect line. Species were considered dominant if they provided the greatest percentage cover, either in the canopy or the understory. Where several species were roughly equal in percentage cover, they were recorded as co-dominant. Where total foliose algal cover was less than 20%, no species was considered dominant. The points on the transect at which changes occurred in the relative dominances of species were recorded. Rock-pool inhabitants were noted separately. Small or taxonomically difficult species were collected for identification in the laboratory.

Survey data were converted to heights above chart datum, using as a reference point the predicted height of the low tide at the nearest reference or secondary port in the Canadian Tide and Current Tables and interpolating as required. The study sites rarely coincided with reference ports, and owing to variations caused by atmospheric pressure and wave action, error for intertidal levels is estimated to be about 0.3 m. Widdowson (1965) found that variation in surveyed algal limits was 0.1-0.2 m.

The upper and lower distributional limits of algae were plotted or tabulated relative to tidal levels (Table I). These tidal levels reflect the percentage of time spent exposed to the air (Lewis, 1964; Underwood, 1978) but are not meant to represent significant discontinuities in the intertidal environment.

Sublittoral observations were performed by divers swimming a compass course perpendicular to the shore, starting from the low-water level. Sublittoral transects were continuations of intertidal transects except where the intertidal region was barren or too steep to survey. In most cases the diver swam seaward to 20 m depth, noting the depth ranges of macrophytes, the relative abundances of species and the type of substratum. Depths were measured using a simple pressure gauge and were therefore inaccurate at 0 to 10 m depth, and accurate within about 1 m in deeper water. Our distributional limits for sublittoral species are therefore accurate only to 1-2 m. Separate plant collections were taken within 2-5 m depth intervals, or, in the case of Gulf sites, at randomly numbered points on a transect line. In treacherous

water or on a wide shoal, divers were dropped at intervals from a boat. Depths were converted to depth below chart datum (= CD) using tide tables and merogram (Hanic, 1974).

As many field workers were involved in this survey, variability in assessment of relative abundance was inevitable. Where broad areas were dominated by 100% cover from one or two species, as in the case of stands of intertidal fucoids or sublittoral kelps, there was no problem with the abundance scale. In sublittoral areas not occupied by dense kelp beds, use of a subjective abundance scale was particularly difficult. Distributional patterns in such areas must be viewed in general terms, with little importance given to minor differences.

Nomenclature for subdivisions (shores) of each coastal environment follows Owens and Bowen (1977) except that their southern Fundy and eastern Atlantic shores are further subdivided (Fig 2b). Our species list (Appendix 2) includes species that were rarely, if ever, dominant or were seasonal in occurrence; these will not be considered in detail. In Appendix 2 shores have been grouped in sectors on the basis of general coastal aspect and wave exposure.

Upper and lower limits of common macroalgae were analysed using analysis of variance for unbalanced designs and stepwise linear regression, from the SAS statistical package (SAS Institute Inc., 1987). As it is likely that many relationships are not linear, linear regression gives conservative indications of the correlations of vertical limits with the tested variables.

Results

Geographical distributions of algae. We identified 189 algal species; 77 red, 68 brown and 44 green. These macroalgae represent roughly half of the known algal taxa of eastern Canada (South, 1984). To avoid misrepresentation of distributions, the species recorded at various shore levels in each sector of the coastline have been tabulated (Appendix 2) together with data (in brackets) from sources other than the present survey. The macroalgal flora of the Atlantic coastal environment, with 177 species, was found to be more diverse than that of the Gulf (158 species) or the Bay of Fundy (153 species). For the eastern Atlantic coast alone (shores 10-15, exclusive of the Fundy approaches), 168 species were recorded. We found only 118 species on shores 1-5 of the inner Bay of Fundy.

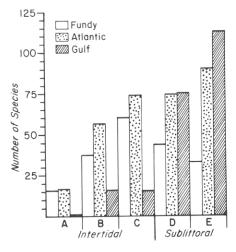
The majority of species were found in all three coastal environments. The warmtemperate species Chondria baileyana and Chaetomorpha aerea were found only in the southern Gulf, as were a number of species having a more restricted southern distribution but with their northern limits in or just north of the Gulf (Striaria attenuata, Ascocyclus distromaticus, Delamarea attenuata, species of Giffordia and Vaucheria, and Audouinella dasyae). Others of southern or more widespread distribution were present on the Gulf and Atlantic shores but not in the cooler (in summer) Bay of Fundy (Derbesia vaucheriae formis, Stylonema alsidii, species of Callithamnion, Polysiphonia elongata and P. subtilissima). Some species having southerly distributions (Ceramium deslongchampii, Gloiosiphonia capillaris, Spongomorpha spinescens, Monostroma pulchrum, Porphyra miniata, Porphyra leucosticta, Polysiphonia lanosa, Phymatolithon lenormandii) were not found in the southern Gulf but have been recorded from the middle of the Gulf, on the Magdalen Islands or Gaspé Peninsula (Cardinal, 1968). Scinaia forcellata, another southern species, has been recorded only in the Gulf and Fundy approaches, Furcellaria lumbricalis presently occurs only in the Gulf, on Atlantic shore 12 and on the northeast tip of shore 10, but its distributional limits are expanding in western Prince Edward Island (McLachlan, pers. obs.). Fucus serratus had a distribution similar to that of F. lumbricalis, but it has

also been found in abundance on the Fundy approaches (Edelstein et al., 1972) and very recently at one site in Lunenburg County (McLachlan, pers. obs.). Alaria esulenta and Ascophyllum nodosum were absent from our Gulf sites, although A. nodosum is known from some localities in this coastal environment (Lobban and Hanic, 1984). The foliose phase of Mastocarpus stellatus was absent from the Gulf although the crustose phase, Petrocelis cruenta, has been recorded (Bird et al., 1983). Foliose plants of this species were present occasionally on the Atlantic coast and often dominant in the Bay of Fundy (Fig 6).

A number of cold-temperate to Arctic species (Ralfsia fungiformis, Elachista lubrica, Enteromorpha groenlandica, Audouinella purpurea) were absent from the southern Gulf but present on the colder Atlantic or Fundy shores. However, a few cold-temperate to Arctic species found on Atlantic or Gulf shores (Dilsea integra, Halopteris scoparia, Stictyosiphon griffithsianus, S. tortilis) were not found in the Bay of Fundy. Four species (Melanosiphon intestinalis, Scytosiphon dotyi, Blidingia chadefaudii and Spongomorpha sonderi) were found only in the Bay of Fundy and/or Fundy approaches.

Vertical distributions of algae: general intertidal patterns. Despite considerable variation in both the vertical limits of species and species compositions of each shore (Appendix 3) some trends could be discerned in distributional patterns. There was an increase in species diversity moving from the head to the mouth of Fundy and from eastern to western Atlantic sites (Fig 4). The intertidal regions of all Gulf sites and Atlantic sites 42-44 (Fig 2a, Appendix 1) were greatly or completely denuded by ice scour. The sublittoral region was relatively impoverished in the Bay of Fundy and relatively diverse in the Gulf (Fig 4).

On those sites having significant intertidal vegetation, three zones were generally recognisable, conforming to the typical zonation pattern for North Atlantic shores (Fig 1). The littoral fringe was dominated, in season, by various species, including Enteromorpha, Porphyra, Ulothrix, Prasiola, Urospora, cyanophytes and lichens. The midlittoral zone was dominated by 80-100% cover of one or more fucoids. Kelp species, the indicators of the sublittoral fringe, were not always present intertidally.



Numbers of species at different intertidal and sublittoral levels in three Fig 4 coastal environments of the Maritime Provinces. A = above HHWN; B = HHWN to LLWN; C = 0 - 2 m depth; D = 2-20 m depth.

Table V The average upper and lower limits (relative to HHWS, where HHWS = 100) of common species of Fucus and Ascophyllum found intertidally along the Bay of Fundy and Atlantic coasts.

		Fun	dy		Atlantic					
				Fundy ap	proaches	Eastern /				
Species		upper	lower	upper	lower	upper	lower			
F. spiralis	avg	89	84	72	58	83	76			
	SE (n)	3.4 (5)	3.5 (5)	2.9 (7)	4.77 (7)	3.5 (9)	4.4 (9)			
F. vesiculosus	avg	78	26	69	20	76	25			
	SE (n)	2.0 (20)	2.0 (20)	2.8 (9)	4.6 (9)	3.9 (11)	4.7 (11)			
A. nodosum	avg	76	23	68	12	76	25			
	SE (n)	3.0 (20)	1.7 (20)	2.7 (9)	2.5 (9)	3.9 (11)	4.6 (11)			
F. evanescens	avg	33	19	17	5*	28	5*			
	SE (n)	3.0 (14)	1.6 (14)	5.9 (7)	1.5 (5)	4.8 (9)	6.3 (8)			
F. serratus	avg SE (n)	nd	nd	32 22 (2)	5 5 (2)	16 (1)	< CD			

^{*} only for sites where limit was > CD. SE = standard error; nd = no data; < CD = below chart datum.

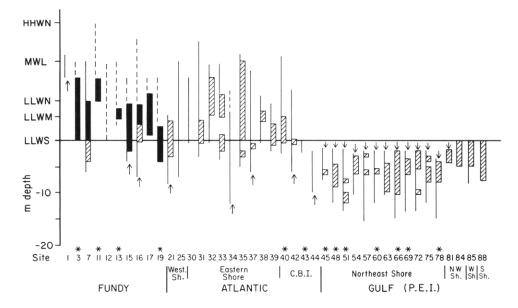


Fig 5 Limits of Chondrus and Mastocarpus at selected sites. Arrows = junctures with soft substrata; * = lower limit bordered by sea urchins. Thick bars denote dominance; thin lines, presence. Chondrus = diagonal bar and solid line; Mastocarpus + Chondrus = solid bar and dashed line.

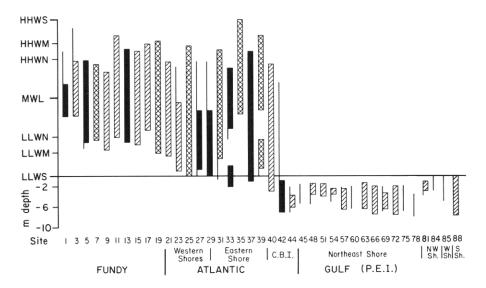


Fig 6 Limits of the fucoid belt. Thick bars denote dominance; thin lines, presence. Patterns indicate wave exposure index of site (Table IV): sheltered or semi-sheltered = solid; semi-exposed = diagonal; exposed = cross-hatched.

Depending upon conditions, a red algal turf, fucoids or ephemeral species could dominate or co-dominate the lowest intertidal region.

The fucoid species consistently occupied particular shore levels relative one to another (Table V). Fucus spiralis, and F. distichus, when present, occupied the highest level, alone or together with F. vesiculosus or Ascophyllum nodosum or both. Fucus vesiculosus and A. nodosum dominated the middle of the intertidal region and often graded, at their lower limits, into more open stands of F. evanescens or F. serratus. Because vegetative F. evanescens is difficult to distinguish from evesiculate F. vesiculosus, upper limits of this species were likely underestimated. All fucoid species, except the relatively rare F. distichus and F. serratus, occurred in all conditions of wave exposure. There was a tendency, however, for F. vesiculosus to be the most abundant species at the most wave-exposed sites (site 35, Appendix 3), while A. nodosum could be relatively abundant on more sheltered sites (sites 26, 30, Appendix 3). Fucoid holdfasts occupied little primary space. Chondrus crispus or Mastocarpus stellatus or both occupied the understory, reaching above MWL in some localities (Fig 5). Holdfasts of these understory species, the encrusting algae Hildenbrandia rubra and H. Crouanii and marine lichens (species of Verrucaria) occupied increasing amounts of primary space moving seaward.

Sites in the Bay of Fundy and on shore 8 of the Fundy approaches varied from most Altantic sites in that fucoids did not exclusively dominate the lower reaches of the midlittoral zone (Fig 6). Except where the low intertidal was covered by sediment (sites 1, 4) or denuded by sea urchins (sites 10, 13), the gap between that area totally dominated by fucoids and the upper limit of kelp was occupied by a dense turf of *Chondrus crispus* or *Mastocarpus stellatus* or both (sites 2-21, Appendix 3).

Upper and lower limits of distribution in the intertidal region: variation within and among coastal environments. Progressing from the Fundy to Atlantic to Gulf environments, the upper limits (in m relative to CD) of major belts of vegetation dominated by fucoids, turfing red algae (Chondrus and Mastocarpus) and kelp shifted downwards (Table VI). This was predictable because the reduction in tidal amplitude (from 15 m to 2 m) from the Bay of Fundy to the outer coast reduces the possible vertical extent of all marine organisms, while ice scouring in the Gulf limits the upward extent of macrophytes.

