STUDIES ON THE LITTORAL LICHENS OF MORTHEASTERN NORTH AMERICA

Dissertation for the Degree of Ph. D. MICHIGAN STATE UNIVERSITY RONALD MAXWELL TAYLOR 1974



This is to certify that the

thesis entitled

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presented by

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ABSTRACT

STUDIES ON THE LITTORAL LICHENS OF NORTHEASTERN NORTH AMERICA

By

Ronald Maxwell Taylor

Lichens were collected along the coast of the United States from the southern tip of New Jersey to Lubec, Maine as well as in the province of Nova Scotia and the island of Newfoundland, in a zone restricted to that part of the rocky coast covered by tides or splashed by waves. The resulting collection is the most extensive collection of this unique and little studied flora to be made to date in North America.

Studies were made of vertical distribution patterns and interspecific associations as well as general geographic distribution of the species collected. Environmental conditions such as rock structure, water characteristics and atmospheric conditions were studied and related to the distribution and abundance of the littoral lichens and their general diversity. Indices of diversity, dominance and evenness were computed. A chi square test of association was used to evaluate the significance of apparent associations among littoral lichens and the coefficients of those associations were determined. A multiple regression analysis was utilized to determine the effect of environmental parameters on the species distribution and general diversity. Although zones of maximum growth were identified, unlike other studies, no specific biologically defined zones were observed. Two species, Verrucaria ditmarsica, and Verrucaria striatula, were found to have a significant positive association. Environmental influences on distribution and diversity were found to consist of complex interactions rather than

independent actions by one or two dominant factors.

A taxonomic key to the twenty-one species comprising the flora is accompanied by detailed discussions of the species contained.

Because of the unique and generally unfamiliar structure of the species of the genus *Verrucaria*, the principal genus of the area, the morphology of this genus is discussed in detail, with emphasis on morphological variations and environmentally induced modifications. Included under the discussion of each species is a list of specimens seen and literature records. Five of the species collected are new to North America: *Caloplaca microthallina*, *Stigmidium marinum*, *Verrucaria amphibia*, *V. ditmarsica* and *V. internigrescens*.

STUDIES ON THE LITTORAL LICHENS OF NORTHEASTERN NORTH AMERICA

Ву

Ronald Maxwell Taylor

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1. INTRODUCTION

The littoral zone of coastal New England from Cape May, New Jersey northward to Lubec, Maine and of coastal Nova Scotia and Newfoundland was the subject of this study, with emphasis on the distribution, ecology and taxonomy of the lichen component.

The term littoral, as applied here, includes the littoral zone and supralittoral fringe of Stephenson and Stephenson (1949) and, to a limited extent, zones one and two of the supralittoral zone as defined by Ferry and Sheard (1969).

Some species, such as *Verrucaria maura* and *V. erichsenii* are obligate littoral species in that they are only found where they come in contact with salt water. Other species found in this zone, such as *Xanthoria parietina*, are facultative and commonly occur remote from the sea. Facultative members are included in this treatment if they are found in the same collection with, or at the same height above high tide as obligate littoral species.

Since a comprehensive study of littoral lichens has not previously been made in this hemisphere, an attempt is made in this work to describe the ecology of littoral species in North America and then make comparisons with published European findings.

Recognizing the complexity of the habitat studied and the fact that lichens are an intergral part of the biota therein, the contents and style of presentation of this paper were chosen to both encourage and serve all naturalists who might wish to study this fascinating environment. It is evident from the literature and from inquiries directed to me that the littoral lichen flora presents an interesting enigma to biologists of diverse disciplines. It is hoped that this paper will help them in studying and accurately reporting the lichens of the littoral zone.

II. HISTORY

Littoral lichens to date have been studied on two fronts and these must be treated separately even though they share the same time span. Consideration will be given first to the taxonomic history and then to an appraisal of previous ecological studies.

A. Taxonomy

Littoral lichens were apparently first collected in Scandinavia by Wahlenberg and described in Acharius (1803) as Verrucaria maura, V. ceuthocarpa, V. mucosa and V. striatula.

Although this was a necessary first step, the description of such species did not herald a study of littoral lichenology per se.

Rather, lichenologists merely included them as the extreme lower limit of exploration of terrestrial lichens. At the same time, phycologists observed littoral lichens and felt obliged to report them as incidental inclusions in the upper limits of their explorations.

Throughout the nineteenth and early twentieth century littoral lichens were included in general floras and a number of new species were described and added to the list. Unfortunately the littoral species of *Verrucaria* are highly variable and difficult to recognize. The result has been the naming of populations with ecological modifications as separate species. By way of illustration, in discussing his new species, *Verrucaria convexa*, Lynge (1928, p. 17) writes, "It is nearly related to *Verrucaria maura* and the specific distinction can be contested, so much the more as only one plant was collected and nothing can be known of its range of variation".

New reports and increasing numbers of specimens enabled taxonomists to gain a better view of the variations of the littoral

lichens and a broader sense of species. Zschacke (1924), for example, attempted to develop a rather conservative view in his treatment of the littoral *Verrucariae*. Some species previously considered distinct, were reduced to synonyms or treated as forms or varieties. On the other hand, Zschacke described *V. lorrain-smithii*, a species treated by later workers as a minor variation. Santesson (1939) furnished considerable insight into the variations of selected species and showed greater appreciation for the variability of littoral species in general. Unfortunately, his "Amphibious Pyrenolichens I" has not been continued and the taxonomy of this difficult group of lichens was neglected for nearly a decade until Lamb (1948) published a comprehensive work on the pyrenocarpous lichens of the Antarctic, including a new species, *Verrucaria serpuloides*.

What attention the littoral lichens have received, since the aforementioned works, has been of an ecological nature and almost invariably showed a lack of understanding of the taxonomy of the littoral species involved. Ferry and Sheard (1969, p. 43) state that,

"Species of the littoral fringe and the eulittoral zone are omitted from this quantitative survey, partly because of the acute problems of field identification of these species, especially of extreme forms and also because the ecology and taxonomy of these lichens is the subject of current work elsewhere."

Examination of their key shows that a species here considered valid is treated as an "atypical form" of *V. microspora* and a normal variation of *V. striatula* is treated as "atypical". Lewis (1972), in an excellent study of shore zonation, demonstrates his unfamiliarity with littoral *Verrucariae* with his reference to the "dark green patches" of *V. microspora* forming a band along the shore. It is

evident from the description and ecology that the reference is to V. mucosa, and not V. microspora.

Hopefully, despite the difficulty of this group of poorly understood lichens, more investigations will be made into the variation of the species and the influences of environment upon their morphology.

B. Zonation

Nylander (1861) observed three belts of lichens on the rocky shores. These belts consisted, in ascending order, of Lichina pygmaea, Verrucaria maura and Lichina confinis. Rather than define zones according to vegetation, Weddell (1875) chose to classify the zones according to nature of habitat and classified them accordingly as "marine", "semi-marine" and "maritime or littoral". Cotton (1912), a phycologist, attempted to include littoral lichens in his zonation studies but recognized that he lacked detailed knowledge of the lichen species. Knowles (1913) described five lichen zones in detail. The lowest of these zones was the "Belt of marine Verrucarias". The word "marine" referred to the fact that this belt is submerged at high tide. Above this belt she defined the "Verrucaria maura Belt". Placed immediately above the "Verrucaria maura Belt" was the "Lichina Vegetation". Above the "Lichina Vegetation" she described the "Orange Belt", comprised primarily of species of Caloplaca and Xanthoria. The uppermost belt was the "Ramalina Belt".

DuRietz (1925) introduced a new classification of zones
based on the influence of salt water. While retaining the term
"marine" for the intertidal zone, he introduced the term "hygrohalin"

for the region affected by waves and salt spray in the form of drops of sea water. This zone was subdivided into lower and upper. He named the region affected by airborne salt "aërohalin". All else was called "ahalin". Later DuRietz (1935) renamed the marine zone "hydrohalin" to make it consistent with his other zones.

Santesson (1939) preferred a scheme of zonation based on belts of algae, animals, lichens or combinations thereof. His lowest belt was the "Fucus serratus-belt". Above this was the "Fucus vesiculosus-Balanus-belt". This belt was subdivided, in ascending order into the "Ascophyllum-horizon", the "Fucus vesiculosus-horizon" and the "Fucus spiralis-horizon". His next higher belt was the "Calothrix-Verrucaria maura-belt" which was subdivided, in ascending order, into the "Pelvetia-horizon" and the "Verrucaria maura-horizon without pelvetia". His uppermost belt was the "Caloplaca marina-belt".

Feeling that there should be a standard zonation classification system rather than rampant synonymy and believing that their observations bore out the feasibility of such a scheme, Stephenson and Stephenson (1949) proposed a "universal system designed for use throughout the world but not incorporating any specific data on lichens, due to lack of detailed taxonomy. Their system (see figure 1) recognizes three "zones", the interfaces of which form two "fringes" of variable width. The zone that lies below low tide was named the "infralittoral zone". The region lying between the mean high tide and the mean low tide was "midlittoral zone". The uppermost zone was called the "supralittoral zone". The fringes may be flexibly

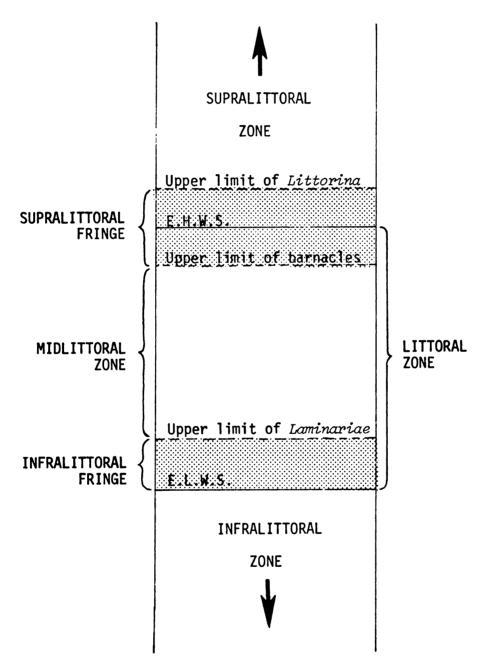


Figure 1. Seashore zonation (after Stephenson and Stephenson, 1949 p. 299).

determined. In the illustration used (Stephenson and Stephenson, 1949, p. 299, f. 3) the infralittoral fringe extended from the extreme low water line to the "upper limits of (e.g.) Laminarians". The supralittoral fringe extended from the upper limits of barnacles, through the extreme high water line to the upper limits of Littorina, etc. Prior to this, the span between the two extreme tide limits had been known simply as littoral.

Kenny and Haysom (1962) studied the zonation of Macquarie Island. They reported that there were several species of lichens "the most obvious being *Verrucaria* sp. and an unidentified bright yellow form". Fuller (1967) reporting on preliminary studies of Marion and Prince Edward Islands observed a striking similarity between the zonation observed there and that described by Kenny and Haysom (1962). In the lichen zone he noted "a conspicuous yellow lichen, probably *Verrucaria* sp.". Morton and Miller (1968) observed lichens as components of the zones on New Zealand shores. They did not suggest names for the lichens but merely described them, in descending order, as grey or greenish white, bright yellow, and, finally, sooty black.

Ferry and Sheard (1969), in describing zonation in Pembrokeshire, England, followed the scheme of the Stephensons but described only the supralittoral range, including the supralittoral fringe.

This was divided into four zones, biologically defined according to characteristic species. Zone one is characterized by Caloplaca marina, C. thallincola, Lecanora actophila, and L. helicopis. Zone two is characterized by Xanthoria parieting, Ramalina siliquosa, Buellia chlorophaea, and Ochrolechia parella. Zone three is characterized

by Rhizocarpon constrictum, Anaptychia fusca, and Lecanora atra.

Zone four, the uppermost zone is characterized by Pertusaria

pseudocorallina, and Lecidea subincongrua.

III. LITTORAL LICHENOLOGY IN NORTHEASTERN NORTH AMERICA

A. Taxonomy

The earliest collections of littoral lichens that I have been able to discover in northeastern North America are an undated collection by E. Tuckerman from Mount Desert Island, Maine, and an undated collection by H. Willey. The location of the Willey collection was listed only as Massachusetts and it is not included in the list of New Bedford lichens (Willey, 1892). A specimen of Verrucaria striatula was collected by H. L. Jones at Nahant, Massachusetts, in April of 1893. The Fink Herbarium (MICH) includes a collection by W. G. Farlow from Campobello, New Brunswick, in 1898. Eckfeldt (1895) and Arnold (1896) reported a collection of V. maura made by Rev. A. C. Waghorne at Shoal Point, Newfoundland in 1895, which appears to make it the first littoral record to be reported in the literature from North America. The herbarium of the Smithsonian Institution (US) contains a collection by G. K. Merrill, presumably from Rockport, Maine, dated 1919 and a collection by W. R. Taylor from Mt. Desert Island, Maine, dated 1920. The remainder of the littoral collections in the Smithsonian Institution were collected by C. Plitt from Mt. Desert Island on dates ranging from 1922 through 1932. Hedrick (1933) reported a new species, Verrucaria silicicola Fink, from Long Island, New York, collected by Roy Latham in 1926.

Degelius (1942) added two new records (*Verrucaria microspora* and *V. erichsenii*) for North America from his collections at Prince Point, Maine, and also confirmed the occurrence of *Verrucaria striatula* from the same place. He also made a valuable comparison between European and North American littoral lichen floras, a

contribution for which he was uniquely equipped. It is interesting to note that Plitt collected *V. erichsenii* in 1922, 1931, and 1932, and identified the material as *V. striatula*. He also collected *V. microspora* in 1928 and 1931, but failed to publish his findings. The specimens mentioned above are in the material that I have examined from the Smithsonian Institution.

Lamb (1954) reported *V. erichsenii* as a new Canadian record from Cape Breton Island, Nova Scotia. He noted that it was the only littoral *Verrucaria* seen there.

Brodo (1968) included two littoral Verrucariae (V. microspora and V. silicicola) in his study on Long Island, New York.

For a summary of the foregoing, see table number 1.

B. Zonation

Shoreline zonation in North America was first studied by

Johnson and Skutch (1928a, 1928b). Their investigation was restricted

to a specific headland known as Otter Cliffs on Mt. Desert Island,

Maine, and dealt with "submersible or strictly littoral vegetation",

including the tide pool environment. Only one lichen, Verrucaria

striatula, was reported and the reference to its "jet black crusts"

makes me suspect that this lichen was instead probably V. erichsenii.

Johnson and Skutch were primarily interested in plant communities below the high water mark and preferred to classify them by dominant species while listing also the tidal data for other workers who might wish to classify them with respect to tidal location.

The only other published work on shore line zonation in northeastern North America is the one by Stephenson and Stephenson (1954). Regrettably, they skipped from North Carolina to Nova Scotia, thus

omitting all of New England. In Nova Scotia they restricted their investigations to the region on the Atlantic coast around Peggy's Cove.

Table 1. CHRONOLOGY OF LITTORAL LICHEN COLLECTIONS IN NORTH AMERICA

COLLECTOR	DATE	LOCALITY	PUBLICATION	HERBARIUM
E. Tuckerman	Unknown	Mr. Desert Island, Maine	Unpublished	MICH
H. Willey	Unknown	Massachusetts	Unpublished	МІСН
H. L. Jones	1893	Nahant, Mass.	Unpublished	MICH
A. C. Waghorne	1895	Shoal Point, Nfld.	Eckfeldt (1895)	ЬН
W. G. Farlow	1898	Campobello, N. B.	Unpublished	МІСН
G. K. Merrill	1919	Maine	Unpublished	NS
W. R. Taylor	1920	Mt. Desert Island, Maine	Unpublished	NS
c. c. Plitt	1922-1932	Mt. Desert Island, Maine	Unpublished	NS
R. Latham	1926	Long Island, N. Y.	Hedrick (1933)	MICH
G. Degelius	1939	Prince Point, Maine	Degelius (1942)	Degelius
I. M. Lamb	1954	Cape Breton Is., N. S.	Lamb (1954)	CAN
I. M. Brodo	1965	Long Island, N. Y.	Brodo (1968)	MSC

IV. THE STUDY AREA

My study area consisted of the shorelines of eastern North

America from Cape May, New Jersey, Northward to Nova Scotia and

Newfoundland. The Nova Scotia side of the Bay of Fundy was included

as was the north side of the Minas Basin. Sites were selected for

investigation within the limits of accessibility, to provide a

reasonably diverse sample of the flora of the approximately two

thousand miles of shoreline. The specific sites are discussed in

detail under their own headings.

A. Geology

The New Jersey coast is a part of the Atlantic Coastal Plain formed by a process of emergence of the continental shelf and is composed largely of barrier reefs (Fenneman, 1938). Long Island and Cape Cod, also a part of the Coastal Plains, were formed by glacial deposits on old ridges of Cretaceous rock. Long Island Sound is a sunken lowland (Fenneman, 1938).

Narragansett Bay lies in Carboniferous rock composed largely of metamorphic schists and quartzite. In contrast, Pt. Judith is composed of the Narragansett Pier granite with intrusions of pegmatite. Masons Island is a minor monadnock in the submerged Precambrian of which western Rhode Island and eastern Connecticut are composed (Eardley, 1962). Pegmatite intrusions were also found in this pink granite.

The Gulf of Maine is believed to be formed by a 1200 ft. depression of the coastal plain under the weight of glacial ice followed by a recoil of up to four hundred feet. In fact the entire coast from the Hudson River northward has been described as a "drowned coast" (Fenneman, 1938). The emergence is believed to be responsible

for the narrow coastal plain between Cape Ann, Massachuetts, and Portland, Maine (Fenneman, 1938).

Casco Bay is a reentrant bay in a mostly Carboniferous basin eroded into fingers by the seaward movement of the glacier (Fenneman, 1938).

Mt. Desert Island and the surrounding bays, Blue Hill Bay and Frenchman's Bay, and their shores are the remains of igneous intrusions into overlaying strata. The overburden was removed by erosion and glaciation, and the remaining monadnocks were depressed. They became a part of the drowned coast of the Gulf of Maine (Chapman, 1962).

Quody Head is the easternmost point of the United States.

Geologically it is composed of volcanic rocks which are an extension of the southern highlands of New Brunswick (Eardley, 1962). It stands at the west side of the Bay of Fundy and overlooks Campobello Island and Grand Manan.

The Bay of Fundy is generally agreed to be the result of a down-fault in Triassic beds made up for the most part of a soft red conglomerate except for basaltic North Mountain on the east shore where Digby is located. North of the Minas Basin, in the vicinity of Joggins, the shore is Carboniferous fossil bearing sandstone and extensive coal measures (Eardley, 1962).

Along the north shore of the Minas Basin, east of Parsboro, a broken basaltic ridge of the same time and composition as North Mountain forms Partridge Island, the Five Islands, and Gerrish Mountain (Bird, 1972). Most of the remainder of the Minas Basin is red Triassic conglomerate.

From Yarmouth eastward to beyond Halifax, the region known as

Atlantic Uplands, consists mostly of Devonian schists, slate and granite. Schists abound near Yarmouth but this gives way primarily to granite eastward beyond Halifax (Eardley, 1962).

Cape Breton Island is divided into the famous highlands at the northwest tip and into the lowlands south and east. The main massif of Cape Breton Highlands is a tilted block which is principally granitic, with the remainder mostly sandstone and gypsums (Bird, 1972). The lowlands of Cape Breton Island are sandstones, gypsum, shales, and limestone (Eardley, 1962).

Newfoundland is mostly uplands except for the west coast, northern tip and the Notre Dame Bay region. The west coast is predominantly limestone interbedded with shales and dolomite, all of Cambrian to Ordovician age. These formations extend to and include the northern tip in the area of St. Anthony and south to Englee on Canadian Bay. Cape Ray at the southwestern end is in the southern end of the Long Range Mountains. The rocks here are quite similar to those of the lowlands of Cape Breton Island (Bird, 1972). The west side of White Bay is Mississippian clastics such as sandstones, conglomerates and shales (Bird, 1972). The Avalon Peninsula and the west side of Trinity Bay are covered by Cambrian and Ordovician sediments. On the west side of Trinity Bay the rocks are mostly folded while on the Avalon Peninsula folding is less common and faulting accounts for most of the relief (Eardley, 1962).

B. Climate

The region is exposed to three climates as shown on map 1. (Köppen, 1931; Griffiths, 1966). In the Köppen system of classification climates are given a three letter code, with first letter capitalized.

The entire region under consideration is characterized by Df climates; i.e., every month with at least two to four inches of precipitation and one or more months with a mean temperature of less than 64°F, none with a mean below 27°F, and at least one with a mean above 50°F. The southernmost region has a Dfa climate, i.e., a hot summer with the mean temperature of the hottest month above 72°F. The middle region has a Dfb climate, i.e., a warm summer with the mean of the hottest month \leq 72° and at least four months \geq 50°F. The northern region has a Dfc climate, a cool summer with the mean of the hottest month \leq 72°F and one to three months \geq 50°F (Köppen, 1931).

Although cloudiness is fairly uniform throughout the study area, summer fogs vary extremely (see map 2). Fog may be observed in St. John's Newfoundland, on forty-seven days each year and at Port Aux Basques on forty-nine days. At the northern end of Newfoundland, in summer alone, as many as 146 days may be foggy. In the month of July the Avalon Peninsula of Newfoundland experiences fog during 45 percent of all observational hours; Cape Breton Island 20 percent; Halifax 15 percent; Maine 20 percent; Cape Cod 15 percent; Long Island 10 percent; New Jersey 5 percent or less. Fogs south of Cape Cod are usually land fogs (Kendrew, 1961).

C. Water Characteristics

Little is known about the physical characteristics of the intertidal environment and adjacent waters.

1. CIRCULATION

The entire study area is influenced by a single current, the Labrador Current, which flows southward around Newfoundland and along the coast of North America past New Jersey. A finger of this

current forms a barrier between the New Jersey coast and the northward-moving Gulf Stream. Ocean currents however, do not invade the Cape Cod Bay or Nantucket Sound. Rather, the Labrador Current passes Cape Cod and its neighboring islands. Details concerning circulation within Cape Cod Bay are still unpublished (Bumpus, 1972). The waters of Buzzards Bay and Cape Cod Bay communicate through the Cape Cod Canal.

2. SURFACE TEMPERATURES

There are two sources of instantaneous measurements and one source of means and ranges. Instantaneous measurements were made during the course of my collecting and some data are available from oceanographic cruises. Measurements, including means and ranges, have been taken and compiled by lightships and oceanographic stations. The cruise data have two disadvantages. Not only are they instantaneous but they are never taken closer than several miles to the shore. The lightship and oceanographic station measurements provide means and extremes but, again are usually not as near to actual collecting sites as would be desired. My measurements proved quite compatible with the ranges provided by lightships, etc. Only surface temperatures are considered since these would be the ones affecting the shore.

A winter comparison is limited not only by the available data but by the fact that much of the Newfoundland shoreline is ice-locked in winter. My own measurements were taken from mid-June to late August.

It is necessary to rely mostly on my own data for Canadian waters. August measurements along the eastern side of Newfoundland range from 8 to 12°C, the warmer ones occurring in the more sheltered Hare Bay area. Along the west coast of Newfoundland the water is

somewhat warmer, between 15 and 18°C. The warmer temperature of this embayed area also holds for the tip of Cape Breton Island at the mouth of the Cabot Straits. However, the Atlantic side of Nova Scotia is colder, feeling the effect of the Labrador Current and lacking the tempering influence of the embayed waters. Temperatures range from about 10°C at Lousibourg Light on Cape Breton Island to 16°C at Halifax and Yarmouth. I shall use the highs reported for the shores of the United States since they compare more favorably in terms of dates with my Canadian measurements. Since I normally started in Massachusetts area and worked north, the Canadian measurements were made in July through late August.

The temperatures thus derived are slightly more moderate for the Gulf of Maine than those found on Atlantic Nova Scotia. The temperatures range from 19°C in the Bar Harbor area to 20°C at Portsmouth, New Hampshire. At the east entrance to Cape Cod Canal in Cape Cod Bay the August temperature is about 23°C. On the south side of Cape Cod the temperature is about 25°C and then for the remainder of the collecting area southward the water temperature is about 26°C (Day, 1959).

Water at the shoreline is much warmer in the Bay of Fundy owing to the extensive shallow areas covered by high tide. In August I measured the water temperature at Joggins to be 23°C. Detailed data for individual collecting sites may be found in Section VII.

3. SALINITY

The salinity of the waters is remarkably uniform except where influenced by fresh water flow from estuaries. As in the case with

temperatures, my own measurements must be used for Canadian waters. Water was collected in glass bottles equipped with Bakelite caps and conical polyethylene seals. Salinity was determined by the density method (Cox, 1954) with the use of Knudsen's tables (Knudsen, 1953). For a discussion of this method see appendix C.

Along the east coast of Newfoundland the salinity ranged between 31.34 ppt and 33.61 ppt (parts per thousand). The lower parts of the range occurred in bay areas influenced by fresh water. On the west coast of Newfoundland I measured salinity as 32.28 ppt in an area receiving considerable flow from rivers.

The tendency of salinity around Cape Breton Island parallels that of temperature. That is, the salinity is tempered by the flow from the St. Lawrence River. Salinity was 33.36 ppt at Louisbourg Light on the northeast point and 32.48 ppt at the mouth of the Cabot Straits. The Atlantic Coast of middle to lower Nova Scotia exhibits a salinity of about 32 ppt.

In the United States many of the collecting sites are near or at estuaries. The estuaries reduce salinities to below 20 ppt in the spring rainy season with the maximum influence occurring in late April to early May. The extremes may reach 34 ppt to 35 ppt but the means tend to fall around 31 ppt (Day, 1959).

4. SEDIMENTS

On the Bay of Fundy and the Minas Basin, sediments were observed in the intertidal zone. The poorly consolidated conglomerate forming the basin erodes readily. Many ravines flood at high tide and deliver sediments from their beds to the Bay. These sediments tend to cover barnacles and lichens, presumably interfering with light

reception and gas exchange.

In the Cape Cod region and south, sand as a sediment factor appears to be abundantly involved. I am convinced that abrasion by sand carried by waves must be a major factor in reducing the lichen population. In most places the only substrate suitable for littoral lichens is man placed rock found in "sand catchers" along beaches and jetties protecting channels. It is apparent that, since their purpose is to impede the movement of sand, they must be impacted by it.

V. BIOMETRIC METHODS

A. Collecting Procedures

Collecting methods were not designed to produce completely random samples but rather to try to insure that all species present were represented in the collection. On the other hand, the nature of the flora is such that species determination in the field is extremely difficult and no attempt was made at field identification.

Depending upon the nearness of the turning of the outgoing tide, collections were begun at low tide and continued upward to the upper limits of the "black zone" or were begun at that upper edge and continued down to the water at ebb tide. In either case, an attempt was made to collect continuously at all levels and to include all of the different microhabitats. Unfortunately, the shape and texture of the rocks influence, to some extent, the sample data since only lichens in favorable locations could be removed. Under the circumstances I believe that there is sufficient randomization to provide statistical validity.

B. Community Analysis

Three community characteristics were calculated: dominance, evenness and diversity.

Dominance was calculated according to the Simpson method (Odum, 1971). The equation is given below:

$$c=\Sigma(ni/N)^2$$

c= concentration of dominance

ni= number of individuals of given species

N= total of all individuals

The value of "c" varies between zero and one. Of course, the value

will never equal zero; but if all individuals present were of the same species the value would be one.

Evenness is computed according to a method advanced by Pielou (1966):

$$J = \frac{H}{\log S}$$

J= evenness

H= diversity according to the Shannon method (see below)
S= number of species

The value for "J" varies between zero and one.

The Shannon Index of Diversity (Shannon and Weaver, 1963) is computed by the equation:

H= index of diversity

pi= number of individuals of a given species divided by the total of all individuals (=ni/N in Simpson's Index of Dominance).

log pi= the natural log of pi.

There is no absolute upper limit to the value of "H", but if there is only one species, the value is zero.

C. Interspecific Association

One can hardly help, when examining collections, being impressed with the repeated occurrence of certain species with certain other species on a single piece of rock. Certain similarities in vertical distribution are evident from figures 3 through 10. Concurrence and separate occurrence of certain species on various collecting sites are also evident. One tends to form intuitive judgements from these observations as to association tendencies. The measurements of association given by Cole (1949) were utilized in an effort to obtain

unbiased estimates of association to verify initial intuitive $\label{eq:judgements} \mbox{judgements.} \mbox{ The significance of association was determined by a χ^2 test:}$

$$\chi^2 = \frac{(ad-bc)^2 n}{(a+b)(a+c)(c+d)(b+d)}$$

df=1

a= the number of occurrences of two species together.

b= the number of occurrences of the first species in the absence of the second species.

c= the number of occurrences of the second species in the absence of the first.

d= the number of samples from which both the first and second species are absent.

n=a+b+c+d.

For a probability of significance at the 95 percent confidence level, the χ^2 value must be equal to or greater than 3.84146 (Li, 1964).

In order to measure the degree of association and indicate whether the association is positive or negative, the coefficients of association and their standard errors were computed. The same a,b,c,d, and n values are identical to those in the χ^2 calculations. When ad \geq bc, the equation is:

$$C=\frac{ad-bc}{(a+b)(b+d)} \pm \frac{(a+c)(c+d)}{n(a+b)(b+d)}$$

When bc \geq ad and d \geq a the equation is:

$$C = \frac{ad-bc}{(a+b)(a+c)} \pm \frac{(b+c)(c+d)}{n(a+b)(a+c)}$$

When bc \geq ad and a \geq d, the equation is:

$$C = \frac{ad-bc}{(b+d)(c+d)} \pm \frac{(a+b)(a+c)}{n(b+d)(c+d)} \cdot$$

The value of "C" varies between +1 and -1. Positive values indicate association while negative values indicate avoidance.

