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The biogeographic structure of the western North Atlantic rocky intertidal[1]

*Walter H. ADEY[a] * and Lee-Ann C. HAYEK[b]*

[a]*National Museum of Natural History, Department of Botany, NHB-166,*
P.O. Box 37012, Smithsonian Institution, Washington D.C. 20013-7012, USA

[b]*National Museum of Natural History, Statistics and Mathematics,*
NHB-P.O. Box 37012, Smithsonian Institution, Washington D.C. 20013-7012,
USA

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Abstract — The shallow water, coastal flora and fauna from Cape Cod to southern Labrador in the northwestern North Atlantic have been biogeographically regarded as a single unit, although the northern half has been only weakly sampled. The recent "Adey/Steneck biogeographic model" for the subtidal has shown the northern half of this coast as a core Subarctic Region, while the southern half is mixed Boreal/Subarctic (the North Atlantic Boreal being centered in the British Isles). In this study, quantitative sampling, and statistical and graphic analyses of the dominant intertidal biota shows the two areas to be quite different based on species biomass or number of individuals/m^2. *Ascophyllum nodosum*, highly dominant in the southern part of the area becomes an occasional in the north, with *Fucus vesiculosus* in part replacing it, while *Fucus distichus*, a minor species in the south, becomes a dominating element on the northern rocky shores. The ubiquitous, intertidal, understory of the bushy-red alga *Chondrus crispus* and its associated algae in the Gulf of Maine and Nova Scotia, virtually disappears in the northern half of the region, being replaced by the large, filiform, brown alga *Chordaria flagelliformis* and its complex of ecologically-associated species. The characteristic, intertidal mollusc fauna shows a parallel change, with the abundant *Littorina littorea* of the southern coast being replaced by *L. saxatilis* northwards. Those species dominating the intertidal coastal biota surrounding the Strait of Belle Isle (center of the Subarctic core) provide 85% of the number/area/biomass count, but are only 13% of that count in the Gulf of Maine. These results provide further support for the Adey/Steneck theoretical model and demonstrate the necessity for using quantitative area/biomass data, as opposed to only species presence/absence data, in biogeographic analyses.

benthic invertebrates / biogeography / biogeographic model testing / community structure / marine algae / quantitative ecological analysis / rocky intertidal / western North Atlantic

Résumé — Structure biogéographique de la zone intertidale rocheuse de l'Ouest de l'Atlantique nord. La flore et la faune des eaux peu profondes et côtières du Cap Cod, au sud du Labrador, dans l'Atlantique nord occidental, ont été considérées comme une seule unité au plan biogéographique, bien que la partie nord n'ait été que faiblement étudiée. Le

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[1] The authors are very pleased to dedicate this paper to Dr Isabella Aiona Abbott in celebration of her 85th birthday, and in appreciation for "Izzie's" monumental contributions to phycology.

* Reprints and correspondence: adeyw@nmnh.si.edu
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récent modèle biogéographique Adey/Steneck utilisé pour la zone subtidale a montré que la moitié de la partie nord de cette côte appartient au cœur de la région subarctique, tandis que sa partie sud est un mélange boréal/subarctique (l'Atlantique nord boréal étant centré sur les Îles britanniques). Dans la présente étude, un échantillonnage quantitatif, ainsi que des analyses statistiques et graphiques des biontes intertidiaux dominants, montrent que les deux aires diffèrent sensiblement par la biomasse spécifique ou le nombre d'individus par m^2. *Ascophyllum nodosum*, hautement dominant dans la partie sud de l'aire étudiée devient un occasionnel dans le nord, *Fucus vesiculosus* le remplaçant en partie, tandis que *Fucus distichus*, espèce mineure du sud, devient un élément dominant sur les plages rocheuses du nord. L'algue rouge de sous-strate, buissonnante, ubiquiste, intertidale, *Chondrus crispus*, ainsi que les algues qui lui sont associées, dans le Golfe du Maine et en Nouvelle Écosse, disparaîssent virtuellement dans la partie nord, remplacées par l'algue brune, grande et filiforme, *Chordaria flagelliformis* et son cortège d'espèces écologiquement associées. La malacofaune intertidale caractéristique montre un changement parallèle, avec l'abondant *Littorina littorea* de la côte sud remplacé par *L. saxatilis* du Nord. Ces espèces dominant les biotopes intertidaux costaux autour du détroit de Belle Isle (centre Subarctique) représentent 85 % des comptages nombre/aire/biomasse, mais seulement 13 % des comptages dans le Golfe du Maine. Ces résultats fournissent des arguments supplémentaires en faveur du modèle théorique Adey/Steneck et démontrent la nécessité d'utiliser des données quantitatives aire/biomasse, en contrepartie des seules données présence/absence de l'espèce, dans les analyses biogéographiques.

Algues marines / analyse écologique quantitative / Atlantique nord occidental / biogéographie / modèle biogéographique expérimental / structure de communauté / zone intertidale rocheuse / invertébrés benthiques

INTRODUCTION

An extensive review by Mathieson *et al*. (1991) brought together a century of work on the intertidal biota of the northwest Atlantic rocky shore. The dominant algae and sessile invertebrates of the intertidal region were mainly shown as they relate to wave exposure and tide height (Mathieson *et al*., 1991: fig. 7.4; = Fig. 1 herein, with outlines delimiting the extent of the major biotic components). Their characterization of the southern half of the NW Atlantic intertidal biota (ca. 40° – 47° N latitude: Gulf of Maine, Nova Scotia, Prince Edward Island) was mostly derived from several studies, while the northern half (ca. 47° – 54° N: Gulf of St. Lawrence, Newfoundland and S. Labrador) was represented by a single study (Bolton, 1981). Based on a highly exposed shore at Bay Bulls, Newfoundland, Bolton (1981) showed that along with *Semibalanus balanoides* and *Mytilus edulis*, the macroalgae *Fucus distichus* subsp. *edentatus* and *Pylaiella littoralis* were the common elements, and that none of the dominant intertidal algal species shown by Mathieson *et al.* (1991; i.e., *Ascophyllum nodosum, Fucus vesiculosus* and *Chondrus crispus*) were found. All of the dominant algal species known to occur throughout the region were based solely on presence/absence data (South & Tittley, 1986; Lüning, 1990); little quantitative ecological data is available on their abundance in a geographical context.

Mathieson *et al.* (1991) noted that intertidal shores in the northern part are often devoid of algae due to winter ice scour. However, ecologically it is far more complex than a simple correlation of winter sea ice and barren shores, e.g., the inner portions of bays of the Maine coast are often ice-bound in winter, and this is where the largest biomass of perennial fucoids (especially *Ascophyllum*) is

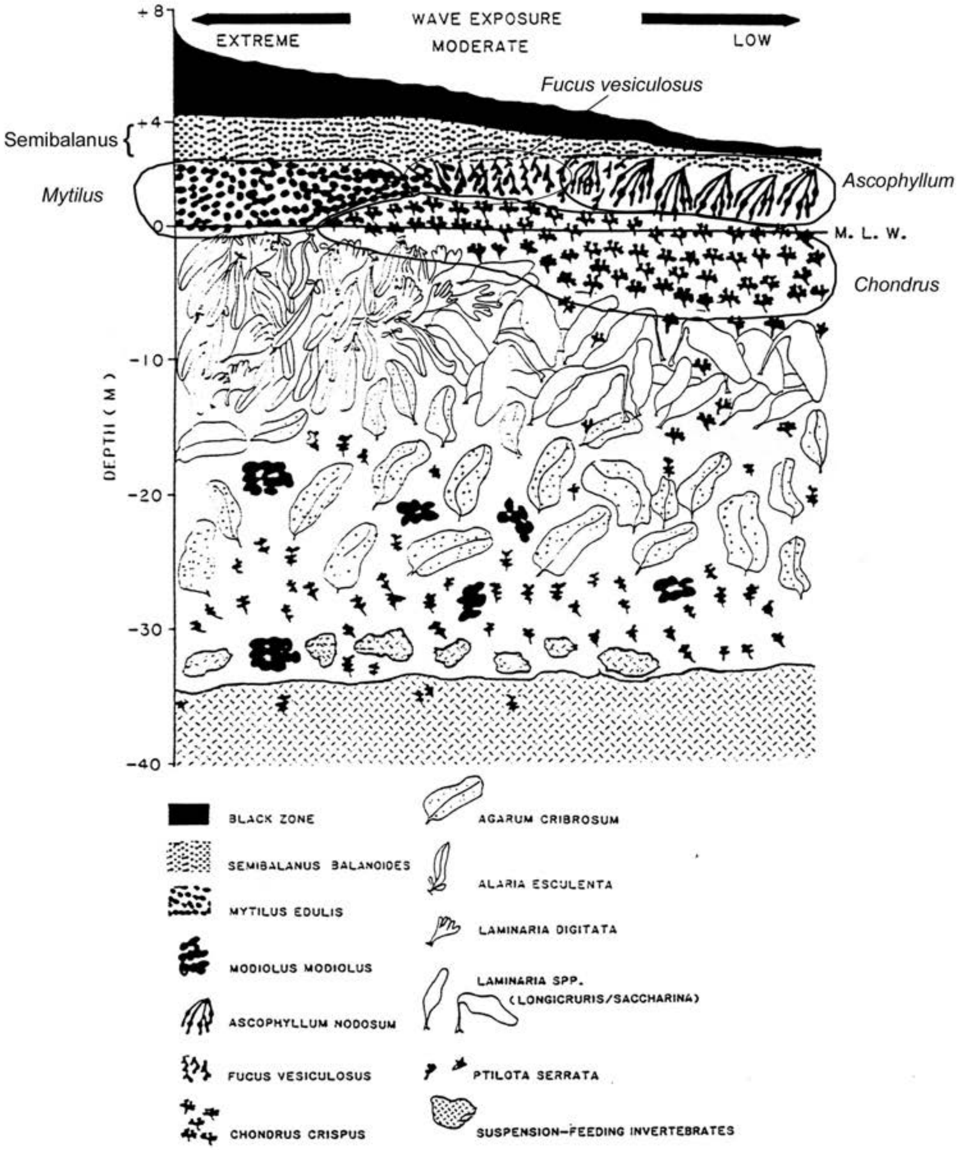

Fig. 1. Major benthic organisms on Northwest Atlantic rocky shores. Dominant bands or zonation patterns of the intertidal are outlined for emphasis (from Mathieson *et al.*, 1991).

typically found. Similarly, the southern coast of Labrador, ice-bound for six months of the year, can have a dense cover of fucoid and other macroalgae, wherever an "ice-foot" (or shore-fast ice band) forms early in the winter season, or where crevices, boulders and tide pools provide protection from ice scour. Likewise, these shores often have exceptionally rich populations of littorinid snails. We found that the presence of shore-fast winter ice is not a deterrent to the development of strong eulittoral (and infralittoral) algal biomass and large invertebrate populations. Where a significant ice foot is formed and maintained through the winter, significant fucoid bands are often present (Figs 2-3). It is where substantial wave action works loose pack ice against an unprotected shore that ice scour occurs and removes perennial macrophytes and sessile animals. However, especially in the Subarctic, the quantity of sea ice varies from year to year, and

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Fig. 2. Dense fucoid algal cover on a eulittoral bench, mouth of Bras D'Or Bay, Quebec Shore, near the SW entrance to the Strait of Belle Isle. In a typical winter, this shore is ice-covered for 5-6 months of the year.