The relationships between various variables and both upper and lower limits of distribution of common macrophytes were tested by linear regression analysis. Regression analyses were performed firstly on all data (Table VIIa) and then on the subset of sites having intertidal algae (Table VIIb). The upper and lower limits of fucoids, and the upper limits of red turf species and of kelps were strongly related to tidal range and ice scour. On ice-scoured sites the larger macroalgae were confined to the sublittoral region, and the intertidal region was either bare or bore dense populations of small ephemeral algae and occasional juvenile fucoids (site 42, Appendix 3).

The fucoid zone contracted where there were unstable substrata in either the upper intertidal or sublittoral regions (Table VII). The lower limits of fucoids were significantly correlated with the upper limits of red turf algae. Red turf species tended to have higher upper limits on sites having sublittoral sand borders, these being predominantly Atlantic sites. Upper limits of intertidal kelp were positively correlated with wave exposure and intertidal slope. On sites that were sheltered, semi-sheltered or gently sloping, kelp could be absent from the intertidal region (sites 30, 34a, 37, 40, Appendix 3).

Although a difference in absolute height of algae on the shore is an obvious feature of changing tidal range, variation in the limits relative to tidal levels (expressed as % HHWS) is not an obvious consequence. We found that proceeding from the Bay of

Table VI Limits (m from CD) of common macroalgae in each coastal environment.*

	Fuc	oids	Red	turf	Ke	elp	Agarum	Phyllophora spp
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Upper
FUNDY								
mean	7.2	2.0	3.8	-0.9	1.3	-3.1	-0.6	4.4
SE	0.5	0.3	0.4	1.0	0.1	0.7	1.3	2.8
n	20	20	19	12	16	10	11	
ATLANTIC SHORES								
8-9								
mean	3.6	0.3	1.5	-3.3	0.4	-6.0		
SE	0.2	0.1	0.2	3.7	0.1			
n	9	7	9	2	8	1		
10-13								
mean	1.7	-1.3	1.0	-3.6	0.1	-9.3	-7.3	-4.3
SE	0.1	0.5	0.1	1.1	0.2	1.1	0.9	2.2 7
n	11	10	11	10	12	11	9	7
14-15								
mean	-0.3	-6.3	-0.5	-6.7	-2.0	-7.7		
SE	0.9	0.3	8.0	1.8	0.0	1.2		
n	3	3	3	3	3	3		
GULF								
mean	-1.9	-5.9	-1.8	-10.8	-5.2	-14.8	-14.7	-7.0
SE	0.2	0.2	0.2	0.5	0.3	0.3	0.8	0.5
n	41	41	45	45	45	44	7	40

^{*} Abbreviations as in Table V.

Table VII Stepwise linear regression modelling of vertical limits (m from CD) of common macroalgae.

Species (variables tested)	Type of Limit (n)		Significant Variable	Effect	Partial R ²	Model R²	Prob. > F
a) All sites							
Fucoids	upper	(84)	t.	+ve	0.91	0.91	0.0001
(tigwh)		, ,	i	-ve	0.05	0.95	0.001
, ,			h	-ve	0.001	0.95	0.15
Fucoids	lower	(76)	i `	-ve	0.81	0.81	0.0001
(tigwlubRK)		, ,	t	+ve	0.06	0.87	0.0001
,			b	-ve	0.01	0.88	0.01
			R	+ve	0.01	0.89	0.02
Red turf	upper	(87)	t	+ve	0.74	0.74	0.0001
(tigwlub)	• • •	, ,	i	-ve	0.07	0.81	0.0001
,			b	+ve	0.01	0.82	0.05
Kelp	upper	(84)	i	-ve	0.71	0.71	0.0001
(tigwlub)			t	+ve	0.07	0.72	0.11
o) Sites with intertidal algae							
Fucoids	upper	(41)	t	+ve	0.95	0.95	0.0001
(tigwhs)		(/	h	-ve	0.004	0.96	0.05
Fucoids	lower	(29)	t	+ve	0.70	0.70	0.0001
(tigwlsR)		, -/	R	+ve	0.10	0.80	0.001
Red turf	upper	(40)	t	+ve	0.63	0.63	0.0001
(tigwlubs)		, ,	u	+ve	0.03	0.66	0.08
			g	+ve	0.02	0.68	0.11
Kelp	upper	(36)	ť	+ve	0.39	0.39	0.0001
(tigwlubs)	• •	, ,	i	-ve	0.16	0.55	0.001
· , -			S	+ve	0.09	0.64	0.01
			w	+ve	0.07	0.71	0.01
			1	+ve	0.02	0.73	0.13

Abbreviations: Fucoids = Fucus and Ascophyllum; Red turf = Chondrus and Mastocarpus; Kelp = Laminaria, Alaria, and Saccorhiza; t = Tide range of spring tides in m; i = Ice scour; u = sea urchins; g = geology; w = wave exposure (Table II); h/I = presence of sand in upper or lower intertidal zone; b = presence of sublittoral sand border; s = slope (m m⁻¹); R = Upper limit of red turf spp; K = upper limit of kelp spp.

The variables tested in each case are indicated in brackets.

Fundy towards the Atlantic coast, the lower limit of the composite fucoid belt and the upper limit of kelps shifted downward relative to tidal levels (Figs 6-7).

Within the Bay of Fundy, on both north and south shores and regardless of wave exposure or geology, the lower limit of the fucoid belt was generally above LLWM and occasionally was above LLWN (Fig 6; sites 2-19, Appendix 3). Along the Fundy approaches (Fig 6; sites 21-26, Appendix 3) the fucoid belt progressively dropped to as low as LLWS. On the east Atlantic shore (Fig 6; sites 30-44, Appendix 3), fucoids commonly extended into the sublittoral region where they formed mixed stands with laminarians, Chondrus and various red algae to 1-2 m below chart datum (CD). In a statistical comparison of intertidal limits in the Bay of Fundy, Fundy approaches and eastern Atlantic shores, differences among the environments in both upper and lower limits of the fucoid belt (relative to tidal levels, see Table V) were significant (ANOVA, p < 0.05), as were the differences in the upper limits of Fucus spiralis and F. vesiculosus and the lower limits of F. spiralis, Ascophyllum nodosum, and F. evanescens. Differences in the upper limits of kelps were non-significant (p = 0.06). On both Fundy and Atlantic shores, kelp species occurred as high as LLWN (Fig 7), but only in the Bay of Fundy formed dominant canopies to this level.

Regression analyses showed that the upper limits of all fucoid species (relative to tidal levels) were significantly and positively correlated with intertidal slope, and the upper limit of the fucoid belt as a whole was also correlated with wave exposure (Table VIII); in other words, these species occurred at higher levels on steep or wave-exposed shores. The upper limit of the fucoid belt lay above HHWN under semi-exposed and exposed conditions and reached HHWS only at Prospect (site 35, Appendix 3), which was both steep and wave-exposed. The tendency for the upper limit of the fucoid belt to be higher on hard bedrock than on sandstone or shale was not significant (p = 0.06).

Lower limits of Fucus spiralis were closely correlated with the upper limits of Ascophyllum nodosum; for the other species, their lower limits were closely correlated with the upper limits of red turf algae (Table VIII). A dramatic rise in the lower limit of fucoids to MWL was evident at Prospect (site 35, Appendix 3). In cases of moderate wave exposure on a steep lower shore (sites 32, 33, 36) C. crispus dominated the steeper slopes but F. evanescens was co-dominant in the more gently sloping areas. Lower limits of A. nodosum were lower in wave-sheltered conditions, while F. evanescens extended lower on more gradual slopes (Table VIII) F. vesiculosus extended into the sublittoral region at a wave-sheltered site but not at a nearby, semi-exposed site (sites 37-38, Appendix 3).

The heights, relative to tidal levels, of the upper limits of the red-turf species (Chondrus and Mastocarpus) did not vary significantly between Fundy and Atlantic shores (Fig 5) and were not significantly correlated with any of the variables tested (Table IX); however, the upper limits of dominant (or co-dominant) turfs of these algae were positively correlated with wave exposure and with the lower limits of fucoid algae (Table IX). For kelp species (Fig 7), intertidal upper limits were correlated with slope and geology, with tidal range being not significant (Table IX). Kelps extended farther up on steep shores and on hard substrata; the upper limits were not correlated with lower limits of dominant red turf. The upper limits of dominant stands of intertidal kelp were related to intertidal slope.

A few other species exhibited consistent differences in vertical distribution in the different coastal environments. Species usually restricted to the sublittoral region (Agarum cribrosum, Callophyllis cristata, Phycodrys rubens and species of Phyllophora) were found in the intertidal region in the Bay of Fundy and, to varying extents, on shore 9 of the Fundy approaches (Table VI; Appendix 2). All of these species were confined below 3 or 5 m depth and became common below 8 to 10 m depth on the Atlantic eastern shore and in the Gulf.

Table VIII Stepwise linear regression modelling of intertidal limits, relative to HHWS, of common fucoid species.*

Species (variables tested)	Type of Limit (n)		Significant Variable	Effect	Partial R ²	Model R²	Prob. > F
Fucoids	upper	(41)	w	+ve	0.14	0.14	0.01
(tigwhs)			S	+ve	0.09	0.23	0.04
			g	+ve	0.07	0.30	0.06
Fucoids	lower	(16)	g D	+ve	0.52	0.52	0.002
(tigwlsDP)			S	+ve	0.14	0.66	0.04
			Р	-ve	0.06	0.72	0.14
F. spiralis	upper	(21)	W	+ve	0.26	0.26	0.02
(tigwhs)	• • • • • • •		S	+ve	0.26	0.52	0.006
F. spiralis	lower	(21)	Α	+ve	0.75	0.75	0.0001
(tigwhsA)			W	+ve	0.05	0.79	0.06
A. nodosum (tigwhs)	upper	(40)	S	+ve	0.09	0.09	0.06
A. nodosum	lower	(40)	w	+ve	0.11	0.11	0.04
(tigwls)		` ,	S	+ve	0.05	0.16	0.13
A. nodosum	lower	(33)	D	+ve	0.55	0.55	0.0001
(tigwlsD)		` ,	t	-ve	0.04	0.59	0.09
F. vesiculosus	upper	(41)	s	+ve	0.19	0.19	0.005
(tigwhs)		. ,	W	+ve	0.09	0.28	0.03
F. vesiculosus (tigwlsD)	lower	(39)	D	+ve	0.29	0.29	0.002
F. evanescens	upper	(30)	S	+ve	0.16	0.16	0.03
(tigwls)	• • •	. ,	w	+ve	0.15	0.31	0.02
F. evanescens (tigwls)	lower	(21)	S	+ve	0.32	0.32	0.007
F. evanescens	lower	(15)	D	+ve	0.64	0.64	0.0004
(tigwlsD)		, ,	S	+ve	0.07	0.71	0.11

^{*} Abbreviations: A = upper limit of A. nodosum; D = upper limit of dominant Chondrus and Mastocarpus; P = upper limit of dominant Laminaria, Alaria, and Sacchoriza.

All other abbreviations given in Table VII.

Table IX Stepwise linear regression modelling of intertidal limits (relative to HHWS) of common macroalgae.*

Species (variables tested)	Type Limit (Significant Variable	Effect	Partial R ²	Model R²	Prob. > F
Red turf	upper	(39)	X	+ve	0.09	0.09	0.07
(tigwlsX)	apps.	()	t	-ve	0.06	0.15	0.12
Dominant Red turf	upper	(34)	W	+ve	0.16	0.16	0.02
(tigwls)		, /	S	+ve	0.07	0.22	0.11
Dominant Red turf	upper	(29)	F	+ve	0.38	0.38	0.0003
(tigwlsF)		, ,	t	-ve	0.08	0.46	0.06
Kelp	upper	(34)	S	+ve	0.12	0.12	0.04
(tigws)		, ,	W	+ve	0.07	0.19	0.11
(3.83.3)			t	-ve	0.09	0.28	0.06
			g	+ve	0.09	0.37	0.05
Kelp (tigwsM)	upper	(19)	M	+ve	0.15	0.15	0.10
Dominant Kelp	upper	(14)	S	+ve	0.56	0.56	0.002
(tigwsM)			g	+ve	0.10	0.66	0.10

^{*} Abbreviations: F = lower limit of Fucoids; M = lower limit of dominant Red turf; X = lower limit of dominant fucoids. All other abbreviations given in Tables VII & VIII.

