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Part 1

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Marine fungi of the Bay of Fundy VI: Growth and metabolites of *Leptosphaeria oraemaris*, *Sphaerulina oraemaris*, *Monodictys pelagica* and *Dendryphiella salina*. J.D. Miller, Y.E. Moharir, J.A. Findlay and N.J. Whitney 1

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Editor: G. Hicks

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**MARINE FUNGI OF THE BAY OF FUNDY VI:
GROWTH AND METABOLITES OF LEPTOSPHERIA
ORAEMARIS, SPHAERULINA ORAEMARIS,
MONODICTYS PELAGICA AND
DENDRYPHIELLA SALINA**

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The growth of four lignicolous marine fungi on a variety of carbon sources was measured quantitatively. The fatty acids and sterols of the marine fungi were also investigated. The fungi grew on constitutive wood sugars and grew poorly on polysaccharides and hydrocarbons. The major sterol of the fungi tested was ergosterol. The relative amounts of the fatty acids produced was somewhat different than that of terrestrial fungi.

La croissance de 4 champignons marins lignicoles, exposés à diverses sources de carbone, a été mesurée quantitativement. Les acides gras et les stérols de ces champignons marins ont aussi été étudiés. Les champignons croissaient en utilisant les sucres constitutifs du bois mais parvenaient difficilement à croître sur des polysaccharides et des hydrocarbures. Le principal stérol des champignons testés est l'ergosterol. Les quantités relatives d'acides gras produites étaient un peu différentes de celles des champignons terrestres.

Introduction

The number of studies on the carbon nutrition of higher marine filamentous fungi is surprisingly low. Kohlmeyer and Kohlmeyer (1979) list approximately 250 species of higher marine fungi and about 12 have been tested quantitatively for growth on a range of carbon compounds in liquid culture (Henningsson 1978; Meyers 1966; Meyers & Scott 1967; Sgueros et al. 1973), and about 8 using agar plate cultures (Barghoorn & Linder 1944,; Johnson et al. 1959).

Chesters and Bull (1963) tested 6 lignicolous marine fungi for laminarase, five of which produced a low amount of the enzyme. Tubaki (1969) tested three lignicolous marine fungi for growth on laminarin, carrageenan, and Na-alginate. All of them produced "luxuriant" growth on laminarin, "moderate" to "good" growth on carrageenan (which form of carrageenan not stated) and "scanty" to "moderate" growth on Na-alginate.

*C.B.R.I. Contribution No. 1418

The ability of yeasts and filamentous terrestrial fungi to degrade petroleum under saline conditions is well known (Ahearn & Myers 1976; Ahearn & Crow 1980; Cerniglia & Perry 1973). The authors are not aware of any reports with respect to the ability of marine filamentous fungi to degrade petroleum or hydrocarbons. Based on circumstantial evidence, Kirk (1983) suggested that marine fungi may play a role in the degradation of hydrocarbons.

Very few reports exist concerning the sterols and fatty acids of higher marine fungi (Kirk & Catalfomo 1970; Kirk et al. 1974), although much data exist with respect to terrestrial fungi (Weete 1980).

The purpose of this study was to measure the growth of four higher marine fungi on a variety of carbon sources and to determine their sterols and fatty acids.

Materials and Methods

Growth studies

Cultures of *Leptosphaeria oraemaris* Linder, *Sphaerulina oraemaris* Linder, and *Monodictys pelagica* (Johnson) E.B.G. Jones were obtained from driftwood by placing ascospores or conidia from driftwood on seawater agar (Johnson & Sparrow 1961) containing 0.5 g/L penicillin G and streptomycin sulphate. *Dendryphiella salina* (Sutherland) Pugh et Nicot, was similarly isolated from an oil-contaminated weir pole. Fungi were isolated from wood collected on the New Brunswick coast of the Bay of Fundy as described in Miller and Whitney (1981a).

The growth of *L. oraemaris*, *S. oraemaris*, and *M. pelagica* on various carbon compounds from seaweeds (either from commercial sources or appropriate substitutes) was measured using gravimetric methods (Sguros et al. 1962). The fungi were tested for growth on the carbon sources in artificial seawater (ASW) (NaNO_3 , 0.4 g/L; K_2HPO_4 , 0.06 g/L) at 10 and 20°C (Churchland & McLaren 1976) adjusted to 28‰.

Cellobiose, dextrose, fructose, galactose, maltose, mannitol, mannose, sucrose and trehalose were added as 1 mL volumes of filter-sterilized ASW in 125 ml Erlenmeyer flasks to a concentration of 1.0 g/L. Agar (Difco, special purified), iota carrageenan, kappa carrageenan, lambda carrageenan, alginic acid, sodium alginate, ammonium-calcium alginate (Sigma Chemical Co.), gelatin (Difco)¹, starch (potato)², and Tween 20³ were mixed each in a separate flask into ASW at a concentration of 0.5 g/L. Then 24 mL were dispensed into flasks and autoclaved. All flasks were stoppered with non-absorbent cotton wool.

Inoculum was prepared as described by Sguros et al. (1962). Inoculum suspensions were adjusted to deliver 2.0 mg dry weight in a 1 mL volume of ASW. All flasks were inoculated with 1.0 mL of inoculum for a final volume of 25 mL per flask.