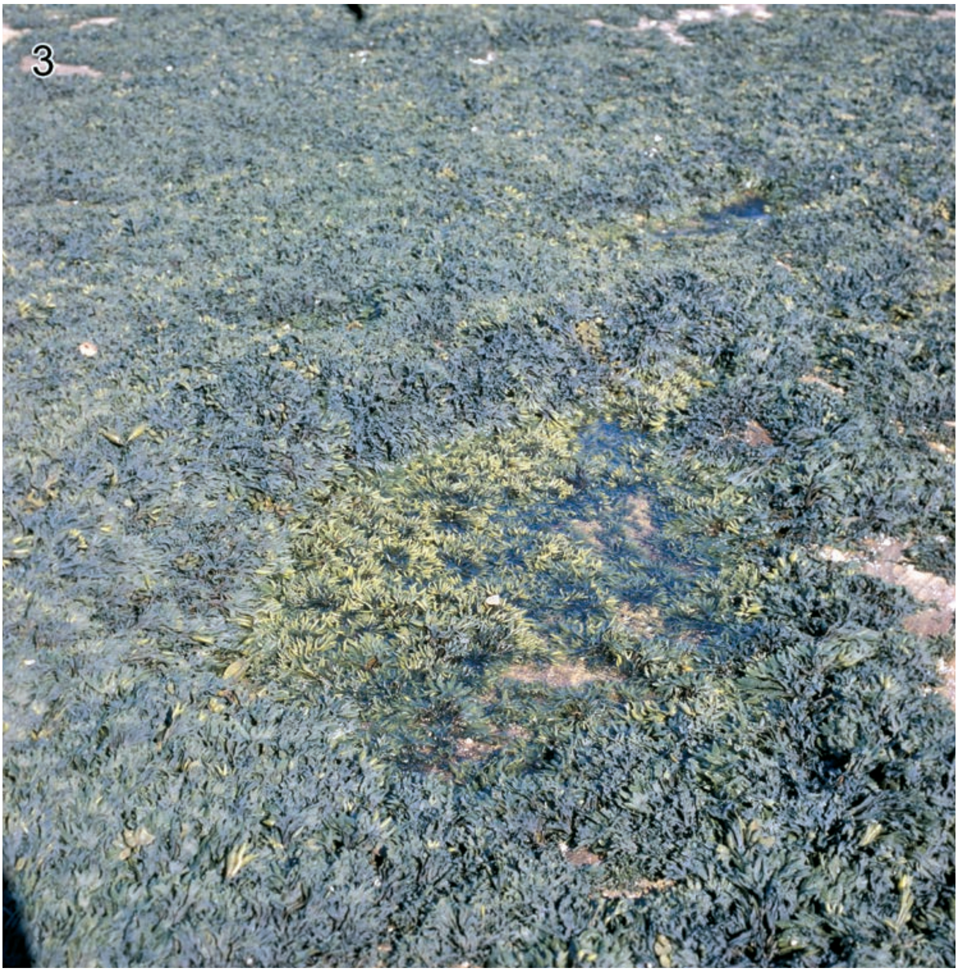


Fig. 3. Close-up of the fucoid-covered bench of Fig. 1, showing the extensive cover and dominance of *Fucus distichus* on the lower shore.

even in the worst ice years, there are shore “polynya” (an area of open water surrounded by sea ice), kept open by winds and currents, as well as the local orientation, geomorphology and composition of the shoreline. Barnes (1999) discusses how sea ice scour can be catastrophic, and the primary determiner of community structure. However, the creviced geomorphology and boulder-strewn of most rocky shores in the western North Atlantic is such that rarely is benthic biotic removal complete over large areas; the creviced and boulder-strewn geomorphology often support well-developed algal and animal communities absent from adjacent elevated and scoured surfaces.

Although quantitative literature on ice-scouring for the northern half of the NW Atlantic region is limited, Keats *et al.* (1985) demonstrate that the composition of infralittoral algae in Conception Bay, Newfoundland, varies considerably between ice scour years and non-ice years. Ice “events” can reduce the subsequent summer algal standing crop to half of its levels in non-ice years (5.4 kg to 2.7 kg wet-weight/m^2). When ice scouring has not occurred, the kelp *Alaria esculenta* tends to strongly dominate. However, when it does occur, other species (along with *Alaria*) become important, including the kelp *Saccorhiza dermatodea*, the large, filiform brown *Chordaria flagelliformis* and the red *Devaleraea ramentacea*. Even though Keats *et al*. (1985) listed and weighed 23 algal species (many being long-lived perennials), *Chondrus crispus* (considered by some to be the characteristic dominant of the Gulf of Maine and Nova Scotia in this zone) was not among them.

Along with the sessile invertebrates *Semibalanus balanoides* ('northern rock barnacle') and *Mytilus edulis* ('blue mussel'), Mathieson *et al*. (1991) note the abundant presence of the grazing snails *Littorina littorea* and *L. obtusata* in the eulittoral, and *L. saxatilis* in the supralittoral. Many studies have shown that these grazers are instrumental in structuring intertidal macroalgal-dominated communities (e.g., Raffaelli & Hawkins, 1996). Although the presence of these characteristic intertidal and supratidal molluscs is often mentioned, their relevant north to south abundance has not been investigated. On this coast the northernmost distribution limits of *Littorina littorea* reaches southernmost Labrador and *L. obtusata* to mid-Labrador; while *L. saxatilis* extends well into the Arctic (Reid, 1995).

Studies on the quantitative distribution of the subtidal, long-lived, crustose coralline algae from Long Island Sound to the northern tip of Labrador (Adey 1966, 1968; Adey & Adey 1973), demonstrated a considerable change in species composition from south to north. Although most coralline species occurred from south to north over the entire western North Atlantic rocky coast (with Cape Cod forming a major break in species distribution and a second, less distinct, break in southern Labrador), their abundance (bottom cover) changed markedly with geography (and summer temperature). Adey & Steneck (2001) in developing their theoretical model of littoral biogeography, used sublittoral coralline distributional data (over the entire northern North Atlantic) to support the model. The same coralline data, herein separated into Boreal species (*i.e.*, those species reaching maximum abundance in the British Isles and S. Norway), Arctic species (*i.e.*, those reaching maximum abundance in N. Labrador), and Subarctic species (*i.e.*, those reaching maximum abundances from the Gulf of Maine to Newfoundland/S. Labrador) are re-plotted and contoured as percent Subarctic (Fig. 7).

In the sublittoral, Subarctic species enter the coralline flora just north of Cape Cod and more-or-less gradually increase to a peak of cover greater than 90% of the flora in Newfoundland, N. Gulf of St. Lawrence and S. Labrador. These Subarctic species are then gradually replaced in cover by Arctic species extending up the N. Labrador Coast. Several "holes" or retrenchment areas occur, especially around Prince Edward Island and W. Newfoundland, where locally the abundance of Subarctic species drops (and Boreal species increase) due to warmer summer seawater temperatures produced by local geography. The Northumberland Strait and Prince Edward Island to Chaleur Bay coast is very shallow with a small tidal range and is strongly affected by terrestrial warming in summer; at 35%, this area achieves the highest abundance of Boreal corallines north of Cape Cod and the SW Nova Scotia area. In summer, the W. Newfoundland coast is warmed by the "piling up" of surface waters off the Gulf of St. Lawrence due to the prevailing summer southwesterly winds, achieving a Boreal coralline abundance of 16% in a latitudinal east/west band that otherwise is less than 4%.

The coralline flora of the sublittoral of the coasts of Gulf of Maine, central and eastern Maine and Nova Scotia, where most of the studies were conducted (Mathieson *et al.*, 1991), is approximately 65% Subarctic and 35% Boreal (Fig. 7). The northern half of the NW North Atlantic region (excepting the warmer coast of W. Newfoundland), is characterized by a sublittoral coralline flora that is approximately 95% Subarctic in its cover (with roughly 3% Arctic and 2% Boreal). In our study we examine the dominant eulittoral biota of the "core" Subarctic Region of E. and N. Newfoundland, S. Labrador and the N. Gulf of St. Lawrence to test whether or not this biota reflects the considerable difference that exists in sublittoral coralline algal composition. The NW Atlantic rocky shore has been characterized by studies in an apparently strongly transitional area where Boreal elements form a major part of the biota. We ask: what is the character of the "core" Subarctic eulittoral, and how does it compare with the Gulf of Maine eulittoral?

MATERIALS AND METHODS

Ecological methods. Intertidal stations north of 47°N with the coasts of Newfoundland, Labrador and the N. Gulf of St. Lawrence were studied in the summers of 2001 and 2002 (Fig. 7); and the Gulf of Maine stations in the summers of 1993-1995. Divided into sub-regions, sectors of these coasts were selected for their relatively even geographic distribution. Station locations were shorelines that were accessible by a drivable trail, or within a half-km hike from a road, and for a few, by local boats. Within these stations selected, sectors were stratified for wave exposure, vertical height and substrate.

In the northern three geographic subsets (i.e., NE part of E. Newfoundland subregion, N. Newfoundland and Labrador, and NW Gulf of St. Lawrence) a further station character was required since most were on exposed shores, where ice scouring can reduce macro algal biomass to very low levels. In these regions, significant biomass occurs primarily in crevices, in boulder fields and/or in rock fractures. Stations reported were in wide areas of well-developed algal biomass thus providing mean quantitative algal biomass maxima.

Station localities in exposed areas were defined as those dominated by bedrock ledge and boulder, and in more protected areas by bedrock ledges, boulders and cobbles. Shores with greater than about 20% pebbles (more protected) or cobbles/small boulders (more exposed) were rejected as unsuitable for developing significant algal biomass, as were those with an overall slope greater than about 30°. All stations selected were on primarily granite, gneiss, schist, sandstone, volcanic, and/or rarely limestone substrata. Substratum that easily eroded or friable was not used. Glacial till - derived boulders and cobbles were often present, and in mineral composition, largely represented the local bedrock. Randomness was achieved within the strata by throwing quadrat squares. To avoid statistical boundary problems, local vertical or near vertical slopes are not included (since thrown quadrats would not stay on these slopes), and only quadrats that lay against the base of a local vertical slope were sampled.