Many common species, including Cystoclonium purpureum, Ectocarpus siliculosus, Petalonia fascia, Ulva lactuca, Ulvaria oxysperma, Palmaria palmata, Devaleraea ramentacea, and Dumontia contorta were found in the intertidal region at all wave exposures but extended farther up the shore in the more wave-exposed sites (Appendix 2). Alaria esculenta dominated the sublittoral fringe only in semi-exposed and exposed conditions, with the exception of Mascabin Point (site 13), where there is a swift tidal current. A. esculenta was often present but not dominant on semi-sheltered shores and absent from sheltered shores.

Patterns of distribution in the sublittoral region. Sublittoral vegetation was extremely patchy and variable (Appendix 3). At all sites and depths, hard substrata were occupied by encrusting coralline algae. The canopy of wave-exposed, Atlantic and Fundy sites was often dominated by 90-100% cover by species of Laminaria and Desmarestia.

Where the kelp canopy was dense, the understory often consisted of scattered Chondrus crispus and Corallina officinalis, whereas under more open canopies species of Polysiphonia and Rhodomela confervoides were co-dominant. On Atlantic shores Dumontia contorta, Devaleraea ramentacea and Cystoclonium purpureum were common in the understory down to 6 m depth; Phycodrys rubens, Callophyllis cristata, Ptilota serrata and, occasionally, species of Phyllophora, Odonthalia dentata and Neodilsea integra provided the understory in deeper water (Appendix 3).

In sheltered sites where sea urchin herbivory had recently ceased or been drastically reduced (sites 34a, 37, Appendix 3), species of *Laminaria* were either rare or did not form dense stands, and a variety of smaller red and brown algae were codominant. Laminarians were also rare where the bottom was unstable (site 44, Appendix 3).

When many sea urchins were present in the sublittoral region (Fig 7) Laminaria was usually rare, particularly at depths greater than 2-4 m. The vegetation could be reduced to crustose corallines, or consist mainly of Desmarestia, Agarum and scattered individuals of Phyllophora, Chondrus and Polysiphonia (sites, 3, 11, 40-42, Appendix 3).

The upper and lower boundaries of Laminaria varied both among and within the coastal environments (Fig 7, Table VI). Where kelp was confined to the sublittoral region, the upper limit was correlated with ice scour (Table X). A friable substratum such as occurs in the Gulf sites may exacerbate the effect of ice scour. However, kelp occurred intertidally on sandstone and shale in the Bay of Fundy (sites 7, 17), suggesting that a friable substrate does not by itself prevent the occurrence of macroalgae in wave-swept environments.

On the ice-scoured sites of Cape Breton Island (sites 42, 44, Appendix 3), as in the Gulf (sites 65-69, Appendix 3), fucoids, Chondrus crispus, or small ephemeral brown algae replaced Laminaria in shallow water. These gave way, at 4-8 m depth, to C. crispus or Desmarestia, Rhodemela confervoides and species of Polysiphonia and Phyllophora. On shore 17 of the Gulf (sites 65-83, Appendix 3) and also at some north-shore sites (McLachlan et al., 1987), a shallow-water belt of fucoids and Chondrus crispus often gave way to Furcellaria lumbricalis to about 10 m and then to species of Phyllophora to about 20 m. On these and other Gulf shores, mussels could dominate extensive areas (site 83, Appendix 3). Laminaria was rare down to 3-6 m. Individual kelp plants were small (< 1 m long) compared to plants of Atlantic and Fundy shores, and cover by the canopy rarely exceeded 60%.

Lower limits of species of *Laminaria* were correlated with tidal range, sublittoral sand, sea urchin activity and ice scour (Table X). The lower limits of *Laminaria*, and of foliose algae in general, were much shallower in the macrotidal Bay of Fundy than on the Atlantic coast and in the Gulf (Tables VI, XI). The lower limit of significant foliose

 Table X
 Stepwise linear regression modelling of sublittorally occurring limits of common macroalgae.*

Species (variables tested)	Type Limit		Significant Variable	Effect	Partial R ²	Model R²	Prob. > F
Fucoids	lower	(51)	i	-ve	0.49	0.49	0.0001
(tigwbuR)			b	-ve	0.03	0.52	0.08
(10)			R	+ve	0.04	0.57	0.03
			g	+ve	0.02	0.59	0.13
			ť	-ve	0.02	0.61	0.15
Red Turf	lower	(69)	i	-ve	0.50	0.50	0.0001
(tigwbulK)		, ,	K	+ve	0.02	0.52	0.06
Kelp	upper	(50)	i	-ve	0.10	0.10	0.03
(tigwbu)		` '	u	+ve	0.05	0.15	0.11
Laminaria	lower	(69)	t	+ve	0.63	0.63	0.0001
(tigwbu)		(/	b	+ve	0.09	0.72	0.0001
(8)			u	+ve	0.02	0.75	0.02
			i	-ve	0.02	0.77	0.02
			W	-ve	0.01	0.78	0.12

^{*} Abbreviations given in Table VII.

Table XI Vertical position and nature of the lower limits of significant foliose algal vegetation in each coastal environment.*

	Total		No. of Site	es with Algal		Nature & Depth of Lower Limits in 0-20 m Depth Range					
	Sites		Limits in Each				o. of each ty		Depth (m)		
	(n)	Int	0-20 m	> 20 m	nd	Sand	Urch	Rock	SE		
Fundy shores											
1-7	21	4	11	0	6	6	5	4	7	1.2	
Atlantic shores											
8-9	9	1	1	1	6	1	0	1	10		
10-13	13	0	11	1	1	11	0	0	11	1.0	
14-15	3	0	3	0	Ö	2	1	0	8	1.2	
Gulf shores											
17-20	39	0	35	4	0	6	15	14	16	0.4	
21-22	5	0	3	2	0	3	0	0	11	0.4	

^{*} Abbreviations: Int = intertidal, Urch = aggregation of sea urchins, Sand = sand or cobble, Rock = bedrock or boulders, nd = no data.

vegetation could occur on shallow, bare rock in the Bay of Fundy and Fundy approaches. Limits on the outer Atlantic coast and in the Gulf only occurred on rock at depths greater than 15 m; otherwise they were defined by unstable bottom or aggregations of sea urchins (Table XI). The correlation between maximum depth of *Laminaria* and ice scour results from the occurrence of deep rock flats at many of the Gulf sites.

Ice scour and the upper limits of red turf were significantly correlated with lower fucoid limits in the sublittoral region (Table X); fucoids extended deeper on disturbed sites, and the lower limits of *Chondrus* were similarly found lower down at ice-scoured sites (Table X). The relationship between the lower limits of red turf and the upper limits of kelp was insignificant.

Where suitable hard substratum was available on Fundy and Atlantic shores, there was a deep-water zone occupied by $Agarum\ cribrosum$ and various red algae which lay either below or overlapping the lower portion of the Laminaria-Desmarestia belt. The upper limit of Agarum was intertidal or to 8 m depth in the Bay of Fundy and at 2-12 m on the Atlantic coast (Fig 7, Table VI). In the Gulf A. Cribrosum occurred at depths > 12 m and was sometimes absent from depths < 20 m.

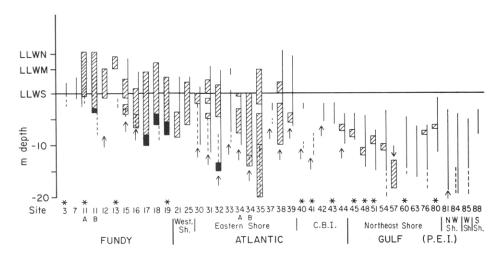
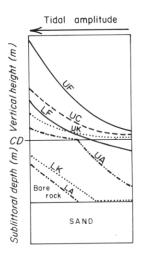


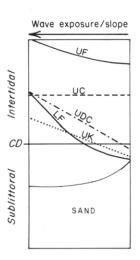
Fig 7 Limits of kelp species in all sublittoral surveys of Fundy and Atlantic coasts and at selected Gulf sites. Thick bars indicate dominance; thin lines, presence. Alaria or Laminaria = diagonal bar and solid line; Agarum = solid bar and dashed line. Other symbols as in Fig 5.

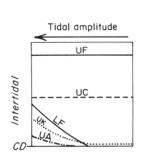
Discussion

The intertidal regions (between HHWS and LLWS) of stable, rocky shores of the north-eastern Atlantic Ocean generally exhibit three vegetational zones: the littoral fringe, the midlittoral zone, and the sublittoral fringe (Stephenson and Stephenson, 1954; Wilce, 1959; Bolton, 1981). Data from our survey support this generalization, but it is obvious that on these shores, differences in tidal amplitude (Fig 8a-b), slope and wave exposure (Fig 8c), ice scour (Fig 8d) and, to a lesser extent, geology affect not only the vertical distance occupied by the various zones but also their positions relative to tidal levels and their species compositions.

Physical factors may limit the vertical extent of intertidal plants by exceeding limits of tolerance of individual species or by affecting competitive balances among species







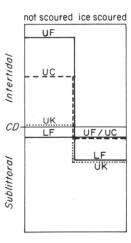


Fig 8 Schematic representations of general patterns of vertical distribution of macroalgae on rocky shores of the Maritime Provinces, Canada. a-b) Changes in heights of algal limits with tidal amplitude; a) absolute heights [m]; b) relative heights (% HHWS). c) Changes in relative heights with slope and wave exposure. d) Changes in relative heights with presence and absence of ice scour. UF/LF = upper/lower limit of fucoids; UC = upper limit of Chondrus crispus and Mastocarpus stellatus; UDC = upper limit of dominant red turfs; UK/LK = upper/lower limits of kelp species, except for Agarum cribrosum; UA/LA = upper/lower limits of A. cribrosum.

(Widdowson, 1965; Kussakin, 1977; Southward and Southward, 1978; Lubchenco 1980; Druehl and Green, 1982). When physical factors are not limiting, the lower and upper boundaries of intertidal and sublittoral algae are largely determined by competition and herbivory (Menge, 1976; Lubchenco and Menge, 1978; Lubchenco, 1980; Underwood and Denley, 1984).

We have found that, as is the case on European shores (Lewis, 1964), upper distributional limits of many intertidal species in eastern Canada are higher on relatively steep, wave-exposed shores (Fig 8c). The relatively depressed upper limits of fucoids along the Fundy approaches (Table V) therefore appear to be related to the fact that all the sites surveyed on these shores were either semi-sheltered or gently sloping (Appendix 1). These upper limits may therefore be influenced by desiccation but experimental tests are needed to determine the effect of herbivory. Wave exposure also influences species composition. Moving from sheltered to steep and/or wave-exposed sites, species of Fucus, Mastocarpus and Alaria replaced Ascophyllum, Chondrus and Laminaria, respectively.

The extension of sublittoral algae and certain invertebrates (Bousfield and Laubitz. 1972) into the intertidal region of the Bay of Fundy is readily explained in terms of decreased illuminance and desiccation in this environment. A similar upward extension of sublittoral species has been documented in foggy and wave-swept environments such as the Faeroes (Price and Farnham, 1982) and the northern shores of

Newfoundland and Labrador (Wilce, 1959).

For fucoid species, the availability of stable and resistant substrata in the upper intertidal region affects upper limits. Similarly, kelp species extend higher in the intertidal on resistant bedrock than on soft rock. The upper limits of all perennial macroalgae in the Gulf and on some Atlantic shores are depressed owing to winter ice scour. On such disturbed substrata ephemerals dominate; perennial fucoids occur sublittorally here, as they do on ice-scoured shores of Newfoundland and Labrador (Wilce, 1959). Where ice scour is relatively minor and rocky substrata are available, the upper limit of fucoids in the Gulf is still depressed (Lobban and Hanic, 1984), probably because of desiccation stress. This coastal environment is characterized by relatively high numbers of sunshine hours and infrequent fog, together with mixed, semi-diurnal tides that sometimes leave the intertidal region exposed for extended periods during day time in summer.

Little is known of competitive interactions among algal species. However, the vertical arrangement of intertidal fucoid species in eastern Canada is similar to that in Britain (Lewis, 1964), where the pattern is largely a result of interspecific competition (Burrows and Lodge, 1951). Competition from Chondrus crispus can prevent fucoids from occupying otherwise favorable areas of the low intertidal (Lubchenco, 1980).

The lower limit of fucoids bordered on dominant stands of Chondrus crispus and Mastocarpus stellatus and these, in turn, frequently bordered on dominant stands of kelp. However, the shore level of the boundaries between fucoids, red turf algae and kelp varied among the coastal environments. Our statistical analyses indicate that, depending upon the species involved, the variations were related to tidal range, intertidal slope, wave exposure and disturbance (Fig 8). These physical factors may, therefore, be important to the outcome of competitive interactions.