Three replications of each treatment plus controls (carbon-free solutions) were done. With careful inoculum preparation, accurate dispensing of all solutions and the use of identical 125 mL flasks (Parberry 1971), standard deviations were about 1% of the mean. Flasks at both temperatures were incubated for two weeks.

At the end of the incubation period, cultures grown on the algal polysaccharides, gelatin, and Tween 20 were brought just to boiling (2 min) to reduce viscosity prior to filtration through pre-weighed HA 0.45 µm Millipore filters. Filters and filtered material were washed with warm distilled water. All filters were dried at 100°C and weighed.

The fungi above and *Dendryphiella salina*⁴ were grown on a series of hydrocarbons in 25 mL sterilized ASW (28‰) in 125 mL flasks each containing one of

¹ a protein source.

² Percival (1968) suggests that potato starch is similar to Floridean starch.

³ Tween 20 is a convenient lipid source.

⁴ Data on the growth of an isolate of *D. salina* on the other carbon compounds are given in Miller and Whitney (1981b).

n-undecane, *n*-dodecane, *n*-tetradecane, *n*-hexadecane, *n*-octadecane, or *n*-eicosane, added aseptically to give 0.5 g/L. The methods were as described above. There were 3 trials with hydrocarbons and carbon-free controls. Filtered material and filters were washed with chloroform (2-3 mL) to ensure that no hydrocarbon remained on the filter. Filters were dried and weighed.

Analysis of selected metabolites

Cultures of *L. oraemaris*, *S. oraemaris*, *M. pelagica* and *D. salina* were grown in three 2.8 L Fernbach flasks containing 560 mL ASW (28‰, NaNO₃, 0.4 g/L; K₂HPO₄, 0.06 g/L; dextrose, 5 g/L) at 20°C for three months. At the end of the incubation period, cultures were filtered through HA 0.45 μm Millipore filters. The hyphae were scraped from the filters and homogenized in chloroform. The filtrate was separately extracted with chloroform.

The total crude extracts were each hydrolyzed in 10 ml of 1N HCl for 3 h at 100°C. The reaction mixture was cooled and extracted with chloroform (3x15 mL). The chloroform extract was washed with water (2x15 mL) and then evaporated under reduced pressure after drying with anhydrous sodium sulphate.

The residue was treated with a mixture of anhydrous methanol (18 mL), chloroform (1 mL), concentrated hydrochloric acid (2 mL) and heated under reflux for 2 h. After cooling to room temperature, the reaction mixture was concentrated under vacuum, diluted with water (50 mL) and extracted with chloroform (3x20 mL). The chloroform extract was washed with water (2x50 mL), dried over anhydrous sodium sulphate and evaporated under vacuum. The oil was subjected to preparative TLC on Kieselgel 60F₂₅₄, (hexane:ether:glacial acetic acid, 80:20:1). The fatty acid methyl ester fractions ($R_f = 0.5 - 0.55$) thus separated (Table I) were analysed (Tables II, III) on a fused silica capillary column, SP-2330, i.d. 0.32 mm x 30 m, film thickness 0.20 μm, using temperature programmed runs, 40°-160° at 10°/min, 160°-200° at 5°/min and isothermal at 200°C using helium gas (16 psi back pressure) until all components emerged.

All the analyses were performed using a Finnigan 4000 series GC/MS, equipped with the Finnigan 9610 GC and INCOS data system.

The sterol fractions ($R_f = 0.2 - 0.25$) were separated (Table I) and analysed as their TMS ethers on a fused silica capillary column DB-1, I.D. 0.32 mm x 30 m, film thickness 1.0 μm, using temperature programmed runs, 40°-180° at 40°/min and isothermal at 280° until all the components emerged (35 min) using helium gas (20 psi back pressure).

Results

Growth studies

The results of the tests for growth of the marine fungi on the 20 algal-derived carbon compounds are shown in Table IV. Most of the fungi grew well on the sugars and mannitol, except *M. pelagica*, which showed limited growth on mannitol. None of the fungi showed any growth on agar or on the carrageenans. Alginic acid supported some growth of all three fungi, whereas Na-alginate and NH₄ Ca alginate did not. Gelatin was used by *M. pelagica* but not by the other fungi. Starch was not used. Tween 20 was used by *L. oraemaris*, *S. oraemaris* and *M. pelagica*.

In general the marine fungi tested did not grow on *n*-hydrocarbons but *Sphaerulina oraemaris* did grow on dodecane, tetradecane and hexadecane. Although the isolate of *D. salina* used was obtained from petroleum-contaminated wood, no growth was observed on any of the hydrocarbons tested.

Table I Amount of fatty acids and sterols of marine fungi.

Name	Weight of hyphae (g)	Weight of fatty acid methyl esters (g)	Weight of sterol (g)
<i>Monodictys pelagica</i>	0.256	0.003	0.001
<i>Sphaerulina oraemaris</i>	0.403	0.005	0.002
<i>Leptosphaeria oraemaris</i>	0.782	0.008	0.003
<i>Dendryphiella salina</i>	1.316	0.013	0.007

Table II Fatty acids of marine fungi (% composition).