D. Environmental Effect

Five independent environmental variables were measured at each site: water temperature, air temperature, solar insolation, salinity of the sea water, and tidal range. These data were used in an effort to explain the variation in abundance of each of eight species and in the diversity of littoral lichen species at each site.

Inasmuch as the environmental variables do not act independently, a multiple regression analysis was employed. Due to the large number of variables for the number of sites collected, a stepwise multiple regression analysis was used to reduce the list of independent variables to those whose effect was statistically significant.

In addition to the simple variables listed above, their cross products were also included to represent the interactions of those variables. Since preliminary work indicated that the effects of the variables were not entirely linear, the squares of the functions were included in the analysis as were the cross products of the squared functions and the other functions.

The multiple regression analysis used provides regression coefficients and their associated standard errors for each variable. However, several variables are measured in different units. The difference in variables is compensated for by converting all units to standard scores. The regression coefficients so corrected are expressed as beta weights and their standard errors are given.

The regression analysis procedure yields a test of the null hypothesis that the variable considered makes no contribution to the explanation of the variation in the dependent variable (i.e., diversity or relative abundance of each species).

The analysis procedure also yields the partial correlation coefficient which is the correlation between the dependent and independent variable if all other variables were held constant.

Finally, the analysis procedure also indicated what percent of the variation would be explained if the variable concerned were eliminated from the analysis.

VI. FACTORS INFLUENCING LICHEN DISTRIBUTION

The environment of littoral lichens is one in an almost constant state of fluctuation. An intertidal lichen is subjected alternately to hot and cold temperatures, submergence and desication, varying salinity, intense sunlight and shade, and pronounced changes in wave action, all within a single day. All of these factors vary also from one extreme to another with the passing of seasons. These plants are also subjected to drenching rain water and crashing waves. The latter transport a wide variety of particles which have an additional erosive effect. The various environmental conditions to which lichens are subjected cannot be isolated in nature and can only be imperfectly measured. Attempts were made, however, to quantify a number of these variables and compute their effects.

If a given environmental factor is selective, its increasing impace will diminish the diversity of species in the habitat by reducing the members to those either most resistant to its detriment or benefiting most from its presence. On this basis, measurable parameters were regressed against diversity as indicated by the Shannon Index of Diversity (Shannon and Weaver, 1963) and against the percent each species comprised of the entire collection at a given site. This percent was used as an indicator of success for that species.

A. Salinity

It would be desirable to know the complete range of salinities for all collecting sites and to know the duration of each condition. Unfortunately such data are not available. The salinity values used are maxima where known. Otherwise, they are instantaneous

summer measurements.

Santesson (1939, pp. 43) stated that "the eumarine species cited...have, as pronounced aquatic plants, a distribution which is first and foremost settled by the content of the submerging water".

Accordingly he classifies as meso-euhalibiae, accepting salinities down to .4 to .6 ppt, Verrucaria maura, V. microspora, V. ceuthocarpa, Lichina confinis, and Arthopyrenia orutensis. He classified as euhalobiae, accepting salinities not lower than 15 to 20 ppt,

Verrucaria erichsenii, V. ditmarsica, V. striatula, V. mucosa and Arthopyrenia sublitoralis=(A. halodytes). I have, however, collected several of the euhalobiae species at sites having seasonal salinities well below the ranges specified by Santesson.

Moore (1958) points out that lowered water temperatures increase the sensitivity of certain marine animals to desalination and this may well apply to lichens as well. Since my collecting area is considerably more southern and warmer than the area studied by Santesson, it is quite possible that the differences in our findings are due in part at least to the difference in latitude between our respective study areas.

B. Heat

It is reasonable to expect some effects of heat on lichen distribution since the literature is replete with maps of vegetation zones based in part or entirely on isotherms (Visher, 1954).

Santesson (1939) alludes to this influence in stating that the reports of *Verrucaria mucosa* were all from arctic or temperate regions. The appearance of a latitudinal gradient in which several species reach southern limits tends to support the hypothesis that increased heat

may be a limiting factor.

One of the most profound characteristics of the intertidal zone is that it is alternately atmospheric and aquatic. In summer, the thalli are heated on dry sunlit rocks at low tide and then cooled by the incoming tide. Conversely, in winter they are frozen by the cold winds of the atmosphere and then thawed by the sea water that flows over them when the tide rises.

1. WATER TEMPERATURES

Since some of the shores in Newfoundland are icebound during much of the winter, it is not possible to compare the water temperature minima over my entire collecting area. Therefore, maximum water temperatures were used. Where records of maxima are not available, instantaneous summer measurements made at the time of collecting were substituted.

2. AIR TEMPERATURES

Average daily maximum air temperatures (U.S. Dept. of Comm., etc., 1971; Atmospheric Environment Service, etc., 1971) were regressed against diversity and species abundance.

3. INSOLATION

It is logical to expect that lichens exposed to sunshine above high tide or after the recession of tidal waters would be affected in some way by this radiation. The observations by Ferry and Sheard (1969) and Lewis (1972) that *Verrucaria maura* grows higher on north-facing rocks than on south-facing rocks suggests that the sun's heat may be a factor in limiting distribution. Fletcher (1973a) attributes the difference in distribution to resulting "wetness". My field data will not support analysis of local effect. However, there

does appear to be a sufficient basis for analysis with reference to geographical distribution. There are approximately twelve degrees of latitude between the northern and southern points of my study area. Figure 2 indicates the langleys (1 langley = 1 calorie per square centimeter) per day striking the surface of the earth at different latitudes at different times of the year.

By interpolation it is evident that the variation is ten langleys

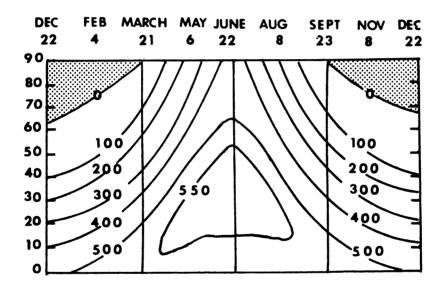


Figure 2. Annual variation in solar insolation in the northern hemisphere. Drawn after Hess (1959, p. 133, f. 9.2).

per day for each degree of latitude in late August. August was selected as the time of interest because it is the warmest month and, therefore, the month in which insolation would have its most rigorous heating effect.

C. Tidal Variations and Wave Action

Those species that fall into the category of littoral as stated earlier are influenced by the impact of changing tide. With the

exception of *Verrucaria serpuloides* (Lamb, 1948, 1973), which does not occur in my study area, there are no lichens that live below the low tide level. It is reasonable then to assume that constant submersion cannot be tolerated by the littoral lichens under consideration. Since there is a limit to the vertical extent of growth above high tide for these lichens, it is reasonable to assume that the presence of sea water to some degree is essential. These upper and lower limits, in accordance with Leibig's law of minimums (Leibig, 1840) and Shelford's law of tolerance (Shelford, 1913) must be established by some environmental factor or the interplay of more than one factor. If tidal range is a limiting factor, it follows that diversity should increase with increasing height of tide.

As already discussed, views differ as to whether vertical distribution should be studied with regard to tide levels or some biological index. Acting on the suspicion that submergence and emergence and wetting and drying would be major factors in establishing survival limits for the various species, I chose to plot the quantitative vertical distribution of species with respect to these factors.

In the field, I noted the estimated heights above and below high tide of each collection. I also noted the distance seaward and leeward from the high tide line on the shore. Inasmuch as the water floods a slope at essentially the same rate as it rises up a vertical face, the horizontal factor is irrelevant to time of submergence or emergence.

In examining figures 4 through 10 one must bear in mind that the heights are indeed estimated and not measured and obviously some error must be present.

A major problem in trying to incorporate all of the data from all localities is the fact that tide range in my study area varies from less than one meter to more than ten meters. If one specifies that a given individual lichen is found three meters below high tide, this could mean that it is still five meters above low tide or that it is actually several meters below low tide (which does not occur in my study area). I settled on an imperfect yet, I believe, useful treatment. Within my study area the rate of tidal variation is fairly uniform. i.e., it is ca. six hours between low and high tides. About the same time elapses between high tide and the following low tide. High tide and low tide each occur twice per day. Disregarding the fact that the rate of change slows slightly at each extreme one could say that, as water rises toward high tide, the bottom sixth of the range will be covered about six hours, the next sixth for five hours, etc., until the water reaches high tide. The upper sixth of the range would be covered one hour. As the water receeds the top sixth of the range will be exposed after one hour, the next sixth after two hours... thus with two tides per day the top sixth would be covered four hours. The next sixth would be covered eight hours. Theoretically those exactly at high tide would never be submerged and those at low tide would always be submerged. The flaws in this are obvious. However, I believe that it is a useful assumption that equal sixths of the tide range represent equal times of submergence and exposure and that this is the most reasonable way of equating distributions over such diverse tide ranges.

In figures 4 through 10, the intervals on the vertical axis below the horizontal axis represent sixths of the tide range. The

bottom of the vertical axis represents low tide and the line of the horizontal axis represents the high tide line. Above that point each interval represents one meter above high tide. Distances above high tide were rounded off by adding .5 to the value and plotting only the integer. Except for high and low tide all points are plotted at mid-interval. In order that the distribution of all species could be compared regardless of their abundance, the values plotted were percents of the total of all collections of that species.

The marine lichen floravis dominated by seven species of Verrucaria and one of Arthopyrenia. I will discuss the Verrucariae first. In figures 4 through 10 it is evident that all species except V. maura show the largest peak to be within one meter of high tide. The mode for V. maura is slightly higher. Except for that peak, V. mucosa, V. ditmarsica, V. striatula and V. microspora grow predominently below high tide when all shores are considered without regard to exposure to waves. Verrucaria ceuthocarpa is more evenly distributed around the high tide line. Verrucaria erichsenii grows to a greater extent above high tide than below. Verrucaria maura, in my experience, was found exclusively at or above the high tide line. These observations are quite compatible with those of Santesson (1939) in Europe. The greatest differences between my observations and those of Santesson are that he found Verrucaria maura and V. erichsenii lower than I did and he found V. ceuthocarpa did not extend as low as I found it. The latter discrepancy is due, in part, to the fact that he regards V. ceuthocarpa as different from his new species, V. degelii. As explained later I regard V. degelii as merely a variant of V. ceuthocarpa.

Arthopyrenia halodytes (see figure 10) is distributed rather

evenly around high tide and has a narrower range than the more aquatic *Verrucariae*. This may, in part, relate to the fact that this species is found most frequently on the calcareous shells of barnacles which occur primarily in this narrow zone.

Considerable emphasis has been placed on exposed versus sheltered shores (Kärenlampi, 1966; Ballantine, 1961; Lewis, 1972). With this in mind the collection sites were divided according to wave exposure and the verticle distributions of each species plotted. There were 18 sheltered and 24 exposed shores. In figures 4 through 10 the solid line represents the distribution on sheltered shores while the dashed line represents the distribution on exposed shores. Points plotted are percents of all collections from the included shores.

Exposure has little effect on the location of the zone of greatest abundance of *Verrucaria mucosa* (figure 8). It only slightly extends the range above high tide. However, it also increases the percentage of abundance below high tide. The effect on *Verrucaria ditmarsica* (figure 4) and *V. striatula* (figure 9) is quite similar to that on *V. mucosa*.

While elevating the level of peak abundance of *V. microspora* (figure 7), exposure approximately reverses the trends above and below high tide for the remainder of the population.

Exposure produces a slight general downward shift in frequency pattern of V. ceuthocarpa (figure 3).

Exposure has a minimal effect on the abundance of *V. erichsenii* (figure 5) below high tide but does extend the range of growth upward about 2.5 meters.

Exposure does not extend the range of V. maura (figure 6) but

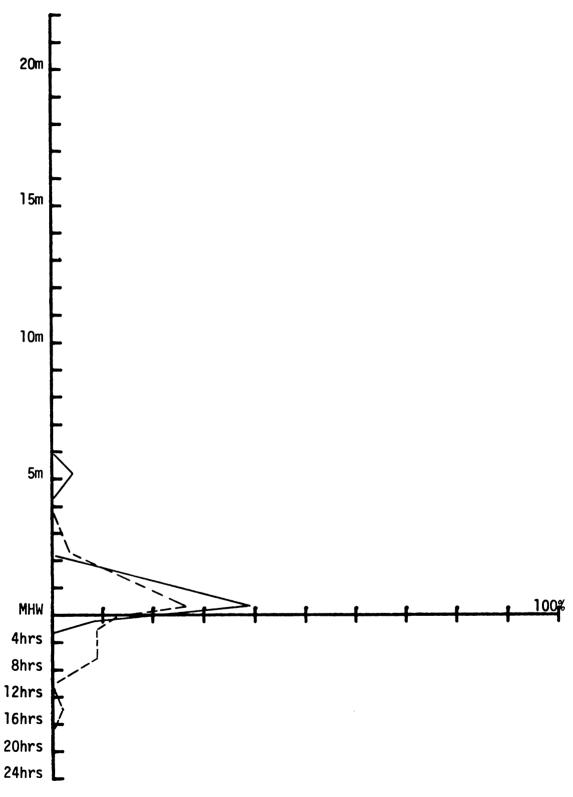


Figure 3. Vertical distribution of Verrucaria ceuthocarpa.

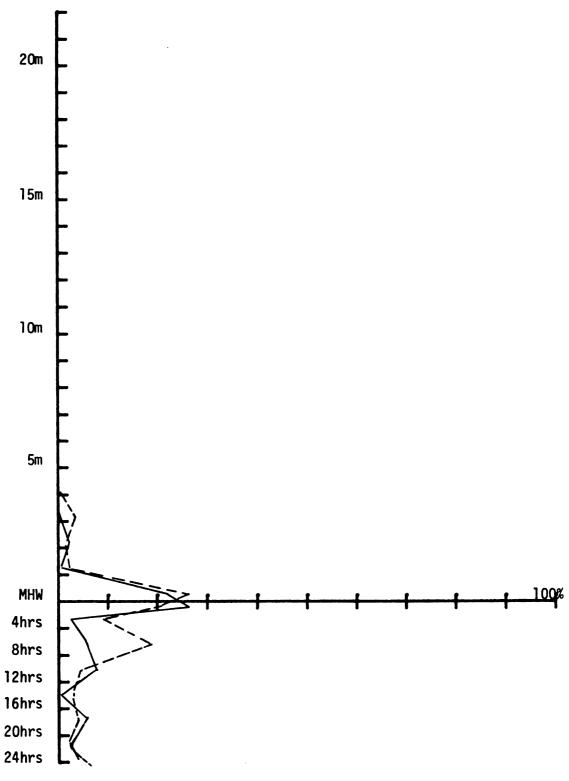


Figure 4. Vertical distribution of Verrucaria ditmarsica.

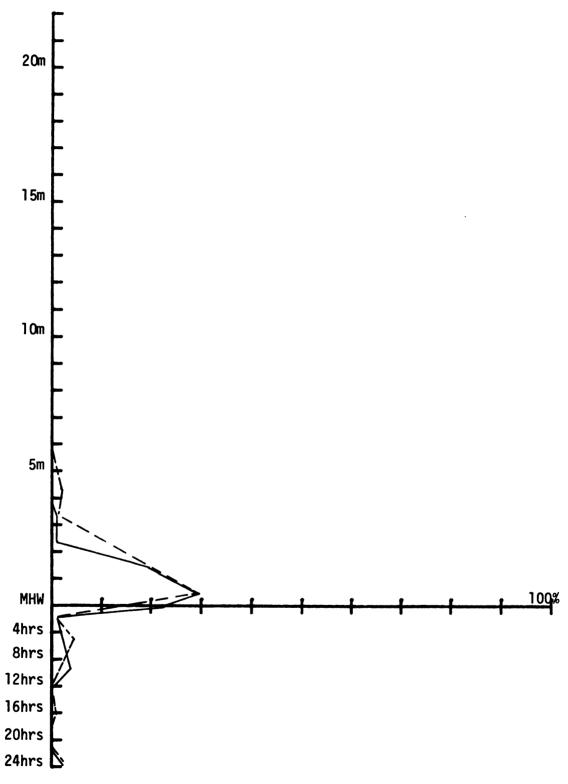


Figure 5. Vertical distribution of Verrucaria erichsenii.

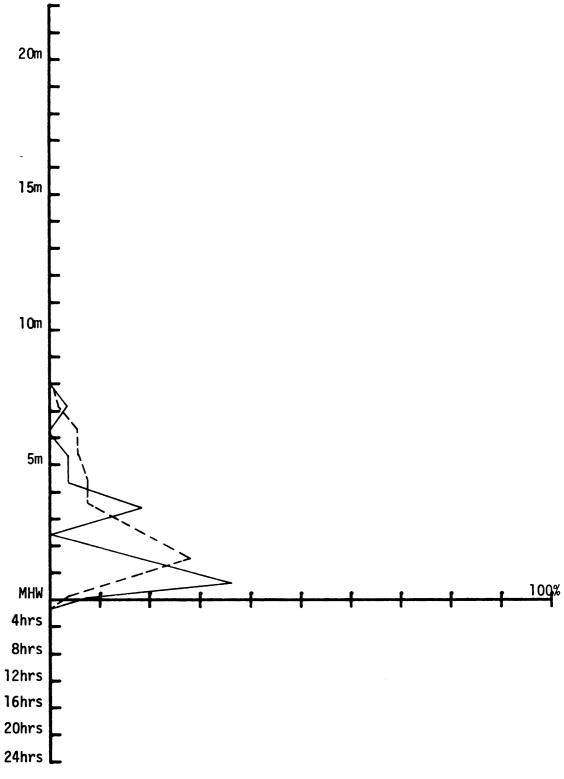


Figure 6. Vertical distribution of Verrucaria maura.

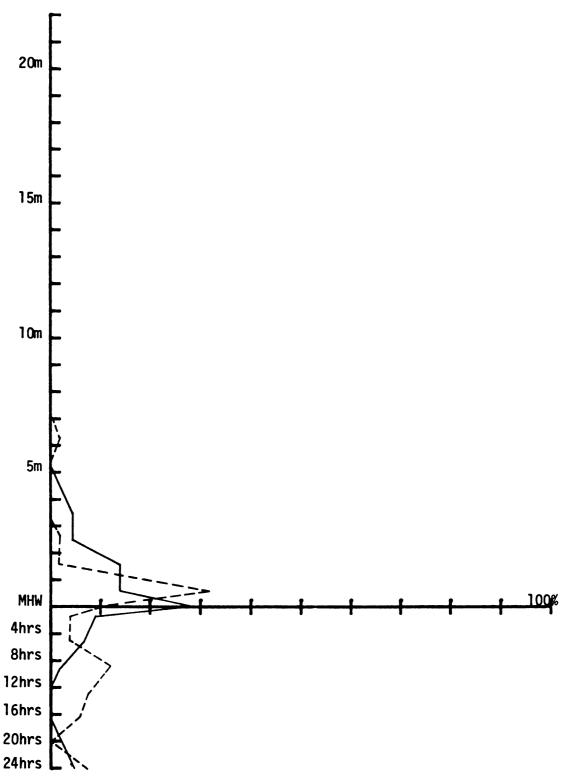


Figure 7. Vertical distribution of Verrucaria microspora.

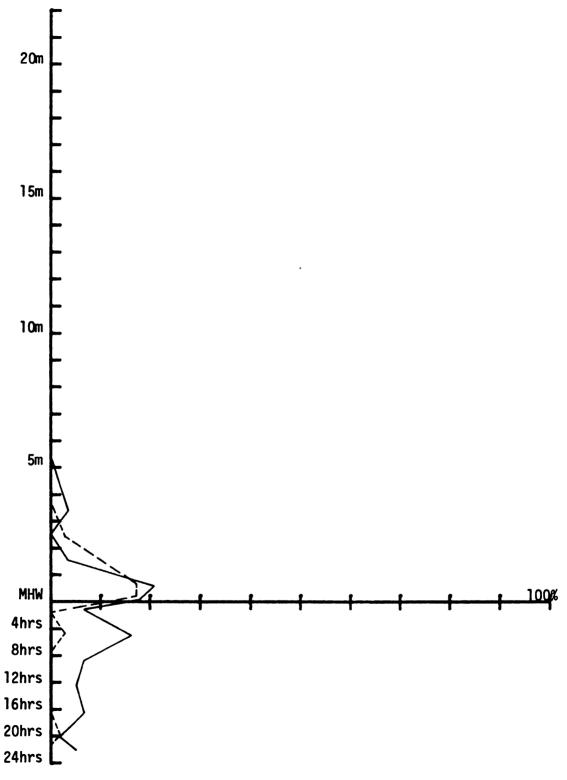


Figure 8. Vertical distribution of Verrucaria mucosa.

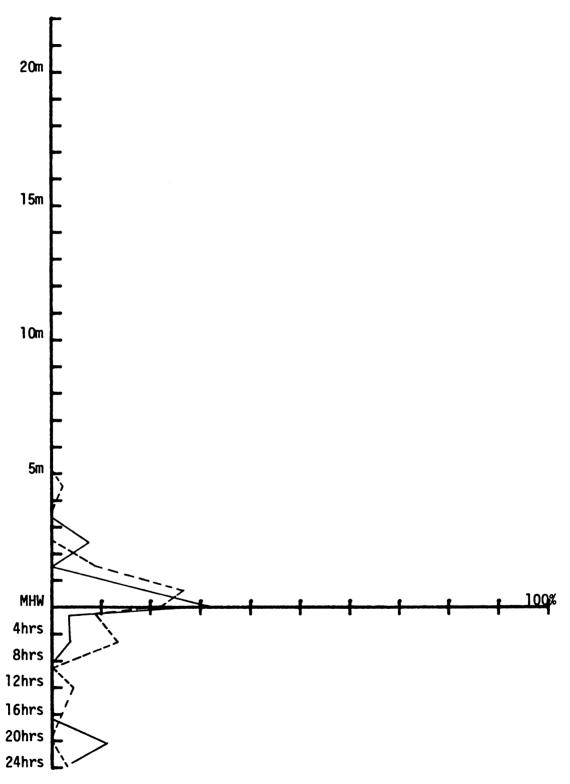


Figure 9. Vertical distribtuion of Verrucaria striatula.

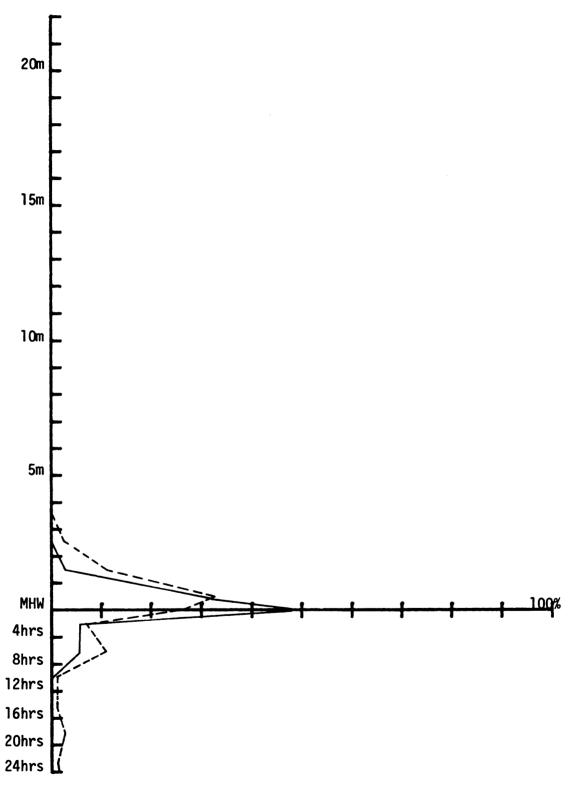


Figure 10. Vertical distribution of Arthopyrenia halodytes.

does slightly increase the percentage distributed at higher levels.

In general, it appears that increased wave action results in an increase in the height at which a species that grows primarily above high tide can survive. Conversely, exposure lowers the level of abundant growth of species that normally have extensive growth below high tide.

It appears that wave action extends the height of "marineness" on a shore line for those species normally living mostly above high tide. I can offer no explanation for the depression of the depth of abundant growth of those species abounding below high tide except that they may be sheltered by the macro-algae at lower levels. My observations and conclusions regarding wave exposure effects are in harmony with those of Fletcher (1973a).

D. Geology

Topography, rock structure, and sediments affect the distribution of littoral lichens.

As observed by Lewis (1972) shore topography to a large extent determines the impact of the sea on the flora and fauna. Vertical faces produce spray action. It was noted that at Cape Bona Vista the slope of the rocks allowed the wave to ride up the rocks rather than break and spray. On sloping terraces such as those at Halibut Point, lichens grow primarily on the vertical sides of the sloping blocks, thus avoiding the scrubbing action of the water rushing up the slope.

Generally speaking, the harder the rock the better the substrate for marine lichens. On the Bay of Fundy much of the rock is quite friable, leading to rapid erosion. This makes a poor substrate for slow-growing lichens. The rocks at Englee, Newfoundland, although

well lithified, are quite soluble and the surfaces weather rapidly. Fracture patterns are important on shores exposed to heavy waves by providing protected niches (Lewis, 1972).

Sediments have two effects as previously discussed. When sediments settle in the intertidal zone they tend to smother the flora and fauna. This was observed in the Bay of Fundy. It was also observed at the New Jersey sites where barnacles showed sand deposits where Arthopyrenia halodytes would normally be found. Abrasion results where sand is the sediment (Lewis, 1972).

E. Analyses of Environmental Effects

The data that supports the following analyses are found in Appendix B (Tables 6-14). Independent variables were eliminated stepwise until all of the variables retained had a significance (of the null hypothesis) of less than .1. Most of the variables retained had significance of .05 or less.

Eleven variables are required to explain 60.9 percent of the variation of abundance of *Verrucaria mucosa*. All parameters measured play a role in this determination. However, the greatest effects are produced by insolation and/or salinity. The greatest significance and the greatest effect on the percent of explanation if deleted belongs to insolation. The effect on the abundance of *V. mucosa* is negative. Second in importance is the influence of salinity, having the next highest significance and effect of deletion. This influence is also negative. The interaction effect of these two factors is complex. The linear aspect of their interaction is positive and third in order of deletion effect. The effect in their non-linear aspect is negative but far less significant and has one of the lesser

deletion effects.

The environmental effects on the distribution of Verrucaria microspora are far more complex. Although 91.3 percent of the variation of abundance of V. microspora is explained by the factors measured, nineteen variables are required for this degree of explanation. Within all of this complexity, however, a few observations are noteworthy. Of all the conditions measured, water temperature exhibited the least effect. Although tidal range alone is not significant in its effect at the 95 percent confidence level. it is involved in the most important interactions. The interactions having the greatest significance and deletion effect are air temperature and tidal range, in both linear and non-linear aspect, and the non-linear interaction of tidal range and salinity. The strongest effect is a negative one in the non-linear aspect of the interaction of tidal range and air temperature. Only slightly less in effect is the positive influence of the linear interaction of the same two factors. The non-linear interaction of tidal range and salinity is intermediate in the degree of effect between the two aspects of the above interaction and has a positive influence. It is interesting to note that none of the variables alone has a really great effect on the explanation if deleted. Such a complex relationship of abundance to environmental variation is not surprising when one considers that the species in question is distributed over the greatest range of latitude of any studied.

Of all of the species investigated the least of the variation of abundance of *Verrucaria erichsenii* is explained by the environmental qualities measured. Only 24.3 percent of the variation in abundance

is explained by seven variables of which only five are significant at the 95 percent confidence level. Tidal range and its interactions with all other variables fail to reach this significance level. Air temperature and its interaction with insolation have a significant effect but they have less deletion effect than the remaining significant factors. The negative linear influence of air temperature has about equal effect to the positive influence of the interaction of air temperature and insolation.

The strongest effects are exerted by salinity and its interaction with insolation. The effect of salinity alone is negative. The effect of the interaction between salinity and insolation is positive in the linear aspect but negative in the non-linear aspect.

Fifteen variables explain 79.9 percent of the variation of abundance of *Verrucaria striatula*. Seven of these are significant to an extremely high level of confidence. However, statistical significance does not necessarily equate with degree of effect. The greatest deletion effect and highest partial correlation coefficients are produced by the interaction of tide with salinity and insolation. Tidal range and insolation interact non-linearly to produce the greatest effect as indicated by the high partial correlation coefficient and the major deletion effect. This influence is negative. The next highest influence is exerted by the interaction of tidal range and salinity with the strength of influence divided almost equally between the positive influence of the non-linear aspect and the negative influence of the linear aspect of their relationship.

Eighteen variables explain 74.3 percent of the variation of abundance of *Verrucaria ditmarsica*. All of these are significant to

at least the 95 percent level. It is difficult to select out any variables for special mention. However, by examining both the beta weights and deletion effects, five variables seem to stand out. These five involve insolation and salinity and their interactions. Each of these independently exert a negative influence except for the non-linear aspect of insolation which has a positive effect. Their interaction effects are divided almost equally between the positive influence of their linear aspect and the negative influence of their non-linear aspect.

Sixteen variables, of which fourteen are significant to the 95 percent confidence level, explain 71.6 percent of the variation of the abundance of *Verrucaria maura*. Of these variables there are four leading members. All four involve air temperature or its interactions with insolation and salinity. Air temperature acting independently in a non-linear mode is the strongest factor based on beta weight; however, based on partial correlation coefficient and deletion effect, the interaction of air temperature with insolation and salinity have greater effects. The influence of air temperature alone is negative. Its influence when interacting with insolation is positive. The influence of the interaction of air temperature and salinity is negative in its linear aspect but positive in its non-linear aspect.