In the Bay of Fundy Chondrus, Mastocarpus and patches of other small algae, either alone or with kelps, usually excluded fucoids below LLWM. In contrast, on the Atlantic coast, particularly at wave-sheltered sites, fucoids usually extended down below LLWS. Only at one steep and wave-exposed site (site 35) were fucoids entirely

excluded from the lower intertidal region of an Atlantic shore.

The features that set the Bay of Fundy apart from the Atlantic and Gulf environments are the extreme tidal range and relatively steep intertidal slopes, factors that are both significantly and positively correlated with the lower limits of the fucoid belt. There are several possible explanations for this correlation.

Daily quantum dose declines steadily from the top to the bottom of any shore and this reduction is greatest where tides are highest (Dring, 1987). In the British Isles, lack of light has been invoked to explain the limited downward extension of fucoids in turbid and macrotidal waters (Gail, 1918; Burrows and Lodge, 1951; Dring, 1987). Lack of light may similarly be the factor restricting the distribution of fucoids in the Bay of Fundy, as the frequent occurrence of spring low tides in the morning and evening, the turbidity of the water, and the large tidal range all limit the light reaching the lower intertidal region. In contrast to fucoids, *Chondrus crispus* has a lower light saturation point (Mathieson and Burns, 1971; Burns and Mathieson, 1972; Neimeck and Mathieson, 1978; Bird et al., 1979). An ability to grow in limited light, together with the fact that the timing of low tides and frequency of fog decrease desiccation, may explain *Chondrus* as a competitive dominant this environment.

Where the tidal range is great, the low intertidal region is subject to long periods of intense tidal currents as well as surface-wave activity (Thomas et al., 1983). The physical stresses of currents and waves are most pronounced on steeply sloping shores. Such mechanical stress may make the low intertidal zone of steep Fundy shores less suitable for larger macrophytes than for tenacious turf forms, and may particularly favor Mastocarpus stellatus. Foliose M. stellatus is abundant in the Bay of Fundy, occasionally present on steep or wave-exposed shores of the Atlantic coast and absent from the Gulf. Like Chondrus crispus, M. stellatus is intolerant of desiccation (Marshall et al., 1949) but it is more prevalent than C. crispus on wave-exposed or current-stressed coasts (Marshall et al., 1949; Mathieson et al., 1977). The cool summer temperatures of the Bay of Fundy may also favor M. stellatus over C. crispus (Burns and Mathieson, 1972; Munda, 1977; Guiry and West, 1983).

When kelps are rare or absent because of disturbance from ice or sand scour, fucoids can form dominant stands to 6-8 m depth. Moderate disturbance can increase diversity (Dayton, 1971) and may facilitate the recruitment of fucoids among otherwise dominant *Chondrus crispus* (MacFarlane, 1952), at least where light is not limiting. The lower limit of fucoids may then be set by dense aggregations of mussels or sea urchins, as is common in Northumberland Strait (Moseley and MacFarlane, 1969), or by competition from species that grow better at low light levels. *Rhodomela confervoides* and species of *Polysiphonia* seem able to out-compete fucoids in the sublittoral region of sheltered Atlantic shores. Dense stands of *Furcellaria lumbricalis* or *Chondrus crispus* often confine the sublittoral fucoid belt in the Gulf. The lower limit of *C. crispus* in turn tends to be deeper at these disturbed sites, perhaps because of the lack of effective competition from kelps. Field experiments are needed to clarify the roles of competition, herbivory and disturbance in this environment.

Three belts of vegetation have been recognized in the sublittoral region of rocky Atlantic shores (Edelstein et al., 1969): a Laminaria-Desmarestia belt to about 15 m, an Agarum-Ptilota belt below 10 m, and, below 30 m, a Phyllophora-Polysiphonia belt. Other workers have described other dominant assemblages, mostly in shallow water on unstable substrata (Moseley and MacFarlane, 1969; Mann, 1972; McPeak, 1980). Our data confirm the existence of a Laminaria-Desmarestia belt along most of the rocky Atlantic and Fundy coasts, but variations occur that are related to the availability of firm substrata and the activity of herbivorous sea urchins. Dominance by sea urchins or by kelp can be viewed as opposite ends of the dynamic continuum that is the "Laminaria-Desmarestia zone" (Schiel and Foster, 1986). At some Atlantic sites, sea urchins had recently died and Desmarestia was dominant. Such sites were probably in transition, and will in time become dominated by Laminaria (Johnson, 1984). In wave-sheltered sites formerly occupied by sea urchins, establishment of

Laminaria and Desmarestia was more erratic, possibly because these sites lack a wave-battered sublittoral fringe which can provide a refuge from sea urchin herbivory and therefore a persistent spore source. The scarcity of Odonthalia dentata and species of Phyllophora on the eastern Atlantic shore where they were once common (Edelstein et al., 1969; Novaczek and McLachlan, 1986) may be due to lack of such deep-water species in shallow-water refugia.

In the Gulf the sublittoral region, with its frequent patches of sand and cobble, was particularly variable. Different vegetation belts replaced the *Laminaria-Desmarestia* zone at different depths and on different substrata. Both in the Gulf and along northeastern Cape Breton Island, the rarity and small size of *Laminaria* could result from the friable substratum, ice scour, sea urchin herbivory and, perhaps, competition from red-algal turfs. Recruitment of *Laminaria* in the sublittoral region can be impeded by dense turfs of red algae (Chapman, 1984). Again, experimental work is required to clarify the roles of various factors.

The Agarum-Ptilota belt (Edelstein et al., 1969) may occur at less than 20 m depth in the Gulf but may also be lacking or confined to deeper water (Bird et al., 1983). We found a similar Agarum-Ptilota belt in shallower water (< 10 m) below the Laminaria-Desmarestia belt on Atlantic and Fundy shores. Because of the depth limits of our survey, we cannot comment on the general occurrence of a deep Phyllophora-Polysiphonia assemblage on Atlantic and Gulf shores. In the Bay of Fundy this vegetation belt is lacking. Even on hard substrata and where sea urchins were not observed, the lower limits of foliose algal growth in the Bay of Fundy were shallow and sublittoral algal cover was sparse compared to other coastal environments. The reasons for this, which need to be studied experimentally, may include turbidity (Logan et al., 1983; Prouse, 1983), herbivory, and tidal currents.

Variation in the complement of species found in the coastal environments may stem from historical as well as environmental influences. For instance, Furcellaria lumbricalis and Fucus serratus were previously restricted to the Gulf. This pattern may reflect the locations where these species were introduced, presumably from Europe. Their limited success in spreading out of the Gulf may be related to physical or biological factors (Edelstein et al., 1972; Dale, 1982; Holmsgaard et al., 1981), although Fucus serratus has now become relatively abundant and generally wide spread along the Fundy approaches. Gulf populations, especially those in shallow embayments, of warm-temperate species appear to be relics of a time 7000 years ago when the Atlantic coastal waters were several degrees warmer (Novaczek et al., 1987).

The rarity of Ascophyllum nodosum in the Gulf is probably owing to the combination of friable substratum and ice scour (Bird et al., 1983). The absence of Alaria esculenta may be primarily a consequence of lethal high summer temperatures (Sundene, 1962) but ice scour (Keats et al., 1985) is also a possible factor.

Other cases of absence of species from coastal environments appear to be related to the summer sea temperature, with southern species often being restricted to the Gulf and northern species restricted to the colder Fundy and Atlantic environments. The number of warm-temperate species and the tendency for normally intertidal algae to occur sublittorally in the Gulf made the sublittoral region of this environment particularly rich in species (Fig 4). The absence of Arctic species from the depauperate sublittoral region of the Bay of Fundy may in some cases be related to the moderate minimum winter temperatures together with limited availability of substratum.

Patterns of nutrient availability can direct the evolution of physiological ecotypes and affect the phenology of an algal species (Espinosa and Chapman, 1983). There is also evidence that on enriched shores of the Bay of Fundy and Fundy approaches both individual plant size and biomass per unit area can be large (MacFarlane, 1952; McPeak, 1980; Pringle and Semple, 1980) relative to that on Atlantic shores (Mann, 1972; Cousens, 1981; Scheibling, 1986) and Gulf shores (Herring and MacBeth, 1973;

McLachlan et al., 1987). Four of the species we recorded were restricted to nutrientenriched shores of the Bay of Fundy and Fundy approaches. However, these were either small or taxonomically difficult and may have been overlooked at other sites. The fact that the number of species recorded for the Atlantic coast increased from 168 to 177 with the addition of data from the Fundy approaches may indicate an increase in diversity related to nutrient enrichment.

Our survey has documented a wealth of variation in the vertical distributions of algal species on rocky shores of the Maritime provinces. There are, however, general trends in the distributions of dominant species (Figs 4-8), which can be attributed to major differences in physical factors among the three coastal environments. From the Bay of Fundy around the Atlantic coast and into the southern Gulf of St. Lawrence, the tidal characteristics, the type of substratum, the slope of the intertidal region and the degree of winter ice scour all change; in the same progression, the belts of dominant algae (fucoids, Chondrus-Mastocarpus, Laminaria-Desmarestia and Agarum-Ptilota) occupy positions farther and farther down the shore. Before we can fully understand the variations within this general pattern, experimental studies of biotic interactions will be necessary. Our analyses suggest that any such experimental program should incorporate controls to test for the influence of variations in tidal range, slope, wave exposure and disturbance on biotic interactions.

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References

- **Adey, W.H.** 1964. The genus *Phymatolithon* in the Gulf of Maine. *Hydrobiologia* 24: 377-420.
- **Adey, W.H.** 1965. The genus *Clathromorphum* (Corallinaceae) in the Gulf of Maine. *Hydrobiologia* 26: 538-573.
- **Bailey, W.B.** 1954. Seasonal variations in the hydrographic conditions of the Bay of Fundy. *Fish. Res. Board Can. Manus. Rept. Biol. Stn. No.* 551.
- **Bell, H.P.** and **MacFarlane, C.** 1933a. The marine algae of the Maritime provinces of Canada. I. List of species with their distribution and prevalence. *Can. J. Res.* 9: 265-279.
- **Bell, H.P.** and **MacFarlane, C.** 1933b. The marine algae of the Maritime provinces of Canada. II. A study of their ecology. *Can. J. Res.* 9: 280-293.
- **Bird, C.J., Greenwell, M.** and **McLachlan, J.** 1983. Benthic marine algal flora of the north shore of Prince Edward Island (Gulf of St. Lawrence) Canada. *Aquat. Bot.* 16: 315-335.
- **Bird, N.L., Chen, L.C.-M.** and **McLachlan, J.** 1979. Effects of temperature, light and salinity on growth in culture of *Chondrus crispus, Furcellaria lumbricalis, Gracilaria tikvahiae* (Gigartinales, Rhodophyta) and *Fucus serratus* (Fucales, Phaeophyta). *Bot. Mar.* 22: 521-527.
- **Blair, S.M.** 1983. Taxonomic treatment of the *Chaetomorpha* and *Rhizoclonium* species (Cladophorales: Chlorophyta) in New England. *Rhodora* 85: 175-211.
- **Bolton, J.J.** 1981. Community analysis of vertical zonation patterns on Newfoundland rocky shores. *Aguat. Bot.* 10: 299-316.