Fatty Acid ¹	<i>Monodictys pelagica</i>	<i>Sphaerulina oraemaris</i>	<i>Leptosphaeria oraemaris</i>	<i>Dendryphiella salina</i>
dodecanoic	0.2	0.1	0.2	0.2
tridecanoic	-	0.07	0.1	0.1
12-methyl tridecanoic	-	-	-	0.1
tetradecanoic	3.5	3.0	2.4	8.3
12-methyl tetradecanoic	-	0.4	0.1	1.8
pentadecanoic	0.7	1.3	4.5	2.4
12-methyl pentadecanoic	-	0.1	-	-
hexadecanoic	42.4	42.2	53.5	39.8
11-hexadecenoic	5.1	7.7	-	3.2
15-Methyl hexadecenoic	0.8	0.8	6.8	1.9
octadecanoic	7.2	12.9	17.7	-
10-octadecenoic	17.8	9.0	1.6	22.3
hexadecadienoic ²	0.3	0.8	0.2	1.0
octadecadienoic ²	0.6	-	0.4	-
nonadecanoic	-	0.1	-	-
eicosanoic	1.1	0.6	0.8	1.0
$\Delta^{8,11}$ octadecadienoic	4.7	2.4	1.1	2.5
$\Delta^{11,14}$ octadecadienoic	8.0	4.4	3.1	1.3
docosanoic	-	0.5	1.1	1.3
tricosanoic	-	-	0.3	-
tetracosanoic	-	0.4	2.3	3.2
unidentified ³	6.6	12.8	3.3	8.5

¹Analysed as their methyl esters and identified tentatively on the basis of comparison with data in the mass spec. library of the Finnigan 4000 series GC/MS instrument.

²Position of the double bonds not confirmed.

³see Table III.

Analysis of selected metabolites

Ergosterol accounted for 99.9% of the sterols of *Monodictys pelagica*, *Sphaerulina oraemaris* and *Leptosphaeria oraemaris*. However, in the case of *Dendryphiella salina*, ergosterol accounted for only 70.7% of the sterols. Two isomers of ergosterol, not yet identified, accounted for most of the remainder (5.2% and 22.4%). Cholesterol and cholestanol were not found.

The fatty acid methyl esters of the various fungi are listed in Table II, with the relative retention times (to C₁₆) of unidentified esters listed in Table III. The fatty

acids of these marine fungi were generally similar. However, the relative percentages of tetradecanoic, 12-methyltetradecanoic, 10-octadecenoic, octadecadienoic and tetracosanoic acids of *D. salina* were distinct from the other three fungi.

Discussion

The growth of the marine fungi on the various sugars tested revealed patterns similar to those reported by Henningson (1978), Johnson et al. (1959) and Sguros et al. (1973). A difference was the relative growth of the fungi on cellobiose relative to glucose. Henningson (1978) and Johnson et al. (1959) report more equal (but variable) values for the use of the two sugars by marine fungi. Meyers and Scott (1967) reported that *Corollospora maritima* Werdermann grew on mannitol as did *L. oraemaris* and *S. oraemaris* in this study, whereas *M. pelagica* did not. Henningson (1978) and Meyers and Scott (1967) demonstrated that variability can exist with respect to the use of carbon compounds between strains of the same marine fungus, thus some of these responses may be variable.

Pisano et al. (1964) showed that several marine fungi can grow on gelatin. In the present study, only *M. pelagica* grew on gelatin. None of the isolates tested grew on potato starch. By contrast Meyers (1966), Meyers and Scott (1967) and Johnson et al. (1959) report the growth of several higher marine fungi on "starch" undefined with respect to source.

Generally, there was no growth of the marine fungi on the algal polysaccharides, which supports the observations of Chesters and Bull (1963), but is partly in conflict with the observations of Tubaki (1969). However, Tubaki's methods involved the growth of the marine fungi on agar media made up with laminarin, carrageenan or Na-alginate. This is an inadequate method for this purpose as growth may have resulted from carbon compounds in the inoculum or impure agar.

The fungi were able to grow on alginic acid but not on alginates. This demonstrates the importance both of testing the growth of fungi on the pure constituent polysaccharides as opposed to crude commercial preparations and also of using a number of salts of alginic acid to allow for possible cation toxicity (Hughes 1975).

The tests for growth of the marine fungi on hydrocarbons showed that generally they were unable to grow on these compounds. To the authors' knowledge there are no comparable published results. Marine fungi were less common in areas with oil pollution in the region surveyed by Miller and Whitney (1981a, cf. Kirk, 1983). We did not test whether these marine fungi are able to co-metabolize hydrocar-

Table III Unidentified fatty acid methyl esters.

<i>M. pelagica</i>		<i>S. oraemaris</i>		<i>L. oraemaris</i>		<i>D. salina</i>	
RRT ¹	%	RRT	%	RRT	%	RRT	%
1.13	0.3	0.76	0.4	1.60	0.4	0.63	0.1
1.29	0.2	0.85	0.1	1.90	0.3	0.75	0.4
1.34	0.6	1.14	0.3	1.94	0.5	0.86	0.6
1.52	0.5	1.34	0.1	2.15	0.1	1.26	5.9
1.71	0.8	1.66	1.4	2.89	2.0	1.78	0.2
1.78	0.3	1.89	0.4			1.82	0.1
1.84	1.2	2.57	7.3			1.85	0.6
2.05	0.1	2.89	2.8			2.90	0.6
2.11	0.5						
2.90	2.1						

¹RRT = Relative Retention Time with respect to hexadecanoic acid methyl ester.