Quadrats (0.1 m^2 in size), constructed of plastic and steel, were sampled. Where possible, on low slopes (typically wave-cut benches), these were thrown over the shoulder; on steep slopes, the quadrat was thrown directionally (to avoid its loss) and sometimes several throws were needed to obtain the desired

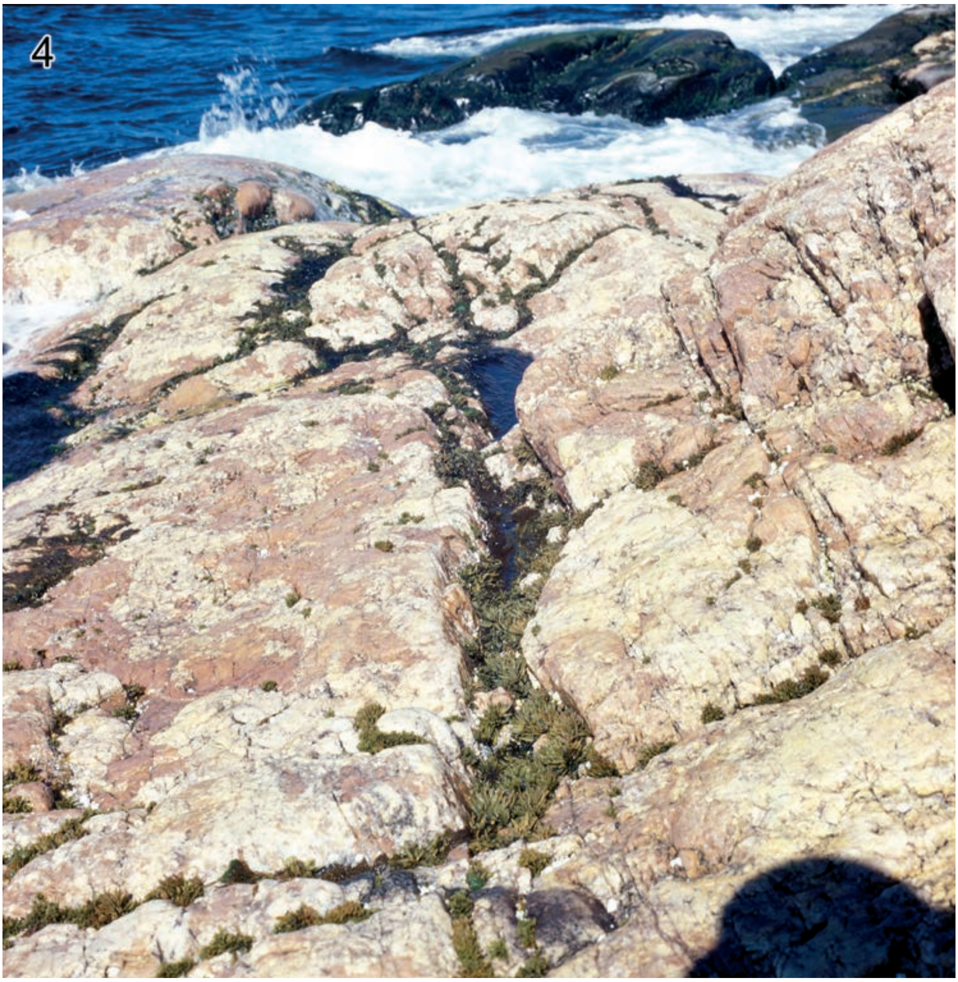


Fig. 4. Highly-exposed (Labrador Sea/ North Atlantic Ocean) mid-tidal shore, Battle Harbour, Labrador. The "open" rock surface is ground free of all macrobiotia by constantly moving winter pack ice for at least six months of the year; however, the crevices have a persistent cover of *Fucus distichus*, a modest amount of *Mytilus* and scattered *Balanus*. While *Littorina littorea* was not found, *L. saxatilis* was abundant throughout the eulittoral.

tidal range. The "bounce" of the quadrat before landing prevented targeting or haphazard selection. If the quadrat landed at least partially in a tide pool, it was thrown again. Tide pools, the supratidal and the infralittoral were given a general visual description, but not quantitatively studied. Infralittoral quadrats with more limited data were used to establish boundary conditions for the contour plots.

Arrival at study sites was scheduled two-three hours prior to the time of low tide ("Tide Tables for the East Coast of North and South America," 2001, 2002). The bottom boundary of the eulittoral was the mean upper line of the infralittoral community (usually a sharp band) as compared against the expected

Fig. 5. Mid-tidal pool, 10m from the locality of Fig. 4. Upper surface of the dense biomass visible is *Fucus distichus*. Figure center about 2 meters across.

low tide level for the day, and the top by the limit of fucoid algae and/or barnacles. Elevation and zone extension due to wave action was noted and compared with the tidal range. On protected shores, "eulittoral" refers to the zone between mean low- and high-water neap tides, and "infralittoral" to the zone between mean low water neap and spring tides. The eulittoral region of about 50 m. of shore was visually divided into three equal vertical zones, low, middle and upper; within each, five successive quadrats (0.1 m^2) were thrown. On more exposed shores with biotic zone elevations (up to 2 meters), the additional elevation was included as part of the eulittoral range.

Quadrats were first photographed using a U/W Nikonos V© 35 mm camera with a Nikonos 35 mm lens, and Fujichrome™ Provia 400 color film, to assess algal cover. Next macroalgae were collected by cutting the holdfasts at the substratum, and significant epiphytes by hand. Collections were sorted to species, placed in a pre-weighed plastic mesh bag, and weighed with a hand-held 5 kg scale (Pesola™ #80005; reads about 0.1 kg, listed as ±0.3% load). Weights below that level were recorded as either trace or an estimated fractional value of 0.1 kg. After macroalgal collection, surface cover of *Mytilus, Semibalanus* and crustose algae on the underlying rock was estimated as a percentage of total surface area. During algal removal, littorinid snails and limpets were picked off or shaken into the quadrat, and then put in a plastic bag (data pooled as a five quadrat set of each zone) and returned as vouchers (USNM). After collection each quadrat "base" was re-photographed to record the type of substratum.

Algae from each quadrat were identified using a Wild M-5 dissection microscope. If species identification was in doubt (e.g., *F. vesiculosus* of the mid-zone of exposed locales sometimes lacked vesicles), color and shape correlation with local algae with vesicles were utilized. Herbarium vouchers are deposited in the Algal Collection of the U.S. National Herbarium (US; herbarium abbreviation follows Holmgren *et al.*, 1990). Littorinid identification was done after drying following the methods of Reid (1996). Larger snails were usually not a problem; *L. littorea* is quite distinctive. Microstriae present on small *L. obtusata* var. *palliata* differentiate it from similar-sized *L. saxatilis* var. *groenlandica* of northern stations. Though rare in Gulf of Maine eulittoral, varieties of *L. saxatilis* and *L. obtusata* were easily differentiated. Juveniles below 4mm in length were not generally retrieved or included in this study.

Statistical Methods. Summary statistics for total biomass and one-way analyses of variance were run for each locality. Descriptive statistics by exposure and levels of tidal height were calculated within each locale and over all 4 locales. Tests for significant mean differences were run using Student's or Satterwaithe t-tests, depending on the results of Hartley's F-max test for homogeneity of variance. Factorial ANOVA designs were evaluated and tests on means run with and without covariate analysis. General linear models were developed separately for each of these sections or locales. Furthermore, all locales were included in an overall factorial model and polynomial trends were assessed within and between locales, over factors of tidal height and exposure. Means, standard errors and station and quadrat frequencies were calculated for the biomass of each species, and exposure and elevation groupings (Figs 1-14; Tabs. 1-8). Statistical modeling and analyses of the subregions are the same as those described above; except the NE and SE Newfoundland areas were combined into a single subregion, "eastern Newfoundland."

Contouring of biomass as a function of exposure and elevation was accomplished with the 10.2 SYSTAT Scatterplot/contouring graphing tool. Although only the contours within close proximity to the data points were used in the diagrams, boundary conditions were established one equivalent step above and below and to the left and right, so as to not constrict the contours. One step above the data, in the very low biomass Black Zone (where fucoids are lacking), total biomass was arbitrarily given a value of 1.0 gram/m^2 [species were all given a biomass of zero in this zone]. Below the diagrams, in the infralittoral, mean values were derived from scattered quadrats during extremely low tides and from more extensive quadrats using SCUBA in 2003. Numbers for boundary conditions on either end of the diagrams (theoretically super-protected & super-exposed), were made by continuing mid to protected and mid to exposed gradient data.

RESULTS AND DISCUSSION

Macroalgae. Results are presented first by locality and then over all localities. In total, 190 biomass measurements were made for the Gulf of Maine (locality 1), 285 in E. Newfoundland (locality 2), 180 in Labrador Straits area (locality 3), and 75 (none possible for mid level) in NW Gulf of St. Lawrence (locality 4) (Tab. 1). At each locality, an equal number of stations were examined at each of the three tidal heights. Each one-way analysis of variance for locality was highly significant, except locality 4 (because of the lack of mid level data). Locality mean biomass at each of the three tidal heights decreased from Maine northwards (Tab. 1; Fig. 12).

Within each factorial ANOVA model (Tab. 3) both tidal height and exposure were highly significant, while each of the interaction terms for exposure by tidal height was non-significant, regardless of locality. Tidal effect size (0.078, 0.046, & 0.022), was the largest in the Gulf of Maine and decreased northwards, with the W. Gulf of St. Lawrence, 0.082, only over two levels.

In considering the entire western North Atlantic sampling area, tests were performed within a 3-way factorial model framework with 730 degrees of freedom. All factors were highly significant, *i.e.*, exposure, tidal height and locality ($p<0.0001$). The 3-way interaction of tidal height by locality and by exposure level was not significant ($p=0.143$, effect size of 0.02). Therefore, a test for the existence of the quadratic trend observed at each of the four localities separately was done over the entire locality set. The result was highly significant, enabling us to fit a single quadratic surface to the data over locality regardless of level of site exposure. This surface is descriptive of the consistent tidal height changes in biomass throughout the western Atlantic (Tab. 4).

Biomass, in grams/m^2 (standing crop) of each significant macroalgal species, was plotted as the means of the indicated number of stations (for exposed, intermediate and protected stations, and upper, middle and lower zones) (Figs 8-11). Within each sub-region, mean biomass of each macroalgal species at all exposure/height zones is shown separately; total biomass is at the top of diagram; standard error and station and quadrat frequency data for each mean also given (Tabs 5-8). In all geographic subregions (Fig. 7), algal biomass reached a peak in the mid-eulittoral zones of protected stations (Figs 8-11). Progressively, it was reduced both upwards and downwards in the eulittoral, as well as towards greater exposure. Exposed stations usually had only half to two thirds of the algal biomass of protected stations, and upper and lower eulittoral zones had roughly half to two thirds of the biomass of the mid-eulittoral.

In the Gulf of Maine (Fig. 8), *Ascophyllum nodosum* followed the same pattern with 94% of the total macroalgal biomass at protected stations, which decreased to 45% at exposed stations. Although *A. nodosum* was present almost everywhere as scattered individuals in the eulittoral, *Fucus vesiculosus* (with smaller proportion of *Fucus spiralis* in the uppermost eulittoral) made up a much smaller amount, only 9% of the total biomass. If only upper zones are considered, *F. vesiculosus* made up 24%, and in the exposed stations 21%. *Fucus distichus* occurred only in the lower zones of more exposed stations, providing almost 33% of the total biomass. Mirroring its frequent, band-forming dominance in the infralittoral, *Chondrus crispus* (and occasionally *Mastocarpus stellatus*) extended up the eulittoral under the fucoid cover, limited in its biomass development by increasing elevation and greater shore protection.

Fig. 6. Dense cover of dominant brown algae near locality of Fig. 3: in the background *Chordaria flagelliformis* and *Petalonia fascia* (upper right; darker brown) extending lower in the infralittoral; and in the foreground *Fucus distichus* extending higher in the lower eulittoral.