- **Bousfield, E.L.** and **Laubitz, D.R.** 1972. Station lists and new distributional records of littoral marine invertebrates of the Canadian Atlantic and New England regions. *Nat. Mus. Nat. Sci.* (Ottawa) Publ. Biol. Ocean. 5: 1-51.
- **Burns, R.L.** and **Mathieson, A.C.** 1972. Ecological studies of economic red algae. II. Culture studies of *Chondrus crispus* and *Gigartina stellata*. *J. Exp. Mar. Biol. Ecol.* 8: 1-6.
- **Burrows, E.M.,** and **Lodge, S.** 1951. Autecology and the species problems in *Fucus. J. Mar. Biol. Assoc. U.K.* 30: 161-176.
- Canadian Climate Normals. 1982. Vol. 7. Bright sunshine. Canadian Climate Program, Environment Canada.
- Canadian Climate Normals. 1984. Vol. 9. Soil temperature, lake evaporation, days with blowing snow, hail, fog, smoke/haze, frost. Canadian Climate Program, Environment Canada.
- Canadian Tide and Current Tables, 1984. Vols. 1, 2. Government of Canada, Fisheries and Oceans.
- **Cardinal, A.** 1968. Répertoire des algues marines benthiques de l'est du Canada. *Cahiers d'Information 48.* Ministère de l'Industrie et du Commerce, Québec.
- **Chamberlain, Y.M.** 1983. Studies in the Corallinaceae with special reference to *Fosliella* and *Pneophyllum* in the British Isles. *Bull. Br. Mus. (Nat. Hist.) Bot.* 11: 291-463.
- **Chapman, A.R.O.** 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelps in St. Margaret's Bay, eastern Canada. *Mar. Biol.* 62: 307-311.
- Chapman, A.R.O. 1984. Reproduction, recruitment and mortality in two species of Laminaria in southwest Nova Scotia. J. Exp. Mar. Biol. Ecol. 78: 99-109.
- **Chapman, A.R.O.** and **Craigie, J.** 1977. Seasonal growth in *Laminaria longicruris:* Relations with dissolved inorganic nutrients and internal reserves of nitrogen. *Mar. Biol.* 40: 197-205.
- **Chapman, A.R.O.** and **Gagné, J.** 1980. Environmental control of kelp growth in St. Margaret's Bay and on the southwest shore of Nova Scotia. *Can. Tech. Rept. Fish. Aguat. Sci.* 954: 194-207.
- Colinvaux, L.H. 1966. Distribution of marine algae in the Bay of Fundy, New Brunswick, Canada. *Proc. Int. Seaweed Symp.* 5: 91-98.
- Colinvaux, L.H. 1970. Marine algae of eastern Canada: A seasonal study in the Bay of Fundy. Nova Hedwigia 19: 139-158.
- Coote, A.R. and Hiltz, R.S. 1975. Distribution of silicate, nitrate and phosphate in the Gulf of St. Lawrence: July-August 1971, June 1972 and February 1975. Bedford Inst. Oceanogr. Rept. Serv. BI-R-75-14, Dartmouth, N.S.
- Coote, A.R. and Yeats, P.A. 1979. Distribution of nutrients in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 36: 122-131.
- **Cousens, R.** 1981. The population biology of Ascophyllum nodosum (L.) Le Jolis. Ph.D. thesis, Dalhousie University, Halifax, N.S.
- **Dale, M.** 1982. Phytosociological structure of seaweed communities and the invasion of *Fucus serratus* in Nova Scotia. *Can. J. Bot.* 60: 2652-2658.
- **Dayton, P.K.** 1971. Competition, disturbance and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389.
- **Dobson, D.** and **Petrie, B.** 1982. Long-term temperature monitoring program 1981. Can. Data Rept. Hydrogr. Ocean Sci. 6: 1-297.
- **Dring, M.J.** 1987. Light climate in intertidal and subtidal zones in relation to synthesis and growth of benthic algae: a theoretical model. In: *Plant life in aquatic and amphibious habitats.* (Ed. R.M. Crawford). Special Publications No. 5, Br. Ecol. Soc., Blackwell Scientific Publ. Oxford, pp. 359-373.

- **Drinkwater, K.** and **Taylor, G.** 1982. Monthly means of the temperature, salinity and density along the Halifax section. *Can. Tech. Rep. Fish. Aquat. Sci.* 1093: 1-67.
- Druehl, L.D., and Green, J.M. 1982. Vertical distribution of intertidal seaweeds as related to patterns of submersion and emersion. *Mar. Ecol. Prog. Ser.* 9: 163-170.
- Edelstein, T., Craigie, J.S. and McLachlan, J. 1969. Preliminary survey of the sublittoral flora of Halifax County. J. Fish. Res. Board Can. 26: 2703-2713.
- **Edelstein, T., Greenwell, M., Bird, C.J.** and **McLachlan, J.** 1972. Investigations of the marine algae of Nova Scotia X. Distribution of *Fucus serratus* L. and some other species of *Fucus* in the Maritime Provinces. *Proc. N.S. Inst. Sci.* 27: 33-42.
- **El-Sabh, M.I.** 1976. Surface circulation pattern in the Gulf of St. Lawrence. *J. Fish. Res. Board Can.* 33: 124-138.
- **Espinosa, J.** and **Chapman, A.R.O.** 1983. Ecotypic differentiation of *Laminaria longicruris* in relation to seawater nitrate concentration. *Mar. Biol.* 74: 213-218.
- **Gagné, J.A.** and **Mann, K.H.** 1981. Comparison of growth strategy in *Laminaria* populations living under different seasonal patterns of nutrient availability. *Proc. Int. Seaweed Symp.* 10: 297-302.
- **Gail, F.W.** 1918. Some experiments with *Fucus* to determne the factors controlling its vertical distribution. *Puget Sound Mar. Biol. Stn. Publ.* 2: 139-151.
- **Garret, C.J.R.** and **Loucks, R.A.** 1976. Upwelling along the Yarmouth shore of Nova Scotia. *J. Fish Res. Board Can.* 33: 116-117.
- **Gran, H.H.** and **Braarud, T.** 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity). *J. Biol. Board Can.* 1: 279-467.
- **Guiry, M.D.** and **West, J.A.** 1983. Life history and hybridization studies on *Gigartina* stellata and *Petrocelis cruenta* (Rhodophyta) in the North Atlantic. *J. Phycol.* 19: 474-494.
- **Guiry, M.D., West, J.A., Kim, D.-H.** and **Masuda, M.** 1984. Reinstatement of the genus *Mastocarpus* Kützing (Rhodophyta). *Taxon* 33: 53-63.
- Hanic, L.A. 1974. A guide to the common seaweeds of Prince Edward Island. P.E.I. Mar. Sci. Club Publ., Charlottetown.
- **Hartnoll, R.G.** and **Hawkins, S.J.** 1980. Monitoring rocky-shore communities: A critical look at spatial and temporal variation. *Helgol. Meeresunters* 33: 484-494.
- Herring, F. and MacBeth, C. 1973. Quantity survey of Chondrus crispus and other marine plants, Covehead to Naufrage, Prince Edward Island. P.E.I. Dept. Fish. Tech. Rep. 130, Charlottetown, P.E.I.
- **Himmelman, J.H.** 1980. The role of the green sea urchin, *Strongylocentrotus droeba-chiensis*, in the rocky subtidal region of Newfoundland. *Can. Tech. Rept. Fish. Aguat. Sci.* 954: 92-119.
- **Holmsgaard, J.E., Greenwell, M.** and **McLachlan, J.** 1981. Biomass and vertical distribution of *Furcellaria lumbricalis* and associated algae. *Proc. Int. Seaweed Symp.* 10: 309-313.
- **Johnson, C.R.** 1984. Ecology of the kelp Laminaria longicruris and its principal grazers in the rocky subtidal of Nova Scotia. Ph.D. thesis, Dalhousie University, Halifax, N.S.
- Johnson, C.R. and Mann, K.H. 1986. The importance of plant defence abilities to the structure of subtidal seaweed communities: The kelp *Laminaria longicruris* de la Pylaie survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. *J. Exp. Mar. Biol. Ecol.* 97: 231-267.
- **Keats, D.W., South, G.R.** and **Steele, D.H.** 1985. Algal biomass and diversity in the upper subtidal at a pack-ice disturbed site in eastern Newfoundland. *Mar. Ecol. Prog. Ser.* 25: 151-158.
- **Kussakin, O.G.** 1977. Intertidal ecosystems of the seas of the USSR. *Helgol. Wiss. Meeresunters.* 30: 243-262.

- **Lauzier, L.M.** 1967. Bottom residual drift on the continental shelf area of the Canadian Atlantic coast. *J. Fish. Res. Board Can.* 24: 1845-1858.
- Lauzier, L.M. and Hull, J.H. 1969. Coastal station data temperatures along the Canadian Atlantic coast, 1921-1969. Fish. Res. Board Canada Tech. Rept. 150: 1-25.
- **Lewis, J.R.** 1964. The ecology of rocky shores. English University Press Ltd., London. **Lindstrom, S.C.** 1985. Nomenclatural and taxonomic studies on *Dilsea* and *Neodilsea* (Dumontiaceae, Rhodophyta). *Taxon* 34: 260-266.
- **Lobban, C.S.,** and **Hanic, L.A.** 1984. Rocky shore zonation at North Rustico and Prim Point, Prince Edward Island. *Proc. N.S. Inst. Sci.* 34: 25-40.
- Logan, A., MacKay, A.A. and Noble, J.P.A. 1983. Chapter 8, Sublittoral hard substrates. In: Marine and coastal systems of the Quoddy Region, New Brunswick. (ed. M.L.H. Thomas). Can. Spec. Publ. Fish. Aquat. Sci. 64: 119-139.
- **Loring, D.H.** and **Nota, D.J.G.** 1973. Morphology and sediments of the Gulf of St. Lawrence. *Fish. Mar. Serv. Bull.* 182: 1-147.
- **Lubchenco, J.** 1980. Algal zonation in the New England rocky intertidal community: An experimental analysis. *Ecology* 61: 333-344.
- **Lubchenco, J.** 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity and plant escapes during succession. *Ecology* 64: 1116-1123.
- **Lubchenco, J.** and **Menge, B.A.** 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 59: 67-94.
- MacFarlane, C.I. 1952. A survey of certain seaweeds of commercial importance in southwest Nova Scotia. Can. J. Bot. 30: 78-97.
- MacFarlane, C.I. 1965. Sublittoral surveying for commercial seaweeds in Northumberland Strait. *Proc. Int. Seaweed Symp.* 5: 169-176.
- Mann, K.H. 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.
- Marine Ecology Laboratory. 1980. Physical oceanography, dissolved nutrients, phytoplankton production, plankton biomass and sedimentation in St. Georges Bay, N.S., 1977. Can. Tech. Rept. Fish. Aquat. Sci. 934: 1-162.
- Marshall, S.M., Newton, L. and Orr, A.P. 1949. A study of certain British seaweeds and their utilisation in the preparation of agar. H.M. Stationery Office, London.
- Mathieson, A.C. and Burns, R.L. 1971. Ecological studies of economic red algae: I. Photosynthesis and respiration of *Chondrus crispus* Stackhouse and *Gigartina stellata* (Stackhouse) Batters. J. Exp. Mar. Biol. Ecol. 7: 197-206.
- Mathieson, A.C., Tveter, E., Daly, M. and Howard, J. 1977. Marine algal ecology in a New Hampshire tidal rapid. *Bot. Mar.* 20: 277-290.
- MacLachlan, J., Greenwell, M., Bird, C.J. and Holmsgaard, J.E. 1987. Standing stocks of seaweeds of commercial importance on the north shore of Prince Edward Island, Canada. *Bot. Mar.* 30: 277-289.
- McPeak, R.H. 1980. A preliminary assessment of the Laminaria resource near Lower Wood Harbour, Nova Scotia, during July 1977. Can. Tech. Rept. Fish. Aquat. Sci. 954: 180-192.
- **Menge, B.A.** 1976. Organization of the New England rocky intertidal community: Role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46: 355-393.
- Miller, R.J. 1985. Succession in sea urchin and seaweed abundance in Nova Scotia, Canada. *Mar. Biol.* 84: 275-286.
- Miller, R.J. and Colodey, A.G. 1983. Widespread mass mortalities of the green sea urchin in Nova Scotia, Canada. *Mar. Biol.* 73: 263-267.
- Moore, D.S. and Miller, R.J. 1983. Recovery of macroalgae following widespread sea urchin mortality with a description of the nearshore hard-bottom habitat on the Atlantic coast of Nova Scotia. Can. Tech. Rept. Fish. Aquat. Sci. 1230: 1-94.