Table IV Growth of lignicolous fungi on various carbon sources in ASW at 10 and 20 C.

Compound	<i>L. oraeumaris</i>	<i>S. oraeumaris</i>	<i>M. pelagica</i>	<i>D. salina</i> ¹
cellobiose	10 ⁰²	5.4 ¹	10.3	5.7
	20 ⁰	7.1	10.9	9.7
dextrose	10 ⁰	7.7	18.7	18.7
	20 ⁰	14.4	35.6	36.2
fructose	10 ⁰	7.8	10.6	10.6
	20 ⁰	13.5	17.4	9.9
galactose	10 ⁰	6.1	11.9	8.7
	20 ⁰	12.7	21.7	21.8
mannitol	10 ⁰	4.4	12.6	4
	20 ⁰	11.4	25.6	-
maltose	10 ⁰	8.2	7.9	11.6
	20 ⁰	12.2	14.9	24.0
mannose	10 ⁰	4.4	5.9	6.1
	20 ⁰	11.2	12.4	6.8
sucrose	10 ⁰	4.0	3.6	4.3
	20 ⁰	7.1	6.6	5.2
trehalose	10 ⁰	9.1	8.0	5.4
	20 ⁰	13.1	10.0	9.3
xylose	10 ⁰	4.7	8.7	11.9
	20 ⁰	7.5	17.1	15.3
agar	10 ⁰	-	-	-
	20 ⁰	-	-	-
i carrageenan	10 ⁰	-	-	-
	20 ⁰	-	-	-
L carrageenan	10 ⁰	-	-	-
	20 ⁰	-	-	-

Compound	10 ⁰	20 ⁰	<i>L. oraeumaris</i>	<i>S. oraeumaris</i>	<i>M. pelagica</i>	<i>D. salina</i>
K carrageenan	10 ⁰	20 ⁰	-	-	-	-
alginate	10 ⁰	20 ⁰	3.7	4.1	5.2	5.2
	10 ⁰	20 ⁰	6.5	5.3	5.4	5.4
Na-alginate	10 ⁰	20 ⁰	-	-	-	-
	10 ⁰	20 ⁰	-	-	-	-
Ca-alginate	10 ⁰	20 ⁰	-	-	-	-
	10 ⁰	20 ⁰	-	-	-	-
gelatin	10 ⁰	20 ⁰	-	-	4.9	4.9
	10 ⁰	20 ⁰	-	-	3.6	3.6
starch	10 ⁰	20 ⁰	-	-	-	-
	10 ⁰	20 ⁰	-	-	-	-
Tween 20	10 ⁰	20 ⁰	3.6	5.4	4.6	4.6
	10 ⁰	20 ⁰	6.5	7.3	12.3	12.3
n-undecane	10 ⁰	20 ⁰	-	-	-	-
	10 ⁰	20 ⁰	-	-	-	-
n-dodecane	10 ⁰	20 ⁰	-	-	-	-
	10 ⁰	20 ⁰	-	5.2	-	-
n-tetradecane	10 ⁰	20 ⁰	-	4.8	-	-
	10 ⁰	20 ⁰	-	4.9	-	-
n-hexadecane	10 ⁰	20 ⁰	-	4.5	-	-
	10 ⁰	20 ⁰	-	4.2	-	-
n-octadecane	10 ⁰	20 ⁰	-	-	-	-
	10 ⁰	20 ⁰	-	-	-	-
n-eicosane	10 ⁰	20 ⁰	-	-	-	-
	10 ⁰	20 ⁰	-	-	-	-

1. See note in text.

2. Flasks incubated for two weeks.

3. mg dry weight hyphae per flask, n = 3, standard deviation ca. 1% of mean value.

4. - equals weight less than 3 mg.

bons with glucose as *Zalerion maritimum* (Linder) Anastasiou has been shown to do with pesticides (Sgueros & Quevedo, 1978).

As expected, the predominant sterol of the marine fungi tested was ergosterol, which is the dominant sterol of Ascomycetes and Fungi Imperfecti (Weete 1980). Kirk et al. (1974) reported that *Leptosphaeria oraemaris* R-13 did not contain ergosterol.

To the authors' knowledge, there are no reports of the fatty acids of marine filamentous fungi, with the exception of a qualitative estimate of some fatty acids of *Corollospora maritima* (Kirk et al. 1974). The fatty acids of terrestrial Ascomycetes and Fungi Imperfecti are discussed by Weete (1980). In several respects, the fatty acids of terrestrial filamentous fungi differ from those of the four marine fungi reported here. The marine fungi contain more tetradecanoic, hexadecanoic, hexadecenoic and eicosanoic and less octadecenoic and octadecadienoic fatty acids (cf. Weete 1980).

The difference in the sterol and fatty acid composition of *D. salina* compared to the other marine fungi may have some ecophysiological significance. This fungus primarily occurred in intertidal regions in New Brunswick (isolate used obtained at Station 5, Miller & Whitney 1981a) and generally has a lower salinity tolerance than some other higher marine fungi (Jones & Bryne 1976).