The positive influence of insolation alone and when interacting with air temperature leads me to question whether the predisposition of *V. maura* to grow on less illuminated sides of rocks might relate to some factor other than sunshine.

To explain 57.9 percent of the variation of abundance of

Verrucaria ceuthocarpa, nineteen variables are required, four of which do not reach the 95 percent confidence level. The greatest influences are exerted by air temperature, insolation and salinity and their interactions. The influence of the interaction of air and water temperature has a small beta weight but has significance. The partial correlation coefficient and deletion effect make it stand out as the largest single influence. Insolation is the predominant remaining factor acting independently and in interaction with salinity. Insolation has a negative effect in its linear aspect with a positive effect of about equal strength in its non-linear aspect. Its interaction with salinity is positive in influence. Salinity, acting independently in a non-linear mode, has a negative influence; when interacting with non-linear air temperature, it has a substantial positive effect.

Only 41.7 percent of the variability of abundance of Arthopyrenia halodytes can be explained by the seven environmental variables measured. All these variables play some role in determining abundance of this species. Two of the three major influences involve interactions of air temperature and salinity. The interaction has a positive influence in its linear aspect and a negative influence in its non-linear aspect. Water temperature and insolation interact with a positive effect. Water temperature itself has a considerable negative effect. It is difficult to say whether the effects are really upon the lichen or upon the barnacles that commonly serve as substrates for the lichen.

Three variables composed of two parameters explain 59.1 percent of the variation in general diversity of species. All three variables are highly significant. Salinity alone is not as effective as is its

interaction with insolation. The independent effect of salinity is negative. When insolation interacts non-linearly with salinity, the effect is negative. The linear interaction of insolation with salinity is positive.

While my findings do not bear out Santesson's (1939) conclusion that salinity is the determing factor in lichen distribution, it does support the position that it is one of the major factors. By tallying the number of times that each environmental factor is involved as one of the most important causes, the following frequencies resulted: salinity, 21; insolation, 15; air temperature, 12; tidal range, 7; and water temperature, 2. The emergence of salinity and insolation as the prime explainers of general diversity is consistent with the role of these factors in determining individual species abundance. Certainly the relationship of environment to abundance is a complex one as is the environment itself. Perhaps the wide tolerances of these species accounts for their presence in this environment. Fletcher (1973a) postulates that "wetness" is the primary factor influencing distribution. Unfortunately his sampling procedures were not accompanied by statistical analyses.

F. Biotic Factors

"Competition for space is always keen. Young muscles and Fucus sporelings develop on and between barnacles; barnacle larvae settle on old barnacles, muscles and limpets; small algae grow on limpets, and lithothamnia overgrow barnacles (Lewis, 1972, p. 295)."

The intertidal lichens share the world discribed above. I have seen, in a single field of view of a dissecting microscope, an example of such competition. *Hildenbrantia* surrounded the hold-fast of *Fucus*. Part of the *Hildenbrantia* was overgrown by *Lithothmnia* which was

largely overgrown by bryozoa. Another part of the *Hildenbrantia* was overgrown by *Verrucaria mucosa*, much of which, in turn, was covered with a shellac-like glaze where a barnacle had been attached. At the microhabitat level, if not above, the distribution of a littoral lichen must be affected by its ability to compete with other littoral lichens as well as the myriad of other organisms seeking to occupy a space on the rock.

The degree to which the rocks are clothed by macro-algae affects the distribution of littoral lichens in three ways. The first of these, spatial competition, has already been discussed; the other factors are reduced desiccation and shading.

When the tide ebbs, the algae hang limply and the outer layers dry. Beneath this outer layer, however, moisture is conserved. The lichens at their bases are kept from drying. This action and its favorable effect were noted by Santesson (1939).

When the tide returns, the fronds of the macro-algae float outward and upward, spreading and intercepting maximum light. The shading effect is similar to that of maple trees over understory on land. Thus the lichens in the macro-algae belts are shaded to an extraordinary degree under all tidal conditions. I have observed that the lichens included in these belts contain, to a large extent, shade-modified thalli.

A biotic factor affecting marine lichens that is only occasionally seen in my area is predation by animals. Santesson (1939) reports morphological differences due to predation. Lewis (1972) reports several examples of bare rock cleared as the result of such predation on blue-green algae. While he does not report such grazing

damage by gastropods on littoral lichens, the incidents reported occur in a zone normally occupied by them. He includes an excellent photograph (pl. 38) of tracks made by rasping radulae. I have occasionally seen similar marks on lichen thalli especially of Verrucaria mucosa.

VII. COLLECTING SITES

Sites are numbered here to correspond with maps of distribution. Inasmuch as collecting sites close together are represented on the map as a single circle, collecting sites so represented are designated with the same number but with different letter suffixes. The order in which sites were collected was often dictated by time of tide with respect to daylight or by other events such as hurricanes. Collection numbers for the sites listed below are contained in appendix A. Gaps in collection number sequences are caused by collections during that time period not relevant to this discussion or by a return to the site at a later date for further collection. Air temperatures given are average values for a year unless otherwise stated. All temperatures for air and water are in degrees Celsius. Water temperatures given are the high temperatures for the month of August unless otherwise specified.

la. Wingersheek Beach (Essex County, Massachusetts)

Tidal range: 2.66 m

Surface water temperature: 23°C

Salinity: 29.88 ppt (Instantaneous, June 21)

Insolation: 384 langleys

Average air temperatures: min.= 5°C; mean= 9.3°C; max.= 13.2°C

Diversity index: .588

Dominance index: .320

Evenness index: .841

The site consists of a public bathing beach strewn with granitic glacial erratic boulders up to four meters high and ten meters in diameter. Wave action at this site is minimal since the

beach is in a protected bay. Algae were not abundant, only a few fucoid and a few laminarioid types being present. Barnacles were present but not abundant.

1b. Halibut Point (Essex County, Massachusetts)

Tidal range: 2.66 m

Surface water temperature: 23°C

Salinity: min.= 12.8 ppt; mean= 29.7 ppt; max.= 34.2 ppt

Insolation: 384 langleys

Average air temperatures: min.= 5°C; mean= 9.3°C; max.= 13.2°C

Extreme air temperatures: -25°C and 37°C

Diversity index: .769

Dominance index: .209

Evenness index: .866

This is a granitic outcrop at the tip of Cape Ann. The rocks dip slightly seaward in terraces, forming ramps upon which the waves break and flow up. It is evident that exposure to wave action is always present at low or high tide. It is further evident that during storms waves keep the rocks barren to a distance of 30 meters back of the mean high tide. The rocks were heavily clothed in macroalgae with *Fucus* dominating and *Chondrus crispus* present at the lower levels. Laminarioid algae were observed below low tide. Barnacles were small and not particularly abundant.

2a. Recompence Shores (Cumberland County, Maine)

Tidal range: 2.7 m

Surface water temperatures: -2°C to 21°C

Salinity: 28.1 ppt to 33.55 ppt

Insolation: 371.7 langleys

Average air temperatures: min.= 4.4°C; mean= 8.9°C; max.= 13.3°C

Extreme air temperatures: -24.4°C and 36.6°C

Diversity index: .363

Dominance index: .583

Evenness index: .603

The site consists of a small granitic outcrop at the end of a long bay. At low tide a long mud flat is exposed. Due to the mud there is little bare rock below the high tide level. At high tide the rock extends no more than .6 meters above the water. Despite a brisk wind that prevails at this point, the wave action is minimal. Neither algae nor barnacles were in evidence.

2b. Bailey's Island (Cumberland County, Maine)

Tidal range: 2.7 m

Surface water temperature: 21°C

Salinity: 25.8 ppt to 32.4 ppt

Insolation: 371.4 langleys

Average air temperatures: min.= 4.4°C; mean= 8.9°C; max.= 13.3°C

Extreme air temperatures: -25.6°C and 36.7°C

Diversity index: .891

Dominance index: .144

Evenness index: .891

The rocks of the island are garnetiferous schists high in mica. The layers of rock are strongly tilted into a nearly vertical position forming ridges which extend into Casco Bay. The wave action is largely perpendicular to these ridges except at the point of the island. The nature of the folds that have produced this inclination tends to cause the formation of terraces exposed at low tide whereas

at high tide the waves usually strike against vertical faces of cliffs. The rocks were clothed in *Fucus* and *Ascophyllum*. In tide pools and below low tide *Lithothamnia*, *Corallina* and *Laminaria* were abundant. A dense population of barnacles gathered around the high tide line. Blue clams, sea stars and sea urchins abounded in the tide pools.

2c. Reid State Park (Sagadahoc County, Maine)

Tidal range: 2.7 m

Surface water temperature: 21°C

Salinity: 25.8 to 32.4

Insolation: 371.2 langleys

Average air temperatures: min.= 4.4°C; mean= 8.9°C; max.= 13.3°C

Extreme air temperatures: -25.6°C and 36.7°C

Diversity index: .941

Dominance index: .117

Evenness index: .986

Most of the shore is a sand beach but there are some flat granitic outcrops which are, for the most part, submerged at high tide. The shore is unprotected and wave action is continual. The algal and lichen floras were minimal because the rocks were dominated by a dense and expansive barnacle population.

3a. Great Head (Hancock County, Maine)

Tidal range: 3.2 m

Surface water temperature: 19°C

Salinity: min.= 26.9 ppt; mean= 31.6 ppt; max.- 34 ppt

Insolation: 366.2 langleys

Average air temperatures: min.= 2.9°C; mean= 7.4°C; max.= 12.8°C

Extreme air temperatures: -29.4°C and 36.6°C

Diversity index: .991

Dominance index: .116

Evenness index: .918

Great Head is a point of rock on the northeast corner of Mount

Desert Island. It is composed primarily of granite but contains

breccia and basaltic intrusions. The rocks rise abruptly out of the

sea and are subjected to very heavy wave action. Sea caves occur at

several points along the shore. Fucus, Ascophyllum and Chondrus

crispus predominated in the algal flora with laminarioid types

abundant in the tide pools and below low tide. Barnacles extended in a

conspicuous band from just above high tide to below high tide where

they are joined or replaced by blue clams.

3b. Schoodic Peninsula (Hancock County, Maine)

Tidal range: 3.05 m

Surface water temperature: 19°C

Salinity: min.= 2.9 ppt; mean= 31.6 ppt; max.= 34 ppt

Insolation: 386.2 langleys

Air temperatures: min.= 2.9°C; mean= 7.4°C; max.= 12.8°C

Extreme air temperatures: -29.4°C and 36.6°C

Diversity index: .952

Dominance index: .119

Evenness index: .952

Schoodic Peninsula is primarily grantitic but with many intrusions of basalt and veins of epidote. Terracing of the shoreline resulted from the characteristic exfoliation pattern of granite. The ledge exposed at low tide drops precipitously to a depth of

eighty feet. Wave action at this point is spectacular. The wave action plus the shape of the shore made the most exposed part too hazardous to collect. However, it appeared that filamentous blue green and red algae, rather than lichens, predominated.

3c. West Point Near Otter Cove (Hancock County, Maine)

Tidal range: 3.2 m

Surface water temperature: 19°C

Salinity: min.= 26.9 ppt; mean= 31.6 ppt; max.= 34.0 ppt

Insolation: 374.7 langleys

Average air temperatures: min.= 2°C; mean= 7.6°C max= 12.8°C

Extreme air temperatures: -29.4°C and 36°C

Diversity index: .738

Dominance index: .191

Evenness indes: .948

The rocks of this site include granite and basalt as is typical of Mount Desert Island. The rather steep cliffs give way seaward to boulders or miniature sea stacks that emerge prominently at low tide and are awash at high tide. Wave action, though not as spectacular as at Schoodic Peninsula is always present. The algal flora was similar to that at Great Head except that Ascophyllum was even more abundant. The band of barnacles at high tide with blue clams below is typical here as it is on most of the island.

4. Quody Head (Washington County, Maine)

Tidal range: 4.8 m

Surface water temperature: 14°C

Salinity: min.= 28.9 ppt; mean= 32.0 ppt; max.= 34.4 ppt

Insolation: 361.9 langleys

Average air temperatures: Unknown

Extreme air temperatrues: -26.7°C and 33.9°C

Diversity index: .836

Dominance index: .163

Evenness index: .926

The rock at Quody Head is primarily basaltic. Included in the site is a cliff and a conical mass of rock that is barely accessible at low tide. The site is quite protected by Campobello Island, and wave action is minimal. The algal flora was almost entirely made up of Ascophyllum. The barnacle population was minimal.

5a Prospect Point (Halifax County, Nova Scotia)

Tidal range: 1.35 m

Surface water temperature: 14°C (Instantaneous, Aug. 15)

Salinity: 32.66 ppt (Instantaneous, Aug. 15)

Insolation: 363.8 langleys

Average air temperatures: min.= 1.4°C; max.= 10.1°C

Extreme air temperatures: -28°C and 37.5°C

Diversity index: .699

Dominance index: .200

Evenness index: 1.000

The rocks at Prospect Point are granitic. The shoreline which consists of small boulders and well weathered bedrock outcrops, receives severe wave action. Algal and barnacle growth was minimal. Only a brief visit was made to this site and most material collected was non-littoral. When returning to these shores I collected at Peggy's Cove which is the next point of rock towards Halifax.

5b. Peggy's Cove (Halifax County, Nova Scotia)

Tidal range: 1.35 m

Surface water temperature: 14°C (Instantaneous, July 3)

Salinity: 32.66 ppt (Instantaneous, July 3)

Insolation: 363.3 langleys

Average air temperatures: min.= 1.35°C; mean= 7.6°C; max= 17.5°C

Extreme air temperatures: -27.5°C and 38.5°C

Diversity index: .874

Dominance index: .179

Evenness index: .839

This site is an exposed point at the mouth of Peggy's Cove and consists of low granitic outcrops. Wave action is substantial despite the impression one would gain from the name of the site. The algal flora was minimal and consisted primarily of Ascophyllum. Barnacles made a token appearance at the high tide line.

6. Joggins (Cumberland County, Nova Scotia)

Tidal range: 10.2 m

Surface water temperatures: Unknown

Salinity: 31.08 ppt (Instantaneous, Aug. 12)

Insolation: 353.2 langleys

Average air temperatures: min.= .51°C; mean= 9°C; max.= 12.4°C

Extreme air temperatures: -37.5°C and 37°C

Diversity index: .301

Dominance index: .500

Evenness index: .631

The shores of Joggins are sandstone and erosion has been great.

Despite the tidal range of 10.2 meters, the water does not reach the

cliff at high tide except in a storm. No lichens were observed on the cliff. A few lichens were found on the flat slabs of sandstone over which the incoming tide rides. Only occasional *Ascophyllum* plants could be found and these appeared stunted.

7. Five Islands Provincial Park (Colchester County, Nova Scotia)

Tidal range: 11.25 m

Surface water temperatures: Unknown

Salinity: 31 ppt (Estimated from Joggins)

Insolation: 356.3 langleys

Average air temperatures: min.= .51°C; mean= 9°C; max.= 12°C

Extreme air temperatures: -37.5°C and 37°C

Diversity index: .301

Dominance index: .500

Evenness index: .631

Most of the Five Islands area is a soft friable conglomerate. The more resistant structures, which were the only ones bearing lichens, are of a more lithified conglomerate. Due to the structure of the Minas Basin only about 4 meters of the 11.25 meter tidal range extends up the resistant rock. As the tide receeds it leaves a deposit of sediment on the resistant rocks and their inhabitants. Despite the strong winds that frequent the Minas Basin, such as the fifty to seventy mile per hour winds I experienced while at the site, little wave action occurs on the lichenized shores.

8. Yarmouth Lighthouse (Yarmouth County, Nova Scotia)

Tidal range: 4.25 m

Surface water temperature: 14°C (Instantaneous, June 28)

Salinity: 31.09 ppt (Instantaneous, June 28)

Insolation: 372 langleys

Average air temperatures: min.= 3.2°C; mean= 9°C; max.= 10.8°C

Extreme air temperatures: -23°C and 33°C

Diversity index: .878

Dominance index: .159

Evenness index: .878

Yarmouth Lighthouse is situated on a point of rock protecting Yarmouth harbor. The collections were made on the seaward side of the point. The rocks here are predominantly chlorite schists but include some granite. They rise out of the water as pyramids or as nearly vertical slabs. Although it was relatively quiet during my visit, the height of the black zone indicated strong wave action much of the time. The intertidal algae were Fucus, Porphyra and Ascophyllum. Barnacles formed the characteristic band in the vicinity of high tide.

9. Digby Lighthouse (Digby County, Nova Scotia)

Tidal range: 6.6 m

Surface water temperature: 14°C

Salinity: 32.54 ppt (Instantaneous, June 29)

Insolation: 373.7 langleys

Average air temperatures: min.= 1.6°C; mean= 7.5°C; max.= 17.5°C

Extreme air temperatures: -26.5°C and 39°C

Diversity index: .911

Dominance index: .150

Evenness index: .875

The rocks at Digby Lighthouse are primarily basaltic, being a part of North Mountain. The cliff upon which the lighthouse is

situated rises steeply from the water with a slight wave-cut terrace at its base. The prevailing winds provide Digby with considerable wave action. The algal flora was restricted almost entirely to Ascophyllum in the intertidal range.

10. West Point (Shelburne County, Nova Scotia)

Tidal range: 1.45 m

Surface water temperature: 14°C (Instantaneous, June 30)

Salinity: 32.66 ppt (Instantaneous, June 30)

Insolation: 372.7 langleys

Average air temperatures: min.= 1.36°C; mean= 7.6°C; max.= 17.5°C

Extreme air temperatures: -27.5°C and 38.5°C

Diversity index: .871

Dominance index: .166

Evenness index: .871

The shoreline consists of very large boulders between fifteen and twenty meters in length and about ten meters high. They are well rounded and I cannot assess whether they are large glacial erratics or exposed bedrock. Wave action at the site is substantial. Algal and barnacle populations were minimal.

11. Neil's Head (Victoria County, Nova Scotia)

Tidal range: .77 m

Surface water temperature: 16°C (Instantaneous, July 6)

Salinity: 32.54 ppt (Instantaneous, July 6)

Insolation: 342.8 langleys

Average air temperatures: min.= 1.5°C; mean= 7.8°C; max.= 10.8°C

Extreme air temperatures: -28°C and 38°C

Diversity index: .792

Dominance index: .225

Evenness index: .792

The shore at Neil's Head is granite rising abruptly from the water. It is not sheltered, but is exposed to the full force of waves from the Atlantic Ocean. The tops of the rocks are only about three meters above high tide and are constantly receiving spray. The algal flora was primarily fucoid. The barnacles formed the usual white zone around high tide and were fairly abundant.

12. Louisbourg Light (Cape Breton County, Nova Scotia)

Tidal range: 1.75 m

Surface water temperature: 10°C (Instantaneous, July 10)

Salinity: 33.36 ppt (Instantaneous, July 10)

Insolation: 351 langleys

Average air temperatures: min.= 1.09°C; mean= 6°C; max.= 10.6°C

Extreme air temperatures: -27.5°C and 38.5°C

Diversity index: .802

Dominance index: .174

Evenness index: .949

The rocks at Louisbourg are a limestone conglomerate much like those of Cape Ray, Newfoundland. The point at the lighthouse was uncollectable at the time I was there because of the active fog horn which was oppressive even around the point in a protected area. This site was quite protected from wave action except during storms. The algal flora was almost exclusively <code>Ascophyllum</code>. Barnacles were abundant and moderately large along the high tide mark.

13. Cape Ray Lighthouse (Newfoundland)

Tidal range: .99 m

Surface water temperatures: 16°C (Instantaneous, July 15)

Salinity: 32.54 ppt (Instantaneous, July 15)

Insolation; 334.2 langleys

Average air temperatures: min.= 1.46°C; mean= 4.19°C; max.= 7.2°C

Extreme air temperatures: -26°C and 30°C

Diversity index: .818

Dominance index: .211

Evenness index: .785

The rocks at Cape Ray are composed of a limestone conglomerate similar to that at Louisbourg Light. The rocks form a shelf which is dissected by vertical cracks. Wave action is heavy and the shelf is mostly awash at high tide. I was frequently splashed when collecting at low tide on a mild day. The rocks were heavily clothed in *Fucus*. Barnacle growth was moderate.

14. Deer Cove (Newfoundland)

Tidal range: .16 m

Surface water temperature: 18°C (Instantaneous, July 21)

Salinity: 32.48 ppt (Instantaneous, July 21)

Insolation: 300 langleys

Air temperatures: min= -.1°C; mean= 3.8°C; max.= 7°C

Extreme air temperatures: -32°C and 33°C

Diversity index: .817

Dominance index: .191

Evenness index: .817

The collecting site at Deer Cove consists of a very small cove

Seaward terraced shelves dip into the water and waves ride over them, striking the cliff. Very little was collected on the seaward side of the cliff because of the extreme wave action that inundated the area. The force of the wind along this shore was indicated by its pruning action on the evergreens growing near the shore. At this site I found the nearest thing to an "orange belt" of any place collected. Sighting down the shore one could see a tinge of orange on the high points of the cliff. The continuity was broken by irregularities in the height of the cliff. Algal growth was minimal. Barnacles were present near the high tide mark but were not abundant.

15. Goose Cove (Newfoundland)

Tidal range: .61 m

Surface water temperature: 12°C (Instantaneous, July 27)

Salinity: 32.48 ppt (Instantaneous, July 27)

Insolation: 300 langleys

Average air temperatures: min.= -1.8°C; mean= 1.7°C; max.= 5.2°C

Extreme air temperatures: -32°C and 31°C

Diversity index: .712

Dominance index: .240

Evenness index: .843

Goose Cove is a moderately protected cove just inside Hare Bay. It is a broad cove with a sloping shore of limestone. There was a scant population of Fucus and a few barnacles.

16. Englee (Canada Bay, Newfoundland)

Tidal range .61 m

Surface water temperature: 12°C (Instantaneous, July 28)

Salinity: 33.15 ppt (Instantaneous, July 28)

Insolation: 335 langleys

Average air temperatures*: min.= -.1°C; mean= 3.8°C; max.= 7°C

Diversity index: .802

Dominance index: .187

Evenness index: .888

*Temperatures are based on interpolations.

The rocks on the shore at Englee are largely marble. Broken terraces extend into the water from a cliff that extends steeply to about four meters above the terraces. Wave action is moderate. Most of the lichens were quite near the high tide mark above which the rocks weather rapidly. The rapid weathering causes the rock to be a poor lichen substrate. Areolate lichens survived only as scattered crumbs. Fucus and barnacles were present but rather scant.

17. Jacksons Arm (White Bay, Newfoundland)

Tidal range: .76 m

Surface water temperature: 12°C (Instantaneous, July 30)

Salinity: 33.13 ppt (Instantaneous, July 30)

Insolation: 321.7 langleys

Average air temperatures: min.= -.38°C; mean- 1.45°C; max.= 8.8°C

Extreme air temperatures: -43°C and 35°C

Diversity index: .828

Dominance index: .156

Evenness index: .980

The shore at Jacksons Arm is comprised of slate dipping into the sea. The site at Jacksons Arm is extremely protected with minimal wave action. A few fucoid algae formed a narrow zone at the high tide line. Barnacles were abundant and unusually large.

18a. Salvage (Bona Vista Bay, Newfoundland)

Tidal range: .76 m

Surface water temperature: 12°C (Instantaneous, Aug 1)

Salinity: 31.32 ppt (Instantaneous, Aug. 1)

Insolation: 328.5 langleys

Average air temperatures: min.= -.27°C; mean= 3.6°C; max.= 7.2°C

Extreme air temperatures: -35°C and 35°C

Diversity index: .821

Dominance index: .176

Evenness index: .909

The collecting site is slightly west of Salvage, in the direction of Eastport. It consists of a terrace of limestone overlooked by a four meter cliff and is quite sheltered, having minimal wave action. Only a moderate growth of Fucus and Ascophyllum was present near the high tide level. The barnacle population was equally moderate.

18b. Terra Nova National Park (Newfoundland)

Tidal range: .78 m

Surface water temperature: 16°C (Instantaneous, Aug. 9)

Salinity: 31.32 ppt (Instantaneous, Aug. 9)

Insolation: 324.5 langleys

Average air temperatures: min.= .28°C; mean= 3.6°C; max.= 7.2°C

Extreme air temperatures: -35°C and 35°C

Diversity index: .756

Dominance index: .215

Evenness index: .895

This site is located south of Route 39 on an arm of Alexander Bay. The rock is principally slate. The tide of only .8 meters must pass through a narrow channel under a bridge on Route 39 and then through a still narrower channel under a causeway within the park in order to reach this extremely well protected shore. The causeway also serves as a wind shelter. Blue clams and an occasional barnacle were observed but macroalgae were not evident.

19. Chance Cove (Trinity Bay, Newfoundland)

Tidal range: .76 m

Surface water temperature: 12°C (Instantaneous, Aug. 3)

Salinity: 33.60 ppt (Instantaneous, Aug. 3)

Insolation: 334.8 langleys

Average air temperatures: Unknown

Diversity index: .898

Dominance index: .136

Evenness index: .941

The shore is moderately sloping limestone. The collecting site is reasonably sheltered with moderate wave action. The algal growth was primarily enteromorphoid and filamentous. Barnacles were very scant.

20. Cape Bonavista (Bonavista Bay, Newfoundland)

Tidal range: .76 m

Surface water temperature: 13°C (Mercer, 1966)

Salinity: 33.61 ppt (Instantaneous, Aug. 6)

Insolation: 328.5 langleys

Air temperatures: min.= 1.4°C; mean= 4.5°C; max.= 7.8°C

Extreme air temperatures: -24°C and 30.5°C

Diversity index: .830

Dominance index: .161

Evenness index: .919

The collecting site is called "Cabot's Landfall". It is a limestone cliff dipping into the Atlantic at about a sixty degree angle. The layers of limestone are tipped on end at that angle. It is a very exposed point with a very unusual form of wave action. I have not seen the site during a storm and the pattern may change under such circumstances but, at the time of my observation, the waves did not break on the rocks; rather they flowed up the incline and back down. The algae seen were entirely filamentous reds and blue-greens. Barnacles were present within a meter of high tide but were not abundant.

21. Cape Freels (Newfoundland)

Tidal range: .76 m

Surface water temperature: 12°C (Instantaneous, Aug.7)

Salinity: 31.1 ppt (Instantaneous, Aug. 7)

Insolation: 314.8 langleys

Average air temperatures: min.= .25°C; mean= 3.9°C; max.= 7.2°C

Diversity index: .330

Dominance index: .570

Evenness index: .692

The collecting site consists of a large mass of limestone jutting out into the Atlantic Ocean on the west side of the mouth to

Bonivista Bay. It is not visibly continuous with similar rocks along the shore. Sea stacks are visible farther down the shore and perhaps this piece or rock represents an incompletely severed sea stack. The site is bordered by sand beaches on either side, while smaller boulders flank it in the water. It is quite exposed and only an occasional *Fucus* or barnacle could be found.

22a. Great Island (Witless Bay, Newfoundland)

Tidal range: 1.1 m

Surface water temperatures: -1°C to 15°C (Templeman, 1968)

Salinity: 31 ppt to 32 ppt (Templeman, 1968)

Insolation: 337.0 langleys

Average air temperatures: min.= 1.5°C; mean= 5.2°C; max.= 9.8°C

Extreme air temperatures: -25°C and 30.5°C

Diversity index: .888

Dominance index: .142

Evenness index: .931

Great Island is composed largely of slate. It rises precipitously from the sea on all sides. The only access by boat is in a small cove on the north end of the island. The island is part of a sea bird sancturary inhabited princially by puffins and gulls. All exposed rock not washed by the sea is coated with bird droppings. The island is topped with a shallow layer of soil into which the nesting puffins burrow. While the island is generally exposed, the cove in which I collected is sheltered. The algae were filamentous greens and reds above low tide and laminarioid types below low tide. Barnacles were moderately abundant.

22b. Bauline (Newfoundland)

Tidal range: 1.1 m

Surface water temperatures: -1°C to 15°C (Templeman, 1968)

Salinity: 31.0 ppt to 32.0 ppt (Templeman, 1968)

Insolation: 337.0 langleys

Average air temperatures: min.= 1.5°C; mean= 5.2°C; max= 9.8°C

Extreme air temperatures: -25°C and 30.5°C

Diversity index: .979

Dominance index: .125

Evenness index: .907

The collecting site is a cove in Witless Bay. It consists of a gently sloping terrace with a cliff that rises about four meters above the terrace about four meters back of the high tide line. The rocks are largely slate, as on Great Island. The cove offers a little shelter but opens directly toward the Atlantic Ocean, therefore receiving considerable wave action. There were very few intertidal algae although laminarioid types were abundant below low tide. Barnacles were moderatley abundant and of good size at the high tide line. A slight "orange belt" of lichens could be seen at three meters above high tide.

23. Cape Cod Canal Jetty (Barnstable County, Massachusetts)

Tidal range: 2.66 m

Surface water temperature: 26°C

Salinity: min.= 16.6 ppt; mean= 30.7 ppt; max= 34.6 ppt

Insolation: 395 langleys

Average air temperatures: min.= 4.1°C; mean= 9.5°C; max.= 15.4°C

Extreme air temperatures: -18.9°C and 37.8°C

Diversity index: .369

Dominance index: .506

Evenness index: .733

This jetty guards the Cape Cod Canal. It is composed of large granite quarried rocks about two meters long, one meter wide and one meter thick. The collections came from the side facing a sand beach. The canal side of the jetty had been treated with creosote above the low tide line and was uninhabitable. The jetty is moderately exposed although wave action in the area is not extreme except in periods of storms to which the area is susceptible. Fucus was the only alga observed and it was not abundant. Barnacles were moderately abundant.