- Moore, D.S., Miller, R.J. and Meade, L.D. 1986. Survey of shallow benthic habitat: Eastern shore and Cape Breton, Nova Scotia. Can. Tech. Rept. Fish. Aquat. Sci. 1546: 1-49.
- Moseley, C.M. and MacFarlane, C.I. 1969. Sublittoral seaweed investigation in Northumberland Strait and George Bay 1967-1968. Nova Scotia Research Foundation Corp., Seaweeds Division, Dartmouth, N.S.
- Munda, I. 1977. The structure and distribution of Gigartina stellata (Stackh.) Batters and Chondrus crispus Stackh. associations in Icelandic waters. Bot. Mar. 20: 291-301.
- Neish, I.C. and Dunn, R.S. 1971. Atlantic Mariculture Ltd. rockweed report, New Brunswick Dept. Fish. & Environ., Fredericton, N.B.
- **Niemeck, R.A.** and **Mathieson, A.C.** 1978. Physiological studies of intertidal fucoid algae. *Bot. Mar.* 21: 221-227.
- Novaczek, I. and McLachlan, J. 1986. Recolonization by algae of the sublittoral habitat of Halifax County, Nova Scotia, following the demise of sea urchins. *Bot. Mar.* 29: 69-73.
- Novaczek, I., Bird, C.J. and McLachlan, J. 1987. Phenology and temperature tolerance of the red algae Dasya baillouviana, Chondria baileyana, Griffithsia globifera, and Lomentaria baileyana, in Nova Scotia. Can. J. Bot. 65: 57-62.
- Owens, E.H. 1976. The effects of ice on the littoral zone at Richibucto Head, eastern New Brunswick. Rev. Géogr. Montr. 30: 95-104.
- Owens, E.H. and Bowen, A.J. 1977. Coastal environments of the Maritime Provinces. Mar. Sed. 13: 1-31.
- Platt, T. and Irwin, B. 1970. Primary productivity measurements in St. Margaret's Bay, 1968-1970. Fish. Res. Board Can. Tech. Rept. 203: 1-68.
- **Platt, T.** and **Irwin, B.** 1972. Primary productivity and nutrients in St. Margaret's Bay, 1966. Fish. Res. Board Can. Tech. Rept. 327: 1-21.
- Price, J.H. and Farnham, W.F. 1982. Seaweeds of the Faroes 3: Open shores. Bull. Br. Mus. (Nat. Hist.) Bot. 10: 153-225.
- **Pringle, J.D.** and **Semple, R.E.** 1980. The benthic algal biomass, commercial harvesting and *Chondrus* growth and colonization off southwestern Nova Scotia. *Can. Tech. Rept. Fish. Aquat. Sci.* 954: 144-168.
- **Probyn, T.A.** and **Chapman, A.R.O.** 1983. Summer growth of *Chordaria flagelliformis* (O.F. Mull.) C. Ag.: Physiological strategies in a nutrient-stressed environment. *J. Exp. Mar. Biol. Ecol.* 73: 243-271.
- **Prouse, N.J.** 1983. Primary production measurements in the Bay of Fundy from March 1979 to November 1980. Can. Tech. Rept. Fish. Aquat. Sci. 1167: 1-82.
- **Roland, A.E.** 1982. Geological background and physiography of Nova Scotia. N.S. Inst. Sci., Halifax, N.S.
- **Scheibling, R.** 1986. Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. *Oecologia* (Berl.) 68: 186-198.
- **Schiel, D.R.** and **Foster, M.S.** 1986. The structure of subtidal algal stands in temperate waters. *Ann. Rev. Oceanogr. Mar. Biol.* 24: 265-307.
- South, G.R. 1984. A checklist of marine algae of eastern Canada. Can. J. Bot. 62: 680-704.
- **Southward, A.J.** 1958. The zonation of plants and animals on rocky sea shores. *Biol. Rev.* 33: 137-177.
- **Southward, A.J.** and **Southward, E.C.** 1978. Recolonization of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. *J. Fish. Res. Board Can.* 35: 682-706.

- Stasko, A.B., Amaratunga, T. and Caddy, J.F. 1977. Nineteen seventy-five Northumberland Strait project, Part II: Commercial shellfish data. Fish. Mar. Serv. Manu. Rept. 1432: 29.
- **Stasko, A.B., Campbell, A.** and **Graham, D.E.** 1980. Sea urchin (*Strongylocentrotus droebachiensis*) distribution around western Nova Scotia. Can. Tech. Rept. Fish. Aquat. Sci. 954: 225-236.
- **Steele, D.H.** 1983. Coarse sedimentary shores. In: Marine and coastal systems of the Quoddy Region, New Brunswick. (ed. M.L.H. Thomas.) Can. Spec. Publ. Fish. Aguat. Sci. 64: 74-94.
- **Stephenson, T.A.** and **Stephenson, A.** 1954. Life between tide-marks in North America IIIB. Nova Scotia and Prince Edward Island: The geographical features of the region. *J. Ecol.* 42: 46-70.
- **Stephenson, T.A.** and **Stephenson, A.** 1972. *Life between tidemarks on rocky shores.* W.H. Freeman, San Francisco.
- **Steven, D.M.** 1974. Primary and secondary production in the Gulf of St. Lawrence. *Mar. Sci. Centre Manus. Rept. No. 26, McGill University, Montreal, 1-116.*
- **Sundene, O.** 1962. The implications of transplant and culture experiments on the growth and distribution of *Alaria esculenta*. *Nytt. Mag. Bot.* 9: 155-174.
- Sutcliffe, W.H. Jr., Loucks, R.H. and Drinkwater, K.F. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J. Fish. Res. Board Can. 33: 98-115.
- **Taylor, A.R.A.** 1973. Studies of populations of *Chondrus crispus* (Irish moss) and *Furcellaria fastigiata* in Prince Edward Island waters during 1971. *Indust. Devel. Br. Environ. Can. Tech. Rept. Series* 65: 1-109.
- **Taylor, A.R.A.** 1975. The *Chondrus crispus-Furcellaria fastigata* community at Campbell's Cove, Prince Edward Island. *Indust. Devel. Br., Fish. Mar. Serv., Environ. Can. Tech. Rept.* 88: 1-72.
- **Taylor, W.R.** 1957. Marine algae of the northeastern coast of North America. University of Michigan Press, Ann Arbor, MI.
- **Thomas, M.L.H., Arnold, D.C.** and **Taylor, A.R.A.** 1983. Rocky Intertidal Communities: In: *Marine and coastal systems of the Quoddy region, New Brunswick,* (ed., M.L.H. Thomas), Can. Spec. Publ. Fish. Aquat. Sci. 64: 35-73.
- Underwood, A.J. 1978. A refutation of critical tide levels as determinants of the structure of intertidal communities on British shores. J. Exp. Mar. Biol. Ecol. 33: 261-276.
- Underwood, A.J. and Denley, E.J. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: Ecological communities, conceptual issues and the evidence. (eds. D.R. Strong Jr., D. Simberloff, L.G. Abele and A.B. Thistle), Princeton University Press, Princeton, NJ. 151-180.
- Weiler, J.D.M. and Keeley, J.R. 1980. Monthly sea surface temperature for the Gulf of St. Lawrence. Dept. Fish. Oceans, Mar. Environ. Data Service Tech. Rept. 7: 1-43.
- Wharton, W.G. 1980. The extent of destructive grazing by the green sea urchin Strongylocentrotus droebachiensis on the eastern and southwestern shores of Nova Scotia. Fish. and Oceans Canada. DSS Contract No. ISC 7900058, Halifax, N.S.
- Wharton, W.G. and Mann, K.H. 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. Aguat. Sci.* 38: 1339-1349.
- **Widdowson, T.B.** 1965. A survey of the distribution of intertidal algae along a coast transitional in respect to salinity and tidal factors. *J. Fish. Res. Board Can.* 22: 1425-1454.

- Wilce, R.T. 1959. The marine algae of the Labrador peninsula and northwest Newfoundland (ecology and distribution). Nat. Mus. Can. Bull. 158, Biol. Ser. 56, 1-103.
- Wilson, J.S., Bird, C.J., McLachlan, J. and Taylor, A.R.A. 1979. An annotated checklist and distribution of benthic marine algae of the Bay of Fundy. *Memorial Univ. Nfld. Occ. Pap. Biol.* No. 2: 1-65.
- **Woelkerling, W.J.** 1973. Morphology and systematics of the *Audouinella* complex (Acrochaetiales, Rhodophyta) in northeastern United States. *Rhodora* 75: 1-621.
- Yabu, H. 1978. Chromosome numbers in species of *Porphyra* from Nova Scotia, Canada. *Jap. J. Phycol.* 26: 97-104.

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Appendix 1

List of surveyed sites, indicating the type of transect (I = intertidal, S = sublittoral), dates of surveys and the wave exposure (Table II), geology, presence of sea urchins (o = none seen, 1 = few, 2 = common or abundant), spring-tide range and intertidal slope in each locality, nd = no data.

Site No. & Name	Transect type:	Wave Exp	Geology	Sea Urch	Tide Range	Slope
	da-mo-yr	Index			(m)	$(m m^{-1})$
BAY OF FUNDY: shores 1-2, 5-7						
1 Scots Bay	I, 13-05-77	2	basalt	0	14.6	0.09
2 Cape D'Or	1, 02-07-77	3	basalt	0	13.0	0.19
3 Hampton	I, 14-06-84	3	basalt	0	11.6	0.08
	S, 22-08-84			2		
4 Martin Head	1, 06-07-78	3	sandstone	0	11.1	0.16
5 Quaco Head	1, 05-07-78	2	sandstone	0	11.0	0.08
6 Delap Cove	I, 31-05-77	3	basalt	0	9.8	0.2
7 Cape Spencer	1, 04-07-78	4	sandstone	0	.9	0.2
, ,	S, 05-07-78			0		
8 Musquash Head	1, 24-05-78	4	basalt	0	9.1	0.15
9 Welch Cove	1, 23-05-78	3	basalt	0	8.2	0.01
10 Deer Point	1, 20-06-78	1	basalt	2	8.1	0.23
11 E. Quoddy Head	1, 20-06-78	3	basalt	0	7.7	0.21
•	S, 18-07-78			2		
11b	S, 18-07-78			0		
12 Dinner Head	I, 21-06-78	3	basalt	0	7.7	0.06
	S, 18-07-78			0		0.00
13 Mascabin Point	1, 23-05-78	2	basalt	2	.8	0.2
	S, 23-05-78			2		· · · ·
14 Gulliver Cove	1, 03-07-77	2	basalt	0	7.9	0.07
15 Sandy Cove	1, 02-06-77	3	basalt	0	7.8	0.09
•	S, 02-06-77			0		0.00
16 Ingalls Head	1, 22-06-78	3	basalt	0	7.3	0.04
	S, 22-06-78			0		0.0.
17 Swallowtail Light	1, 23-06-78	3	shale	0	7.3	0.29
0	S, 23-06-78		5. 17/10/20	0		0.23
18 Dark Harbour	1, 22-06-78	4	basalt	0	6.0	0.1
	S, 20-07-78		47.730.7	0		0.1

Appendix 1 (C

Site No. & Name	Transect type: da-mo-yr	Wave Exp Index	Geology	Sea Urch	Tide Range (m)	Slope (m m ⁻¹)
20 North Point	1, 04-06-77	3	basalt	0	6.6	0.12
ATLANTIC: Funday approaches: shores 8-9						
21 Meteghan	I, 02-06-77 S, 02-06-77	3	slate	0	6.2	0.08
22 Cape St. Mary	1, 01-08-77	3	slate	0	5.8	0.04
23 Burns Point	1, 03-08-77	3	slate	0	5.7	0.05
24 Cheggogin Point	1, 02-08-77	3	slate	0	5.7	0.04
25 Chebogue Point	1, 02-08-77	4	slate	0	4.7	0.02
is chesogue rount	S, 02-08-77	-		. 0		
26 Comeau Hill	1, 03-08-77	2	granite	0	4.7	0.02
7 Lower E. Pubnico	I, 17-05-84	2	granite	0	4.5	0.1
28 St. Ann Point	I, 16-05-84	2	slate	0	4.2	0.05
29 West Head	I, 17-05-84	2	granite	0	3.8	0.14
Eastern Atlantic: shores 10, 11-15						
30 Ingomar Point -	I, 18-05-84	2	granite	0	2.7	0.05
	S, 31-07-84			0		
31 Western Head	I, 10-07-84	4	quartzite	0	2.4	0.07
	S, 10-07-84			0		
32 Ovens	1, 05-07-84	3	slate	0	2.2	0.02
	S, 05-07-84			0		0.00
33 Fox Point	1, 19-06-84	2	granite	0	2.2	0.08
	S, 16-08-84			0		
34 Northwest Cove	1, 08-06-84	1	granite	0	2.1	0.22
	S, 16-08-84	1		0		
34b	S, 16-08-84	2		0		