In all E. Newfoundland sub-regions (Fig. 9), total macroalgal biomass was less than two-thirds of that in the Gulf of Maine. *Ascophyllum nodosum* made up only 37% of the regional total, and was limited or absent at exposed stations and markedly reduced at mid exposure stations. In contrast, *Fucus vesiculosus* (with *F. spiralis*), rose to 44% of the total regional biomass, becoming the dominant in the mid and upper zones of outer stations. *Fucus distichus* dominated in the lower zones of mid and exposed stations, much as in the Gulf of Maine. In E. Newfoundland, *F. distichus* generally penetrated much further upwards in the eulittoral and to more protected stations, and also strongly into the infralittoral, whereas in the Gulf of Maine it was only an occasional. *Chondrus crispus* was still

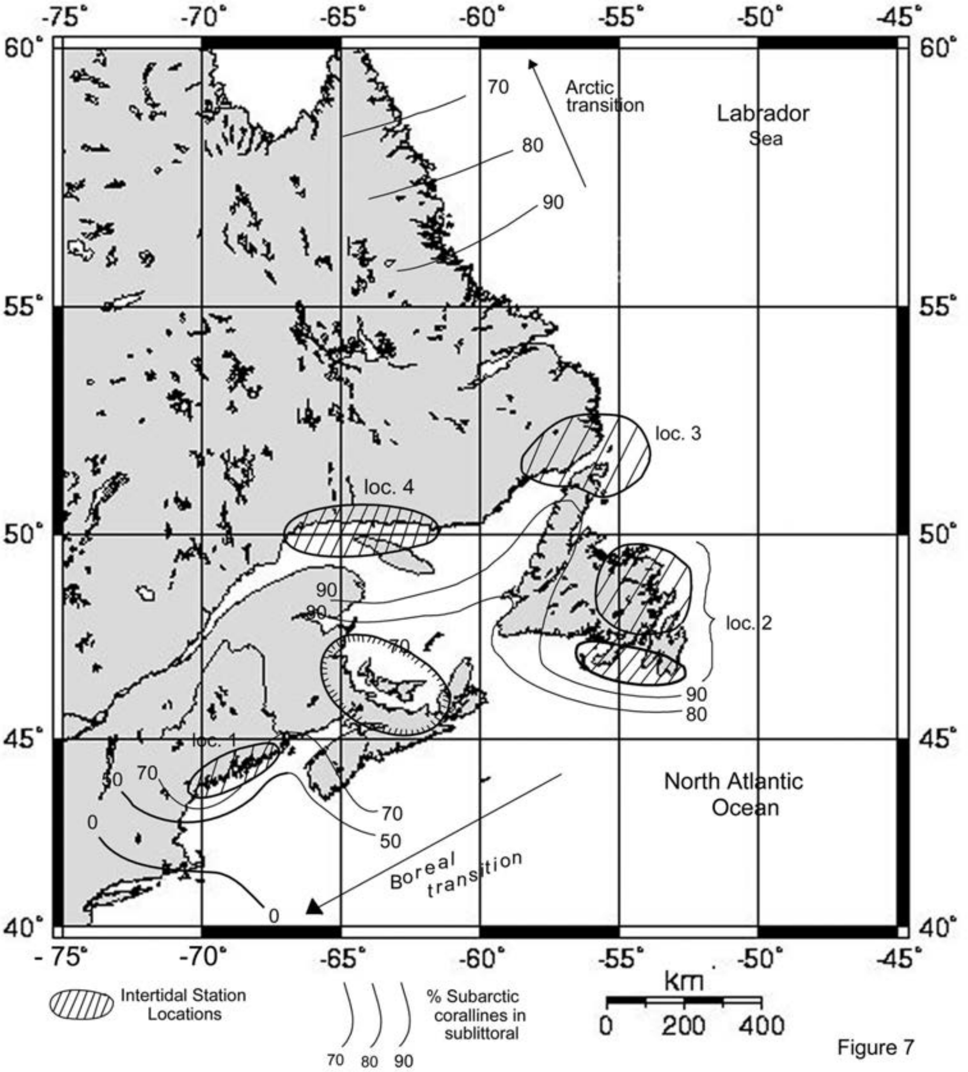


Fig. 7. Distribution (% cover) of Subarctic corallines in the western North Atlantic. The areas of station localities of this study are shown as diagonal hachures.

common in the lower zones, but members of the *Chordaria*-complex (numbers in squares) began to appear as measureable biomass in outer stations and lower zones. This *Chordaria*-complex, usually dominated by *C. flagelliformis*, also included varying amounts of *Petalonia fascia*, *Pilaiella littoralis*, *Scytosiphon lomentaria* and *Devaleraea ramentaceum.* At ice-scoured stations (mostly exposed stations in the northeast; significant sea ice does not occur in the southeast), macroalgal biomass was negligible (trace, as indicated by “Tr.” in the figures). On ice-scoured shores, macroalgae were found in crevices and fractures, with dwarf *Fucus distichus* clearly dominating at all tide levels.

Table 1. Estimated marginal means by factor and level for each locality, with 95% confidence intervals.

A. Grand Mean by locality

Locality	*Mean*	*Standard Error*	*95% confidence Interval*	
1	14494.4	998.3	12524.57,16464.32	Gulf of Maine
2	8936.2	392.9	8162.83,9709.60	Eastern Newfoundland
3	5513.9	347.2	4828.53,6199.25	N. Peninsula Nfld. & S. Labrador
4	6952.8	539.1	5877.22,8028.33	northwestern, Gulf of St. Lawrence

B. Exposure by locality. 1 = Exposed sites; 2= Mid exposure; 3= protected sites

Locality	*Exposure*	*Mean*	*Standard Error*	*95% confidence Interval*
1	1	9673.3	1768.9	6182.97,13163.70
	2	14248.3	1768.9	10757.97,17738.70
	3	19561.7	1646.8	16312.31,22811.02
2	1	6155.6	686.2	4804.71,7506.41
	2	9449.3	751.7	7969.55,10929.12
	3	11203.8	594.3	10033.88,12373.62
3	1	3921.7	601.4	2734.60,5108.74
	2	5011.7	601.4	3824.60,6198.74
	3	7608.3	601.4	6421.26,8795.41
4	1	5888.9	682.0	4528.41,7249.37
	3	8016.7	835.2	6350.42,9682.91

Table 2. Tidal Height by locality. (1= upper; 2=mid; 3=low).

Locality	*Tidal Ht*	*Mean*	*Standard Error*	*95% confidence Interval*
1	1	11160.0	1708.9	7787.99,14532.01
	2	19921.7	1708.9	16549.65,23293.68
	3	12401.7	1768.9	8911.30,15892.03
2	1	8102.3	680.5	6762.73,9441.82
	2	10304.8	680.5	8965.29,11644.38
	3	8401.5	680.5	7061.98,9741.07
3	1	4601.7	601.4	3414.60,5788.74
	2	6893.33	601.4	5706.26,8080.41
	3	5046.7	601.4	3859.60,6233.74
4	1	5125.00	933.8	3262.08,6987.92
	2	7450.00	933.8	5587.08,9312.92
	3	8283.33	933.8	6420.42,10146.25

Table 3. Factorial 2-way ANOVA with interaction test results for each of the four Western Atlantic sites. Abbreviations used: *df*: degrees of freedom for the test; *Obs. P*: probability level calculated form observed data; *Obs*. Power: the power of the test calculated form the observed data assuming a type 1 error rate of 5%.

Locality 1. Gulf of Maine

Source	*df*	*F*	*Obs. p*	*Effect Size*	*Obs. Power (α = 0.05)*
Exposure	2	8.427	0.000	0.085	0.963
Tidal height	2	7.645	0.001	0.078	0.945
Interaction	4	2.066	0.087	0.044	0.608
Error	181				
Corrected Total	189				

Locality 2. Eastern Newfoundland

Source	*df*	*F*	*Obs. p*	*Effect Size*	*Obs. Power (α = 0.05)*
Exposure	2	15.572	0.000	0.101	0.999
Tidal height	2	3.082	0.047	0.022	0.591
Interaction	4	1.110	0.352	0.016	0.348
Error	276				
Corrected Total	284				

Locality 3. The northern peninsula of Newfoundland plus southern Labrador

Source	*df*	*F*	*Obs. p*	*Effect Size*	*Obs. Power (α = 0.05)*
Exposure	2	9.919	0.000	0.104	0.983
Tidal height	2	4.0830	.0190	.046	0.719
Interaction	4	0.1860	.9460	.004	0.089
Error	171				
Corrected Total	179				

Locality 4. Western Gulf of St. Lawrence

Source	*df*	*F*	*Obs. p*	*Effect Size*	*Obs. Power (α = 0.05)*
Exposure	1	3.894	0.052	.053	.494
Tidal height	2	3.0720	.053	.082	.575
Interaction	2	0.8840	.418	.025	.196
Error	69				
Corrected Total	74				

Table 4. The Western Atlantic Region.

Tidal Height.

Tidal Ht	*Mean*	*Standard Error*	*95% confidence Interval*
1	7779.6	604.2	6593.49,8965.77
2	11815.1	604.2	10629.00,13001.28
3	8591.0	608.8	7395.7,9786.4

Exposure by Tidal Height

Exposure	*Tidal Ht.*	*Mean*	*Standard Error*	*95% confidence interval*
1	1	5545.8	954.80	3671.21,7420.46
	2	7112.5	954.8	5237.88,8987.12
	3	6571.3	954.8	4696.63,8445.87
2	1	8388.7	1065.1	6297.44,10479.90
	2	12162.3	1065.1	10071.10,14253.56
	3	8158.3	1065.1	6067.10,10249.56
3	1	8623.1	990.00	6679.47,10566.78
	2	15330.6	990.00	13386.97,17274.28
	3	10839.1	1012.7	8850.72,12827.40

Table 5. Gulf of Maine. Statistics for Biomass Data (Fig. 8) (+S.E.., station frequency, quadrat frequency)

		Protected *(5,25)*	*Mid* *(4,15)*	*Exposed* *(4,20)*
	Upper	±2220,5,24	±1970,4,10	±1710,4,12
Ascophyllum	Mid	±4985,5,25	±3950,4,16	±1670,4,14
nodosum	Lower	±2520,4,20	±3525,3,13	Tr,1,1
Fucus vesiculousus	Upper	±650,5,11	±525,4,7	±755,4,14
and	Mid	±415,3,6	±220,2,2	±885,4,11
Fucus spiralis	Lower	±300,4,9	±265,4,5	±150,2,2
	Upper	0	0	0
Fucus distichus	Mid	0	0	±1000,3,14
	Lower	0	0	±1190,3,14
	Upper	Tr,1,1	±100,1,2	Tr,3,4
Chondrus complex	Mid	±20,2,2	±70.4.8	±70,4,16
	Lower	±70,4,10	±460,3,8	±535,4,19

Table 6. Eastern Newfoundland. Statistics for Biomass Data (Fig. 9) (+ S.E., station frequency, quadrat frequency)

		Protected *(8,40)*	*Mid* *(5,25)*	*Exposed* *(6,30)*
	Upper	±1025,8,29	±1725,3,10	±2,1,3
Ascophyllum	Mid	±1345,7,32	±1190,4,10	±400,2,5
nodosum	Lower	±1435,7,29	0	0
Fucus vesiculousus	Upper	±640,8,35	±860,5,24	±605,6,30
and	Mid	±910,8,25	±925,5,21	±870,4,12
Fucus spiralis	Lower	±730,7,29	±270,4,8	±285,1,1
	Upper	0	±1,2,2	±120,3,11
Fucus distichus	Mid	0	±770,5,15	±465,6,26
	Lower	±685,5,21	±935,5,25	±565,6,30
	Upper	Tr,1,1	±1,1,2	±1,1,2
Chondrus complex	Mid	±50,4,10	±95,4,14	±105,3,12
	Lower	±130,6,15	±165,5,20	±280,3,10
Chordaria complex	Upper	0	±1,1,2	±5,2,3
	Mid	Tr,1,1	±1,4,5	±70,3,7
	Lower	Tr,1,,2	±55,5,14	±65,6,13

Table 7. N. Peninsula Newfoundland & S. Labrador. Statistics for Biomass Data (Fig. 10). (±S.E., station frequency, quadrat frequency)