24a. Beaver Tail Light (Newport County, Rhode Island)

Tidal range: 1.1 m

Surface water temperature: 26°C

Salinity: min.= 16.6 ppt; mean= 30.7 ppt; max.= 34.6 ppt

Insolation: 395.5 langleys

Air temperatures: min.= 4.1°C; mean= 9.5°C; max.= 14.5°C

Extreme air temperatures: -30°C and 32.2°C

Diversity index: .627

Dominance index: .270

Evenness index: .897

Beaver Tail is a point of rock composed largely of quartzite which often contains nodules of limonite. The shoreline slopes at about a 30° angle into Narragansett Bay. Although at the seaward point of the island, Beaver Tail is relatively sheltered within the bay. Intertidal algae were Fucus and Ascophyllum. Calothrix was abundant above high tide, comprising the bulk of the black zone.

Barnacles were moderately abundant within a meter of high tide.

24b. Conanicut Light (Newport County, Rhode Island)

Tidal range: 1.05 m

Surface water temperature: 26°C

Salinity: min.= 16.6 ppt; mean= 30.1 ppt; max.= 34.6 ppt

Insolation: 395.7 langleys

Average air temperatures: min.= 4.1°C; mean= 9.5°C; max.= 15.4°C

Extreme air temperatures: -30°C and 32.2°C

Diversity index: .453

Dominance index: .496

Evenness index: .648

The only rocks exposed for habitation by lichens are boulders dumped along the shore to retard erosion and a few boulders lying in the water and exposed at low tide. Most of these rocks were of chlorite schist. The site is quite sheltered and even the near passage of a hurricane did not produce much wave action on this point. The only intertidal algae observed was a thin, transparent green film that slightly colored the rocks. Barnacles were moderately abundant within a meter of high tide.

25. Point Judith Light (Washington County, Rhode Island)

Tidal range: .99 m

Surface water temperature: 26°C

Salinity: 32 ppt

Insolation: 396.3 langleys

Air temperatures: min.= 4.1°C; mean= 9.5°C; max.= 15.4°C

Extreme air temperatures: -30°C and 37.2°C

Diversity index: .377

Dominance index: .500

Evenness index: .790

The rocks at this site are mostly granite or pegmatite.

Although a few boulders emerge at low tide, most of the lichens are found on bed rock or on quarried rock placed around the point to retard its erosion. Calothrix comprised most of the black zone above high tide. The intertidal algae were mostly Fucus and Ascophyllum. Barnacles were moderately abundant within a meter of the high tide level.

26. Masons Island (New London County, Connecticut)

Tidal range: .75 m

Surface water temperature: 27°C

Salinity: min.= 1.3 ppt; mean= 9.5 ppt; max.= 32.1 ppt

Insolation: 396.8 langleys

Average air temperatures: min.= 3.1°C; mean= 9.5°C; max.= 16°C

Extreme air temperatures: -29.4°C and 37.8°C

Diversity index: .538

Dominance index: .316

Evenness index: .894

The island might be regarded as a low monadnock on the Connecticut Coast. Although the island only rises about four meters out of the water, it is solid granite bedrock with intrusions of pegmatite. The rock shore slopes at twenty to thirty degrees into the mouth of Long Island Sound. The site is quite sheltered by a small but long offshore island. The only alga observed above low tide was Calothrix. Barnacles were present but not abundant.

27. Brant Rock (Plymouth County, Massachusetts)

Tidal range: 3.05 m

Surface water temperature: 23°C

Salinity: min.= 29.1 ppt; mean= 31.4 ppt; max.= 33.7 ppt

Insolation: 389.3 langleys

Average air temperatures: min.= 3.4°C; mean= 10.5°C; max.= 14.8°C

Extreme air temperatures: -18.9°C and 37.8°C

Diversity index: .650

Dominance index: .242

Evenness index: .930

The collecting site is an irregular mass of granite rising about seven meters out of the water at high tide. It lies about a hundred meters from the shore of the mainland and is connected by a narrow causeway formed by the piling up of quarried granite blocks. Being slightly north of Cape Cod Bay, the site is fully exposed to wave action from the Atlantic Ocean. The principal intertidal alga was Ascophyllum. At the low tide level and below Lithothamnia and Corallina were common with laminarioid types below low tide. Barnacles were moderately abundant.

28. Barnegat Light (Ocean County, New Jersey)

Tidal range: 1.02 m

Surface water temperature: 26°C

Salinity: min.= 26.8 ppt; mean= 31.2 ppt; max.= 35 ppt

Insolation: 412.7 langleys

Air temperatures: min.= 5.6°C; mean= 11.7°C; max.= 17.1°C

Extreme air temperatures: -26.7°C and 41.1°C

Diversity index: .178

Dominance index: .755

Evenness index: .591

The shores in this area are predominantly sandy. The only suitable substrate for lichens is the breakwater made of quarried granite, but even here they have to withstand the scouring of sand. Exposure ranges from the natural waves of the Atlantic Ocean to waves created by fast boats passing nearby. In the intertidal zone an enteromorphicid green alga formed a dense moss-like cover over much of the rock. At the high tide line blue-green algae formed a leathery cover which rode up over the barnacles, which were abundant.

29. Cape May (Cape May County, New Jersey)

Tidal range: 1.54 m

Surface water temperature: 26°C

Salinity: min.= 20 ppt; mean= 28.7 ppt; max= 32.8 ppt

Insolation: 420.4 langleys

Average air temperatures: min.= 8.7°C; mean= 12.4°C; max= 16.2°C

Extreme air temperatures: -19.4°C and 39°C

Diversity index: .217

Dominance index: .680

Evenness index: .721

The collecting site consists of "sand catchers" made by piling up quarried granite rocks. Otherwise the area consists only of sand beaches. The site is exposed directly to waves of the Atlantic Ocean. Barnacles were abundant.

30. Portsmouth Harbor Light (Rockingham County, New Hampshire)

Tidal range: 2.85 m

Surface water temperature: 20°C

Salinity: min.= 9.7 ppt; mean= 28.7 ppt; max.= 34.1 ppt

Insolation: 379.2 langleys

Air temperatures: min.= 1.9°C; mean= 7.8°C; max.= 14.3°C

Extreme air temperatures: -31.7°C and 39.4°C

Diversity index: .803

Dominance index: .170

Evenness index: .950

The site is a slightly terraced outcrop of granite. It receives some shelter from Gerrish Island on the other side of the channel.

Fucus and Ascophyllum comprised the bulk of the intertidal algae.

Barnacles were abundant, forming a white zone near the high tide line.

31a. Sisuit Harbor (Barnstable County, Massachusetts)

Tidal range: 2.85 m

Surface water temperatures: Unknown

Salinity: Unknown

Insolation: 382.8 langleys

Average air temperatures: min.= 5.8°C; mean= 9.8°C; max.= 13.8°C

Extreme air temperatures: -24°C and 37.8°C

Diversity index: .423

Dominance index: .406

Evenness index: .929

The site is a man-made rock jetty separating a boat channel and a swimming beach. Collections were made on the beach side. The jetty serves the purpose of keeping sand from filling the channel. The water temperatures and salinity are not known. They may be similar to the east entrance to the Cape Cod canal but this site is

farther removed from the flow of water through the canal. I would expect this temperature to be warmer and its salinity lower. It is a relatively trapped body of water which receives runoff from the surrounding land. Calothrix above high tide and scant Fucus between the tides were the only algae observed. Barnacles were also scant.

31b. Bass River Jetty (Barnstable County, Massachusetts)

Tidal range: 1.12 m

Surface water temperature: 25°C

Salinity: min.= 17.4 ppt; mean= 31.7 ppt; max= 35 ppt

Insolation: 393.5 langleys

Average air temperatures: min.= 5.8°C; mean= 9.8°C; max= 13.8°C

Extreme air temperatures: -24.4°C and 37.8°C

Diversity index: .477

Dominance index: .333

Evenness index: 1.000

The site consists of a jetty only about ten meters long and rising only about one meter above high tide. It is made of cemented granite blocks. *Calothrix* predominated among the algae. Scant *Fucus* was observed below high tide. Barnacle growth was minimal.

32. Manomet (Plymouth County, Massachusetts)

Tidal range: 2.85 m

Surface water temperature: 23°C

Salinity: min.= 29.1 ppt; mean= 31.4 ppt; max.= 33.7 ppt

Insolation: 390.9 langleys

Average air temperatures: min.= 3.4°C; mean= 10.5°C; max.= 14.8°C

Extreme air temperatures: -18.9°C and 37.8°C

Diversity index: .670

Dominance index: .228

Evenness index: .959

The site is a rather sheltered boulder strewn beach with

boulders ranging from head sized to two meters in diameter.

Scant amounts of Fucus were present with a moderate number of barnacles.

VIII. DISTRIBUTION IN NORTHEASTERN NORTH AMERICA

A. General Account

The distribution of littoral lichens of northeastern North

America (either collected or examined by me) is represented on

maps 11 through 31. Site numbers are indicated on map 3. Due to

the scale of the map it is sometimes necessary to include more than

one site under a single number when they are in close proximity of

each other. Magnifications of these areas are shown on maps 4

through 10. The localities shown for species of Caloplaca,

Xanthoria, and Lecanora represent only the littoral distribution

of those species. The species may be found higher on the shore or

farther back from the sea at the same localities or at localities

not indicated. Essentially, if such facultative species were contained

in the same collection as, or were found at the same level as, such

obligate littoral lichens as Verrucaria maura or V. erichsenii they

were included as littoral lichens in this study.

The most southerly species of *Verrucaria* in this area is *V. microspora*. It occurs abundantly at Cape May, New Jersey, the most southerly of my collection sites. It should, however, not be presumed that this is its southern limit. The thallus accomodates itself well to irregular and friable surfaces, a character alluded to by Santesson (1939). This could explain its occurrence at Joggins and Five Islands, Nova Scotia, where only one other species could be found on the rapidly-eroding surfaces characteristic of that area.

Verrucaria mucosa is widely distributed over most of northeastern North America. It is the other species mentioned above that persists at Joggins and Five Islands, Nova Scotia. This species, so common

throughout most of New England, exhibits an interesting distribution in the vicinity of Cape Cod, Massachusetts. At Manoment, Massachusetts, near the mouth of Cape Cod Bay, the characteristic dark, smooth thallus of this species is scattered in abundant and conspicuous spots over the boulders strewn on the beach. Yet, just ten miles south of that spot at the mouth of the Cape Cod Canal it is absent from the jetty protecting the canal. A single specimen of V. mucoba was found at Sesuit Harbor on the north coast of Cape Cod. Intrigued by this anomaly, I searched all around Cape Cod for further evidence of this species and found that littoral lichens in general were rare. The limited presence of littoral lichens in the Cape Cod area may well be due to the absence of suitable natural substrates and the relative newness of rock works made by man. A single specimen of V. mucoba was also found in the Narranansett Bay. I believe that this area represents the southern limit of this species.

Northeastern North America. I collected it at thirty-seven of my forty-two sites. I have also examined a specimen collected by Farlow at Nahant, Massachusetts. This speices was collected as far north as Goose Cove, Newfoundland and as far south as Masons Island, Connecticut. Verrucaria erichsenii, rather than V. maura as in Europe, is the principal lichen component of the black zone in New England, a phenomenon also observed by Degelius (1942).

Verrucaria ditmarsica and V. striatula have almost identical geographical distributions as well as having similar vertical distributions on a given shore. While not predominating in the littoral community, both species were found over the entire range of latitude

from Narragansett Bay northward. I did not find either species south of Narragnasett Bay.

Verrucaria maura is widely distributed on the shores of Nova

Scotia and Newfoundland. Although I have seen specimens collected

by others on Mt. Desert Island, Maine, I did not find it there myself.

Fink (1935) reports V. maura from Massachusetts but I have not seen

specimens from that area. On the contrary, a collection from Nahant,

Massachusetts collected by Fink and labeled V. maura actually

contained only V. mucosa and V. striatula.

The most southerly specimen of *Verrucaria ceuthocarpa* that I have seen is one that I collected at Halibut Point in Massachusetts which I believe to be the southern limit of the range of that species. I also collected this species at my most northern point, Goose Cove, Newfoundland. I have no reason to assume this to be the northern limit of the species, especially since Lynge (1921) expressed the view that *V. ceuthocarpa* is the most common arctic littoral lichen. For reasons that I will discuss later I am including *Verrucaria degelii*, Sant. as a modification of *V. ceuthocarpa*. Specimens of *V. ceuthocarpa* conforming to Santesson's description of *V. degelii*, and in part annotated by him as *V. degelii*, have been found throughout the range of *V. ceuthocarpa*.

Verrucaria amphibia was found at only three sites, all in eastern Newfoundland.

Verrucaria intermigrescens was found at only one site, Bauline, Newfoundland. Since Erichsen (1957) refers to this species as both littoral and non-littoral, it should be regarded as a facultative species.

Arthopyrenia halodytes, although more common in New England, is also found at several localities in Nova Scotia and Newfoundland. It is commonly found on barnacles but also occurs on rock including siliceous rock.

Stigmidium marinum is parasymbiont found on thalli of

Verrucaria mucosa and V. microspora. Because of the close resemblance

of the Stigmidium perithecium to that of the associated lichen it

if often overlooked. I detected this species from only three localities

but do not presume that this is the limit of its occurrence.

Lichina confinis if generally regarded as an obligate littoral species occurring at the upper limits of the zone included in this study. I found this species only in Newfoundland where it appeared most abundantly at Deer Cove.

The facultative species found at the upper limits of the littoral zone, as treated herein, are Caloplaca granulosa, C. marina,

C. microthallina, C. scopularis, Lecanora grantii, Xanthoria candelaria,

X. elegans, and X. parietina. No member of this group predominated.

Although little can be concluded about their distribution from the small numbers collected, Lecanora grantii and Xanthoria candelaria were found only in Canada.

B. Interspecific Association

Chi square values and coefficients of association were determined for all possible pairs of *Verrucaria mucosa*, *V. microspora*, *V. erichsenii*, *V. striatula* and *V. ditmarsica*. *Verrucaria maura* and *V. ceuthocarpa* were paired only with each other since it was evident that their distribution both geographically and locally was similar to each other but unlike any of those listed above. The associations are

shown in tables 2 through 5. The supporting data are contained in appendix D. Verrucaria mucosa is positively associated with V. erichsenii and V. ditmarsica. The former association is a strong one with a coefficient of $.695 \pm .704$. Verrucaria erichsenii is positively associated with V. striatula and V. ditmarsica. Both associations are weak with coefficients of $.244 \pm .343$ and $.364 \pm .349$ respectively. Verrucaria striatula and V. ditmarsica form a strong association with a coefficient of $1.000 \pm .671$. Although V. maura and V. ceuthocarpa are significantly associated the association is weak with a coefficient of $.262 \pm .607$.

Eighteen of the forty-two collecting sites are sheltered from severe wave action and twenty four are exposed. The same species paired to determine general geographic association were paired for sheltered shores and again for exposed shores (see tables 3 and 4). On sheltered shores, only two pairs are significantly associated: V. maura With V. ceuthocarpa and V. striatula With V. ditmarsica. The former association is weak having a coefficient of only .407 \pm .629. The latter is a strong association having a coefficient of $1.000 \pm .697$. On exposed shores, however, there are six associated pairs. Three associations are strong: V. mucosa and V. erichsenii with a coefficient of 1.000 ± .703, V. mucosa and V. ditmarsica with a coefficient of 1.000 ± .646 and V. striatula and V. ditmarsica having a coefficient of $1.000 \pm .646$. The remaining three are significant but weak. They are V. mucosa with V. striatula having a coefficient of .786 ± .589, V. erichsenii with V. striatula having a coefficient of .333 ± .351 and V. erichsenii with V. ditmarsica with a coefficient of .486 \pm .373.

Of the six pairs shown to be associated generally on a geographical basis, only one pair proves to be associated under both conditions of exposure. This seems to show that one association is independent of the exposure factor whereas the rest require either shelter or exposure.

Two factors compelled me to examine associations within collecting sites. Figures 4 through 10 show that the species paired for the study of associations tend to have similar vertical distributions. Upon examining the many lichen bearing pieces of rock one tends to form intuitive conclusions.

In order to eliminate the geographical factor, only sites at which both numbers of the pair are present were considered. Two species were regarded as concurrent if both were present in a given collection number (see table 5). Three pairs, all involving V. erichsenii were significantly negatively associated: V. mucosa with V. erichsenii having a coefficient of -.723 ± .001, V. microspora with V. erichsenii having a coefficient of -.743 ± .001 and V. ditmarsica with V. erichsenii having a coefficient of -.312 ± .000. These may be regarded as avoiding the microhabitat significantly more often than sharing it. Only one pair was significantly positively associated: V. striatula with V. ditmarsica having a coefficient of .459 ± .000.

Table 2. Overall Geographical Association

	V. ditmarsica	ica	V. striatula	V. erichsenii	V. microspora
	$\chi^2 = 10.572$		$\chi^2 = 3.231$	$\chi^2 = 10.294$	$\chi^2 = .001$
V. mucosa	± 69° = 0	.704	C = .308 ± .648	$.695 \pm .704$ C = $.308 \pm .648$ C = $1.000 \pm .761$ C = $.006 \pm .648$	C = .006 ± .648
	$\chi^2 = .246$		$\chi^2 = .467$	$\chi^2 = 1.106$	
V. microspora C =		.366	.182 ± .366 C =200 ± .293 C =533 ± .507	$ C =533 \pm .507$	
	$\chi^2 = 11.824$		$\chi^2 = 7.135$		
V. erichsenii C =	1	.349	364 ± .349 C = .224 ± .343		V. maura
	$\chi^2 = 24.218$				$\chi^2 = 5.665$
V. striatula C =		.000 ± .671	<u> </u>	V. ceuthocarpa	$ c = .262 \pm .607$

Interspecific Association Considering Only Sheltered Sites Table 3.

		_						- -i
pora		± .652						$ c = .407 \pm .629$
V. microspora	$\chi^2 = .180$.100				V. maura	$\chi^2 = 4.923$.407
Λ.	×2=	2		_		Λ.	×2=	= 3
V. erichsenii	$\chi^2 = 2.813$	= 1.000 ± .839	$\chi^2 = .028$	= .100 ± .839				V. ceuthocarpa
Λ.	× ₂	ت ع	×2.	2		-		7
V. striatula	$\chi^2 = 1.169$.100 \pm .780 C =357 \pm .330 C = 1.000 \pm .839 C = .100 \pm .652	$\chi^2 = 1.169$	438 ± .493 C =357 ± .330 C = .100 ± .839	$\chi^2 = .117$.156 \pm .310 C = .036 \pm .273		
V. ditmarsica	$x^2 = .064$	= ع	$\chi^{2} = .788$	V. microspora $C =438 \pm .493$	$\chi^2 = 1.004$	V. erichsenii C = .156 \pm .310	$\chi^2 = 8.082$	$V. \ striatula \ C = 1.000 \pm .697$
		V. mucosa		V. mic		V. eri		V. str

Interspecific Association Considering Only Exposed Sites Table 4.

<u> </u>						_		
ra		.563						.565
V. microspora	10	+1				a	54	C = .158 ± .565
micı	$\chi^2 = .505$	4(V. maura	$\chi^2 = 1.364$	
<u>V</u>	×2=	ပ္		_		<u>v</u>	×2=	ညီ
::		703		11.				rpa
V. erichsenii	0	+1	9	+1				V. ceuthocarpa
eric	$\chi^2 = 8.000$	1.0	$\chi^2 = 1.976$	-1.00				cent
V.	χ ₌ =	2	×2=	2				7
2		$ C = 1.000 \pm .646$ $ C = .786 \pm .589$ $ C = 1.000 \pm .703$ $ C =400 \pm .563$.048 ± .482 C = 0.000 ± .467 C =-1.000 ± .711		351		
V. striatula	203	+1 9	0	+1	0	+1		
stri	$\chi^2 = 12.202$.78	$\chi^2 = 0.000$	0.0	$\chi^2 = 8.000$.33		
7.	×2=	<u>၂</u>	×2=	2	×2=	ပ္		
ia		646		482		1.000 ± .646 C = .333 ± .351		646
ditmarsica	۲۲.	+1		+1	22	+1	۲۱	+1
ditm	16.471	0.1	.067		$\chi^2 = 11.657$	- 00	$\chi^2 = 16.471$	- 0
7.	× ² = 1	2	χ ₂ =	<u></u>	X ² =	<u></u>	χ ² =	"
·		7		V. microspora C =		V. erichsenii C =		V. striatula C = 1.000 ± .646
		V. mucosa		nicro.		srich.		stria
		V. n		V. n		V. 6		ν.

Table 5. Interspecific Association In Microhabitat

_						_		_
V. microspora	$\chi^2 = .006$	$ C =018 \pm .004$		_		V. maura	$\chi^2 = 1.575$	C =495 ± .017
V. erichsenii	$\chi^2 = 40.522$	$ c =723 \pm .001$	$\chi^2 = 23.799$	$ C =743 \pm .001$				V. ceuthocarpa
V. striatula	$\chi^2 = .069$.018 \pm 0.000 C = .020 \pm .001 C =723 \pm .001 C =018 \pm .004	$\chi^{2} = .590$	$285 \pm .001$ C = $228 \pm .005$ C = $743 \pm .001$	$\chi^2 = .055$	302 ± 0.000 C = $.025 \pm .001$		_
V. ditmarsica	$\chi^2 = .153$	$ c = .018 \pm 0.000$	$\chi^2 = 3.149$	$cra C =285 \pm .001$	$\chi^2 = 12.983$	$nii C =302 \pm 0.000$	$\chi^2 = 178.531$	<i>lα</i> C = .459 ± 0.000
		V. mucosa		V. microspora C =		V. erichsenii C =		V. striatula C =

IX. TAXONOMY

A. Collection

In order to collect the full intertidal zone, the tide must be at low ebb, an event that occurs twice a day. Ideally the collection should take place at that time of the year when the tides are the most extreme. In practice, these conditions are rarely met, espically if many localities are to be studied in a limited time. The tide, however, does not turn quickly in most places and usually one has about an hour of useful collection time on either side of actual low tide.

Collection sites are often limited since rocky shores that provide a suitable habitat for littoral lichens are often privately owned, especially in the populated areas of New England. It was my experience that public properties such as lighthouses, piers and beaches tend to be both suitable and accessible. Permission can sometimes be obtained for collecting on private property.

Marine lichens inhabit rocks or the barnacles attached to them. The crustose nature of littoral lichens precludes removing them from the rocks. One must collect pieces of the substrate upon which the lichens grow. I found that rock chisels and a three pound hand mall were most satisfactory for removing pieces of rock. Ideally one should strive to collect specimens on pieces of rock small enough to fit well into herbarium packets. Regrettably the configuration of the substrate may not be conducive to this goal. Despite this fact, the collecting site may afford a better opportunity to reduce the size of a piece of substrate than will the laboratory. Barnacles can be removed from the rocks with a knife.

Once the specimen is removed it must be placed in a suitable container. Paper bags are quite satisfactory if the bag is strong. Unfortunately, the specimens are often wet, and the wet bag may need to be placed in another bag. Plastic or other waterproof bags are not desirable since they retard drying and promote molding.

Proper accounting is of the greatest importance. Each bag should be marked with the collection number in waterproof ink.

To prevent blurring or running of the ink, I have found it desirable to premark bags before going to the site.

Precise field notes are important if any study is to be made following the collection. After experimenting with various methods I found the most satisfactory technique was to make a large rubber stamp (see figure 11) and prestamp the bags. In this way ecological information can be quickly marked in the field in a standard form. More elaborabe notes may also be written on the bag in the field.

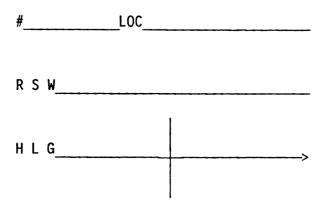


Figure 11. Rubber stamp for collecting bags.

Collection number and locality identification are written on the top line. Rock (R), soil (S), or wood (W) substrates are indicated by circling the appropriate letter. The line following the letters is for further substrate identification. The letters H, L, and G

representing high tide line, low tide line, and ground level respectively are circled to identify the reference line for distances to be noted. The arrowhead represents the seaward direction. Abbreviations of compass direction toward the sea (e.g. N, E, etc.) are written at the end of the arrowhead. The vertical line represents the point at which the water meets the shore. Numbers of meters are written on the appropriate axis; above the horizontal axis if the collection is from above the reference line, below the horizontal axis if below the reference line, right of the vertical if toward the sea and left of the vertical if away from the sea. For littoral collections the ground designation of the horizontal line is inappropriate but is occasionally used for non-littoral collections.

A small canvas bag with a shoulder strap served to carry tools and empty bags. A strong cloth bag with a draw string served as a container in which to carry filled bags. On occasions when longer distances over difficult terrain were to be walked a back pack was substituted for the bag with a draw string.

B. Preparation

The preparation of littoral lichen specimens is, for the most part, the same as for any saxicolous crustose material. The problem with any such material, is in shaping the pieces of rock into suitable size and shape to fit herbarium packets.

A rock saw would seem to provide a fairly ideal solution to the problem. However, when using a rock saw a liquid coolant must be used to protect the blade. In preparing lichen specimens, water is used rather than the oil used in lapidary work. This works well with non-littoral specimens, but with littoral lichens the soaking that

results from the water coolant and the additional water required to rinse the specimen causes excessive reticulation, and is detrimental to future study.

Hydraulic devices are available which break rocks by applying pressure to chisel-like jaws. These produce fractures in the rocks that are not as neat or predictable as the cut of a saw but they do avoid the reticulation and are quite satisfactory.

After sizing, the rocks were glued to cards of suitable size.

This prevents abrasion of the specimens and degradation of the rock.

C. Study

Many of the diagnostic characteristics of littoral lichens are readily observed with a dissecting microscope using a magnification of twenty power. Adequate illumination is important because of the dark color of many of the *Verrucaria* thalli. It is desirable to observe these thalli in both wet and dry conditions. The addition of water to the thallus often increases its transparency, thus revealing any pattern that might be below the surface. As indicated earlier, water was used sparingly to avoid necral reticulation.

Sections of fruiting structures may be made by hand with a razor blade. The small perithecia of many *Verrucariae* make a successful section difficult though not impossible. I found a double edged razor blade broken lengthwise to be most suitable.

Microtome sections are complicated by the thin crustose nature of the thalli and their adherence to the rock substrate. Secondly, the involucrella of pyrenocarpous lichens are hard and brittle and do not respond well to the usual parafin embedding techniques.

I found two techniques involving a freezing microtome to be

satisfactory. One technique involves pouring a shallow layer of agar in a small container. The perithecium is moistened several times with water containing a small amount of wetting agent. The perithecium and the subtending and surrounding thallus are then scooped from the rock with a razor blade, taking care to lift the entire perithecium from the rock. Faulty diagnosis will result if the base of the perithecium is left on the rock. The thallus and perithecium are then transferred to the surface of the agar. A drop of melted agar placed over the lichen material embeds it between the two layers of agar. A cube cut from the agar is then placed on the freezing microtome so that the thallus is perpendicular to the blade and the vertical axis of the perithecium is parallel to the blade. The material is then frozen and sectioned.

The other technique involves commercially available synthetic plastic materials intended for embedding for frozen sections. A mound is built up on the microtome's object disc and frozen. A vertical face is cut facing and perpendiclar to the blade. The lichen material to be cut is prepared as before and then pressed firmly against the embedding material. The pressure melts the plastic and when the pressure is released the plastic and embedded lichen fuse and freeze solid.

Both techniques have the disadvantage of leaving visible residues on the slide surrounding the sections. This is a problem only if the slide is to be photographed.

D. Species Concepts

Crustose lichens in general are highly plastic morphologically, as emphasized by Weber (1962), and species delineations should reflect

this variation. Santesson (1939) discribed a number of environmentally induced morphological variations for littoral lichens in general and described in detail the variations of certain selected species. Both Weber and Santesson expressed the view that the present lichen taxonomy is inflated, and Santesson, both in the publication cited above and in a personal communication, has suggested that several species are superfluous and has described in detail the ecological variations of several other species.

I have traced variations on a single thallus from continuous to areolate and from smooth to ridged. I have also observed variations of perithecia from sunken to prominently raised on a single thallus. Even the darkness of the lower side of the excipulum is quite variable within a single species. Shade modification is well known and predictable among the littoral lichens. Shade causes lighter pigmentation and reduction in size and number of juga. Some species that are distinct in appearance when growing in good illumination appear much less distinct when growing in the shade. The distinguishing features of a species are frequently reduced in the shade modifications, and as a result there is considerable taxonomic confusion among the shade modifications of Verrucaria striatula, V. ditmarsica and, to a lesser degree, V. erichsenii. Also, I feel that too much stress is placed on perithecium size. I have observed variations of perithecium size on a single thallus beyond the range accepted in some taxonomic keys. I feel that the taxonomic character "perithecia slightly smaller (or larger) than... should be regarded with suspicion.