Appendix 1	(Cont'd.)
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Site No. & Name	Transect	Wave	Geology	Sea	Tide Range (m)	Slope (m m ⁻¹)
	type: da-mo-yr	Exp Index		Urch		
35 Prospect	1, 07-06-84	4	granite	0	2.1	0.13
	S, 13-08-84			0		
36 Portuguese Cove	1, 06-06-84	3	granite	0	2.1	0.1
37 Boutiliers Island	I, 12-07-74	1	slate	0	2.0	0.05
	S, 12-07-84			0		
38 Sober Island (W)	I, 11-07-84	3	slate	0	2.0	0.05
	S, 11-07-84			0		
39 Tor Bay	I <i>,</i> 17-07-84	4	quartzite	0	1.95	0.08
	S, 19-07-84			1		
40 Rocky Bay	I, 19-07-74	3	sandstone	0	2.0	0.04
	S, 19-07-84			2		
41 Gooseberry Cove	S, 18-07-84	4	shale	2	1.7	nd
42 Neal Cove	I, 18-07-84	2	sandstone	0	1.7	0.04
	S, 18-07-84			1		
43 Point Aconi	S, 08-08-84	3	sandstone	2	1.25	nd
44 Wreck Point	S, 08-08-84	3	granite	1	1.3	nd
SOUTHERN GULF OF ST LAW	RENCE: shores 17, 20-22					
45:East Point T2	S, 16-05-77	3	sandstone	2	1.1	nd
46:T3	S, 16-05-77	3	sandstone	2	1.1	nd
47:T4	S, 16-05-77	3	sandstone	2	1.1	nd
48:T6	S, 13-05-77	3	sandstone	2	1.1	nd
49:T7	S, 13-05-77	3	sandstone	2	1.1	nd
50:T8	S, 13-05-77	3	sandstone	1	1.1	nd
51:T10	S, 09-05-77	3	sandstone	2	1.1	nd
52:T11	S, 17-05-77	3	sandstone	2	1.1	nd
53:T12	S, 17-05-77	3	sandstone	1	1.1	nd
54:T14	S, 19-05-77	3	sandstone	1	1.1	nd
55:T18	S, 20-05-77	3	sandstone	1	1.1	nd
56:T19	S, 20-05-77	3	sandstone	1	1.1	nd
57:T21	S, 20-05-77	3	sandstone	1	1.1	nd

Site	Transect	Wave	Geology	Sea	Tide	Slope
No. & Name	type: da-mo-yr	Exp Index		Urch	Range (m)	(m m ⁻¹)
58:T24	S, 23-05-77	3	sandstone	1	1.1	nd
59:T25	S, 23-05-77	3	sandstone	1	1.1	nd
60:T26	S, 25-05-77	3	sandstone	2	1.1	nd
61:T29	S, 24-05-77	3	sandstone	1	1.1	nd
62:T30	S, 24-05-77	3	sandstone	1	1.1	nd
63:T32	S, 24-05-77	3	sandstone	1	1.1	nd
64:T33	S, 25-05-77	3	sandstone	2	1.1	nd
65:T34	S, 31-05-77	3	sandstone	1	1.1	nd
66:T35	S, 31-05-77	3	sandstone	2	1.1	nd
67:T36	S, 31-05-77	3	sandstone	2	1.1	nd
68:T37	S, 31-05-77	3	sandstone	1	1.1	nd
69:T38	S, 01-06-77	3	sandstone	2	1.1	nd
70:T39	S, 31-05-77	3	sandstone	1	1.1	nd
71:T40	S, 01-06-77	3	sandstone	2	1.1	nd
72:T41	S, 01-06-77	3	sandstone	1	1.1	nd
73:T42	S, 01-06-77	3	sandstone	1	1.1	nd
74:T44	S, 02-06-77	3	sandstone	1	1.1	nd
75:T45	S, 08-06-77	3	sandstone	1	1.1	nd
76:T46	S, 08-06-77	3	sandstone	1	1.1	nd
77:T48	S, 07-06-77	3	sandstone	1	1.1	nd
78:T49	S, 09-06-77	3	sandstone	2	1.1	nd
79:T51	S, 09-06-77	3	sandstone	1	1.1	nd
80 St. Peters Bay:T57	S, 14-06-77	3	sandstone	2	1.1	nd
81 Doyle's Cove	S, 03-08-85	3	sandstone	1	1.1	nd
82 Cape Tryon	S, 02-07-85	3	sandstone	1	1.1	nd
83 Anglo	S, 29-07-85	3	sandstone	1	1.2	nd
84 Seacow Pond	S, 16-07-85	3	sandstone	1	1.2	nd
85 Norway	S, 31-07-85	3	sandstone	1	1.2	nd
86 Miminegash	S, 19-08-85	3	sandstone	1	1.2	nd
87 Cape Wolfe	S, 15-08-85	3	sandstone	0	1.3	nd
88 Cape Egmont	S, 17-06-85	2	sandstone	0	1.4	nd
89 Amherst Point	S, 14-08-85	2	sandstone	0	2.4	nd

Appendix 2

List of species in each sector of 3 coastal environments of the Maritime Provinces, Canada, indicating the vertical distribution of each species. For locations of shores and sites see Fig 2. P = present, with height or depth undocumented; 1 = rockpool above MWL; 2 = rockpool below MWL; A = above HHWN; B = HHWN to LLWN; C = LLWN to CD; D = CD to 2 m depth; E = below 2 m depth; * = wave exposure 4 only (see Table V); + = site 39 and shore 12 only. Data in brackets are from one of the following sources: Adey (1964, 1965), Cardinal (1968), Edelstein et al. (1969), Wilson et al. (1979), Novaczek and McLachlan (1986), Lobban and Hanic (1984), NRCC herbarium, C.J. Bird unpublished records. Nomenclature follows South (1984) except where noted (see footnotes).

	Sector: I F Hores: 1 Sites: 1	undy 1-5	Outer Fundy 6-7 7-20	Fundy Approaches 8-9 21-29	Eastern Atlantic 10-15 30-44	Open Gulf 16, 17, 20 45-83	Lower Gulf 18, 19, 21, 22 84-89
Phaeophyta							
Acrothrix novae-angliae	[O	-	(P)	(DE)	Ε	(D)E
Agarum cribrosum	(CD	2CDE	(E)	Ė	Ε	È
Alaria esculenta	(CD	2CDE	D	1*2B*CDE	-	-
Ascocyclus distromaticus	-		-	-	-	D	(E)
Ascophyllum nodosum	A	ABC	12ABC	1ABCD	2ABC	(P)	(P)
Chorda filum	((P)	(P)	ED	CDE	DE	(CD)E
Chorda tomentosa		C	2CDE	CD	CDE	E	(P)
Chordaria flagelliformis	2	2C	12BCD	12CD(E)	12BCDE	(B)CDE	E
Delamarea attenuata	-		-	-	(P)	DE	(P)
Desmarestia aculeata	((P)	CDE	(DE)	C*DE	E	Ė
Desmarestia viridis		2CD	CDE	2CDE	2CDE	E	E
Desmotrichum undulatum	-		Р	(P)	(P)	DE	(D)
Dictyosiphon eckmanii	((P)	(P)	(P)	(1)	D	-
Dictyosiphon foeniculaceous	2		12B	2D	12BCDE	CDE	(D)E
Ectocarpus confervoides	-		(P)	(P)	Ε	(P)	(P)
Ectocarpus fasciculatus	((P)	(P)	(E)	CD	DE	-
Ectocarpus siliculosus	(C	C	12D(E)	1*2B*CDE	DE	(D)E
Elachista fucicola	E	BC	BC	BCD	2 BCD	DE	-
Elachista lubrica	-		P	2	(P)	-	-
Eudesme virescens	-		(P)	2(D)	DE	(P)	-
Feldmannia irregularis	-		-	-	-	E	(P)
Fucus distichus	1	1	1	1	1	-	(P)

	Sector: Shores:		Outer	Fundy	Eastern	Open		
		Fundy	Fundy	Approaches	Atlantic	Gulf		
			6-7	8-9	10-15	16, 17, 20		
	Sites:	1-6	7-20	21-29	30-44	45-83	84-89	
Fucus evanescens		BC	BC	2CD	BCDE	DE	(D)	
Fucus serratus		-	-	BCD	CDE	DE	(BC)D	
Fucus spiralis		1A	Α	1AB	AB	(P)	(B)	
Fucus vesiculosus		ABC	1ABC	ABC	2ABCDE	(B)CDE	(B)DE	
Giffordia granulosa		-	-	-	(P)	Ė	(E)	
Giffordia ovata		-	-	-	-	Ε	(E)	
Giffordia sandriana		-	-	-	-	E	<u>.</u> ′	
Giffordia sp.		-	-	-	BCD	E	-	
Halopteris scoparia		-	-	(P)	(E)	DE	DE	
Haplospora globosa		-	(P)	<u>-</u>	2(E)	DE	-	
Isthmoplea sphaerophora		(P)	BC	В	B*CD	-	(P)	
Laminaria digitata		2Ć	12CDE	2CDE	1*2B*CDE	E	-	
Laminaria saccharina ¹		2C	2CDE	2CDE	1*2CDE	E	Ε	
Laminariocolax tomentosoio	les	-	(P)	С	(P)	-	-	
Leathesia difformis		(P)	1D	2CDE	12BC	D	(P)	
Leptonematella fasciculata		B	Р	BC	2BC	E	(P)	
Litosiphon pusillus		-	-	-	-	DE	(P)	
Melanosiphon intestinalis		В	Р	(P)	-	-	-	
Microspongium globosum		-	Р	(P)	(P)	-	(P)	
Myriocladia lovenii		-	_	-	(P)	DE	(E)	
Myrionema strangulans		-	P	(P)	È	D	-	
Myriotrichia filiformis		-	(P)	-	(P)	D	(P)	
Petalonia fascia		12C	2ĆD	1CD	12B*C	(B)DE	Ď(E)	
Petalonia zosterifolia		- `	(P)	BC	(P)	CDE	(D)	
Pilayella littoralis		В	2BC	1BC	2A*BCD	(D)E	(E)	
Pseudolithoderma sp.		-	A	В	(P)	- /-	-	
Punctaria latifolia		-	P	P	1DE	(B)DE	(E)	
Punctaria plantaginea		-	12	C	1*D	DE	(D)	
Ralfsia clavata		_	P	P	CD	DE	(D)E	
Ralfsia fungiformis		BC	2C	2	2	_	(-/-	

Appendix 2 (Cont'd.)

	Sector: Shores: Sites:	Fundy 1-5	Outer Fundy 6-7 7-20	Fundy Approaches 8-9 21-29	Eastern Atlantic 10-15 30-44	Open Gulf 16, 17, 20 45-83	Lower Gulf 18, 19, 21, 22 84-89
 Ralfsia verrucosa		(1)	2	2B	В	(B)CE	(P)
Saccorhiza dermatodea		(P)	2CDE	DE	1*2CDE	E	E
Scytosiphon dotyi		2	C	-	-	-	-
Scytosiphon Iomentaria		1C	12BC	12CD	12BCDE	(B)CDE	(12BE)D
Sorocarpus micromorus		-	-	-	DE	DE	-
Sphacelaria cirrosa		-	(P)	(P)	BCD	D	(D)E
Sphacelaria fusca		-	(P)	-	2	-	-
Sphacelaria plumosa		-	Р	(P)	E	DE	E
Sphacelaria radicans		-	C	E	-	DE	DE
Sphacelaria rigidula		(P)	Р	(P)	1	-	(E)
Sphaerotrichia divaricata		(P)	(P)	CD	B*	DE	D(E)
Spongonema tomentosum		(P)	(P)	В	B*C	(P)	-
Stictyosiphon griffithsianus		-	-	-	(P)	E	(P)
Stictyosiphon tortilis		-	-	-	-	DE	(D)E
Striaria attenuata		-	-	-	-	E	(E)
Tilopteris mertensii		-	-	-	(E)	E	(E)
Chlorophyta							
Blidingia chadefaudii		-	Р	-	-	-	-
Blidingia marginata		P	(P)	В	(P)	-	(P)
Blidingia minima		(A)	1	Α	1AB	(P)	(A)
Chaetomorpha aerea		-	-	-	(P)	CD	(D)
Chaetomorpha brachygona ²	!	(P)	-	-	(1)	DE	DE
Chaetomorpha cannabina		2	1BC	C	(1)	-	(P)
Chaetomorpha linum		-	(P)	D(E)	BE	(P)	(P)
Chaetomorpha melagonium	,	12CD	12CDE	CDE	1*DE	DE	E
Chaetomorpha picquotiana		-	P	E	(P)	-	E
Cladophora albida		D	(P)	С	2CE	DE	E
Cladophora crystallina ⁵		(P)	1	2	(P)	-	-
Cladophora rupestris		Ċ	В	2BC	1*BC	-	-