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SPAWNING OF THE AMERICAN SHAD (*ALOSA SAPIDISSIMA*) IN THE ANNAPOLIS RIVER, NOVA SCOTIA

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Plankton drift-net collections of American shad (*Alosa sapidissima*) eggs indicated that spawning in the Annapolis River, N.S., occurred from 7 May to 19 June in 1976. Spawning was related to water temperatures on the spawning grounds. Peak spawning (80% of eggs collected) occurred from 12-19 May when water temperatures were 14-15°C. Few eggs were netted at < 13°C (3%) or at > 18°C (1%). Spawning occurred throughout the day but most occurred during the evening and at night. Shad spawned in fresh water with the majority (98% of all egg collections) of spawning occurring > 22 km upstream from the tip of the salt wedge in this stratified estuary.

Les récoltes d'oeufs de l'alose américaine (*Alosa sapidissima*) effectuées à l'aide d'un filet planctonique dérivant indiquent que cette espèce s'est reproduite, dans la rivière Annapolis (Nouvelle-Ecosse) entre le 7 mai et le 10 juin 1976. La reproduction était reliée aux températures de l'eau des frayères. Les maxima de reproduction (80% des oeufs récoltés) se sont produits entre le 12 et le 13 mai lorsque la température était inférieure à 13°C (3%) ou supérieure à 18°C (1%). Le frai se produit pendant toute la journée mais la plus grande partie de celui-ci se produit pendant la soirée et durant la nuit. L'alose se reproduit en eau douce: la majorité du frai se produit à une distance supérieure à 22 km en amont de l'extrémité du front salin de cet estuaire stratifié.

Introduction

The American shad (*Alosa sapidissima*), largest member of the herring family (Clupeidae) is native to the east coast of North America from Newfoundland to Florida. Introduced to the Pacific coast in 1871, it occurs from southern California to Cook Inlet, Alaska, and along the Kamchatka Peninsula on the Asiatic side (Scott & Crossman 1973). Shad are anadromous, the precise time of their upstream spawning migration depending on the water temperature (Walburg 1960; Leggett & Whitney 1972; Scott & Crossman 1973; Carscadden & Leggett 1975; Leggett & Carscadden 1978). In Canadian waters spawning occurs in May, June, or even as late as July (Scott & Crossman 1973; Gabriel et al. 1976). The spawning of this species in the United States' rivers has been well documented (Massmann 1952; Walburg 1960; Watson 1968; Chittenden 1976; March 1976), but apart from a detailed account of the shad population in the Shubenacadie River, N.S., by Leim (1924), data on other Canadian shad populations are limited. The Annapolis River shad population is the largest unexploited population in Atlantic Canada (Dadswell et al. 1983a, b) and is a population of great interest because of the recent construction of the Tidal Power Station at Annapolis Royal (Daborn et al. 1983). The objective of the present study was to define the spawning period and area of the native shad population in the Annapolis River during 1976.

Methods

Drift net and egg collections were used to determine the spawning area and period. Collection techniques are described in Williams et al. (1984). Nets used were set from 7 May to 30 June at four stations located at regular distances along the Annapolis River, beginning just downstream from the upper limit of the salt

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Drift net American shad (*Alosa sapidissima*) egg collections made in the Annapolis River, Nova Scotia, during the 1976 shad spawning season

Date	Total no. of eggs collected	% of total	Drift net station no.	Time of day, h	Mean water ^a temperature, °C	No. of eggs collected	No. of eggs per hour
May 7-8	2174	2.7	2 4	1100-1100 1635-1635	11.0 11.0	237 1937	9.9 80.7
8-9	2723	3.3	4	1700-1700	13.0	2723	113.5
12	3948	4.9	2 3 4	0920-1750 0955-1840 1155-2025	14.3 14.1 14.0	133 41 3774	15.7 4.7 444.0
12-13	29036	35.7	2 4	1810-0230 2045-0400	14.3 14.0	22 29014	2.6 4001.9
14	14268	17.6	1 (20) ^b 2 (29) 3 (35) 4 (42)	0030-1230 0120-1350 0222-1515 0330-1800	14.8 14.5 14.7 14.6	198 ^c 15 355 13700	16.5 1.2 27.6 944.8
18-19	21724	26.7	2 3 4	2040-1100 1900-0800 1940-0940	14.6 14.5 14.8	147 ^c 374 21203	10.0 28.8 1514.5
21-22	1611	2.0	2 3 4	0958-0010 0640-1935 0730-2045	12.8 12.8 12.8	7 ^c 29 1575	0.5 2.3 117.5
25-26	596	0.7	2 4	2140-0945 1950-0810	10.5 10.5	2 ^c 594	0.2 48.2
30	2767	3.4	2 3 4	0920-2035 0810-1940 0710-1820	16.8 16.6 16.2	5 ^c 4 2758	0.4 0.4 247.0
June 3-4	1934	2.4	4	2205-1050	17.8	1934	151.7
7	12	0.0	4	0805-1905	18.9	12	1.1
8-9	447	0.6	4	1830-0735	20.3	447	34.2
11	6	0.0	2 4	0915-2035 1220-2400	22.1 22.7	1 ^c 5	0.1 0.4
13-14	1	0.0	4	0045-1247	16.7	1	0.2
16	5	0.0	4	1313-2355	22.2	5	0.5
18-19	2	0.0	4	1950-0922	22.4	2	0.2
Total	81254						

^a(temperature at beginning of set + temperature at end of set)/2.^bDistance above the Annapolis River Causeway in kilometers.^c1.0 m diameter plankton net used; number of eggs collected adjusted to 0.6 diameter net.

wedge in early May, 20 km above the Annapolis River Causeway, to about 42 km above the causeway at Lawrencetown. Station 1 (km 20) was used from 12 May to 30 May, station 3 (km 35) from 12 May to 30 June, and stations 2 (km 29) and 4 (km 42) from 12 May to 30 June. Treatment and identification of samples follows that described by Williams et al. (1984).