If one restricts his study to a few specimens, it is easy to see dichotomy among the specimens examined. As the number of specimens increases, the kinds and degrees of variations also increase and extreme forms are bridged by lesser variations. Since, as discussed earlier, the littoral environment is one of great contrasts and many microhabitats, it is not surprising that considerable taxonomic confusion has resulted.

Weber (1962) used a quotation from Hooker (1855, pp. 35-36) to summarize his article on environmental modification. I would like to quote the same passage as expressing well my own view:

"It is very much to be wished that the local botanist should commence his studies upon a diametrically opposite principle to that upon which he now proceeds, and that he should endeavour, by selecting good suites of specimens, produced under all variations of circumstances, to determine how few, not how many, species are comprised in the flora of his district. The permanent differences will, he may depend upon it, soon force themselves upon his attention, whilst those which are non-essential will consecutively be eliminated. There is no better way of proving the validity of characters than by attempting to invalidate them. The unavoidable tendency of the human mind, when occupied with the pursuit of minute differences, is to sieze upon them with avidity, and to relinquish them with regret; hence the irresistible desire to rest contented with a character, however bad, so long as it is obtained with difficulty, and in the observer's opinion is tolerably constant. It is strange that local naturalists cannot see that the discovery of a form uniting two others they had previously thought distinct, is much more important than that of a totally new species, inasmuch as the correction of an error is a greater boon to science than is a step in advance."

E. Distribution Citations

Distributions of species on the coasts of northeastern North

America are shown on maps 11 through 31. In addition, general and

North American distributions are given following the discussion of
each species. My own collection numbers are listed without collector's
name. Other collection citations are accompanied by the collector's
name and collection number. If no herbarium is given for the collection

cited, the collection is in the Michigan State University Cryptogamic Herbarium (MSC). Where a distribution record is reported from the literature, the reference is cited.

F. Key to Species

1. Thallus prostrate, foliose, orange, KOH+ purple2
1. Thallus erect, fruticose, composed primarily of Calothrix
filaments; ascocarp perithecoidLichina confinis
1. Thallus crustose4
2. Thallus with soredia mostly apical or laminal; Thallus lobes
finely divided (0.2-0.5 mm wide)Xanthoria candelaria
2. Thallus not sorediate3
3. Lobes flattened and broad (1 mm or more wide)
Xanthoria parietina
3. Lobes nodular-convex
4. Ascocarp an apothecium; thallus light (shades of white, gray,
or yellow-orange)5
4. Ascocarp a perithecium; thallus dark (shades of green, brown
or black) or apparently absent9
5. Thallus whitish to gray, KOH+ yellow; spores colorless,
one-celled, 9-15 x 4-7 μLecanora grantii
5. Thallus yellow-orange, KOH+ purple; spores colorless,
polarilocular6
6. Thallus covered with globose isidia; spores 9-14 x 4-6 μ
Caloplaca granulosa
6. Thallus without isidia and without soredia7

7.	Tha	allus forming circular patches with radiating lobes; spores
	10	-15 x 5-7μCaloplaca scopularis
7.	Tha	allus irregular, comprised of scattered, unoriented lobes
	or	numerous granules8
	8.	Thallus citrine, granular (granules 1-3 mm diam.); spores
		10-18 x 3-7μ
	8.	Thallus orange-yellow, determinate, marginal lobules
		subconvex; spores 10-14 x 5-7μ
9.	Spo	ores 2-celled, colorless10
9.	Spo	ores one-celled, colorlessll
	10.	On barnacles or rock; thallus scant to evidently lacking;
		paraphyses persistent, spores fusiform, 9-20 x 4-7.5µ
		Arthopyrenia halodytes
	10.	Parasymbiont on Verrucariae; paraphyses gelatinizing, spores
		10-15 x 3.5-5μStigmidium marinum
11	. TI	hallus without juga (i.e., pegs and ridges lacking)12
11	. TI	hallus with juga (i.e., pegs and/or ridges present)16
	12.	Thallus areolate15
	12.	Thallus continuous or discontinuous but not areolate13
13	. Pe	erithecia elevated, often shiny, dome-shaped to
	he	emispherical or sometimes pointed14
13	. Pe	erithecia submerged to slightly elevated; spores 8-11 x
	4	-5µ; thallus thick, green to greenish-black
	•	Verrucaria mucosa
	14.	Spores 6-11 x 3-5µ
	14.	Spores 18-22 x 8-9µVerrucaria silicicola

15.	Areoles light brown on dark brown prothallus; perithecia
	brown, spores thick-walled, 11.5-17 x 4-6.5
	Verrucaria internigrescens
15.	Thallus prominently fissured; prothallus not evident;
	perithecia black, spores thin-walled, 9-12 x 5-6μ
	Verrucaria ceuthocarpa
1	6. Thallus areolate17
1	6. Thallus not areolate20
17.	Areoles bordered by raised juga18
17.	Areoles not bordered by juga
1	8. Perithecia usually immersed, ostiole border frequently
	raised, spores 9-12 x 5-6 μ ; juga often limited to borders
	of areoles, occasionally scattered within areoles
	Verrucaria ceuthocarpa
1	8. Perithecia elevated, often caterous, juga forming a
	reticulate pattern
19.	Juga appearing as pegs protruding from thallus and also
	to some extent on perithecia; thallus rimose-areolate, usually
	blackish-brown and opaque (wet or dry); perithecia often large,
	0.3-0.7 mm diam., immersed or elevated, gently sloped to
	rising abruptly, sometimes depressed on top, spores 10-20 x
	7-10μVerrucaria maura
19.	Juga raised or immersed, appearing as usually effigurate and
	often furcated ridges, often merging with or continuing over
	perithecia, if immersed appearing as black spots when wet;
	thallus blackish-brown, becoming brown to amber and translucent
	when wet; perithecia spreading and effigurate at base, up to
	0.3 mm diam., spores 8-9 x 4.5-7µVerrucaria erichsenii

20.	Perithecia immersed, spores 9-12 x 5-6 μ ; juga appearing
	as long sharp black ridges on borders and sometimes extend
	across thallus, fissures occasionally develop along juga
	and simulate areolation; thallus usually green to cream
	coloredVerrucaria ceuthocarpa
20.	Perithecia raised and prominent21
21. Ju	ga appearing as pegs to usually short ridges, usually
st	raight but sometimes crescent-shaped, sometimes coalescing
wi	th perithecium at base; thallus usually dark olive-green
bu	t lighter and with fewer juga in shade; perithecia
hei	mispherical, often shiny, spores 6-11 x 3.5-6μ
• • •	Verrucaria ditmarsica
21. Ju	ga broader, effigurate and sometimes furcated22
22.	Juga conspicuous, highly irregular, frequently furcated,
	raised or immersed and appearing as conspicuous black spots
	in wet thallus, often merged with perithecia; wet thallus
	usually brown to amber and translucent; perithecia up to
	0.3 mm diam., spores 8-9 x 4.5-7 μ Verrucaria erichsenii
22.	Juga prominent, black and shiny, much thicker than in
	V. erichsenii, frequently broaden into thick, effigurate
	plates, especially at thallus margin; thallus usually
	grass-green but darker in the sun and depigments rapidly
	in shade or in storage; perithecia typically hemispherical
	to globular with flattened tops but may become quite
	effigurate, angular or dissected, spores 8-10 x 4-6 μ
	Verrucaria striatula

ARTHOPYRENIA

Arthopyrenia halodytes (Nyl.) Arn. Ber. Bayer. Bot. Ges. 1:122. 1891. Verrucaria halodytes Nyl. Mem. Soc. Sci. Nat. Cherbourg 5:212. 1857.

Thallus epilithic on siliceous rock, endolithis on calcareous rock and shells, yellowish if epilithic, greyish or blackish-brown if endolithic, smooth, often obscure, sometimes somewhat granular. Perithecium almost wholly immersed in substrate or sessile with black hemispherical to broadly conical involucrellum, .15 to .5 mm diameter, excipulum colorless to pale brown. Spores 8 per ascus, fusiform-ovoid, 2-celled, one cell usually broader than the other, 9-20 x 4-7.5µ.

Swinscow (1965) considers this to be the only littoral species of the genus and treats A. sublitoralis (Leight.) Arn., A. foveolata A. L. Sm. and A. gyalectoidea Knowles as synonyms and reports a range of 10-20 x 5-10µ in spore size.

Arthopyrenia halodytes is often associated with shells or calcareous rocks but may also be found commonly on siliceous rock.

GENERAL DISTRIBUTION: World-wide on marine shores (Santesson, 1939: 52-63).

NORTHEASTERN AMERICAN DISTRIBUTION: NEW JERSEY: Cape May Co., 2441. CONNECTICUT: New London Co., 2368, 2370. RHODE ISLAND:

Newport Co., 2312, 2315, 2328, 2336, 2348. MASSACHUSETTS: Barnstable Co., 2310, 2460, 2475; Plymouth Co., 2395; Essex Co., 234, 240, 1244, 2481, 2486, 2489, 2490, 2497. MAINE: Cumberland Co., 315, 379, 474; Sagadahoc Co., 502, 506; Hancock Co., 567, 573A, 574, 631A, 656, 855, 863A, 882, 884A, 886, 887; Washington Co., 1068, 1071, 1072. NOVA SCOTIA: Yarmouth Co., 1295A; Digby Co., 1337; Halifax Co., 1403, 1416C,

1421; Victoria Co., 1519; Cape Breton Co., 1580. NEWFOUNDLAND: West Coast Section, 1640; Northern Peninsula Section, 1761A, 1762A, 1763A, 1766A, 1768A, 1769A, 1771A, 1773A, 1778A, 1781, 1790, 1889A, 1915A, 1931, 1932; East Coast Section, 1953, 2055, 2056, 2081, 2082; Avalon Section, 2166, 2181, 2182, 2183, 2183A, 2184, 2193.

CALOPLACA

All of the littoral species of Caloplaca collected belong to the section Gasparrinia.

Caloplaca granulosa (Müll. Arg.) Jatta, Sylloge Lich. Ital. 237. 1900. Amphiloma granulosum Müll. Arg. Mem. Soc. Phys. Genève 16:380, pl. 1, f.1. 1862.

Thallus orange or yellow, up to 4 cm diam., or dispersed, lobes 24 x .25-5 mm, convex, center of thallus areolate, granular, isidia globose to granular. Apothecium .5-1.0 mm, orange or yellow, thalline margin often crenulate. Spores oblong-ellipsoid, polarilocular, isthmus about .3 length of spore, 9-14 x $4-6\mu$.

This species is the only littoral *Caloplaca* which is isidiate. Wade (1965) indicates that the globular nature of the isidia distinguishes *C. granulosa* from all other lobate species of *Caloplaca* in the British Isles.

GENERAL DISTRIBUTION: South Africa (MSC), Italy (Jatta, 1909-1911), Finland (Räsänen, 1927), Novaya Zemlya (Lynge, 1928), England (Ferry and Sheard, 1969).

NORTHEASTERN AMERICAN DISTRIBTUION: MAINE: Sagadahoc Co.,497;

Hancock Co., 869, 870. NEWFOUNDLAND: Avalon Section, 2175A, 2177, 2179.

Caloplaca marina (Wedd.) DuRietz, Method. Grund. Modern.

Pflanzensoziol. 170. 1921. Lecanora marina Wedd. Mem. Soc. Sci.

Nat. Cherbourg 19: 275. 1875.

Thallus orange-yellow to red-orange or (in shade) citrine, orbicular, irregular, or subeffuse, small convex lobes contiguous or, in center of thallus, minutely granular or tuberculate, whitish prothallus sometimes visible. Apothecia reddish-orange, .5-10 mm diam., plane to convex, margins entire or crenulate. Spores ellipsoid, polarilocular, isthmus about .3 length of spore, $10-14 \times 5-7\mu$.

Wade (1965) finds this species often associated with Caloplaca thallincola and Verrucaria maura in the British Isles. Caloplaca thallincola has not been collected, however, in the littoral zone of North America. The white hypothallus is seen in young growth between the small subconvex lobules.

GENERAL DISTRIBTUION: Norway, Sweden, Poland (Nordin, 1972), Finland (Räsänen, 1927), Germany (Erichsen, 1957), Novaya Zemyla (Lynge, 1928), England (Ferry and Sheard, 1969), Wales (Fletcher, 1937b), France Werner 6.viii.56 (MSC).

NORTHEASTERN AMERICAN DISTRIBTUION: MAINE: Cumberland Co., 385, 469; Hancock Co., 575. NOVA SCOTIA: Yarmouth Co., 1289, 1292; Digby Co., 1307; Shelburne Co., 1377, 1380; Halifax Co., 1422. NEWFOUNDLAND: Northern Peninsula Section, 1763B, 1940.

Caloplaca microthallina (Wedd.) Zahlbr. Cat. Lich. Univ. 7:247. 1931. Lecanora microthallina Wedd. Mem. Soc. Sci. Nat. Cherbourg 19:276. 1875.

Thallus citrine, 1-3 mm diam., radiate or irregularly lobed, forming patches on rocks, lobes convex, 1-2 times as long as broad, tending toward granules near center of patches. Apothecia yellow to pale orange, .5-.8 mm diam., margins crenulate or entire. Spores oblong-elipsoid, polarilocular, isthmus about .3 the length of the spores, $10-18 \times 3-7\mu$.

Caloplaca microthallina is distinguished by its minute granular thallus forming patches up to 3 mm in diameter and by its citrine color. Wade (1965) finds it often associated with *Verrucaria maura* in the British Isles. This also holds true for North America. This species is not previously reported from North America.

GENERAL DISTRIBUTION: Norway, Sweden, Finland, Denmark (Nordin, 1972).

NORTHEASTERN AMERICAN DISTRIBTUION: NOVA SCOTIA: Digby Co., 1332; Halifax Co., 1404, 1420; Cape Breton Co., 1570. NEWFOUNDLAND: West Coast Section, 1626; Northern Peninsula Section, 1800, 1926.

Caloplaca scopularis (Nyl.) Lett. Hedwigia 52:242. 1912. Lecanora scopularis Nyl. Flora 66:105. 1883.

Thallus yellow-orange to deep orange, radiate, up to 1.5 cm diam., lobes narrow, .25-.3 x 5-2.0 mm, convex, apices crenulate or bifid, center of thallus usually thickly covered with apothecia.

Apothecia orange, .5-.75 mm diam., margins entire. Spores ellipsoid,

polarilocular, 10-15 x 5-7 μ , isthmus about .3 the length of the spore.

Caloplaca scopularis is unique among the littoral Caloplacae due to its radiating thallus. Wade (1965) indicates that this species resembles a small form of C. heppiana or C. thallincola but is distinguished by ellipsoid spores and the submoniliform nature of the upper parts of the paraphyses.

GENERAL DISTRIBUTION: Novaya Zemlya (Lynge, 1928), Norway, Sweden, Denmark (Nordin, 1972), Finland (Räsänen, 1927), Germany (Erichsen, 1957), Japan (Nylander, 1890).

NORTHEASTERN AMERICAN DISTRIBUTION: MAINE: Cumberland Co., 304; Hancock Co., 575, 576. NOVA SCOTIA: Halifax Co., 1391B; Victoria Co., 1534, 1548. NEWFOUNDLAND: West Coast Section, 1629; Avalon Section, 2208.

LECANORA

Lecanora grantii Magn. Ann. Cryptog. Exot. 5 (1):21. 1932.

Thallus of irregular whitish-grey lumps, K+ yellow (atranorin); medulla with small crystals. Apothecia concave to plane, thalline margin regular to crenulate; hymenium dark reddish-brown, I+ dark blue; epithecium with small crystals, insoluble in KOH. Spores eight per ascus, oblong-ovoid, 9-15 x $4-7\mu$.

Little of this species was collected since it occurs only at the upper limits of the littoral zone. The scant material collected seems to conform to the original material described from a log on a sea beach by Magnusson. GENERAL DISTRIBUTION: Washington (Magnuson, 1932), British Columbia Brodo 9874, 9887 (MSC).

NORTHEASTERN AMERICAN DISTRIBUTION: MAINE: Sagadahoc Co., 496, 497. NEW YORK: Suffolk Co., Latham 817 (MSC). NOVA SCOTIA: Shelburne Co., 1355, 1379, 1387. NEWFOUNDLAND: West Coast Section, 1625.

LICHINA

Lichina confinis (0. Müll.) Ag. Sp. Algar. 1:105. 1821. Lichen confinis 0. Müll. Icon. Pl. Daniae 5:5. 1872.

Thallus fruticose, branches rounded in cross section, blackish-brown, phycobiont *Calothrix*. Ascocarps terminal, globose, with small ostioles. Spores colorless, simple, ovoid, 15-24 x 12-15µ.

Lichina confinis, appearing as black tufts in the upper limits of the littoral zone, is the only fruticose littoral lichen with a perithecioid ascocarp.

GENERAL DISTRIBUTION: England (Ferry and Sheard, 1969),
Wales (Fletcher, 1973b), Finland (Räsänen, 1927), Germany
Grummann vii.1932 (MSC), (Degelius, 1939), Italy (Jatta, 1909-1911),
Norway Havaas 23.viii.1914 (MSC), Sweden Degelius 25.ii.1958 (MSC).

NORTHEASTERN AMERICAN DISTRIBUTION: MASSACHUSETTS: Essex Co. (Tuckerman, 1882). NOVA SCOTIA: Cape Breton Co. (Lamb, 1954). NEWFOUNDLAND: East Coast Section, 1624; Northern Peninsula Section, 1765, 1769B, 1771B, 1789; East Coast Section, 1959, 2027, 2032.

STIGMIDIUM

Stigmidium marinum (Deak.) Swins. Lichenologist 3:55. 1965. Sagedoa marina Deak. Ann. Mag. Nat. Hist. I. 12:40, pl. 4, f. 13. 1854.

Parasymbiont on littoral *Verrucariae*, especially *V. mucosa* and *V. microspora*, lacking a thallus of its own. Perithecia usually resembling that of host lichen, totally immersed on *V. mucosa* and hemispherical on *V. microspora*. Involucrellum black with pigment extending into hyaline excipulum. Spores 8 per ascus, 2-celled with each cell often divided by pseudosepta, upper cell usually slightly wider than the lower, 10-15 x 3.5-5µ.

The perithecia of Stigmidium are easily confused with that of the host. Stigmidium, however, has two-celled spores of $10-15\mu$ (usually nearer 12μ) x $3.5-5\mu$ (usually nearer 4μ). Swinscow (1965) reports spores 10-15 x $4-6\mu$. The combination Stigmidium maximum was made by Swinscow when he united Arthopyrenia maxima (Deak.) A.L. Sm and $A.\ leptotera$ (Nyl.) Arn. Neither of these species appear in the North American checklist (Hale and Culberson, 1970) nor did Swinscow (1965) report a specimen from North America. This appears, therefore, to represent a new record for North America.

GENERAL DISTRIBUTION: Germany, Finland, Ireland, Jersey, England, (Swinscow 1965).

NORTHEASTERN AMERICAN DISTRIBUTION: MAINE: Cumberland Co., 326; Hancock Co., 572. NEWFOUNDLAND: Avalon Section, 2188, 2211, 2212. NEW JERSEY: Ocean Co., 2430.

VERRUCARTA

The species of this genus form crusts which may be continuous or form scattered patches, rimose areolate or divided into discrete areoles or peninsulas. The thalli vary in thickness from 20μ to 500μ , and may be almost completely transparent to entirely opaque. In some species, the transparency of the thallus may be enhanced by wetting, while others remain opaque when wet. The thalli may be smooth or roughened by dark points or ridges. The ridges, called juga (Santesson, 1939), vary in all dimensions (length, width, and thickness). The exact origin and ontogeny of the juga is not known but it appears that they originate at or just below the surface of the thallus. In my experience, they do not extend to the substrate except at the edges of the areoles. Often a distinction is made in keys between point and ridge forms of the juga, but it is common that the points are merely peaks on inconspicuous or hidden ridges.

The perithecia of all of the littoral *Verrucariae*, with which I have worked, have a dark involucrellum which may spread widely or be closely appressed to the excipulum. This darkening may extend into the lower excipulum, terminating a short distance below the involucrellum proper or it may not extend into the lower excipulum at all. The darkening may occur intermittently or continuously throughout the lower excipulum. This darkening is given considerable taxonomic importance by Servít (1954) and by Erichsen (1957) but Swinscow (1968) discounts this importance on the grounds that it is highly variable within a species. I concur with Swinscow in this view. Perithecial size is not, in itself, very useful in distinguishing

species. The diameters vary generally between .05 and .7 mm and these dimensions overlap considerably between species. Although vertical sections are illustrated in figure 12, none is claimed to be typical for there is much variation in many, if not all species.

Santesson (1939) has noted the high variability of spore size in littoral pyrenolichens and suggests that they should not be given great taxonomic importance. All spores in *Verrucaria* are simple and hyaline and, for the most part, thin-walled, occurring eight per ascus. *Verrucaria internigrescens* and *V. silicicola* are the notable exceptions in northeastern North America. The spores of *V. internigrescens* are thick-walled and those of *V. silicicola* are of unusual size. The remainder are ovoid to reniform and exhibit overlapping ranges of size between species.

Verrucaria amphibia R. Clem. Ess. Var. Veg. Andalucia 299. 1807.

Thallus continuous, black when dry, translucent green to amber when wet, with irregular black ridges often enclosing lenticular areas $50\text{--}100\mu$ thick. Perithecia large (13-16 mm), prominently elevated, often flattened or concave on top, vertical and horizontal ridges forming reticular pattern, lenticular areas often enclosed by ridges at base; excipulum hyaline to partly darkened below. Spores hyaline, ovoid, $7\text{--}19 \times 4\text{--}7\mu$.

This species might readily be confused with *V. maura*. Both species have dark thalli with juga forming pegs or ridges and with robust perithecia. However, they are easily distinguished on closer

examination. Whereas V. maura tends to have points raised above the thallus, V. amphibia tends toward ridges. The ridges tend to enclose lenticular areas on a dry thallus giving the impression of ripples on water. When wet, V. amphibia becomes more translucent and light colored against which the black ridges become contrasted. The thallus of V. maura remains dark when wet except on very thin juvenile specimens. The thallus of V. amphibia tends to be continuous whereas that of V. maura tends to be rimose areolate but in neither case are the characters absolute. Verrucaria amphibia produces large steep sided perithecia often strongly depressed on top, a form also produced in some instances by V. maura. Such perithecia of V. amphibia have two characteristics not demonstrated by V. maura; whereas V. maura may have many fine points or pegs covering the perithecium, the design on V. amphibia is a reticulum of vertical and horizontal ridges. Also, where the V. amphibia perithecium meets the thallus, the ridges tend to enclose areas of ovoid shape and appear light and translucent when wet (see fig. 12).

Verrucaria amphibia is little discussed in literature. Santesson (1966) alludes to it but says that it is not known from Scandinavia, although it occurs in England. Ferry and Sheard (1969) include V. amphibia in their key but do not deal with it in detail. I first became acquainted with it by examining herbarium specimens. My measurements should not be regarded as true limits due to the small amount of material available. I find no evidence of a prior report of this species from North America.

GENERAL DISTRIBUTION: England (Ferry and Sheard, 1969), Wales (Fletcher, 1973a), Germany, *Ullrich* 22.ix.1962 (MSC).

NORTHEASTERN AMERICAN DISTRIBUTION: NEWFOUNDLAND: East Coast Section, 2017, 2019, 2151, 2157; Avalon Section, 2214.

Verrucaria ceuthocarpa Wahlenb. in Ach. Suppl. Meth. Lich. 22. 1803.

Thallus rimose, forming peninsulas or discrete areoles, amberbrown-black when dry, amber-brown when wet, prominent black ridges bordering areoles and perithecia, thin to thick ($100-320\mu$). Perithecia sunken to prominently elevated, .1-.25 mm diam., excipulum hyaline to entirely black below. Spores hyaline, ovoid, 9-12 x 5-6 μ .

Verrucaria ceuthocarpa is, I believe, a highly variable species expressing itself in sufficient extremes to cause two extremes to be regarded as distinct species, V. ceuthocarpa s. str. and V. degelii Sant. I find it impossible to distinguish intergrades as belonging to either species. In fact, I found one collection from North America and one from the Falkland Islands where the same thallus graded from one extreme to the other. Santesson (1939, p.20) compared these two species as follows: "In several other strongly cracked Verrucaria species, e.g. in V. ceuthocarpa, where hyphae nearest the cracks are dark-colored, yet not developed in raised juga as in V. degelii". I can find no other reference to the distinction in between these two species. However, a similar pattern of variation is noted by Santesson (1939) for V. striatula when he points out that "extreme shade-forms of V. striatula which are almost lacking the juga, can become very much like V. microspora and V. ditmarsica...". While I would not say that V. ceuthocarpa

is an extreme shade form of *V. degelii* or, conversely, that *V. degelii* is an extreme sun form of *V. ceuthocarpa*, it is evident that the presence and degree of juga is greatly affected by environment and, in light of my observations, I believe insufficient grounds for recognizing distinct species. I consider the material appearing to conform to *V. degelii* in North America to be a modification of *V. ceuthocarpa*.

The thallus of *V. ceuthocarpa* varies greatly in thickness and transparency depending on age or extent of development. It is almost always areolate. I have seen only one exception. In that case, a rather large area of smooth, continuous thallus was surrounded by a raised black ridge and a crack, also bordered by a black raised ridge, extended inward toward the center. At the edges of this patch of thallus was more thallus divided into typical discrete areoles with similar black borders. More commonly a young thallus is thin, nearly transparent, smooth and brown to tan. It is areolate although often divided into peninsulas by a dendritic pattern of grooves. In such a thallus, the grooves are usually hyaline.

Regrettably the ontogeny of these lichens has not been studied and must be inferred from observations of what could as easily be the results of conditions of growth as of aging. It appears, however, that older thalli thicken and develop discrete areoles, often with black borders with black lines often connecting them with the perithecium. These areas of blackness then seem to proliferate under some conditions to produce unelevated patterns or raised juga. Sometimes the black area extends beneath the perithecium and sometimes it does not.

The perithecium is commonly immersed, with or without raised ridges around the ostiole. At times there is a convex area raised around the ostiole. I have seen prominently raised convex perithecia on the same thallus as sunken perithecia. The degree of perithecial elevation appears to be a facultative character of the species.

Spores are ovoid but sometimes pointed when young. Commonly, although not always, a clear spot appears in the center of the younger spores. Santesson (1939) reports ranges for *Verrucaria* degelii as $10-13 \times 5-6\mu$. Lamb (1948) reports $9-12 \times 6-7\mu$ for *Verrucaria ceuthocarpa* in the Antarctia. Zschacke (1924 & 1934) records the spore size for *V. ceuthocarpa* as $8-10 \times 5-8\mu$.

GENERAL DISTRIBUTION: Northern Europe, Spitsbergen, Bear Island, Novaya Zemlya, Siberia, Bering Strait, Greenland, Kerguelen and Antarctica (Lamb, 1948), Falkland Islands: *Imshaug 40519*.

NORTHEASTERN AMERICAN DISTRIBUTION: MAINE: Hancock Co., 563, 568B, 569, 577, 629, 861, 861B, 862, 863C, 881A, 884, 884B;

Washington Co., 1063, 1071. MASSACHUSETTS: Essex Co., 1241.

WASHINGTON: Fink 8878 (determined as V. maura by Zahlbruckner).

NOVA SCOTIA: Yarmouth Co., 1259B, 1263, 1267, 1300; Digby Co., 1309, 1311, 1324, 1325, 1326, 1327, 1329, 1331, 1336B, 1347;

Halifax Co., 1403. NEWFOUNDLAND: West Coast Section, 1622;

Northern Peninsula Section, 1886, 1912, 1913; East Coast Section, 2023, 2025, 2026, 2048B, 2049, 2130; Avalon Section, 2167, 2179A.

Verrucaria ditmarsica Erichs. Schriften Naturwiss. Vereins Schleswig-Holstein 22:90.1937.

Thallus entire, olivaceous, with pegs to short ridges, thin $(20-50\mu)$, opaque to translucent when dry, more translucent when wet. Perithecia slightly dome-shaped to globose (usually hemispherical), .1-.25 mm diam., usually shiny; excipulum hyaline to dark below. Spores ovoid to reniform, colorless, 6-11 x 3.5-6 μ .

The thallus of *Verrucaria ditmarsica* is usually olivaceous, but the darkness varies with light exposure. In bright light it is dark olive and if grown in the shade it is a very light olive green. It usually is rather transparent to translucent. The transparency is increased by wetting upon examination. Short, mostly straight ridges are characteristic on the thallus. These become reduced in size and frequency in the shade modification. In this reduced condition it is easily confused with the shade modification of *V. erichsenii* and especially with *V. striatula* whose color is also similar. Ridges often merge with the perithecia at the base.

The perithecia are convex to hemispherical and usually shiny. Darkness of the lower excipulum is a highly variable factor. Generally some carbonaceous granules tend to extend below the involucrellum and may continue somewhat throughout the lower involucrellum (see fig.12). I do not believe, however, that the species should be characterized as having an involucrellum that is dark below, a view adopted in Erichsen (1957).

Erichsen (1957) gives the spore range as 19.5 x 6μ . I measured ten spores from each of five collections, including one from Europe, collected and identified by Santesson. In none of these

collections could I find spores as large as indicated by Erichsen.

GENERAL DISTRIBUTION: Germany (Erichsen, 1957), Norway:

Santesson 18856.