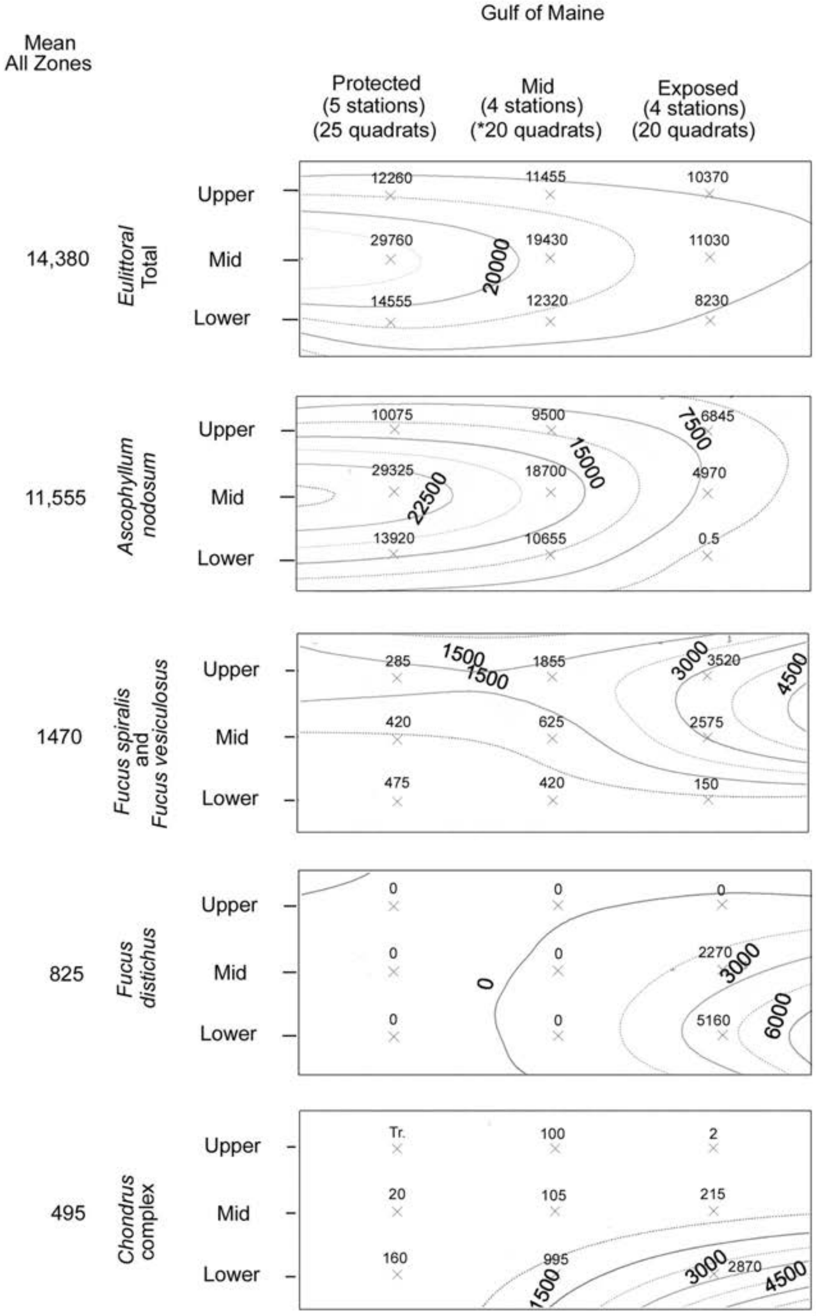
		Protected *(4,20)*	*Mid* *(4,20)*	*Exposed* *(4,20)*
	Upper	Tr,2,2	0	0
Ascophyllum	Mid	±415,2,6	0	0
nodosum	Lower	±275,2,3	0	0
Fucus vesiculousus	Upper	±1400,4,20	±945,4,20	±565,4,16
and	Mid	±1870,4,20	±905,4,18	±610,3,8
Fucus spiralis	Lower	±625,4,11	±225,3,3	0
	Upper	Tr,1,1	Tr,1,1	±295,4,11
Fucus distichus	Mid	±15,2,3	±520,4,13	±785,4,20
	Lower	±580,4,18	±625,4,20	±420,4,20
	Upper	0	0	±1,1,3
Chordaria complex	Mid	0	±1,1,3	±35,4,10
	Lower	±225,3,7	±100,3,9	±115,4,19
	Upper	0	0	0
Chondrus complex	Mid	0	0	0
	Lower	0	Tr,1,2	0

Table 8. Northwestern Gulf of St. Lawrence. Statistics for Biomass Data (Fig.11) (+ S.E., station frequency, quadrat frequency).

		Protected (2,10)	*Exposed* (3,15)
	Upper	±235,2,3	±195,2,6
Ascophyllum	Mid	±950,1,2	±1,1,1
Nodosum	Lower	±1,1,2	±1,1,1
Fucus vesiculousus	Upper	±970,2,10	±495,3,15
and	Mid	±1320,2,10	±875,1,3
Fucus spiralis	Lower	±2000,1,5	0
	Upper	0	±392,1,4
Fucus distichus	Mid	±1515,1,3	±760,3,13
	Lower	±1495,2,6	±2040,3,15
	Upper	0	0
Chondrus complex	Mid	0	0
	Lower	0	0
	Upper	0	±1,1,1
Chordaria complex	Mid	±1,1,1	±1,2,4
	Lower	±555,1,4	±345,3,14

Northwards to the N. peninsula of Newfoundland and S. Labrador (Fig. 10), total algal biomass at non-ice scoured stations dropped to about one-third of the Gulf of Maine. Although total biomass zonal and exposure distribution patterns were quite similar to those of the Gulf of Maine, *A. nodosum* had ceased to be a significant component, found only in mid to lower zones of some protected stations (sometimes only with a search). *Fucus vesiculosus*, usually with an irregular uppermost component of *F. spiralis*, became the dominant algal biomass at upper zones and protected stations, while *F. distichus* achieved dominance in lower zones and more exposed stations. *Chondrus crispus* and *Mastocarpus stellatus* were rare, appearing only as trace in two of 180 quadrats. The *Chordaria*-complex replaced *Chondrus* in both the infralittoral and in the understory of the eulittoral lower zones, notably at mid and outer stations. As in NE Newfoundland, where ice-scouring is a significant factor in the eulittoral, fractures and crevices were usually dominated by dwarf *Fucus distichus*, as well as algae of the *Chordaria*-complex.

More limited data for NW Gulf of St. Lawrence, only 5 stations, (Fig. 11) suggests a pattern quite similar to N. Newfoundland and S. Labrador. *Ascophyllum nodosum* was uncommon, except at the most protected stations where it was mostly a minor component. *Fucus vesiculosus* dominated upper zones and protected stations, and *F. distichus* the lower zones and more exposed stations. Algae



S.E., station frequency & quadrat frequency in Table 5, * one station of 5 quadrats pooled

Fig. 8. Standing crop (biomass) of dominant macroalgae in the upper, middle and lower eulittoral of protected, middle exposure and exposed stations in the central Gulf of Maine (see Fig. 7).

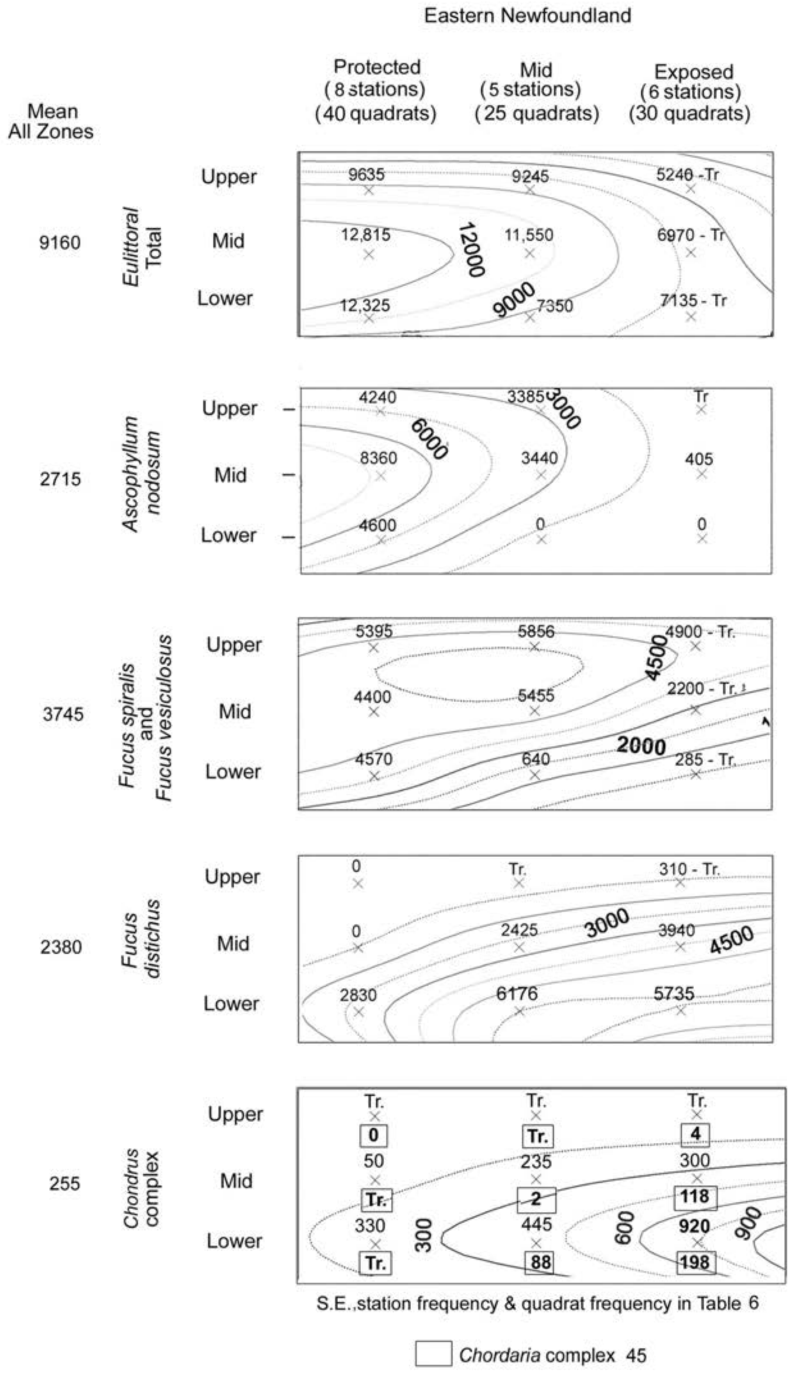
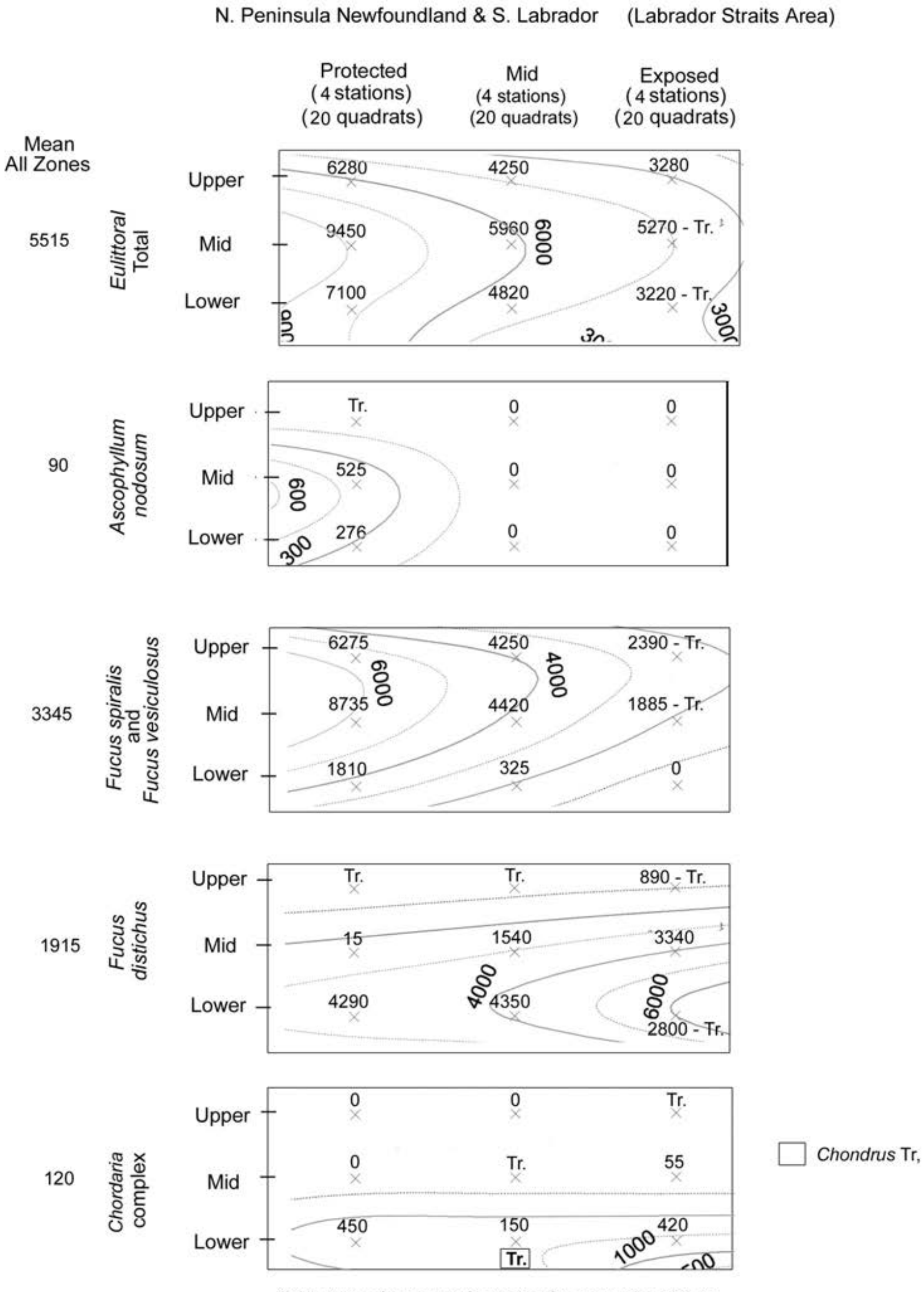