Results and Discussion

Shad definitely spawned in the Annapolis River from 7 May to 19 June in 1976. A total of 81,254 eggs was collected during this period (Table I). Spawning was already in progress when sampling commenced on 7 May; however, since relatively few eggs were netted initially and optimum spawning temperatures were not reached until later, spawning may have just started. Virtually all egg collections (99.4%) were made between 7 May and 4 June with the period from 12-19 May being most productive (80.0%). Leim (1924) also found that shad in the Shubenacadie River, Nova Scotia, spawned in May and June, but peak egg collections were made in late May or early June during the four years of his study. Similarly, Gabriel et al. (1976) noted that spawning occurs from mid-May in the St. John River, New Brunswick.

Shad spawning in the Annapolis River was related to water temperatures. Increasing water temperatures to $>13^{\circ}\text{C}$ approximately coincided with egg collections while rapid temperature drops to $<13^{\circ}\text{C}$ resulted in temporary cessation of spawning (Fig 1). Although shad eggs were collected in water that ranged from $10.5\text{-}22.7^{\circ}\text{C}$, most eggs (96%) were netted at temperatures between 13 and 18°C with peak spawning (12-19 May) occurring when water temperatures were $14\text{-}15^{\circ}\text{C}$. Few eggs were collected when temperatures were $<13^{\circ}\text{C}$ (3%) or when temperatures exceeded 18°C (1%). Similarly, Leim (1924) found that shad in the Shubenacadie River spawned in the spring after water temperatures had reached 12°C and that a depression to $<12^{\circ}\text{C}$ caused almost complete cessation of spawning. Peak spawning occurred at temperatures between 14 and 16°C over the four years of his study. In Virginia rivers shad eggs are also not collected in abundance until water temperatures reach 12°C (Massmann 1952).

Egg collection times indicate that although shad in the Annapolis River may spawn during the day most spawning probably occurred during the evening and at night (Table I). This is in general agreement with other authors (e.g. Leim 1924; Massmann 1952; Mansueti & Kolb 1953; Mansueti & Hardy 1967; Chittenden 1976; Marcy 1976).

Shad spawned in the freshwater ($< 0.1\text{‰}$ salinity) section of the Annapolis River. All egg collections were made in fresh water except one: on 14 May 198 eggs were captured at station 1 (km 20) when the mean salinity was 0.5‰ . However, since these eggs were near hatching they had undoubtedly originated in the freshwater section upstream. The main spawning area was located upstream from station 4 (km 42) since that station accounted for 98.1% of all eggs collected (Table I). During peak spawning the tip of the salt wedge fluctuated near station 1 (km 20), about 22 km downstream from the main spawning area (Williams 1978; Daborn et al. 1979). By the end of the spawning season in June the salt wedge was near station 2 (km 29).

Evidently most shad spawning occurred in the more slowly flowing section of the Annapolis River. The river upstream from station 4 (km 42) is shallow, usually < 1.5 m, and widening, with a bottom composed of sand and mud interspersed with granite and basalt rocks and boulders. Few eggs (2%) were collected in the area downstream from station 4, a region characterized by deeper water, a faster current, and a more sandy bottom. Similar shad spawning areas have been described