NORTHEASTERN AMERICAN DISTRIBUTION: MAINE: Cumberland Co., 366, 368, 372B; Sagadahoc Co., 507A, 508; Hancock Co., 566, 627A 656, 852. NOVA SCOTIA: Yarmouth Co., 1247, 1247B, 1257, 1262; Digby Co., 1304, 1315; Shelburne Co., 1361, 1363; Halifax Co., 1413, 1416A, 1417; Victoria Co., 1508. 1512, 1513, 1514, 1515, 1516. NEWFOUNDLAND: West Coast Section, 1611, 1616, 1621, 1634; Northern Peninsula Section, 1775, 1776, 1777, 1778, 1779, 1780, 1782, 1783, 1784, 1785, 1786A, 1787A, 1790, 1791, 1792, 1793, 1794A, 1795. 1796, 1882, 1889, 1914, 1915B, 1916, 1921, 1938A, 1947, 1951; East Coast Section, 2015A, 2020A, 2021A, 2061A, 2062, 2066A, 2081A; Avalon Section 2164, 2169, 2171A, 2180, 2183B, 2189A, 2190, 2196, 2197A, 2198A, 2199A. RHODE ISLAND: Newport Co., 2314, 2336, 2403. MASSACHUSETTS, Plymouth Co., 2377, 2378, 2380; Essex Co., 2478, 2479, 2483. NEW HAMPSHIRE: Rockingham Co., 2448, 2450.

Verrucaria erichsenii Zsch. in Erichs. Verh. Bot. Vereins Prov. Brandenburg 70:192. 1928.

Thallus entire or areolate, black to blackish-brown dry, amber and more translucent when wet, roughened by rows of pegs or ridges; ridges often furcated, sometimes submerged in thallus and visible only when wet; thallus $30\text{--}70\mu$ thick. Perithecia elevated, conical to hemispherical, spreading in irregular pattern at base, often with pegs or ridges as on thallus, .1-.3 mm diam.; excipulum hyaline below.

Spores ovoid, colorless, 8-9 x $4.5-7\mu$.

Verrucaria erichsenii demonstrates considerable thallus variation. It is usually considered to be clearly rimose or areolate. Typically this is so but it is not uncommon to find a thallus of V. erichsenii continuous under wet circumstances. When in an especially wet environment, the thallus becomes thick and gelatinous. When dry the thallus is usually blackish-brown to black. A form was collected in the Narragansett Bay area that was grey with a texture like that of graphite in pencils. When moistened during examination the thallus increases in transparency. This is one of the best tests of questionable thalli. When wetted they reveal a pattern of black markings typical of the pattern of ridges usually seen above the surface. The thallus of V. erichsenii is typically decorated with short, often bifurcated irregular ridges or rows of points. These are often confluent with or continue up over the perithecia. The ridges are longer than wide and rarely very high. In extreme circumstances the ridges become higher and sharper forming cusps and arêtes. In other extremes they may be immersed within the thallus to be revealed only by wetting.

The most consistant character of the perithecium appears to be the irregular spreading base which seems most pronounced when viewed from above a wet thallus or when the thallus has been peeled from the rock and placed on a slide and illuminated from below. The diameters of perithecia tend to fall between .1 and .3 mm but these figures should not be regarded as restrictive.

Zschacke (1934) and Erichsen (1957) both list a spore range of $8-12 \times 5-7\mu$.

GENERAL DISTRIBUTION: Germany (Erichsen, 1957), British Columbia: Ohlsson 2667B, Sweden: Santesson 18649, Norway: Santesson 18976A, Wales: Brodo 5130, Scotland: Brodo 5254.

NORTHEASTERN AMERICAN DISTRIBUTION: MAINE: Cumberland Co., 290, 291, 292, 293, 294, 295, 296, 298, 316, 328, 363, 366, 373, 380, 381, 384A, 389B, 391, 463, 464; Sagadahoc Co., 501, 509; Hancock Co., 562, 568, 573, 573B, 577, 631B, 863B, 864, 866, 880, 881, Plitt 22.viii.31(MICH), Tuckerman (MICH ex Fink hb 11972): Lincoln Co., Merrill 234; Washington Co., 1069. Massachusetts: Essex CO., 197, 1232, 1233, 1235, 1236, 1237, 1238, 1239, 1240, 1241, 1242, 2489, 2490, 2491, 2492, 2493, 2494, 2495, 2496, 2498, 2499, 2502, Jones 9.v.1893, Farlow (MICH ex Fink hb 11351); Bristol. Co., Willey (Mich ex Fink hb 11351A); Plymouth Co., 2382, 2384, 2385, 2386, 2387, 2390, 2392, 2393, 2394, 2471, 2472; Barnstable Co., 2303, 2304, 2305, 2306, 2307, 2308, 2456, 2457, 2458. RHODE ISLAND: Newport Co., 2314, 2315, 2316, 2317, 2320, 2321, 2322, 2323, 2324, 2326, 2327, 2332, 2333, 2352, 2401; Washington Co., CONNECTICUT: New London Co., 2358, 2362, 2363, 2366, 2367, 2369. NEW HAMPSHIRE: Rochingham Co., 2423, 2424, 2435; NOVA SCOTIA: Yarmouth Co., 1248, 1249, 1254, 1256, 1259A, 1260, 1261A, 1264, 1265, 1268, 1270, 1295, 1297; Digby Co., 1310, 1316, 1320, 1321, 1322, 1323, 1325, 1336A, 1344, 1345, 1346; Shelburne Co., 1349, 1350, 1352, 1353, 1354, 1357A, 1367, 1376, 1389, 1390; Halifax Co., 1396, 1398, 1399, 1403, 1404, 1410, 1418, 1419, 1421; Victoria Co., 1506, 1509, 1516, 1518, 1527, 1528, 1532, 1535, 1536A; Cape Breton Co., 1588, 1589. NEWFOUNDLAND: WEST COAST SECTION, 1614, 1615, 1616, 1617, 1619, 1620, 1623A, 1634, 1635, 1637, 1641, 1642; Northern Peninsula Section, 1761, 1764, 1766, 1768B, 1771, 1773B, 1774, 1775, 1776, 1778B, 1786B, 1787B, 1788, 1792,

1794B, 1797A, 1799, 1887, 1888A, 1891, 1897, 1901A, 1902, 1915C, 1916, 1917, 1918, 1919A, 1920, 1921, 1930; East Coast Section, 1950, 1955, 2015B, 2020, 2020C, 2021C, 2028, 2030, 2048, 2057, 2061B, 2062, 2080A, 2132, 2139, 2158, 2159; Avalon Section, 2183C, 2198C, 2203, 2204.

Verrucaria internigrescens (Nyl.) Erichs. Verh. Bot.

Vereins Prov. Brandenburg 70:193. 1929. Verrucaria aethiobola

var. Internigrescens Nyl. In Brenner, Meddeland. Soc. Fauna
Fl. Fenn. 13:125. 1886.

Thallus of brown areoles connected by darker brown prothallus. Perithecia brown, convex, .2-.34 mm diam., excipulum hyaline or intermittently darkened below. Spores hyaline, thick-walled, fusiform, $11.5-17 \times 4-6.5u$.

The brown prothallus, thallus, and perithecia are distinctive. The thallus is thin by comparison to other areolate forms such as V. maura and V. ceuthocarpa. The spores are distinctive, being fusiform and thick-walled. Erichsen (1957) reports a spore range of 15-27 x 7-12 μ and lists this species as both littoral and non-littoral. Thus it may be assumed to be facultative in its habits. I found this species at only one locality in North America and to my knowledge this is the first record from North America.

GENERAL DISTRIBUTION: Germany (Erichsen 1957).

NORTHEASTERN AMERICAN DISTRIBUTION: NEWFOUNDLAND:

Avalon section, 2202, 2210, 2215.

Verrucaria maura Wahlenb. in Ach. Suppl. Meth. Lich. 19. 1803. Thallus dark, usually black to brownish black, sometimes green, opaque (wet or dry), rimose areolate, usually with small black pegs or points (sometimes obscured by epithallic algae), thin to thick (75-300μ). Perithecia small to large (usually large) .1-17 mm diam., sunken to prominently raised, tops rounded to concave, may be covered visibly by pegs, excipulum entirely black below. Spores ovoid, hyaline, 10-20 x 7-10μ.

Verrucaria maura is probably one of the most widely used names among the littoral lichens. This is often a detriment leading to the report of the species based on the most cursory examination. The species is highly variable and its variation has probably been best understood and described by Santesson (1939 and 1966). Since I can add little to the description of variation provided by Santesson (1966). I would like here to merely record my concurrence and quote Santesson's description (*) of typical V. maura as:

"1. Indistinct or dark prothallus, 2. definite black thallus, 3. areolate thallus, 4. thallus surface with distinct but little conspicuous points, 5. rounded conical conspicuous perithecia, 6. rounded, not impressed perithecia tops, and 7. spores with a width of 7-10 mic. (length 10-19 or at most 20 mic.)"

Santesson continues by describing seven deviations with which he associates names of varieties or what he considers to be synonyms:

- "1. With white or light brown clear prothallus.

 'V. zschackeana Erichs.'
- 2. With green-gray or greenish black thallus.
 'var. fumosocinerea Vain.'

^{*}The material quoted was submitted to me in Swedish by Santesson.

- 3. With connected or triflingly fissured thallus.

 'V. scoting Wedd.'
- 4. Thallus surface with many strongly conspicuous pegs. 'V. aractina Wg.'
- 5. a. With perithecia almost entirely sunken into the thallus.

 'V. malmei Serv.'
 - b. With hemispherical to nearly spherical perithecia. 'var. prominula Vain.'
- 6. With clearly impressed, frequently somewhat irregular perithecium tops. 'V. trachinodes Norm.'
 'V. häyrenii Erichs.', 'var aractinoides Vain.',
 'f. evoluta Th. Fr.'
- (?7 Spores with a width of 11-15 mic. 'V. finrmarkica Zsch.')"

I have seen all of these forms in North America except "V. finnmarkicia". A common source of variation is a result of frequent washing with water. The thallus color and texture becomes obscured by epithallic algae which produce a smooth greenish surface. I have not been able to distinguish between normal, shade and sun forms. I have seen some extreme variations of the thallus from British Columbia, but feel ill prepared to deal with this in detail due to limited experience with it. However, the thallus under question is thick with lobed margins tending to nearly a subfoliose condition and overrunning normal V. maura. It is a most remarkable form requiring more study.

GENERAL DISTRIBUTION: Novaya Zemyla (Lynge, 1928), Finland (Räsänen, 1927), Germany (Erichsen, 1957), Spain to Finland (Degelius 1935), Italy (Jatta, 1909-1911), India (Awasthi, 1965), Japan (Nylander, 1890), Greenland, Iceland, Bear Island, Spitsbergen, Siberia, Bearing Strait, Fuegia, Patagonia, Chile, Falkland Islands and New Zealand (Lamb, 1948), Norway: Santesson 18817, Sweden: Santesson 12982, Wales

(Fletcher, 1973a), England (Ferry and Sheard, 1969), British Columbia Brodo 10515.

NORTHEASTERN AMERICAN DISTRIBUTION: NOVA SCOTIA: Yarmouth Co., 1266, 1295, 1295B; Digby Co., 1321, 1333, 1343; Shelburne Co., 1353, 1356, 1364, 1365, 1366, 1367, 1379, 1380, 1381, 1383, 1385; Halifax Co., 1393, 1424; Victoria Co., 1536B; Cape Breton Co., 1572, 1574, 1579.

NEWFOUNDLAND: West Coast Section, 1623B, 1625, 1627, 1638, 1639, 1642, 1644, 1645A, 1646, 1647; Northern Peninsula Section, 1762B, 1766, 1766B, 1769C, 1771C, 1797, 1797B, 1798, 1809, 1886, 1887, 1890, 1891, 1892, 1893, 1905, 1918, 1923, 1925. East Coast Section, 1958, 1961, 1968, 2028, 2029, 2031, 2048A, 2059, 2071, 2073, 2074, 2083, 2084, 2085, 2131, 2133, 2134, 2135, 2137, 2138, 2139, 2160; Avalon Section, 2170, 2175, 2175B, 2179, 2179C, 2188, 2188B, 2194, 2195A, 2204, 2205, 2211B, 2212B. NEWBRUNSWICK: Campobello, Farlow ix.1898 (MICH).

Verrucaria microspora Nyl. Ann. Sci. Nat. Bot. IV. 3:175. 1855. Thallus usually brown to amber, sometimes green or gray, smooth thin, 20-30μ continuous or in patches but never areolate, translucent when dry, more transparent when wet. Perithecia domeshaped (slightly arched) to hemispherical, sometimes pointed, .05-.3 mm diam., excipulum entirely hyaline below. Spores hyaline, reniform to ovoid, 6-11 x 3-5μ.

Verrucaria microspora is characterized by a thin, normally brown to amber thallus which is either continuous or in scattered patches but never areolate. The thallus is devoid of pegs or ridges but may contain artifacts that might superficially resemble pegs or ridges.

In some instances tests have proven these to be perithecial remains. The thallus becomes translucent to quite transparent when wet. Erichsen (1957) recognized a var. *taetevirens* as characterized by a leek-green thallus which is less transparent. I have also observed this in material from the southern part of its range in North America. I also observed a dark gray thallus in the same area. The dark gray thallus has a color and texture resembling graphite used in pencils. Upon wetting, the dark color disappears.

The perithecia are brown to black and may be shiny or dull.

Their shape may range from that of a slightly arched dome to more nearly hemispherical and pointed. The diameter of the perithecia is reported as .15-.25 mm (Lamb, 1948), .1-.3 mm (Santesson, 1966),.2-.3 mm (Zschacke, 1924), .2-.3 mm (Erichsen, 1957). Erichsen (1957) also recognized var. friesiaca as having a smaller perithecia of only .1-1.5 mm diameter. I measured 230 perithecia (10 each from 23 specimens) and found a range of .08 -.28 mm except for a single collection in which the range was .16-.48 mm with 4 out of 10 exceeding .3 mm. In no other collection did the diameter exceed .3 mm. Clusters of smaller or larger perithecia may be found and, due to the normal patchy appearance of the thalli, one may be tempted to consider such patches as distinct species. I do not believe that perithecium size is of taxonomic significance in this species.

Spores of *V. microspora* are thin-walled and will change shape somewhat with osmotic changes. Generally they are ovoid to slightly reniform. The species name infers smallness of spores, but this is not noticeably different from *V. ditmarsica* and *V. striatula*. Spore sizes have been reported as 7-12 x 4-5u (Lamb, 1948); 7-11 x 5-7u

(Zschacke, 1924); 7-11 x 4-5 μ (Erichsen, 1957). Erichsen (1957) also recognized var. mucosula Sands. with spores 5-9 x 4-9 μ . My own spore measurements give a range of 6-11 x 3-5 μ .

GENERAL DISTRIBUTION: Germany (Erichsen, 1957), *Ullrich* 11.v.1963, England (Ferry and Sheard, 1969), Greenland, Japan, Chile, Antarctica (Lamb, 1948), Wales (Fletcher, 1973a), Norway: *Santesson 18772B*, Scotland: *Brodo 5249*, Australia: *Willis* vii.41 (MICH).

NORTHEASTERN AMERICAN DISTRIBUTION: MAINE: Cumberland Co., 337A, 383A, Sagadahoc Co., 503, 507B; Hancock Co., 627B. MASSACHUSETTS: Essex Co., 1233, 1237, 2479, 2480, 2481, 2484, 2485, 2486, 2487; Plymouth Co., 2389, 2467, 2470, 2474; Barnstable Co., 2456, 2458. RHODE Newport Co., 2311, 2312, 2313, 2315, 2317, 2318, 2319, 2325, 2326, 2327, 2328, 2330, 2332, 2334, 2336, 2348, 2349, 2350, 2351, 2353, 2354, 2400, 2402, 2403, 2404, 2405, 2409. CONNECTICUT: New London Con., 2356, 2357, 2360, 2363. NEW JERSEY: Ocean Co., 2426, 2427, 2429, 2434, 2435, 2436; Cape May Co., 2437, 2438, 2439, 2441. NOVA SCOTIA: Colchester Co., 1182; Cumberland Co., 1190, 1192, 1199; Yarmouth Co., 1252; Digby Co., 1317, 1322, 1326, 1338; Shelburne Co., 1358, 1359; Victoria Co., 1527. NEWFOUNDLAND: West Coast Section; 1613, 1636; Northern Peninsula Section, 1761B, 1901B, 1922; East Coast Section, 1957.

Verrucaria mucosa Wahlenb. in Ach. Suppl. Meth. Lich. 23. 1803.

Thallus grass green to blackish green, smooth and tough, continuous, often with necral cracks in herbarium specimens, 130-150µ.

thick, usually opaque (wet or dry); juga absent; prothallus, if present, whitish. Perithecia submerged to slightly raised, sometimes with prominent ostioles surrounded by chimney, excipulum clear below, involucrellum .05-.2 mm diam. Spores simple, colorless usually ovoid, $8-11 \times 4-5\mu$.

Thallus of this species is easily recognized in the field or in the herbarium. In old herbarium specimens it is brown. Upon drying it develops cracks that are strictly necral artifacts not to be confused with the rimose areolation typical of *V. maura*. A whitish prothallus is often seen around a thallus on smooth rock.

Perithecia are normally flush to slightly raised or sunken. When ripe, the involucrellum tends to evaginate somewhat presenting a conspicuous ostiole with a short chimney around it. One often sees whitish pits in the thallus which are the remains of old perithecia divested of their involucrellum.

The thallus of *V. mucosa* is quite aggressive and often grows over crustose algae, such as *Hildenbrantia* and *Lithothamnia*. It also is commonly found growing over other *Verrucariae* where the perithecia of the overgrown material project through the thallus of *V. mucosa* causing a potential source of misidentification.

Spores of V. mucosa are not distinctive in either shape or size. Santesson (1939) reports the size of spores to be highly variable, 7-15 x 4-8 μ .

Pycnidia are quite common on *V. mucosa* thalli. They appear as slits ringed with brown and occur widely scattered or in cluster. It is not uncommon to find mounds made up of aggregated pycnidia.

GENERAL DISTRIBUTION: Sweden, Norway, Finland, Iceland, Faroe

Islands, Germany, Ireland, France (Santesson, 1939), England (Ferry and Sheard 1969) Wales (Fletcher, 1973a), Greenland, Sibera, Fuegia, Aukland Islands, Campbell Island, New Zealand (Lamb, 1948), British Columbia: *Brodo 10143B*.

NORTHEASTERN AMERICAN DISTRIBUTION: MASSACHUSETTS: Essex Co., 183, 196, 199, 237, 2479, 2482, 2485, 2503, Fink 3474, 20.v.1795; Jones 3440; Plymouth Co., 2375, 2376, 2377, 2379, 2381, 2462, 2467, 2470, 2473. NEW HAMPSHIRE: Rockingham Co., 2444, 2446, 2448, 2451, MAINE: Cumberland Co., 320, 326, 367, 372A, 377B, 383C, 461; Sagadahoc Co., 504, 508; Hancock Co., 628, 632, 633, 644, 657, 849, 878A, 879, 885, W.R. Taylor 3565; Lincoln Co., Merril 234; Washington Co., 1070. NOVA SCOTIA: Colchester Co., 1110; Cumberland Co., 1189, 1190, 1197; Yarmouth Co., 1253; Digby Co., 1301, 1303, 1304, 1305, 1313, 1316, 1319, 1338; Shelburne Co., 1360; Halifax Co., 1369, 1397, 1400, 1415, 1419; Victoria Co., 1516; Cape Breton Co., 1584. NEWFOUNDLAND: Northern Peninsula Section, 1784, 1792, 1883; East Coast Section, 1960, 2014, 2015, 2015C, 2016A, 2017A, 2020D, 2022, 2055, 2056, 2064B, 2066C, 2068, 2080B, 2081B, 2153, 2154, 2155, 2156, 2157, 2158, 2162, 2163; Avalon Section, 2171B, 2185, 2189B, 2192, 2197, 2197B, 2198, 2198B.

Verrucaria silicicola Fink in Hedrick, Mycologia 25(4): 305. 1933.

Thallus brownish, continuous to patchy, not areolate. Perithecia shallow domes to hemispherical, .15-.4 mm broad; excipulum hyaline to dark below. Spores hyaline, $18-22 \times 8-9\mu$.

My personal knowledge of this species, known only from Long Island,

New York, is limited to the examination of available herbarium specimens. The material seen resembled V. microspora to a considerable degree. The thallus was brownish and patchy. The perithecia, for the most part, were shallow domes. Hedrick (1933) gives .15-.4 mm as the diameter of perithecia and those I saw fall within this range. The salient characteristic of this species is the spore size, listed by Hedrick (1933) as $18-22 \times 8-9\mu$. I was unable to find spores but Brodo (1968) reported the range as $16-25 \times 6-10\mu$.

NORTHEASTERN AMERICAN DISTRIBUTION: NEW YORK: Suffolk Co., Brodo 2710, 2826; Latham 36755, 36780.

Verrucaria striatula Wahlenb. in Ach. Suppl. Meth. Lich. 23. 1803.

Thallus entire, light to dark green, usually opaque when dry, more translucent when wet, containing numerous black, rather broad ridges often furcated, ridges especially common at thallus margins. Perithecia hemispherical to globular, often irregular, flattened and/or dissected, shiny, .07-.3 mm diam., excipulum hyaline to entirely dark below. Spores ovoid, may be pointed at one end, 8-10 x 4-5µ.

Verrucaria striatula is most noted for the strikingly large carbonaceous structures termed juga by Santesson (1939). The juga rise above the thallus and tend to be broad and often branched. They commonly encompass a perithecium. Near the edge of the thallus they often radiate out from the center, marking the leading edge of thallus lobes. They are different from the ridges of V. erichsenii and V. ditmarsica, being more like flattened plateaus and buttes than

narrow ridges.

The thallus is normally a bright green when fresh but darkens in more intense sunlight. It becomes quickly depigmented in the shade. In the herbarium the thallus soon becomes colorless and scarcely visible, a condition causing early workers to think that the juga were the entire thallus (Santesson, 1939). The thallus is continuous but often shows necral cracks upon drying.

The perithecia are often amorphous, coalescing with juga or appearing as spheres often with flattened tops. The perithecia often are cracked or dissected and usually a shiny black.

In the shade modification the perithecia become more nearly spherical or may be elongated vertically. The juga become reduced, causing the shade modification of *V. striatula* to resemble *V. ditmarsica*. However, even in the shade modification the juga usually retain their flatness and are reduced in size, but still are broad by comparison to the other ridged species. Perithecium diameters are in the general range of 1.5-3 mm. Zschacke (1934) lists the spore range as 8-12 x 4-5µ and Erichsen (1958) as 8-11 x 4-5µ.

Santesson (1939) questioned the occurrence of this species in North America since several specimens he had examined from this area had been misidentified. I have found many such incorrect identifications in early herbarium material. The true identity was usually *V. erichsenii*. This is quite understandable since *V. striatula* predates *V. erichsenii* as a recognized species by 125 years and most of the errors were made prior to the publication of *V. erichsenii* or certainly before specimens were disseminated for comparison. Degelius (1942), however, confirmed the presence of *V. striatula* in North America

from his own collection in Maine.

GENERAL DISTRIBUTION: Sweden, Norway, Denmark, Iceland, Ireland, France, Spain, Portugal (Santesson 1939), Wales (Fletcher, 1973a), Scotland: *Brodo 5246*, England: *James* 5.iv.1956.

NORTHEASTERN AMERICAN DISTRIBUTION: MASSACHUSETTS: Essex Co.,

191, 2485, 2493, 2504, 2505; Plymouth Co., 2382, 2382, 2386, 2387,

2392, 2472A, 2474; RHODE ISLAND: Newport Co., 2314, 2328, 2392,

2331, 2336; NEW HAMPSHIRE: Rockingham Co., 2448, 2449. MAINE:

Cumberland Co., 297, 366, 383, 384B, 388A, 389A, 390, 463; Hancock Co.,

553, 568A, 851, 852, 854, 861A, 880, 882, 883A. NOVA SCOTIA: Yarmouth

Co., 1247A, 1248, 1254, 1256, 1258, 1261; Digby Co., 1322, 1323;

Shelburne Co., 1357B, 1362A, 1363, 1389, 1390; Halifax Co., 1396, 1397,

1409, 1416B; Victoria Co., 1509, 1520, 1533. NEWFOUNDLAND: West

Coast Section, 1634; Northern Peninsula Section, 1792, 1794, 1888B,

1889, 1889C, 1919B, 1938B; East Coast Section, 1950, 1952, 1956,

2016B, 2017B, 2018, 2019, 2020B, 2021B, 2080C, 2153, 2156, 2158;

Avalon Section, 2197C. NEW BRUNSWICK: Grand Manan, W. R. Taylor

6122 (MICH).

Xanthoria candelaria (L.) Th. Fr. Gen. Heterolich. Europ. 61. 1861. Lichen candelarius L. Sp. Pl. 1141. 1753.

Thallus foliose, light gold, diffuse or forming rosettes, KOH+ purple. Lobes small (.2-.5 mm broad) plane to convex, lacerated, sorediate, soredia mostly apical or laminal, lobes tend to rise off substrate. Apothecia about 2 mm broad with thalline margin. Spores eight per ascus, polarilocular, 9-13 x 4-6µ.

This species superficially resembles members of the genus Candelaria for which it is named but differs in reaction to KOH and spore type. The Candelariae are KOH- and the spores are not polarilocular. There is also a resemblance between Xanthoria candelaria and X. fallax when the latter displays lobe widths at the narrow end of the range for that species. However, in such a case the location of soredia will distinguish them. In X. candelaria the soredia are apical or laminal as opposed to the labrose mode in X. fallax.

GENERAL DISTRIBUTION: New York (Brodo, 1968), Alaska (Krog, 1968), South Dakota (Wetmore, 1967), Nevada (Imshaur, 1957), Washington (Howard, 1950), Utah (MSC), California (MSC), British Columbia (MSC), west central Canada (Bird, 1970), Cuba (Montagne, 1838-1842), Greenland (Lynge, 1932), Novaya Zemlya (Lynge, 1932), France (Harmand, 1909-1913), Germany (Erichsen, 1957), Nepal (Awasthi, 1965), England (Ferry and Sheard, 1969).

NORTHEASTERN AMERICAN DISTRIBUTION: NOVA SCOTIA: Cape Breton Co., 1570. NEWFOUNDLAND: Avalon Section, 2176, 2208.

Xanthoria elegans (Link) Th. Fr. Lich. Arct. 69. 1860. Lichen elegans Link. Ann. Naturges. 1:37. 1791.

Thallus foliose, red-orange to citrine, rising off of substrate at least at tips, KOH+ purple, forming rosettes about 2-5 cm diam., lobes nodular-convex, including tips. Apothecia orange-yellow to red-orange, about 1-2 mm broad. Spore colorless, polarilocular, 10-13 x 5-8u.

Upon cursory inspection this species may appear to be crustose

but it does have a developed lower cortex and lifts off the substrate at least at the tips. The lobes have a tubular appearance but of quite irregular width and thickness, giving it a rather nodular appearance. Like X. parietina it is devoid of soredia.

GENERAL DISTRIBUTION: Washington (Howard, 1950), Alaska (Krog, 1968), South Dakota (Wetmore, 1967), New Mexico (Rudolph, 1953), Arizona (MSC), Colorado (MSC), Wyoming (MSC), Montana (MSC), Iowa (MSC), Michigan (MSC), Minnesota (MSC), Maine (MSC), New York (MSC), Mexico (MSC), Manitoba (MSC), Northwest Territory (MSC), Nova Scotia (Lamb, 1948), Greenland (Lynge, 1932), Finland (Räsänen, 1927), India (Awasthi, 1965), China (Magnusson, 1940), New Zealand (Nylander, 1888).

NORTHEASTERN AMERICAN DISTRIBUTION: MAINE: Sagadahoc Co., 496, 498; Hancock Co., 649, 865, 867. NOVA SCOTIA: Digby Co., 1341; Shelburne Co., 1387; Halifax Co., 1391A; Victoria Co., 1534; Cape Breton Co., 1571. NEWFOUNDLAND: West Coast Section, 1628; Northern Peninsula Section, 1832, 1927.

Xanthoria parietina (L.) Th. Fr. Lich. Arct. 67. 1860. Lichen paritinus L. Sp. Pl. 1143. 1753.

Thallus foliose, orange to citrine, radiate, often rosette-like KOH+ purple, lobes flat, wrinkled, about 1 mm broad, usually bifid at the tips, soredia absent. Apothecia numerous, about 5 mm broad, plane to concave with thin thalline margine disappearing with age. Spores 8 per ascus, polarilocular, colorless, $10-13 \times 6-9\mu$.

This widespread oceanic species is easily distinguished from all other littoral *Xanthoriae* by its relatively broad, thin, distinctly

wrinkled thallus divided dichotomously at the tips. The apothecia often contrast with the thallus by being more red colored.

GENERAL DISTRIBUTION: New York (Brodo, 1968), Massachusetts (MSC), Montana (MSC), Maine (MSC), Greenland (Lynge, 1937), Novaya Zemlya (Lynge, 1928), Sweden (Degelius, 1935), Finland (Räsänen, 1927), Italy (Jatta, 1909-1911), India (Awasthi, 1965), Cuba (Montange, 1838-1842), Tenerife (MSC), England (Ferry and Sheard, 1969), Wales (Fletcher, 1973b).

NORTHEASTERN AMERICAN DISTRIBUTION: MAINE: Cumberland Co., 455; Sagadahoc Co., 496,497; Hancock Co., 599, 646, 866. NOVA SCOTIA: Halifax Co., 1121; Yarmouth Co., 1279; Digby Co., 1328; Shelburne Co., 1368,1378.