Fig. 9. Standing crop (biomass) of dominant macroalgae in the upper, middle and lower eulittoral of protected, middle exposure and exposed stations in eastern Newfoundland (see Fig. 7).



S.E.,station frequency & quadrat frequency in Table 7

Fig. 10. Standing crop (biomass) of dominant macroalgae in the upper, middle and lower eulittoral of protected, middle exposure and exposed stations on the northern Peninsula of Newfoundland and in southern Labrador (see Fig. 7).

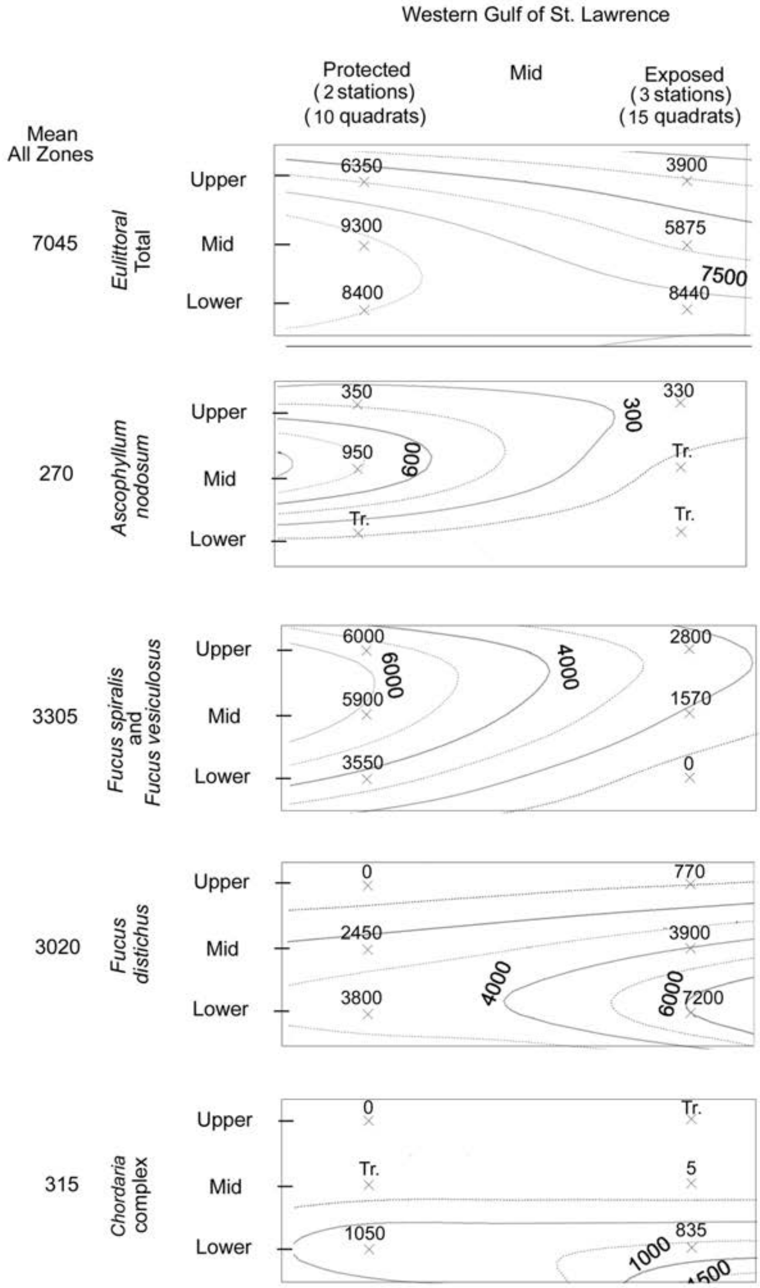
of the *Chordaria*-complex were abundant in the lower zones and in the infralittoral. Unlike *Chondrus* in the Gulf of Maine and E. Newfoundland, members of the *Chordaria*-complex did not extend to a significant degree up the eulittoral? under the fucoid cover. Although reported in the N. Gulf of St. Lawrence (South & Tittley, 1986), no specimens of *Chondrus crispus* or *Mastocarpus stellatus* were seen in reconnaissance or in quadrats.

Mean biomass for all nine zone/exposure units is given on the left of each diagram subunit (Figs 8-11), with sum-values plotted as a function of latitude to detect north/south changes in macroalgal biomass (Fig. 12). The E. Newfoundland region is divided into north and south components (Fig. 12), with the biomass of the *Chondrus*- and *Chordaria*-complexes plotted separately on an expanded scale at the top. Ignoring the complication of ice scouring to only consider "potential biomass," the eulittoral algal biomass dropped more or less directly with latitude. The *Chondrus*-complex in the southern and more central Subarctic region was replaced by the *Chordaria*-complex northwards. *Fucus vesiculosus* and *F. distichus* generally increased their biomass from the Gulf of Maine to the core Subarctic, while *A. nodosum* progressively lost biomass northwards, accounting for nearly all of the algal biomass loss with latitude.

Invertebrates. Percent cover of the sessile *Semibalanus balanoides* ('northern rock barnacle'; Fig. 13a) and *Mytilus edulis* ('blue mussel;' Fig. 13b), and the numbers (per m^2) of the mobile *Nucella lapillus* ('dogwinkle'; Fig. 13c) were plotted against exposure and intertidal height. Coverage of the two sessile species was more irregular than macroalgal abundance, probably because data were visual estimates (though framed in relatively small individual quadrats), rather than scaled weights of the marcoalgae. The basic pattern of Mathieson *et al.* (1991) for the Gulf of Maine is easily discerned. While the Cape Elizabeth station of this study (one of the most exposed on the inner Gulf of Maine coast) showed a pattern of barnacle and mussel distribution that was similar to that demonstrated for the region as a whole, the relative importance of barnacle and mussel cover relative to macroalgal biomass was apparently greater than found in this investigation. Intertidal barnacle cover increased with exposure and higher levels and mussel cover increased with exposure and lower levels (possibly the levels of exposure in the stations used in this study are not as high as in their work).

In northern subregions, the abundance of barnacles was considerably and consistently lower than in the Gulf of Maine. However, a slight recovery in N. Newfoundland from the very low level of occurrence in E. Newfoundland may be related to the dropping out of its principal predator, *Nucella lapillus* (see: Fig. 13c). Blue Mussel cover, on the other hand, increased in E. Newfoundland while it maintained its characteristic abundance (increasing in lower zones and more exposed stations). In N. Newfoundland and Labrador, the abundance of mussels at exposed stations began to drop significantly. Abundance of the predatory *Nucella lapillus* in the Gulf of Maine was similar to that of *Mytilus*, increasing with exposure and depth in the intertidal. This pattern breaks down with depth in E. Newfoundland, and these molluscs disappear in the Labrador Straits area, paralleling the apparent lack of *N. lapillus* in the Cote Nord, NE Gulf of St. Lawrence (Brunel *et al.*, 1998).

Littorina littorea (Fig. 14a), at a mean of 166 snails/m^2, was the dominant herbivore in the Gulf of Maine intertidal. While long considered to be largely restricted to grazing microalgae on rock surfaces, *L. littorea* can also have a significant effect on macroalgae by grazing newly-settled sporelings (Mathieson *et al.,* 1991). Larger and older individuals mostly move to the sublittoral in winter, so it is primarily a summer grazer in the intertidal. Except for exposed stations in



S.E.,station frequency & quadrat frequency in Table 8

Fig. 11. Standing crop (biomass) of dominant macroalgae in the upper middle and lower eulittoral of protected, middle exposure and exposed stations in the western Gulf of St. Lawrence (see Fig. 7).