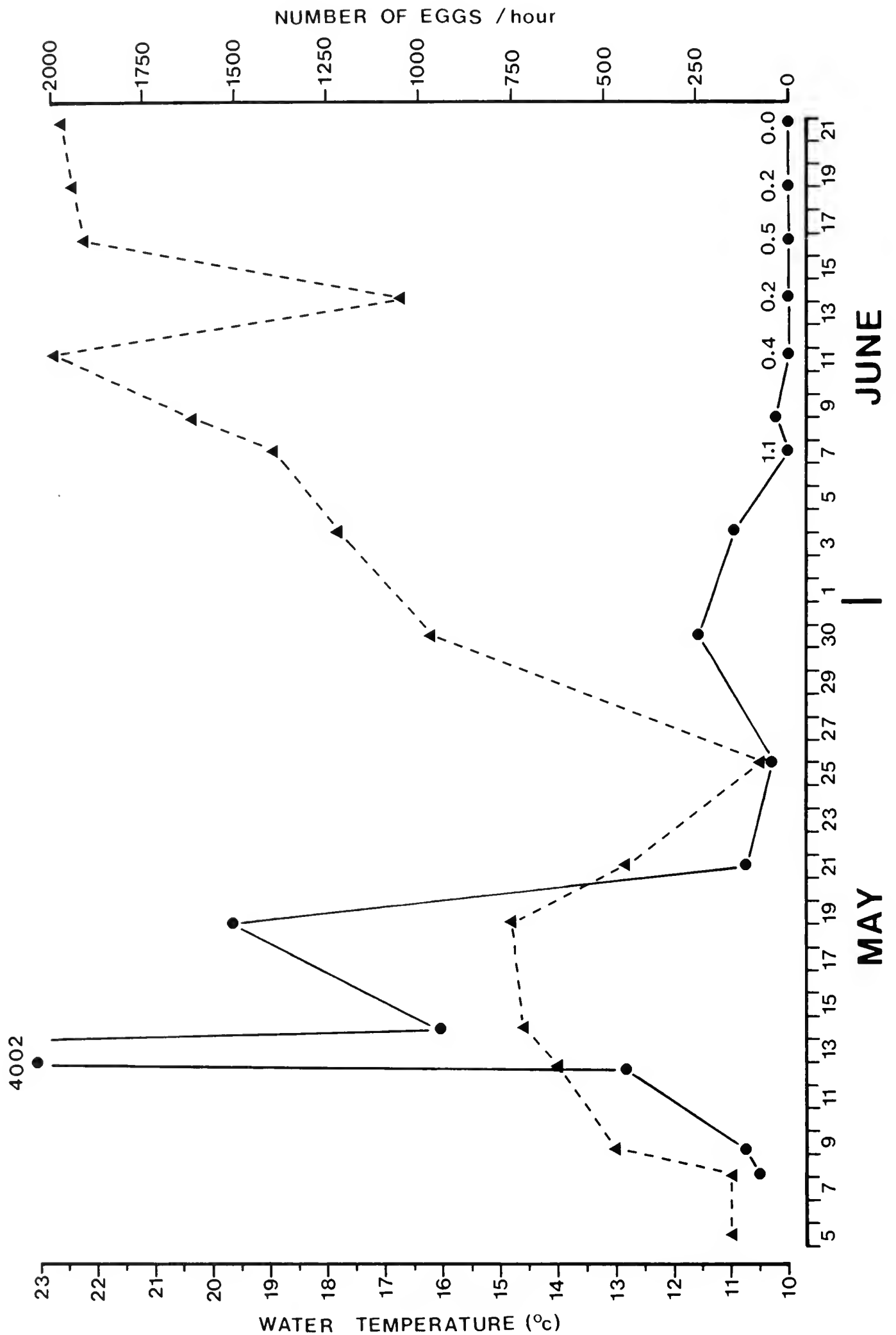


Fig 1. Relationship between water temperature and the number of shad eggs collected per hour at Annapolis River drift net station 4 (km 42) in 1976. ▲, mean water temperature (see Table I); ●, number of eggs collected per hour.

elsewhere although considerable variation exists (e.g. Leim 1924; Massmann 1952; Mansueti & Kolb 1953; Carl et al. 1959; Walburg 1960; Mansueti & Hardy 1967).

Shad larvae were relatively abundant in the Annapolis River from Station 2 (km 29) upstream after 12 May (Williams 1978).

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SPAWNING OF THE STRIPED BASS (*MORONE SAXATILIS*) IN THE ANNAPOLIS RIVER, NOVA SCOTIA

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Plankton net collections of striped bass (*Morone saxatilis*) eggs in the Annapolis River, N.S., indicated that spawning occurred in early June 1983, in freshwater (< 0.1‰ salinity) along a 19 km section of river. Spawning was closely related to water temperatures on the spawning grounds. Most spawning occurred at temperatures $\geq 18^{\circ}\text{C}$ while rapid temperature drops to 15-16°C resulted in temporary cessation of spawning. Peak spawning was from 7-10 June (65% of all egg collections) when water temperatures were 19.0-24.4 C. Spawning behaviour is described.

Des récoltes d'oeufs de la perche commune (*Morone saxatilis*) ont été effectuées dans la rivière Annapolis, N.S., à l'aide d'un filet planctonique. Ces collections indiquent que le frai s'est produit au début du mois de juin 1983, en eau douce (salinité < 0.1‰) le long d'une section de 19 km de cette rivière. Le frai était fortement relié à la température de l'eau des frayères. La plus grande partie du frai eut lieu à des températures $\geq 18^{\circ}\text{C}$; des baisses subites de température à 15-16°C résultèrent en un arrêt temporaire du frai. Le maximum de reproduction fut enregistré du 7 au 10 juin (65% de tous les oeufs récoltés) lorsque les températures de l'eau étaient de 19.0°C-24.4°C. Le comportement pendant le frai est aussi décrit.

Introduction

The striped bass, *Morone saxatilis* (Walbaum), is an anadromous coastal species distributed along the Atlantic coast of North America from the St. Lawrence River (49°N) to the St. Johns River in northern Florida (29°N) and along the Gulf of Mexico in fresh and brackish tributaries of western Florida, Alabama, Mississippi, and Louisiana (Scott & Crossman 1973). Introduced to the Pacific coast in 1879 and 1882 it now ranges from Barkley Sound at 49°N on Vancouver Island (Forrester et al. 1972) to just south of the Mexican border at 32°N (Radovich 1961).

In the United States, the striped bass is an important commercial and sport fish that has been extensively studied on both coasts (see Rogers & Westin 1975; Horseman & Kernehan 1976). Canadian populations, however, have not been studied as intensively and scientific literature is limited. This is probably a result of its restricted distribution, and fluctuating abundance.

The present study was initiated to provide basic information on striped bass inhabiting the Annapolis River, Nova Scotia. The population supports a valuable and popular sport fishery, although in recent years the minimum age of bass caught by angling has been increasing, indicating a failure of recruitment (Jessop & Doubleday 1976; Jessop 1980). This paper presents information on spawning time and location in 1976, and observations on spawning behaviour.