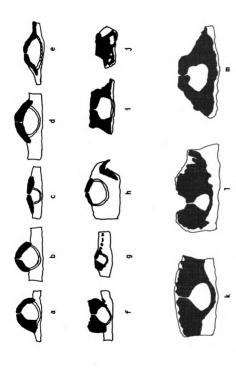


Figure 12. Vertical Sections of Verrucariae. V. silicicola, Brodo 2828; b.

V. striatula, 568A; g. V. mucosa, 2135; ία, 2019 (tangential section); V. maura, 1798 (elevated and indented form); m. V. maura, erichsenii, 1508; e. V. intermigrescens,

X. SUMMARY AND CONCLUSIONS

A. Zonation

Contrasts between European and northeastern North American zonation are evident. It is common in Europe to find three distinct zones: a black zone, and orange belt and a *Ramalina* belt. In northeastern North America only the black zone is distinct. A minimal and indistinct orange belt is rare and a *Ramalina* belt does not occur. The black zone is comprised of diverse *Verrucariae* whose vertical ranges overlap, producing a mixture of species at all levels. Even the heights on the shore at which the various species grow most abundantly tend to overlap. The littoral zone contains relatively few facultative species which normally occur outside that zone. All obligate littoral lichens are found several meters above high tide and most of them extend down to low tide.

B. Ecology

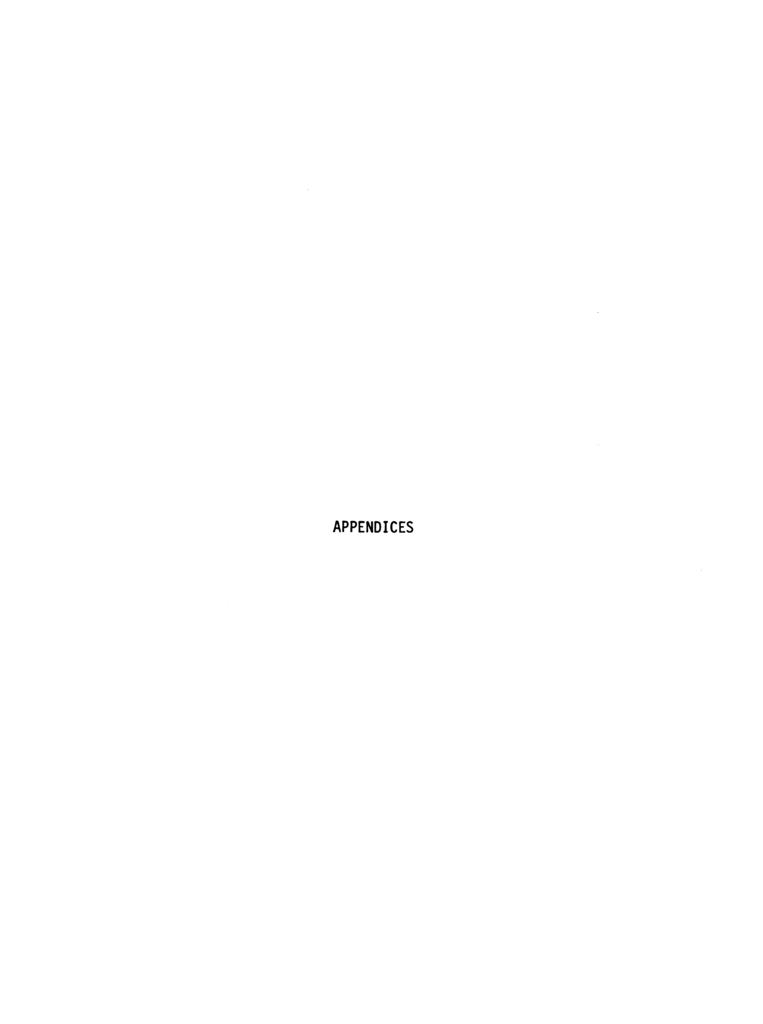
The relationships of environmental conditions to littoral lichen abundance and general diversity are very complex and it is impossible to attribute abundance or diversity to a single environmental condition measured, but rather to the interaction or combined effects of several factors. Two pairs of littoral lichen species are significantly associated geographically on sheltered shores: V. maura with V. ceuthocarpa and V. striatula with V. ditmarsica. Six pairs are significantly associated on exposed shores: V. mucosa with V. erichsenii, V. mucosa with V. ditmarsica, V. striatula with V. ditmarsica, V. mucosa with V. striatula, V. erichsenii with V. striatula, V. erichsenii with V. ditmarsica. Verrucaria ditmarsica and V. striatula have a significant positive association at the microhabitat level, while three pairs have a

significant negative association: V. erichsenii with V. mucosa, V. erichsenii with V. microspora, and V. erichsenii with V. ditmarsica.

C. Taxonomy

The littoral lichen flora of northeastern North America is comprised of twenty-one species representing seven genera. Five of the species collected, Caloplaca microthallina, Verrucaria amphibia, V. ditmarsica, and V. internigrescens were previously unreported from North America.

Four species, Caloplaca microthallina, Lecanora grantii, Xanthoria candelaria, and Xanthoria elegans are found in the littoral zone in northeastern North America but not commonly reported from Europe in that zone. Verrucaria internigrescens is uncommon on both continents while V. silicicala is endemic to Long Island, New York. Caloplaca thallincola, Lecanora helicopis, L. actophila, Lichina pigmaea, and Ramalina siliquasa are commonly reported from European shores but are not found on those of northeastern North America. Although Xanthoria parietina is found in the littoral zone on both European and North American shores, Degelius (1942) commented on the relative rarity of that species on the North American shores.



APPENDIX A

COLLECTION SITES

Collection sites are first listed with collection numbers in consecutive order. Following that complete listing, another listing is given with collecting site numbers in consecutive order to provide a cross-reference.

APPENDIX A

COLLECTION NO.	SITE NO.	LOCALITY.
183-205	la	MASSACHUSETTS (ESSEX COUNTY): Sand beach with rock outcrop Wingersheek Beach near Gloucester. 29 June 1965.
206-240	16	MASSACHUSETTS (ESSEX COUNTY): Along the Shore, Halibut Point near Pigeon Cove. 30 June 1965
290-312	2a	MAINE (CUMBERLAND COUNTY): Along the shore, Recompence Shores south of Freeport. 5 July 1965.
313-328	2b	MAINE (CUMBERLAND COUNTY): Along the shore, Bailey Island. 7 July 1965.
359-392	2b	MAINE (CUMBERLAND COUNTY): Along the shore, Bailey Island. 9 July 1965.
448-475	2b	MAINE (CUMBERLAND COUNTY): Along the shore, Bailey Island, 10 July 1965.
496- 510	2c	MAINE (SAGADAHOC COUNTY): Along the shore, Reid State Park. 15 July 1965.
553-587	3a	MAINE (HANCOCK COUNTY): Great Head shore- line, Mt. Desert Island. 20 July 1965.
627-657	3a	MAINE (HANCOCK COUNTY): Great Head shore- line, Mt. Desert Island. 20 July 1965
829-877	3 b	MAINE (HANCOCK COUNTY): Along the shore, Schoodic Peninsula near Winter Harbor. 25 July 1965.
878- 888	3c	MAINE (HANCOCK COUNTY): Shore line near Otter Cove, Mt. Desert Island. 26 July 1965.
1063-1073	4	MAINE (WASHINGTON COUNTY): Quody Head, S. Lubec. 8 August 1965.
1110-1111	7	NOVA SCOTIA (COLCHESTER COUNTY): Along the shore near Moose Island, Five Islands Provincial Park. 11 August 1965.
1118-1133	5a	NOVA SCOTIA (HALIFAX COUNTY): Along the shore at Prospect Point, near Halifax. 13 August 1965.

1182-1185	7	NOVA SCOTIA (COLCHESTER COUNTY): Along the shore near Moose Island, Five Islands Provincial Park. 14 August 1965.
1188-1198	6	NOVA SCOTIA (CUMBERLAND COUNTY): Shore near the wharf at Joggins. 15 August 1965.
1199	7	NOVA SCOTIA (COLCHESTER COUNTY): Along the shore near Moose Island, Five Islands Provincial Park. 15 August 1965.
1232-1238	la	MASSACHUSETTS (ESSEX COUNTY): Sand beach with rock outcrop, Wingersheek Beach near Gloucester. 21 June 1967.
1239-1246	1b	MASSACHUSETTS (ESSEX COUNTY): Along the shore of Halibut Point near Pigeon Cove. 22 June 1967.
1247-1300	8	NOVA SCOTIA (YARMOUTH COUNTY): Shore at Yarmouth Lighthouse, Yarmouth. 28 June 1967.
1301-1348	9	NOVA SCOTIA (DIGBY COUNTY): Shore at Digby Lighthouse, Digby. 29 June 1967.
1349-1390	10	NOVA SCOTIA (SHELBURNE COUNTY): West Point near Lockport. 30 June 1967.
1391-1425	5b	NOVA SCOTIA (HALIFAX COUNTY): Shore near Peggy's Cove. 3 July 1967.
1428-1429	5b	NOVA SCOTIA (HALIFAX COUNTY): Shore near Peggy's Cove. 3 July 1967.
1493-1567	11	NOVA SCOTIA (VICTORIA COUNTY): Shore at Neils Head at Neils Harbour. 6 July 1967.
1568-1610	12	NOVA SCOTIA (CAPE BRETON COUNTY): Shore at Louisbourg Lighthouse, Louisbourg. 10 July 1967.
1611-1659	13	NEWFOUNDLAND (WEST COAST SECTION): Shore at Cape Ray Lighthouse west of Port Aux Basques. 15 July 1967.
1761-1801	14	NEWFOUNDLAND (NORTHERN PENINSULA SECTION): Shore of Deer Cove, 10 miles south of River of Ponds, west side of Northern Peninsula. 21 July 1967.

1886-1911	15	NEWFOUNDLAND (NORTHERN PENINSULA SECTION): Goose Cove south of St. Anthony, east coast Northern Peninsula. 27 July 1967.
1912-1929	16	NEWFOUNDLAND (NORTHERN PENINSULA SECTION): Englee, east coast of Northern Peninsula, end of Routh 75. 28 July 1967.
1930-1944	17	NEWFOUNDLAND (NORTHERN PENINSULA SECTION): Jacksons Arm on White Bay, east side of Northern Peninsula. 30 July 1967.
1947-1978	18a	NEWFOUNDLAND (EAST COAST SECTION): Between Eastport and Salvage on Bonivista Bay. 1 August 1967.
2014-2054	19	NEWFOUNDLAND (EAST COAST SECTION): Chance Cove, Isthmus of Avalon on Trinity Bay. 3 August 1967.
2055-2100	20	NEWFOUNDLAND (EAST COAST SECTION): Cape Bonivista, Cabot's Landfall. 6 August 1967.
2124-2141	21	NEWFOUNDLAND (EAST COAST SECTION): Cape Freels near Wesleyville. 7 August 1967.
2151-2163	18b	NEWFOUNDLAND (EAST COAST SECTION): Southwest arm of Alexander Bay, West of Bonivista Bay, Terra Nova National Park. Collected by Joseph Karakes. 9 August 1967.
2164-2186	22a	NEWFOUNDLAND (AVALON SECTION): Great Island, Witless Bay Sea Bird Sanctuary near Bauline, south of St. John's. 10 August 1967.
2187-2218	22b	NEWFOUNDLAND (AVALON SECTION): Shoreline at Bauline, Witless Bay, south of St. John's. 11 Aguust 1967.
2219	4	MAINE (WASHINGTON COUNTY): Quody Head near Lubec. 21 August 1967.
2303-2310	23	MASSACHUSETTS (BARNSTABLE COUNTY): Cape Cod canal Jetty at Scusset Beach. 24 August 1971.
2311-2337	24a	RHODE ISLAND (NEWPORT COUNTY): On rocks protecting lighthouse, Beaver Tail Light, Conanicut Island in Narragansett Bay. 26 August 1971.

2338-2347	25	RHODE ISLAND (WASHINGTON COUNTY): On rocks protecting lighthouse, Point Judith Light, south of Narragansett at the mouth of Narragansett Bay. 27 August 1971.
2348-2355	24b	RHODE ISLAND (NEWPORT COUNTY): On boulders on the beach, Conanicut Light Conanicut Island in Narragansett Bay. 28 August 1971.
2356-2373	26	CONNECTICUT (NEW LONDON COUNTY): On rocky shore of Mason's Island near Mystic. 30 August 1971.
2374-2399	27	MASSACHUSETTS (PLYMOUTH COUNTY): Point of rock at public beach, Brant Rock. 31 August 1971.
2400-2409	24b	RHODE ISLAND (NEWPORT COUNTY): On rocks on the beach and in adjacent shallow water, Conanicut Light, Conanicut Island in Narragansett Bay. 1 September 1971.
2424-2436	28	NEW JERSEY (OCEAN COUNTY): On rocks at boat channel at Barnegat Light, Barnegat. 20 August 1972.
2437-2441	29	NEW JERSEY (CAPE MAY COUNTY): On rock sand catchers at public beach, Cape May. 20 August 1972.
2442-2452	30	NEW HAMPSHIRE (ROCKINGHAM COUNTY): On rocks protecting lighthouse, Portsmouth Light, Portsmouth Harbor. 25 August 1972.
2453-2459	31a	MASSACHUSETTS (BARNSTABLE COUNTY): On jetty, Sesuit Harbor, E. Dennis on Cape Cod. 28 August 1972.
2460-2461	31b	MASSACHUSETTS (BARNSTABLE COUNTY): Bass River jetty near Dennis Port on Cape Cod. 28 August 1972.
2462-2474	32	MASSACHUSETTS (PLYMOUTH COUNTY): Boulder strewn area at south end of public beach, Manomet. 29 August 1972.
2475-2476	23	MASSACHUSETTS (BARNSTABLE COUNTY): Cape Cod canal jetty at Scusset Beach. 29 August 1972.

2447-2505

1b

MASSACHUSETTS (ESSEX COUNTY): On rocks at reservarion, Halibut Point near Pigeon Cove. 30 August 1972.

CROSS-REFERENCE

SITE NO. COLLECTION NOS.

la. 183-205, 1232-1238.

1b. 206-240, 239-1246, 2477-2505.

2a. 290-312.

2b. 313-328, 359-392, 448-475.

2c. 496-510.

3a. 627-657.

3b. 829-877.

3c. 556-587, 878-888.

4. 1063-1073, 2219.

5a. 1118-1133.

5b. 1391-1425, 1428-1429.

6. 1188-1198.

7. 1110-1111, 1182-1185, 1199.

8. 1247-1300.

9. 1301-1348.

10. 1369-1390.

11. 1493-1567.

12. 1568-1610.

13. 1611-1659.

14. 1761-1801.

15. 1886-1911.

16. 1912-1929.

1	7.	1930-1944.
1	1.	1930-1944.

- 18a. 1947-1978.
- 18b. 2151-2163.
- 19. 2014-2054.
- 20. 2055-2100.
- 21. 2124-2144.
- 22a. 2164-2186.
- 22b. 2187-2218.
- 23. 2303-2310, 2475-2476.
- 24a. 2311-2337.
- **24b.** 2348-2355, 2400-2409.
- 25. 2338-2347.
- 26. 2356-2373.
- 27. 2374-2399.
- 28. 2424-2436.
- 29. 2437-2441.
- 30. 2442-2452.
- 31a. 2453-2459.
- 31b. 2460-2461.
- 32. 2462-2474.

APPENDIX B

MULTIPLE REGRESSION ANALYSIS DATA

Key to the abbreviations:

VAR. = Independent variables.

REG. COEF. = Regression coefficient.

STD. ER. = Standard Error (for the value in the preceeding column).

BETA WTS. = Beta Weights.

SIG.= The probability that the independent variable had no effect on the dependent variable.

PT. CR. COEF. = Partial correlation coefficient.

R² DEL.= The value that R² would assume if that variable were deleted from the regression equation. (R² does not appear, as such in the appendix. In the expression, "...variables explain...% of the variation...", it is the R² value that is expressed in percent.)

W= Water temperature.

A= Air temperature.

I= Solar insolation.

T= Tidal range.

S= Salinity.

Products of the above variables (e.g. IXS) represent interactions.

A variable squared (e.g. IXI) represents a variable in a non-linear condition.

Table 6 Multiple Regression Analysis Data: Verrucaria mucosa

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R ² DEL.	.51209	.54664	. 29585	.51887	.41959	.51254	.53771	.51175	.46120	.52447	.53765
PT. CR. COEF.	.44533	37044	66672	43246	57104	44451	39229	.44595	.52349	42124	.39243
SIG.	.015	.048	<0.0005	.019	.001	.016	.035	.015	.004	.023	.035
STD. ERR.	8.28991	7.87373	11.31833	4.43440	9.68772	8.62497	11.40130	4.52746	53.12837	51.38760	29.54987
BETA WTS.	21.42483	-16.31675	-52.60993	-11.05143	-35.01581	-22.23944	-25.26554	11.72125	169.61581	-124.01976	65.51179
STD. ER.	14.84503	22.98131	3.57085	30.88964	75.19213	.45280	1.47601	.08279	.42555	.00063	.00042
REG. COEF.	38.36619	-47.62423	-16.59803	-76.98337	-271.77840	-1.16754	-3.27087	.21433	1.35861	00152	.00093
VAR.	3	۷	H	-	S	MXS	AXA	IXI	IXS	IXIXS	IXIXA

Table 7 Multiple Regression Analysis Data: Vermucaria microspora

Nineteen variables explain 91.29% of the variation of abundance of this species

P <0.0005
cuer. Siu. Ek.
228.98982 98.57778
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-3.30860 1.06589
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3.28221 1.35460
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.85831 .23149

Table 8 Multiple Regression Analysis Data: Verrucaria erichsenii

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24.32%
es explain 24.32%
Seven variables
Seven

P= .232

F = 1.4229

R ² DEL.	.13999 .08323 .15818 .09299 .15558
PT. CR. COEF.	.34638 .41769 31775 40692 42342
SIG.	. 048 . 016 . 072 . 068 14
STD. ERR.	6.86465 12.47665 5.50262 1.91222 5.60907 13.36973 8.83476
BETA WTS.	-14.11294 31.93477 -10.26718 -4.74278 10.62442 -34.79177
STD. ER.	35.81299 .17863 68.51240 26.52827 .18333 .00029
REG. COEF.	-73.62631 .45721 -127.83524 -65.79681 .34725 00076
VAR.	AXI IXIXS IXIXS AXI

Table 9 Multiple Regression Analysis Data: Verrucaria striatula

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variables
Fifteen

P <0.0005

F = 6.1041

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R ² DEL.	.69883 .73167 .71110 .52455 .74177 .75212 .49122 .59689 .63977 .72701 .64618 .70447 .51747	0000
PT. CR. COEF.	57835 50180 .55234 .76009 .47174 43595 77807 .66534 .51437 .56627 56627 56627	701-0-1
S1G.	.002 .004 .0017 .017 .029 .0005 .0006 .009 .003 .003	
STD. ERR.	42.75836 33.23017 10.48844 11.96393 5.00677 2.31902 12.95075 35.10632 41.28947 43.22406 11.42048 26.06474 14.07064	2000000
BETA WTS.	-145.37912 -92.4528 33.32826 67.11293 12.84650 -5.38737 -76.93113 169.02613 176.47961 124.33560 47.82131 -85.88130 -79.94277 -9.90198	746.00000
STD. ER.	100.11419 8.41011 58.60968 .33838 .30964 .72370 .03226 3.64586 2.80915 .01516 .16753 .200330 2.36987	?
REG. COEF.	-340.38992 -23.39850 186.23919 1.89819 .79449 -1.68125 -19161 17.55370 12.00688 .04360 .70148 -13.46446	10.101.1
VAR.	TXTXT TXTXX TXXXX TXXXX TXXXX AXXX AXXX	זעעע

Table 10 Multiple Regression Avalysis Data: Verrucaria ditmarsica

Eighteen variables explain 74.29% of the variation of abundance of this species

7
P= .007
2109
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₽,

R ² DEL.	.61540	.59157	.57963	. 59528	.68591	.62016	.68217	.66237	.54967	.68298	. 59638	.54389	.57942	.67234	. 56538	.57747	.56727	.54679
PT. CR. COEF.	57581	60873	62325	60398	42603	.56849	.43720	.48843	65508	43481	.60254	.66058	.62350	.46411	63913	62575	63710	.65784
S1G.	.005	.003	.002	.003	.048	900.	.042	.021	.001	.043	.003	.001	.002	.030	.001	.002	.00	.001
STD. ERR.	22.50871	293.37150	69.49090	4.93851	9.36564	28.20583	12.64016	26.36078	14.73450	16.17558	277.23324	24.46051	368.12508	14.80045	12.18165	321.40757	29.05676	19.22539
BETA WTS.	-70.89383	-1006.65180	-247.67875	-16.73685	-19.72338	87.16436	27.47980	65.98626	-57.13083	-34.92868	936.04962	96.25090	1312.90308	34.68053	-45.27155	-1153.08666	-107.40945	75.09749
STD. ER.	40.07138	92.01513	536.20538	.23258	.74022	.10915	.65971	.16576	7.78074	1.36385	.12049	. 44467	2.93140	17.04616	2.54266	. 00392	69680.	1.87141
REG. COEF.	-126.20950	-315.73344	-1911.13781	78823	-1.55885	.33731	1.43421	.41493	-30.16867	-2.94503	. 40681	1.74974	10.45471	39.94270	-9.44947	01405	33153	7.31004
VAR.	3	—	S	MXM	MXA	MXI	MXS	AXI	AXT	AXS	IXI	IXI	IXS	TXT	TXS	IXIXS	TXTXI	TXTXA

Table 11 Multiple Regression Analysis Data: Verrucatia maura

Sixteen variables explain 71.55% of the variation of abundance of this species.

P = .004

F = 3.4579

R ² DEL.	.65251	.66981	.65047	.62235	.64115	. 59206	.58390	.58552	90099.	.61249	.66005	.60561	.60972	19609.	09609.	.66571
PT. CR. COEF.	.42574	.37197	.43131	.49663	45515	55008	.56237	55999	.40383	51556	40385	. 52785	.52059	52080	.52082	38592
SIG.	.038	.073	.035	.014	.025	.005	.004	.004	.050	010.	.050	800.	600.	600.	600.	.063
STD. ERR.	11.07756	17.55551	7.20283	8.37643	18.38383	30.99959	22.66804	12.21340	6.75524	15.99373	21.48070	15.89622	22.51104	19.34529	16.09229	3.28468
BETA WTS.	24.44693	32.99632	16.15079	22.48031	-44.07710	-95.77363	72.30981	-38.72024	13.98650	-45.13768	-44.47818	46.33755	64.37901	-55.35530	46.04946	-6.44494
STD. ER.	31.09803	8.68280	87.64189	1.04397	.11219	6.29141	.22477	1.62386	1.03691	. 45848	.26973	5.23216	.13502	1.06927	. 07833	. 39698
REG. COEF.	68.62985	16.31969	196.51786	2.80176	26898	-19.43740	10717.	-5.14815	2.14689	-1.29394	55851	15.25177	.38614	-3.05963	.22414	77893
var.	3	H	S	MXA	MXI	AXA	AXI	AXS	TXTXA	IXT	IXS	TXS	AXAXS	TXTXS	TXTXI	MXLXL

Table 12 Multiple Regression Analysis Data: Verrucaria ceuthocarpa

Nineteen variables explain 57.85% of the variation of abundande of this species.

F= 1.3722	P= .248						
VAR.	REG. COEF.	STD. ER.	BETA WTS.	STD. ERR.	SIG.	PT. CR. COEF.	R ² DEL.
3	127.58426	56.09851	52.44402	23.05952	.035	.46258	.46369
Ø	1175.32178	446.45832	296.40968	112.59433	910.	.51698	.42469
H	-156.63213	55.15508	-365.44502	128.68464	.010	54588	.39952
-	-875.88281	527.22909	-92.55455	55.71231	.113	35614	.51722
MXA	2.76537	.83163	25.60427	7.70000	.004	.60652	.33313
MXS	-4.72927	1.86876	-66.30978	26.20208	.020	50210	.43636
AXA	-49.77966	18.23684	-283.03971	103.69196	.013	53074	.41314
AXS	-31.04251	12.25635	-269.42109	106.37411	.020	50240	.43613
IXI	.23325	.09124	392.75151	153.63605	.019	. 50589	.43346
IXS	2.80587	1.00193	257.85177	92.07443	.01	.54053	.40445
TXT	252.13910	137.90135	160.20311	87.61920	.083	.38681	.50428
TXS	26.38053	15.93325	92.48771	55.86049	114	.35509	.51763
SXS	-5.60112	2.09541	-34.98607	13.08846	.015	52277	.41992
AXAXS	1.62354	. 58791	312.35679	113.10942	.012	.53518	.40925
IXIXA	00239	.00108	-123.70063	55.79420	.039	45336	.46939
IXIXS	00347	.00157	-208.39988	93.99790	.039	45336	.46939
TXTXA	2.08374	. 97295	15.66507	7.31442	.045	.44098	.47669
TXTXI	26600	.11959	-63.06329	28.35248	.038	45452	.46869
TXTXS	-5.35563	3.23663	-111.81195	67.57256	114	35490	.51770

Table 13 Multiple Regression Analysis Data: Arthopyrenia halodytes

S

oundance of this spec	
of al	
Seven variables explain 41.73% of the variation of abundance	
the	
of	
41.73%	
olain	12
ex	0
Jes	P=
variat	.1720
Seven	F= 3.

_						٠	. ,
R ² DEL.	.29390	.32618	. 29486	.28793	.29614	.28516	.27618
PT. CR. COEF.	41810	36781	.41676	42630	41495	.43000	.44160
SIG.	.015	.035	.016	.013	.016	.013	010.
STD. ERR.	4.06719	1.20829	6.86312	1.89335	6.87733	5.25497	1.65149
BETA WTS.	-10.42268	-2.66098	17.51942	-4.96796	-17.46343	13.93539	4.52575
STD. ER.	6.82999	. 00050	7.45616	62900.	. 02002	.01918	.13135
REG. COEF.	-17.50268	00109	19.03325	01782	05085	.05087	.35995
var.	3	IXI	TXT	AXAXS	TXTXI	MXI	AXS

Table 14 Multiple Regression Analysis Data: Diversity

Three variables explain 59,13% of the variation of diversity of species at the sites considered

ווו בב אמו ומ	illee var lables explain 59.15% of		the variation of alversity of species at the sites constant	y or species at	מוב אורבא כמו	is ider ed.	
F= 16.8793	P<0.0005						
VAR.	REG. COEF.	STD. ER.	BETA WTS.	STD. ERR.	SIG.	PT. CR. COEF.	R ² DEL
SXS IXIXS IXS	00858721 00000457 .00319571	.00167267	-3.06557 -15.68900 16.78453	.59713 2.84843 3.15104	<0.0005 <0.0005 <0.0005	65541 68141 .66912	.28354 .23705 .25999

APPENDIX C

COMPUTATION OF SALINITY

APPENDIX C

COMPUTATION OF SALINITY

The computation of salinity is in accordance with the methods of Knudsen (1953). The computation involves the values S, t, a_{τ} , k, and P17.5.

S= salinity in grams of solid per 1000 grams of sea water.

t= degrees Celsius of sea water.

 $a\tau$ = hydrometer reading minus 1.0 and times 1000.

k= a value derived from Knudsen's tables when given the values of t and $a\tau$.

P17.5= the sum of $a\tau$ and k.

Steps in the computation of Salinity:

- 1. Water temperature is measured and recorded.
- 2. Hydrometer reading is taken and recorded.
- 3. The value for k is found from Knudsen's P17.5 tables by locating the vertical column headed by the water temperature and tracing that column down to the horizontal line headed by the hydrometer reading.
- 4. The k value is added to at to give P17.5.
- 5. The value determined for P17.5 is located on Knudsen's titration table and the value for S is read from the table on the same horizontal line.

APPENDIX D

INTERSPECIFIC ASSOCIATION DATA

Key to abbreviation:

- A= number of times both species are present together.
- B= number of times the first species is present in the absence of the second.
- C= number of times the second species is present in the absence of the first.
- D= number of times neither species was present.
- N = A + B + C + D.