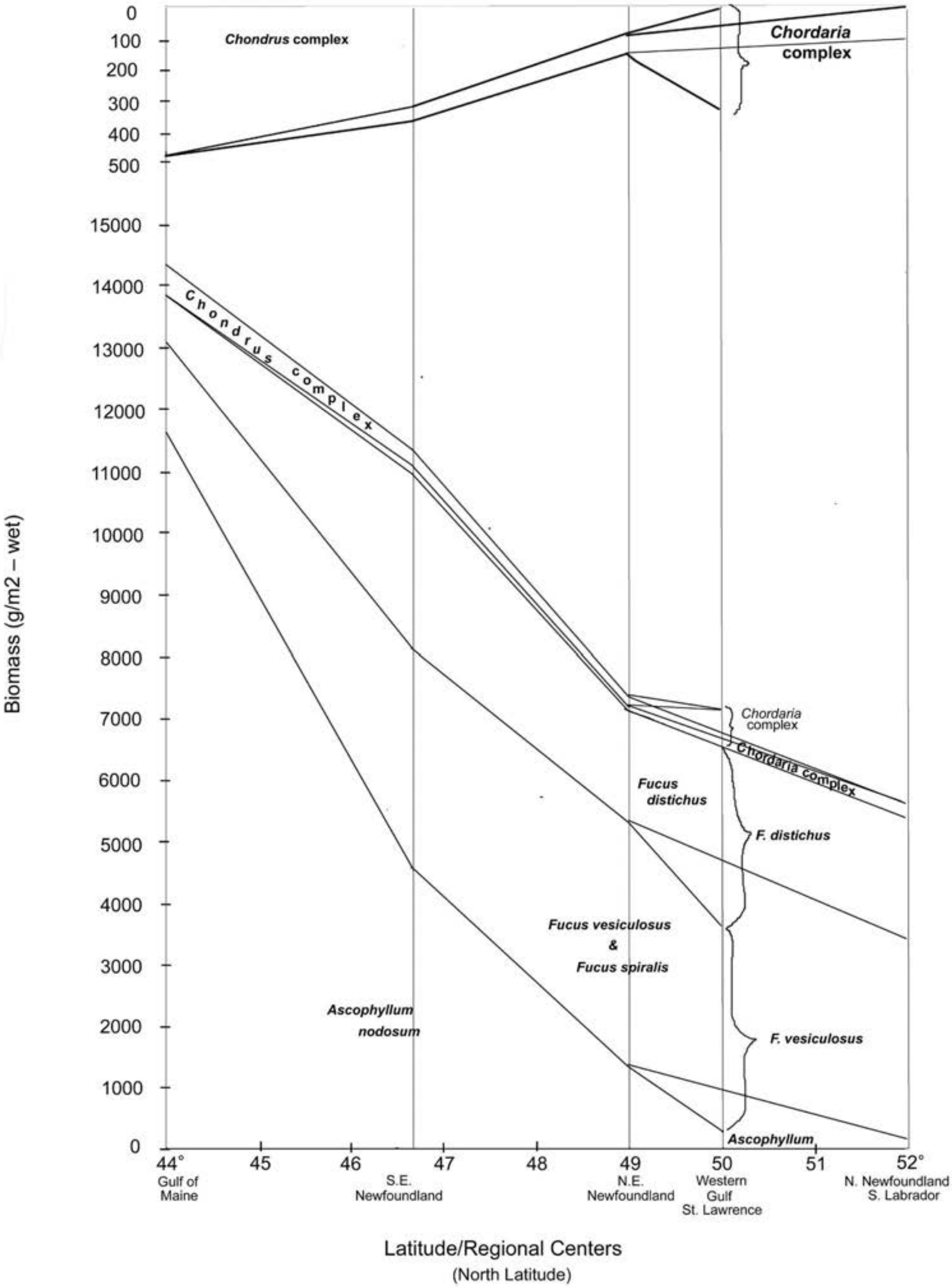


Fig. 12. Mean eulittoral macroalgal biomass (all exposures) as a function of latitude/regional centers. Upper portion of the diagram is a biomass expanded plot for the *Chondrus*- and *Chondaria*-complexes.

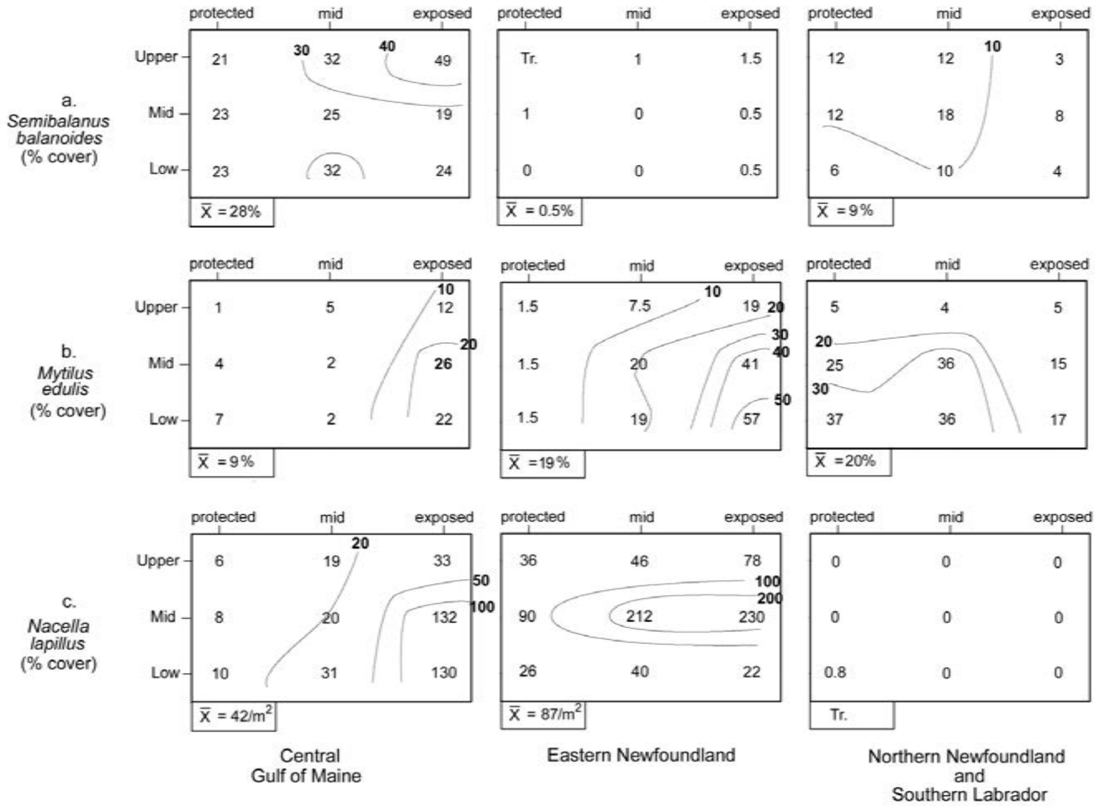


Fig. 13. Percent cover of: (a) *Semibalanus balanoides* (‘northern rock barnacle’) and (b) *Mytilus* (‘blue mussel’); and number (per m^2) of (c) *Nucella lapillus* (‘dogwinkle’) for exposure and intertidal height, and for the primary station groupings shown in Fig. 7.

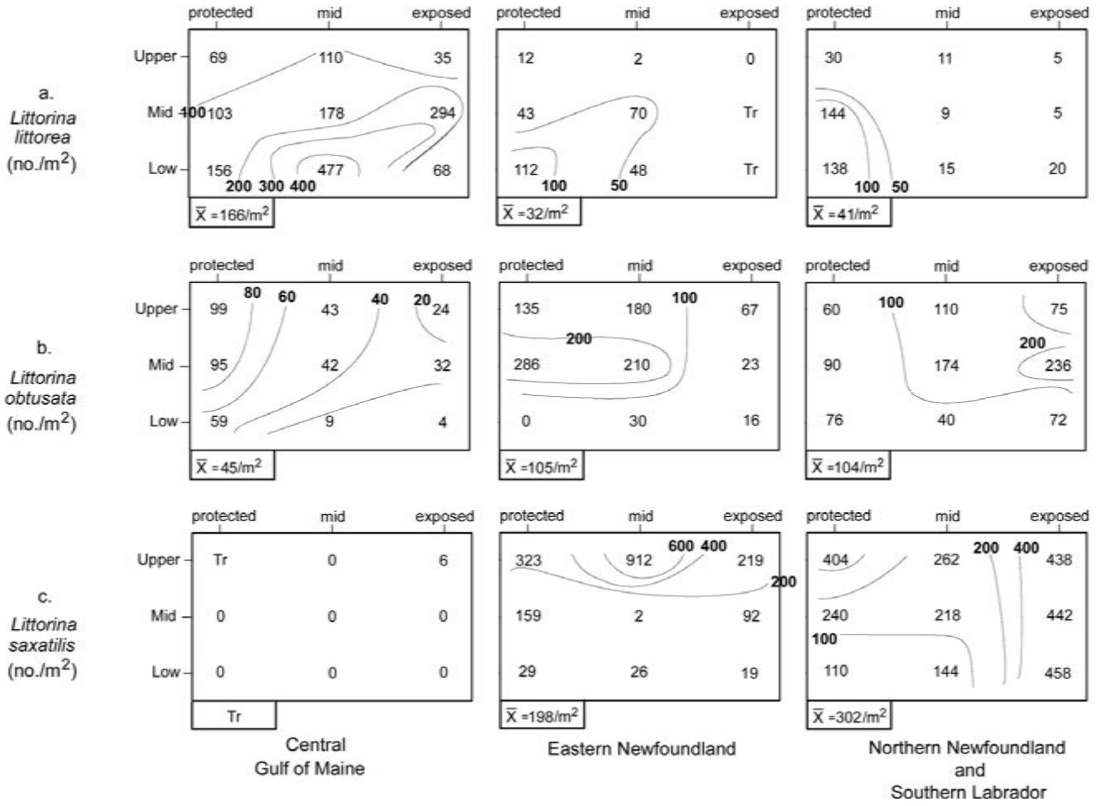


Fig. 14. Number of individuals of littorinid snails (number/m^2): (a) *Littorina littorea*, (b) *L. obtusata* and (c) *L. saxatilis* for the primary station groupings shown in Fig. 7.

the Gulf of Maine, *L. littorea* was most dense in the mid to lower zones. In the core Subarctic, *L. littorea* dropped by 20-25% of its Gulf of Maine abundance. While it remained most abundant in the lower eulittoral, a marked shift to protected (mostly warmer, in summer) stations was clearly seen, a pattern paralleling that of *Ascophyllum nodosum* and *Chondrus crispus*. The relatively few *L. littorea* that occurred in this region were large individuals as compared to a more normal-sized Gulf of Maine population (personal observation).

Littorina obtusata (Fig. 14b) was not nearly as abundant as *L. littorea* in the Gulf of Maine, but was often the dominant grazing snail in more protected and upper zones, where it was often found on macroalgae. A browser of *Ascophyllum* (Mathieson *et al.,* 1991), its distribution only weakly correlated with *Ascophyllum* distribution. In E. Newfoundland, the abundance of *L. obtusata* more than doubled (a well-known relationship; Reid, 1995), though its distribution with eulittoral elevation and exposure was similar to that found in the Gulf of Maine. However, in the Labrador Straits (Strait of Belle Isle), while the numbers remain the same, an apparent marked shift in exposure and elevation distribution occurred. It became more abundant at exposed stations and the morphology shifted from that of *L. obtusata* var. *retusa* to *L. obtusata* var. *palliata*. Seeley (1986) and Trussell & Smith (2000) suggested that these geographic patterns may relate to the abundance and range expansion of the invasive snail predator *Carcinus maenus* ('green crab').

The most striking geographic change in the littorinid community occurred with *Littorina saxatilis* (Fig. 14c). In the Gulf of Maine it was virtually restricted to the supralittoral, occurring in modest numbers, while in the uppermost eulittoral it was relatively rare. Throughout the core Subarctic Region (E. Newfoundland, the Labrador Straits area and in N and W Gulf of St. Lawrence), *L. saxatilis* was by far the dominant littorinid, at 200-300/m^2. While there was still a tendency for *L. saxatilis* to be most abundant in the upper eulittoral at every station and in most quadrats, it was found throughout the eulittoral. At exposed stations in the Labrador Straits, the mean densities of *L. saxatilis* throughout the eulittoral often exceeded 400/m^2.

In summary, across the eulittoral zone of the Gulf of Maine, *L. littorea* represented about 80% of the littorinids, with *L. obtusata* responsible for the entire remainder. In the core Subarctic (Newfoundland, S. Labrador), *L. saxatilis* represented roughly 65% of all littorinid individuals, with *L. obtusata* (mostly *L. obtusata var. palliata)* responsible for 25% and *L. littorea* for 10%.