Sector	r: Inner	Outer	Fundy	Eastern	Open	Lower
	Fundy	Fundy	Approaches	Atlantic	Gulf	Gulf 18, 19, 21, 22
Shores		6-7	8-9	10-15	16, 17, 20	
Sites	s: 1-6	7-20	21-29	30-44	45-83	84-89
Cladophora sericea	, 1 ,	(P)	2(D)	12BCDE	DE	(B)DE
Derbesia vaucheriaformis	-	-	-	DE	-	-
Enteromorpha compressa	1	Р	-	(P)	-	(P)
Enteromorpha flexuosa ssp. parado	oxa P	Р	-	C	(P)	(P)
Enteromorha groenlandica	(P)	В	-	(P)	-	-
Enteromorpha intestinalis	1	12	1	1B	C	(ABD)E
Enteromorpha linza	1	12BC	В	(P)	(B)	(P)
Enteromorpha prolifera ssp. prolife	e ra-	P	(P)	(P)	(P)	(P)
Monostroma grevillii	12C	12CD	(P)	È	(P)	(P)
Monostroma pulchrum	(P)	12C	(P)	B*CD	-	-
Prasiola crispa	À		-	(P)	-	-
Prasiola stipitata	Α	Α	(P)	A	-	(P)
Pringsheimiella scutata	-	(P)	-	(P)	Р	(DE)
Pseudendoclonium submarinum	(P)	-	-	(P)	DE	(D)
Rhizoclonium riparium ²	P	2	2C	1	D	(P)
Rhizoclonium tortuosum ²	1	-	-	2A*DE	E	(D)E
Spongomorpha aeruginosa	-	P	1B	BCDE	DE	(E)
Spongomorpha arcta	2	12BCD	BCD	1*CDE	E	D(E)
Spongomorpha sonderi	C	Р	(P)	-	-	-
Spongomorpha spinescens	BC	12BCD	(P)	12BCDE	-	-
Ulothrix flacca	Α	1A	(P)	(P)	(B)C	-
Ulothrix laetivirens	Α	(P)	-	Α	-	-
Ulothrix speciosa	(P)	AB	-	(P)	-	-
Ulothrix subflaccida	(P)	-	AB	A	-	(P)
Ulva lactuca	(12C)	12CD	(P)	12A*BDE	(B)DE	(D)E
Ulva rigida	2	2D	C(D)	(P)	D	-
Ulvaria obscura v. blyttii	1	2CD	E	(P)	E	(E)
Ulvaria oxysperma	(P)	C	2BC	1*2B*CE	(P)	-
Urococcus foslieanus	-	-	-	A	-	-
Urospora penicilliformis	Α	В	AB	(P)	(P)	-

	Sector: Inner Fundy Shores: 1-5 Sites: 1-6	Outer Fundy 6-7 7-20	Fundy Approaches 8-9 21-29	Eastern Atlantic 10-15 30-44	Open Gulf 16, 17, 20 45-83	Lower Gulf 18, 19, 21, 22 84-89
Urospora wormskjoldii Vaucheria sp.	B -	ABC -	(C) E	(P) -	(B) -	- (E)
Rhodophyta						
Ahnfeltia plicata Antithamnion cruciatum Antithamnion plumula Antithamnionella floccosa Audouinella dasyae Audouinella daviesii Audouinella microscopica ³ Audouinella purpurea Audouinella saviana Audouinella secundata Audouinella spetsbergensis Bangia atropurpurea Bonnemaisonia hamifera ⁷ Callithamnion corymbosum Callithamnion tetragonum Callophyllis cristata Ceramium deslongchampii v. Ceramium elegans Ceramium rubrum Ceratocolax hartzii	2C (P) - (P) - (P) - B - (P) D - - - C t. hooperiC (P)	12CD DE - C - (P) - BC (P) P - P CDE C (P) 12BCDE (P)	2BC(DE) (P) (P) (P) (P) (P) (P) (P) (P) (P) (P	1*2CDE E E B*CDE - 1B 1D (P) - (P) - 1AB 2BCDE E E (P) E E	DE DE - (P) E DE - E C E (B) DE E - E C E (B) DE E - E E DE - E E DE - E E	DE DE (D)E E - E (P) E - DE (D)E - (P) E - (P) E - (P) E - (P) E (DE (DE)
Chondria baileyana Chondrus crispus Choreocolax polysiphoniae Clathromorphum circumscri Clathromorphum compactui	- 12BC P Iptum (P) m DE	12BCDE P (P) (P)	12BCDE (P) C (P)	12BCDE BC C 2DE	CDE - E E	(DE) (12BC)DE E - -

	Sector:		Outer	Fundy	Eastern	Open	Lower	
		Fundy	Fundy	Approaches	Atlantic	Gulf	Gulf	
	Shores:		6-7	8-9	10-15	16, 17, 20	18, 19, 21, 22	
	Sites:	1-6	7-20	21-29	30-44	45-83	84-89	
Corallina officinalis		12CD	12BCDE	12BCDE	2BCDE	DE	(BC)DE	
Cystoclonium purpureum		1BC	1CD	2CDE	2B*CDE	DE	È	
Dermatolithon pustulatum		(P)	C	CD	-	E	D	
Devaleraea ramentacea		12	12BCD	BCD	1*2B*CDE	(CD)	_	
Dilsea integra⁴		-	-	-	E	È	E	
Dumontia contorta		12BC	12C	12CD	1*2BCDE	E	(P)	
Erythrotrichia carnea		- 1	(P)	Р	2	(P)	(P)	
Fimbrifolium dichotomum		-	CDE	-	E	È	-	
Fosliella farinosa (Lamour.) N	1. Howe1	2_	Р	P	(P)		(P)	
Furcellaria lumbricalis		-	- /	-	DÉ ⁺	DE	(Ď)E	
Gloiosiphonia capillaris		(P)		(DE)	DE	· -	-	
Harveyella mirabilis		(P)	Р	P	E	DE	E	
Hildenbrandia spp.8		12ABC	12BCDE	12ABC	12ABCDE	E	-	
Leptophytum laeve		-	E	(P)	-	E	E	
Lithophyllum orbiculatum		E	(P)	(P)	E	-	-	
Lithothamnion glaciale		E	(P)	È	DE	E	E	
Lithothamnion lemoineae		-	(P)	(P)	C*DE	E	_	
Mastocarpus stellatus ¹³		2BCD	2BCDE	CD	BC	-	-	
Membranoptera alata		C	2CDE	(E)	E	E	E	
Odonthalia dentata		(P)	Р	(E)	E	E	E	
Palmaria palmata		BC	2BCDE	BCDE	1*2A*BCDE	DE	E	
Petrocelis cruenta ¹¹		BC	BC	C	(P)	E	_	
Peyssonnelia rosenvingii		E	P	(P)	È	E	_	
Phycodrys rubens		2CDE	2BCDE	2CDE	E	DE	E	
Phyllophora pseudoceranoid	des	CDE	12CDE	2CDE	E	E	Ē	
Phyllophora truncata		(P)	2DE	C(DE)	CE	DE	DE	
Phymatolithon laevigatum		(P)	(P)	BCD	DE	E	-	
Phymatolithon lenormandii		(P)	(P)	В	C	-	_	
Phymatolithon rugulosum		(P)	(P)	В	DE	E	_	

Sites: 1-6 7-20 21-29 30-44 45-8 Plumaria elegans C 12BC P (P) DE Pneophyllum lejolisii - (P) - (P) E Polyides rotundus 2C 12CDE BCDE DE DE Polysiphonia elongata - - - E (P)	17, 20 18, 19, 21, 22 84-89 E (D) DE (P) (P)
Shores: 1-5 6-7 8-9 10-15 16,15 Sites: 1-6 7-20 21-29 30-44 45-8 Plumaria elegans C 12BC P (P) DE Pneophyllum lejolisii - (P) - (P) E Polyides rotundus 2C 12CDE BCDE DE DE Polysiphonia elongata E (P)	84-89 E (D) DE (P) (P)
Plumaria elegans C 12BC P (P) DE Pneophyllum lejolisii - (P) - (P) E Polyides rotundus 2C 12CDE BCDE DE DE Polysiphonia elongata E (P)	E (D) DE (P) (P)
Pneophyllum lejolisii - (P) - (P) E Polyides rotundus 2C 12CDE BCDE DE DE Polysiphonia elongata E (P)	(D) DE (P) (P)
Polyides rotundus 2C 12CDE BCDE DE DE Polysiphonia elongata E (P)	DE (P) (P)
Polysiphonia elongata E (P)	(P) (P)
	(P)
Polysiphonia fibrillosa (E) BDE (P)	
Polysiphonia flexicaulus - P (P) CDE DE	DE
Polysiphonia harveyi (P) (P) E CDE DE	(D)E
Polysiphonia lanosa BC ABC BC ABC -	-
Polysiphonia nigrescens D DE E BCDE DE	DE
Polysiphonia novaeangliae ⁵ - DE D 2CDE D	DE
Polysiphonia subtilissima 1E -	(P)
Polysiphonia urceolata 1CD CDE DE 1*2CDE DE	(D)E
Porphyra leucosticta ⁹ (P) C - (P) -	-
Porphyra linearis (P) (P) - (P) C	-
Porphyra miniata ¹⁰ 1AB 2CD C(D)E BDE -	-
Porphyra umbilicalis ⁹ AB 2ABC A CE (P)	(P)
Ptilota serrata (P) CDE (E) E E	E
Rhodomela confervoides C 2CDE 2DE BCDE DE	DE
Rhodophysema elegans - (P) - E E	E
Scagelia corallina (P) DE - E E	DE
Scinaia forcellata P - (P)	-
Stylonema alsidii (P) DE	DE
Fauna	
Balanus, Pseudobalanus spp. AB 1ABC 12B ABC (AB	B) (BC)E

Sector: Shores: Sites:	Fundy 1-5	Outer Fundy 6-7 7-20	Fundy Approaches 8-9 21-29	Eastern Atlantic 10-15 30-44	Open Gulf 16, 17, 20 45-83	Lower Gulf 18, 19, 21, 22 84-89
Mytilus edulis	BC	BE	2BD	12BCDE	(CD)E	(BD)E
Strongylocentrotus droebachiensis	DE	CDE	-	DE	E	E

¹ Including L. longicruris.

² Sensu Blair (1983).

³ Sensu Woelkerling (1973).

⁴ Lindstrom (1985).

⁵ Sensu Taylor (1957).

⁶ Including R. lycopodioides.

⁷ Tetrasporophyte only, except for occurrence of gametophytes in Fundy approaches and eastern Atlantic.

⁸ H. crouanii and/or H. rubra (C. Maggs pers. comm.).

⁹ Sensu Yabu (1978). Validity of nomenclature is in question (Mitman pers. comm).

¹⁰ Validity of nomenclature is in question (Chen pers. comm.).

¹¹ Guiry et al. (1984).

¹² Chamberlain (1983).

¹³ See also tetrasporophytic phase, Petrocelis cruenta.

Appendix 3

Vertical distributions of macroalgae at Fundy sites 2-19; Fundy Approaches (Atlantic) sites 21-26, eastern Atlantic sites 30-44; and Gulf sites 65-89. Range of dominance or co-dominance (species code in large letters) indicated by a bar; presence beyond this range, by a line. Species common within the same range encoded in small letters. Rock pool and epiphytic species excluded. Intertidal heights relative to tidal levels, sublittoral excluded. Intertidal heights relative to tidal levels, sublittoral depths indicate m below CD. Species are encoded as follows:

BROWN ALGAE

Ac Agarum cribrosum Ae Alaria esculenta

An Ascophyllum nodosum

Cf Chorda filum

Ch Chordaria flagelliformis

Da Desmarestia aculeata

Df Dictyosiphon foeniculaceous

Dv Desmarestia viridis

Fe Fucus evanescens

Fr F. serratus

Fs F. spiralis

Fv F. vesiculosus

Hs Halopteris scoparia

Ld Laminaria digitata

Ls L. saccharina/longicruris

Sd Saccorhiza dermatodea

SI Scytosiphon Iomentaria

GREEN ALGAE

Bm Blidingia minima

Cm Chaetomorpha melagonium

Sa Spongomorpha arcta

Ss S. spinescens

Uf Ulothrix flacca

Ul Ulva lactuca

Ur Urospora spp.

RED ALGAE

Ap Ahnfeltia plicata

Cc Chondrus crispus

Co Corallina officinalis

Cy Cystoclonium purpureum

Di Dilsea integra

Dr Devaleraea ramentacea

Fl Furcellaria lumbricalis

Ms Mastocarpus stellatus

Od Odonthalia dentata

Pa Palmaria palmata

Pb Polysiphonia subtilissima

Pe P. elongata

Ph Phycodrys rubens

Pn Polysiphonia nigrescens

Po Porphyra spp.

Pp Phyllophora pseudoceranoides

Pr Polyides rotundus

Ps Ptilota serrata

Pt Phyllophora truncata

Pu Polysiphonia urceolata

Rc Rhodomela confervoides

Sc Scagelia corallina

ANIMALS

Ba Barnacles Mu Mussels