Table 16. Interspecific Association Data:

Overall Geographical Association

V. mucosa & V. microspora	A=18	B=8	C=11	D=5	N=42
V. mucosa & V. erichsenii	A=25	B=0	C=11	D=6	N=42
V. mucosa & V. striatula	A=20	B=6	C=8	D=8	N=42
V. mucosa & . ditmarsica	A=23	B=2	C=8	D=9	N=42
V. microspora & V. erichsenii	A=22	B=5	C=14	D=1	N=42
V. microspora & V. striatula	A=17	B=11	C=10	D=4	N=42
V. microspora & V. ditmarsica	A=20	B=8	C=11	D=3	N=42
V. erichsenii & V. striatula	A=24	B=11	C=1	D=6	N=42
V. erichsenii & V. ditmarsica	A=30	B=6	C=1	D=5	N=42
V. striatula & V. ditmarsica	A=26	B=0	C=5	D=11	N=42
V. maura & V. ceuthocarpa	A=7	B=9	C=3	D=23	N=42

Table 16. Interspecific Association Data:
Geographical Association, Sheltered Sites

V. mucosa & V. microspora	A= 6	B=4	C=4	D=4	N=18
V. mucosa & V. erichsenii	A=10	B=0	C=6	D=2	N=18
V. mucosa & V. striatula	A=5	B=5	C=6	D=2	N=18
V. mucosa & V. ditmarsica	A=8	B=2	C=6	D=2	N=18
V. microspora & V. erichsenii	A=9	B=1	C=7	D=1	N=18
V. microspora & V. striatula	A=5	B=5	C=6	D=2	N=18
V. microspora & V. ditmarsica	A =7	B=3	C=7	D=1	N=18
V. erichsenii & V. striatula	A=10	B=6	C=1	D=1	N=18
V. erichsenii & V. ditmarsica	A=13	B=3	C=1	D=1	N=18
V. striatula & V. ditmarsica	A=11	B=0	C=3	D=4	N=18
V. maura & V. ceuthocarpa	A=4	B=3	C=1	D=10	N=18

Table 17. Interspecific Association Data
Geographical Association, Exposed Sites

V. mucosa & V. microspora	A=12	B=4	C=7	D=1	N=24
V. mucosa & V. erichsenii	A=15	B=0	C=5	D=4	N=24
V. mucosa & V. striatula	A=15	B=1	C=2	D=6	N=24
V. mucosa & V. ditmarsica	A=15	B=0	C=2	D=7	N=24
V. microspora & V. erichsenii	A=13	B=4	C=7	D=0	N=24
V. microspora & V. striatula	A=12	B=6	C=4	D=2	N=24
V. microspora & V. ditmarsica	A=13	B=5	C=4	D=2	N=24
V. erichsenii & V. striatula	A=15	B=5	C=0	D=4	N=24
V. erichsenii & V. ditmarsica	A=17	B=3	C=0	D=4	N=24
V. striatula & V. ditmarsica	A=15	B=0	C=2	D=7	N=24
V. maura & V. ceuthocarpa	A=3	B=6	C=2	D=13	N=24

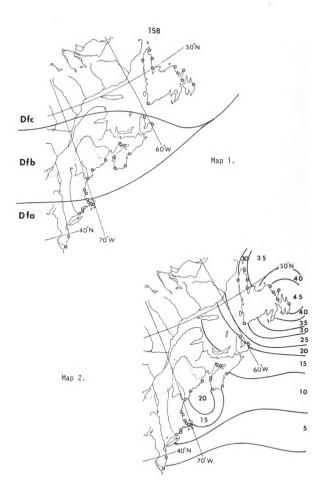
Table 18. Interspecific Association Data
Interspecific Association in Microhabitat

V. mucosa & V. microspora	A=11	B=35	C=56	D=173	N=287
V. mucosa & V. erichsenii	A=10	B=154	C=79	D=162	N=405
V. mucosa & V. striatula	A=14	B=37	C=65	D=188	N=304
V. mucosa & V. ditmarsica	A=30	B=80	C=59	D=174	N=355
V. microspora & V. erichsenii	A=4	B=132	C=29	D=123	N=372
V. micropsora & V. striatula	A=6	B=42	C=45	D=222	N=327
V. microspora & V. ditmarsica	A=15	B=103	C=51	D=202	N=383
V. erichsenii & V. striatula	A=27	B=33	C=138	D=170	N=348
V. erichsenii & V. ditmarsica	A=41	B=97	C=153	D=165	N=444
V. striatula & V. ditmarsica	A=67	B=55	C=1	D=286	N=397
V. maura & V. ceuthocarpa	A=2	B=26	C=12	D=59	N=99

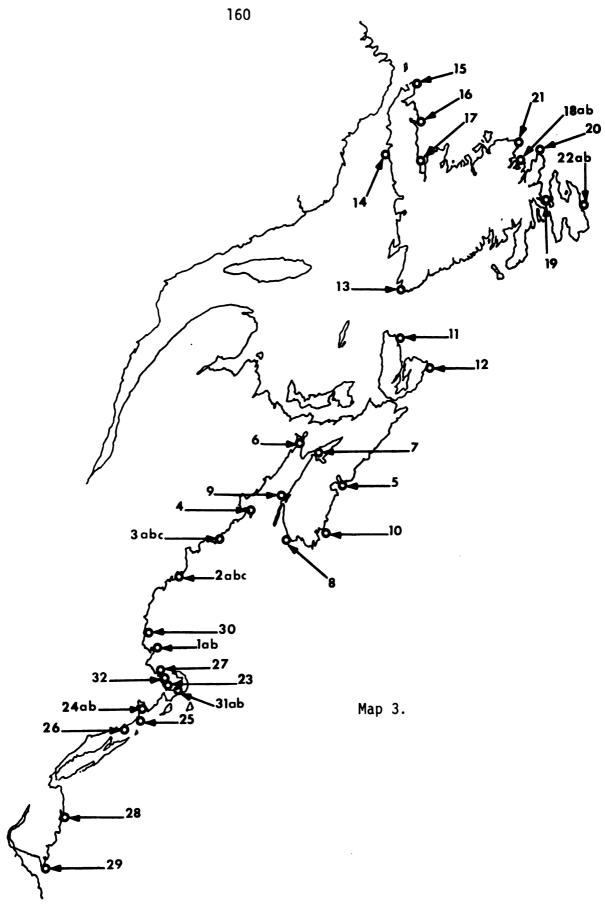
MAPS

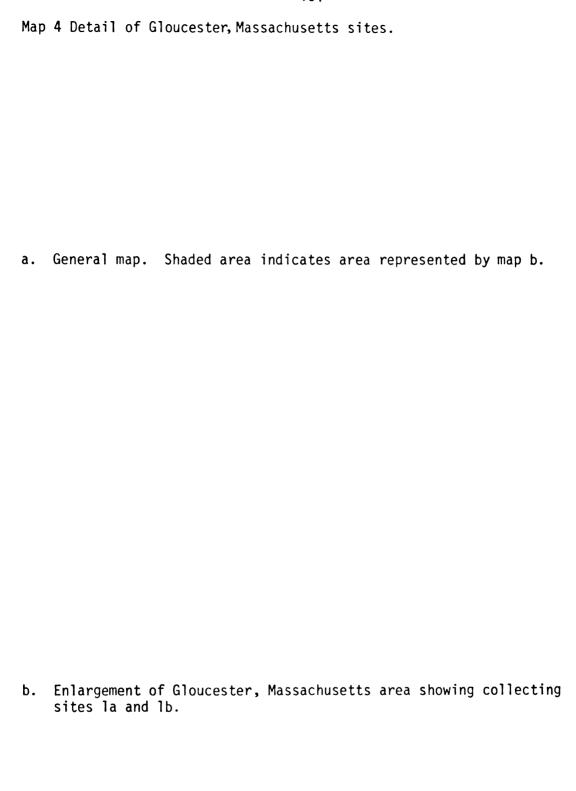
Map 1. Climate classification after Griffiths (1966).

Map 2. Mean frequency of fog at sea in January in percentage of observation hours after Kendrew (1961).



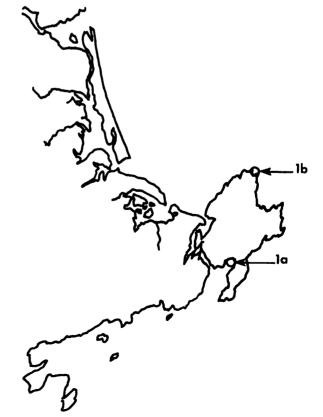
Map 3. General map of collection sites. Circle represent Collecting areas. If a circle represents only one collecting site only the number is given. If a circle represents more than one collecting site, letters follow the numbers indicating which sites are included. Numbers and letters correspond to those in the section and collecting sites and in appendix number. Longer scale maps follow that show the locations of lettered sites within numbered areas.







Map 4a.

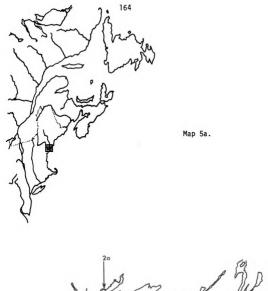


Map 4b.

Map 5. Detail of Brunswick, Maine sites.

a. General map. Shaded area indicates area represented on map b.

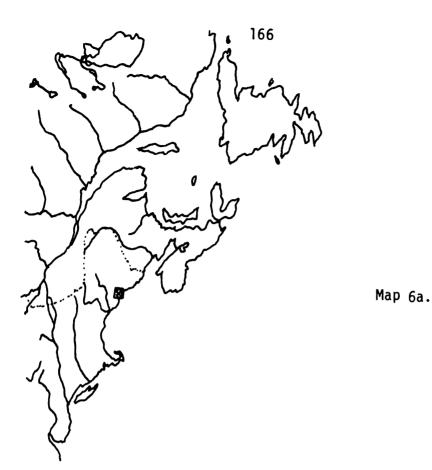
 Enlargement of the area near Brunswick, Maine showing collecting sites 2a, 2b, and 2c.

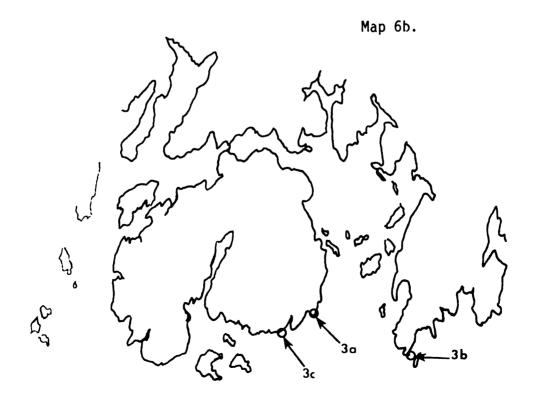


Map 6. Detail of Mt. Desert Island area sites.

a. General Map. Shaded area indicates area represented on map b.

b. Enlargement of Mt. Desert Island and vicinity showing the location of sites 3a, 3b, and 3c.

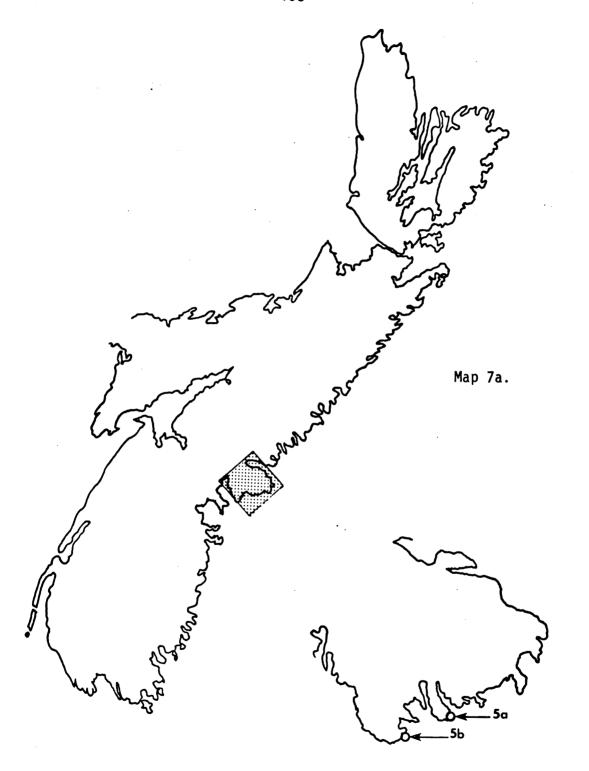




Map 7. Detail of Halifax, Nova Scotia area sites

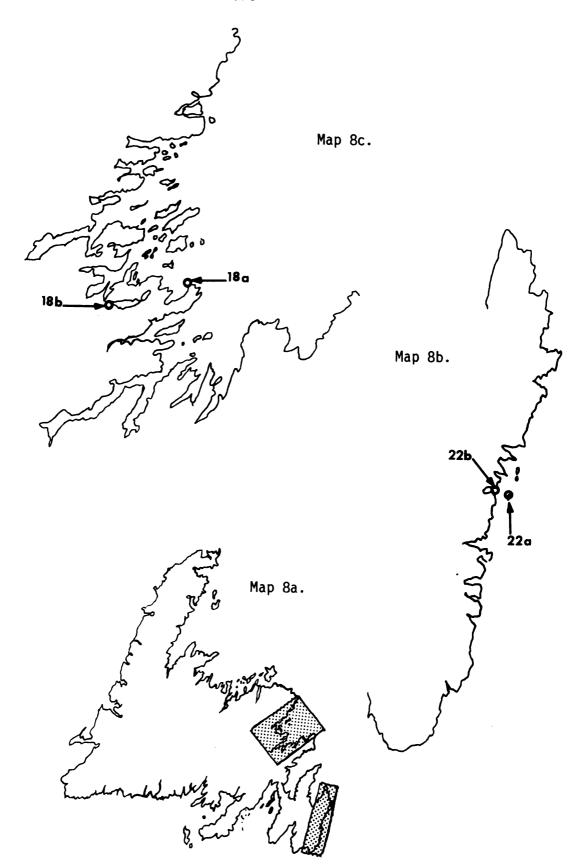
 Nova Scotia. Shaded area indicates the area represented in map number 7a.

b. Enlargement of the vicinity of Halifax, Nova Scotia showing the location of sites 5a. and 5b.



Map 7b.

	169
Мар	8. Detail of Eastern Newfoundland sties.
с.	Enlargement of the east coastal area in the vicinity of St. John's showing the locations of sites 22a. and 22b.
b.	Enlargement of the vicinity of Terra Nova National Park showing the location of sites 18a and 18b.
a.	Newfoundland. Shaded areas indicate the areas represented in Maps b and c.



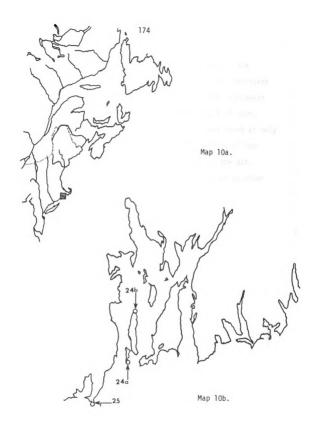
Map 9. Detail of Cape Cod, Massachusetts sites.

a. General Map. Shaded area indicates the area represented on map 9b.

b. Cape Cod area showing the location of sites 23, 31a, 31b, and 32.

Man	10.	Detail	οf	Narragansett	Rav	cites
nap	10.	Detail	UI	Marrayansect	Day	31623.

b. Narragansett Bay and vicinity showing the location of sites 24a, 24b, and 25.

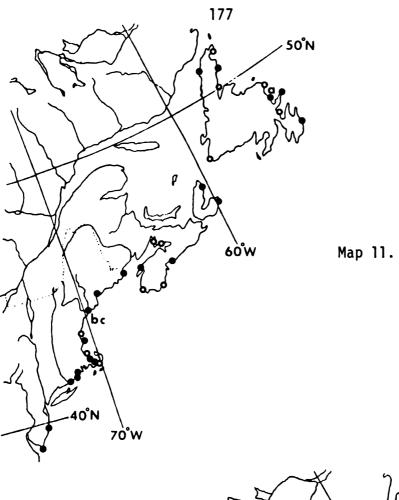


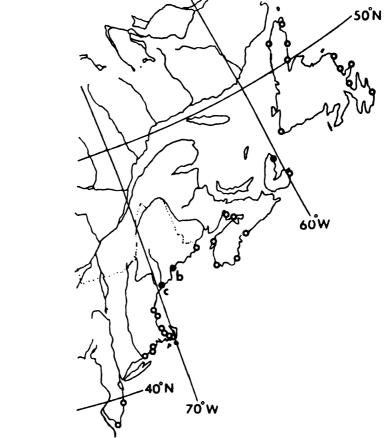
DISTRIBUTION MAPS

On the maps that follow, open circles represent sites collected where the species was not found. Dark dots represent localities where the species was found. If the dot represents more than one site and the species was found at all of them, no special designation is used. If the species was found at only part of the sites represented by the dot, the letters of the sites where the species was found are given beside the dot. Arrowheads represent locations of specimens collected by other collectors which I have examined and cited.

Map 11. Distribution of Arthopyrenia halodytes.

Map 12. Distribution of Caloplaca granulosa.

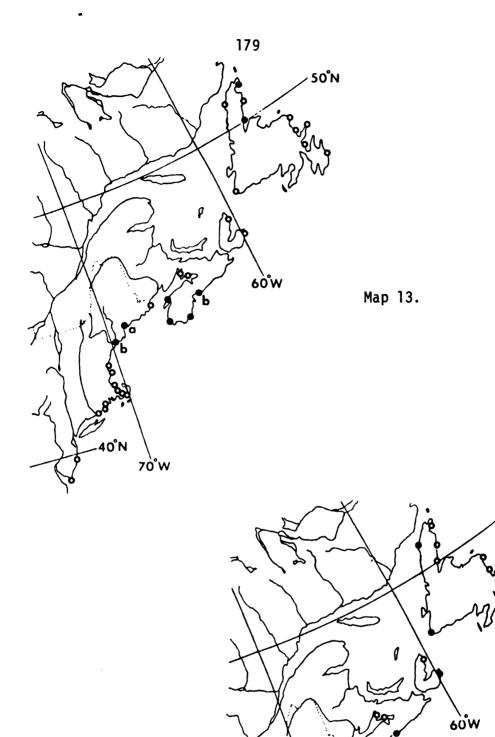




Map 12.

Map 13. Distribution of Caloplaca marina.

Map 14. Distribution of Caloplaca microthallina.



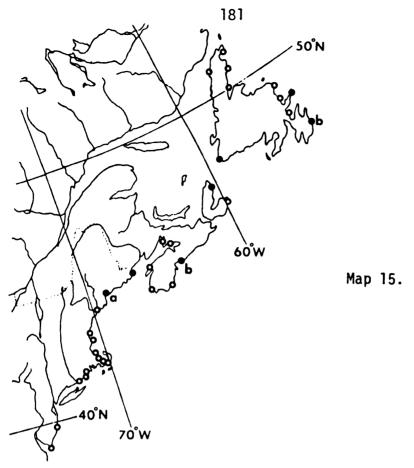
70°W

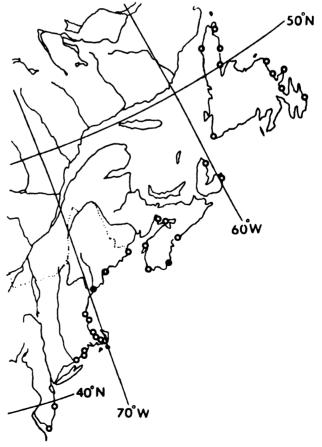
50°N

Map 14.

Map 15. Distribution of Caloplaca scopularis.

Map 16. Distribution of Lecanora grantii.

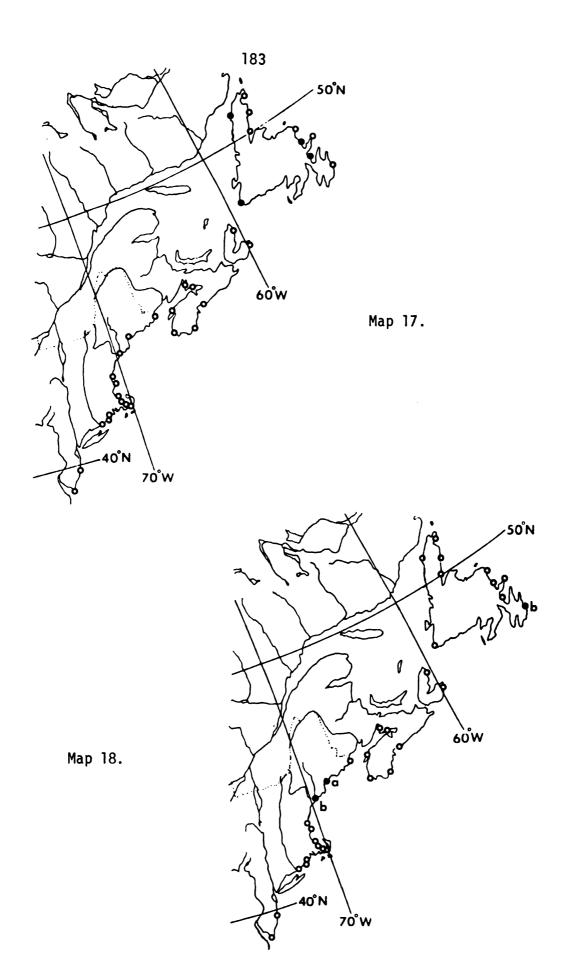




Map 16.

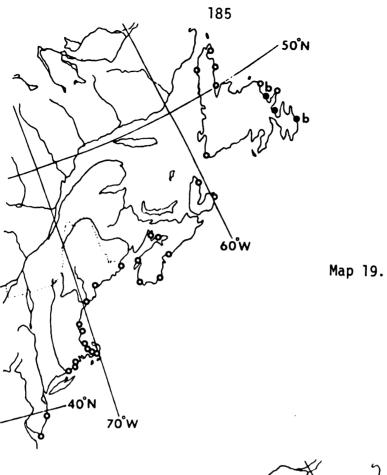
Map 17. Distribution of Lichina confinis.

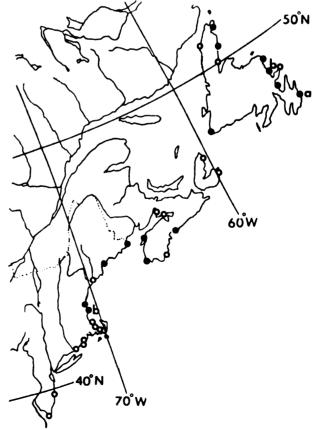
Map 18. Distribution of Stigmidium marinum.



Map 19. Distribution of Verrucaria amphibia.

Map. 20 Distribution of Verrucaria ceuthocarpa.

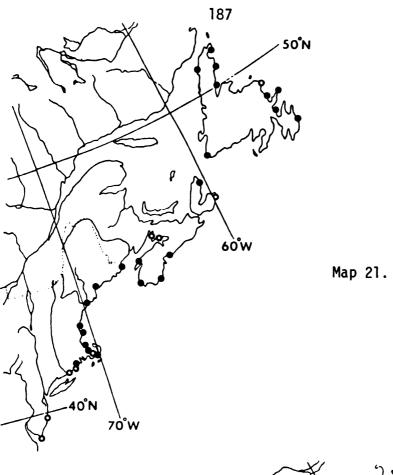


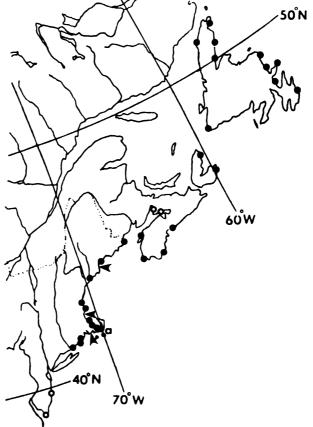


Map 20.

Map 21. Distribution of Verrucaria ditmarsica.

Map 22. Distribution of Verrucaria erichsenii.

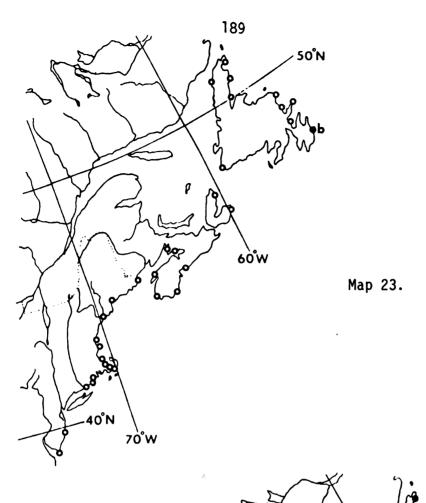




Map 22.

Map 23. Distribution of Verrucaria internigrescens.

Map 24. Distribution of Verrucaria maura.

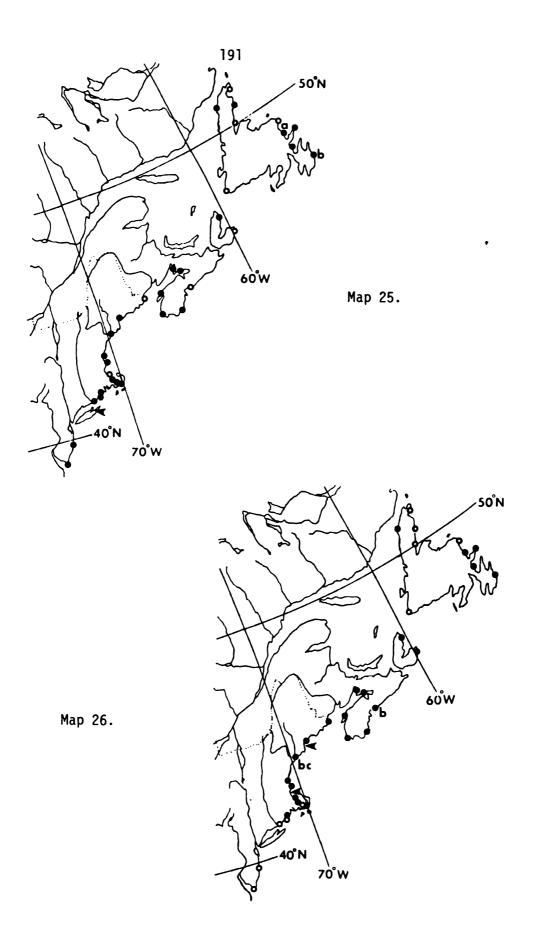


Map 24.

√50°N

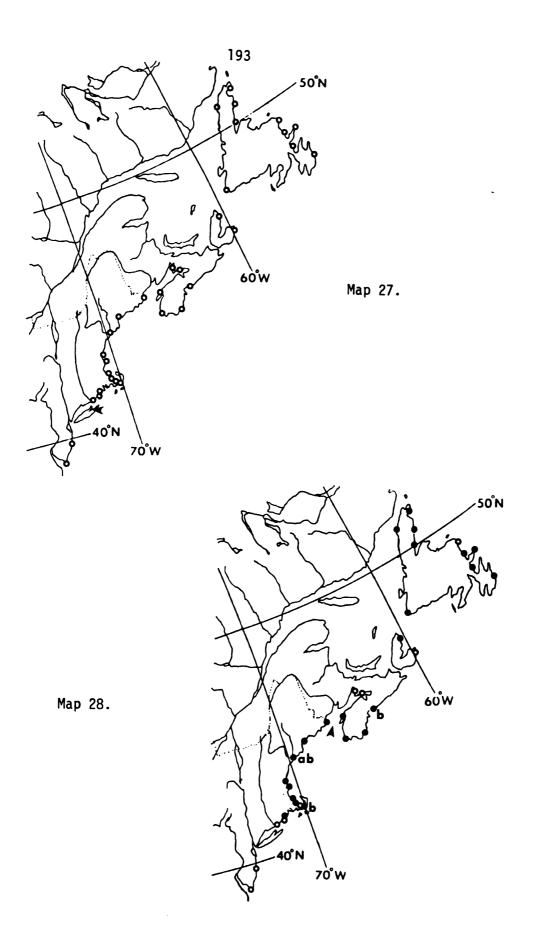
Map 25. Distribution of Verrucaria microspora.

Map 26. Distribution of Verrucaria mucosa.



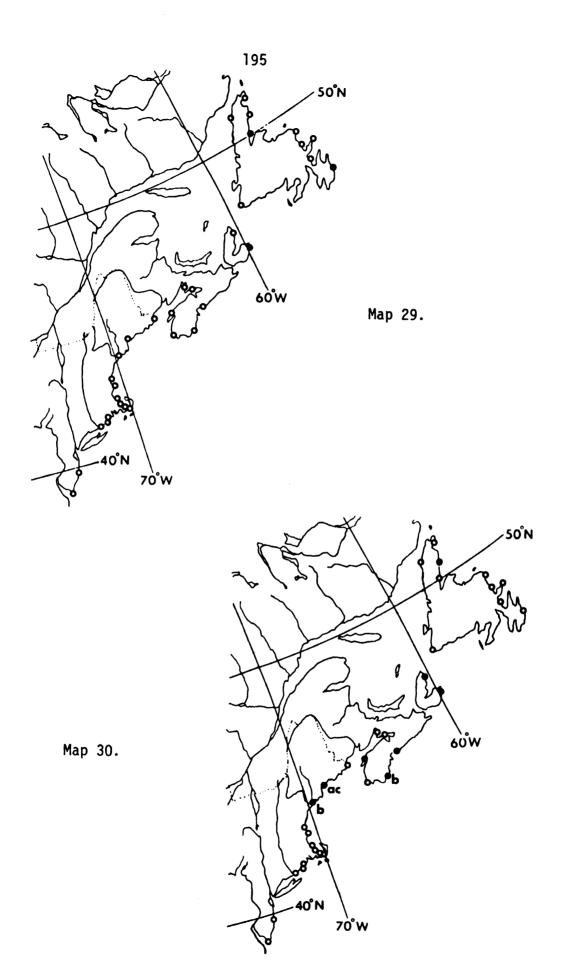
Map 27. Distribtuion of Verrucaria Silicicola.

Map 28. Distribution of Verrucaria striatula.

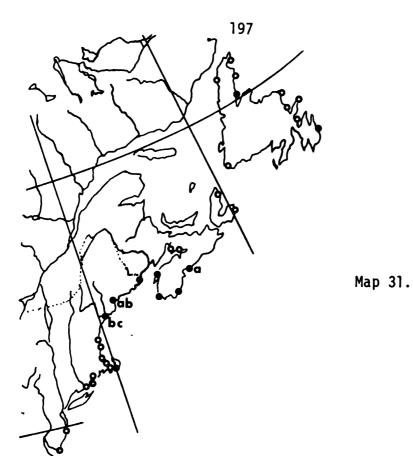


Map 29. Distribution of Xanthoria candelaria.

Map 30. Distribution of Xanthoria elegans.



31. Distribution of Xanthoria parietina.



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LITERATURE CITED

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