Most significant intertidal algal species found at the southern end of the NW Atlantic rocky shore also occur at the northern end and vice-versa. The "presence/absence" distribution maps of Lüning (1990) showed the range of these species extending beyond the north and south limits of this study. *Chondrus crispus* and *Mastocarpus stellatus* are not known north of southernmost Labrador. Hooper & Whittick (1984) also found all the algal species treated in this paper, except *C. crispus* and *M. stellatus*, on the central Labrador coast. However, as we show, the community composition of the eulittoral changes markedly from the Gulf of Maine to the Strait of Belle Isle, Labrador Straits. From intertidal reconnaissance (and quantitative studies during the 2004 field season) and paralleling the distribution of sublittoral corallines, this change is not gradual in relatively warm E. Nova Scotia or S. Gulf of St. Lawrence (or in warm W. Newfoundland), but begins in SE Newfoundland and W. Gulf of St. Lawrence and is fully-developed in the Strait of Belle Isle.

In the eulittoral algal flora, *Ascophyllum nodosum*, the dominant overstory species, and *Chondrus crispus*, the dominant understory species, in the Gulf of Maine are replaced by *Fucus vesiculosus* and *F. distichus* above, and below by a complex of species, often dominated by *Chordaria flagelliformis* (and not including *Chondrus crispus, Mastocarpus stellatus* and *Palmaria palmata*). Based on the quantitative biomass evidence herein, this represents an 82% change from the Gulf of Maine to the Labrador Straits (i.e., species providing 98.2% of the intertidal algal biomass in the Labrador Straits area provide only 15.9% of the biomass in the Gulf of Maine). However, we qualify this, since tide pools and the crevices of ice-scoured shores were omitted from quantitative analysis. Many algal species, some "displaced" from their upper sublittoral habitats, can occur in Gulf of Maine tide pools, e.g., *Chondrus crispus* is one of the commonest tide pool algae, especially in low to mid eulittoral. This is not unexpected considering the general band-forming dominance of this alga in the infralittoral and uppermost sublittoral. In scattered higher pools of exposed shores, *Fucus distichus* f. *filiformis* (= *F. filiformis*) also occurs. Most tide pools in the core Subarctic and especially the central area of the Labrador Straits, except at the highest levels, are densely occupied by a wide morphological array of *F. distichus*. Often these are the large (up to 1m in length), flat-bladed morphology with large terminal receptacles of the more typical form; though in the highest pools, large versions of *F. distichus f. filiformis* can occur. Similarly, *Chondrus crispus* is absent from pools in the Labrador Straits. Species of the *Chordaria*-complex accompany the typically dominant *F. distichus* of E. Newfoundland, with *Chondrus crispus* scattered in tide pools. In the infralittoral on more protected shores, *F. distichus* is not usually out-competed by kelps and *Chordaria*, and its dominance can extend into the sublittoral, especially where significant fresh water input is absent. On ice-scoured shores, the usually abundant crevices throughout the eulittoral are often densely occupied by a dwarf-morph of *F. distichus*, a very distinctive alga of a short, flat-bladed stalk and typically a single bifurcation with proportionally large, relatively flat receptacles. Although components of the *Chordaria*-complex often accompany *F. distichus* in these wave-swept environments, rarely are *Fucus vesiculosus* or *F. spiralis* significant components.

The rocky eulittoral of the core Subarctic region (open rock surface and tide pools), is highly dominated by *Fucus distichus.* In this region over the entire eulittoral, while *F. vesiculosus* and to a lesser extent *F. spiralis* occur, sometimes abundantly, in the upper half of more protected, rocky shorelines, they are secondary in biomass to *F. distichus*. The understory, and usually any notably exposed, persistently wetted areas, are occupied by *Chordaria*-complex. The principal dominants of the Gulf of Maine eulittoral are reduced, often stubby remnants; these are scattered, usually in protected in-bay environments that have higher summer temperatures.

It might be argued that the changes in algal abundance between the southern and the northern half of the NW North Atlantic are due to ice scouring of otherwise dominant species, *Ascophyllum nodosum* and *Chondrus crispus*, from their principle habitat. However, the extensive beds of perennial *Fucus* spp. seen in this study and the work of Keats *et al*. (1985) suggest that such radical effects are unlikely for long coastal stretches. The same patterns of change in the littoral seaweeds were also shown in Iceland, where it is particularly unlikely that ice scouring is a significant factor (Munda, 1991) [note: the pattern of change was the same as those found in the subtidal corallines (Adey, 1968; Adey & Steneck, 2001)].

In this study, it is significant that the proportions of *Chondrus*-complex changes more or less directly with latitude (*i.e.*, 11.5%, Gulf of Maine; 7.3% SE Newfoundland; 3.2% NE Newfoundland; to trace levels in N. Newfoundland and

Labrador). However, SE Newfoundland lacks sea ice, while the NE coast is often beset with sea ice in late winter and early spring. The *Chordaria*-complex shows a more irregular, but significant rise in proportional biomass as the *Chondrus*-complex drops. If sea ice scouring of the infralittoral and lowest eulittoral were key factors, abundant *Chondrus crispus* (and little *Chordaria flagelliformis* and ecologically associated species) would be the norm in SE Newfoundland, with a rapid change up the E Avalon shoreline. More recent studies on a rare, ice-scoured shore on the mid-Atlantic Nova Scotia coast (Cook & Chapman, 1997; Minchinton *et al.,* 1997) have shown a rapid recovery to the typical fucoid structure of the coast as a whole. Also, in current studies of the first author, the crevice communities of the frequently ice-scoured NE coast of Nova Scotia are similar to the remainder of the non-scoured Nova Scotia coast. In community structure, these shores are more similar to the Gulf of Maine than to N. Newfoundland and S. Labrador.

The dominant intertidal invertebrates of the Gulf of Maine are all present throughout the entire rocky western North Atlantic, except *Nucella lapillus*, which disappears in the Labrador Straits and the NE Gulf of St. Lawrence. However, for most species, there is a radical change in abundance and thus in overall community structure. Among the grazing littorinids, *Littorina littorea*, the highly dominant snail of the Gulf of Maine, becomes very limited in occurrence on W Atlantic Subarctic shores, and shows a shift from lower to mid zones across the exposure to more protected habitats. Most visually striking (data not presented here), where *L. littorea* is present they are quite large, though few in numbers (5 of 21 stations did not have a single individual, and another 5 stations had less than 5 individuals for all zones). Thus, the development and settling of larvae or possibly survival and growth of small individuals is limited, while long-term adult survival is more likely. In contrast, *L. saxatilis*, rare in the Gulf of Maine eulittoral, becomes extremely abundant throughout the Subarctic. On most Subarctic shores, *L. saxatilis* also occurs in the supralittoral (as in the Gulf of Maine), reaching its maximum abundance in the uppermost eulittoral. In exposed stations of the Labrador Straits, it achieves large numbers (approx. 400/m^2) throughout the eulittoral, increasing to more than 66% of the littorinid population. Northwards from the Gulf of Maine, *L. obtusata* doubles in total numbers with a shift in local distribution; some attributed this to reduction of a crab predator (Seeley, 1986; Trussell & Smith 2000).

CONCLUSIONS

Mathieson *et al.* (1991) considered the rocky shores from Cape Cod to Labrador to represent a single ecosystem. However, in quantitative biomass and population, we found the dominant macroscopic algal flora and invertebrate fauna of the rocky intertidal to differ radically between: 1) the Gulf of Maine; and 2) the core Subarctic (E Newfoundland, S Labrador, and N Gulf of St. Lawrence). Although the important species are present in both areas, if the mean percentage of biomass, and number or cover (as appropriate) of algal overstory, algal understory, filter feeder cover, predatory snails and grazing snails, are calculated, species that dominate in the core Subarctic (Labrador Straits Area) represent 85% of the biota *versus* only 13% of those same species in the Gulf of Maine.

In this study *Ascophyllum nodosum,* the primary eulittoral fucoid canopy (overstory) species in the Gulf of Maine, was found reduced to occasional status in the central Subarctic area of the Labrador Straits. Moreover, *Chondrus crispus,* the primary understory species of the Gulf of Maine was rare, and its usually associated red algae, *Mastocarpus stellatus* and *Palmaria palmata,* did not occur in the quadrats. *Fucus vesiculosus* and especially *F. distichus* became the dominant eulittoral canopy species in the Labrador Straits, increasing in mean biomass by two to three times over levels in the Gulf of Maine. The *Chordaria*-complex (a suite of species), only occasional in the Gulf of Maine, became the understory dominants in the Subarctic.

The sessile barnacle *Semibalanus balanoides* was greatly reduced in the Labrador Straits, while the mussel *Mytilus edulis* increased modestly over its abundance in the Gulf of Maine (but, conversely at protected rather than exposed sites). Among the primary mobile invertebrates (all molluscs) in more southern areas, *Littorina littorea* and *Nucella lapillus* became considerably reduced further north. *Littorina obtusata* apparently increased modestly in abundance, although it showed a marked morphological change (matching what some have called a separate species and others would attribute to snail predation). *Littorina saxatilis* went from being rare in the Gulf of Maine eulittoral to the most abundant snail in the Labrador Straits. These changes parallel those in the community-structuring macroalgae. In quantitative terms, this study only considered the open rock surface of non-ice scoured areas. However, tide pools and the crevices of ice-swept shores, at all levels were highly dominated by *Fucus distichus.* The ice-scoured areas of open rock eulittoral often had abundant *L. saxatilis.* These species were occasional in these Gulf of Maine environments, thus providing another marked difference between the two areas.

The quantitative, sublittoral biogeographic model of Adey & Steneck (2001) identified the Atlantic Subarctic with a major western Atlantic subset. The North Atlantic test of that model, using coralline algal cover, showed the core areas described in this paper as being comprised of 95% Subarctic species, as compared to 73% Subarctic (27% Boreal) in the part of the Gulf of Maine where the stations were drawn (64% in the Gulf of Maine as a whole). While firm conclusions concerning the regional biogeographic status of the individual species cannot yet be made (because quantitative data are lacking from other regions), there is little question that the NW Atlantic core region (designated as ‘Subarctic’ by Adey & Steneck, 2001) is quite different (in quantitative population/ecological terms) from the transition Boreal-Subarctic area represented by the Gulf of Maine (and the Atlantic Nova Scotia coast). It is also quite clear that the species involved in this difference represent “more northern and more southern” elements. Furthermore, the differences in species composition between the core Subarctic and the mixed zone to the south is quite similar to that of N and E Iceland as compared to S Iceland (Munda, 1991), and the same in the coralline cover (Adey, 1968). Unlike the quantitative data herein, previously published distribution limits of species, mostly based on presence/absence, have produced a confused array of data that does not particularly support (or refute) the Adey/Steneck model. Adey & Steneck (2001) noted that using rarity and great dominance as equivalent in biogeographic analysis (*i.e.*, basing analyses only on species presence and absence) leads to confusion and minimal understanding. Biogeographic and biodiversity analyses in fields as diverse as coral reef fauna (Bellwood & Hughes, 2001) and boreal mountain flora (Fosaa, 2004), have recognized that significant patterns emerge from apparent disarray when quantitative elements of biomass and/or area are considered.

Finally, the presence of sharpness (or lack thereof) of regional and provincial boundaries has often been a point of major dispute in biogeography. Climatic fluctuations of the Pleistocene make sharp regional boundaries highly unlikely (Adey & Steneck, 2001). Nevertheless, as that study demonstrated and this investigation further supports, the presence of biogeographic regions remains quite definitive on both theoretical and real-world bases.

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