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Study Area

The Annapolis River flows for about 142 km through the Annapolis Valley in southwestern Nova Scotia before discharging into the Annapolis Basin (and ultimately the Bay of Fundy) through the Annapolis River Tidal Dam at Annapolis Royal. This dam (constructed in 1960) converted upstream conditions from a vertically homogenous estuary with 10-m tides into a highly stratified salt wedge estuary with 2-m tides; outflowing freshwater (< 2 ‰ salinity) overlies salt water of 16-24 ‰ and a very narrow halocline and thermocline exists (Daborn et al. 1979b). The upper edge of the salt wedge oscillates between km20 and km30 above the dam as a result of tidal flow, manipulation of headpond and river levels, and varying river discharge (Daborn et al. 1979b).

Methods

Striped bass eggs are semibuoyant and float downstream from freshwater spawning areas (Raney 1952; Mansueti 1958; Albrecht 1964; Talbot 1966; Scott & Crossman 1973). Therefore, egg and larvae collections by drift and tow nets were used to determine the spawning area and period. Samples were collected with nylon monofilament plankton nets having apertures of 1.0 m and 0.6 m diameter and pore sizes of 0.5 and 1.0 mm, respectively. The smaller nets were used at stations where current flow was too strong to hold or pull a 1.0-m diameter net.

Drift-net collections were made from 7 May to 7 July at 8 stations located at regular distances along the Annapolis River, beginning just downstream from the limit of saline waters in early May (km20 above Annapolis River Tidal Dam, see Daborn et al. 1979b) to approximately 26 km upstream. Nets were set in mid-channel, just below the surface, for an average of 12-13 hours at about 3-day intervals at any one location. Tow net collections were made from 14 May to 27 June at about 3-day intervals over the same area and alternated with drift net collection periods. Each tow was of 10 min duration and was made in mid-channel with the boat moving upstream. Both drift and tow-net collection periods were staggered in order to cover the diel cycle.

Egg and larval collections were refrigerated when returned to the laboratory, sorted within 1-3 hours and preserved in 8% neutral formalin. Striped bass eggs and larvae were identified and distinguished from those of other fishes using descriptions and diagrams in Pearson (1938), Mansueti (1958, 1964), Mansueti and Hardy (1967), and unpublished data from J. Brown and W. Hasler (addresses in Acknowledgements). Bass eggs are distinguished from those of the American shad (*Alosa sapidissima*) and the alewife (*Alosa pseudoharengus*) by the presence of an oil globule in striped bass eggs and its absence in the latter two species. White perch (*Morone americana*) eggs possess an oil globule also, but are distinctly smaller than striped bass eggs and possess an attachment disc. In addition, bass eggs collected when spawning was observed were directly compared to shad eggs; shad eggs collected on 8 May were kept in an aquarium, hatched on 11 May, the larvae living until 14 May.

A binocular microscope fitted with an ocular micrometer was used to examine the eggs and measure diameters. Developmental stages of eggs were determined by reference to diagrams and descriptions provided by Pearson (1938), Mansueti (1958), and J. Brown and W. Hassler (pers. comm.). Staging was facilitated by staining eggs with alizarin red, which was selectively taken up by the yolk mass, turning it rusty red while leaving the protoplasm white. Eggs were aged by reference to a nomograph (provided by J. Brown & W. Hassler) relating developmental stage to incubation temperature in order to estimate the age in hours.

The origin of each egg was then calculated by multiplying its estimated age by the mean river velocity upstream from the collection site, determined from current velocity readings taken on the same day. For example, a 2-hour-old egg collected below a stretch of river with a 0.5 m/sec mean current velocity would have been spawned about 3.6 km upstream from the collection site (7200 sec x 0.5 m/sec).

Surface-to-bottom water temperatures and salinities were recorded in the field with a YSI model S-C-T meter prior to each plankton net tow and prior to and after each drift net collection. A Peabody-Ryan D-30 thermograph anchored near the shore in about 1 m of water continuously monitored water temperatures on the spawning grounds during the striped bass spawning period.

Results

Spawning Period

The first striped bass eggs were collected on 1 June and the last on 19 June. A total of 3463 eggs and 3 larvae was netted during this interval (Tables I & II). Drift nets collected 2629 eggs and 2 larvae between June 8 and 19 (Table I) while two nets caught 834 eggs and 1 larva between 1 and 13 June (Table II).

Bass spawning was closely related to water temperatures on the spawning grounds (Fig 1.). Increasing temperatures corresponded with collection of eggs while sudden temperature drops coincided with a temporary cessation of spawning. Water temperatures during the spawning period ranged from 15.0-24.4°C. Prior to the initial egg collection (at 18.4°C) on 1 June a rapid rise in water temperature occurred: temperatures increased from 10.5°C, on 26 May, to 19.2°C, on 31 May. A temperature drop to 16.0°C on 2 June (a result of decreasing air temperature) coincided with a temporary cessation of spawning after 1 June, with spawning resuming on 7 June as water temperatures increased. Most eggs and larvae (64.6%) were collected from 7 to 10 June when water temperatures ranged from 19.0-24.4°C (average daily temperature = 20.6°C). A sharp temperature drop after 10 June coincided with a spawning decline and only 2 eggs and 1 larva were netted from 11-15 June. Spawning resumed on June 16 when temperatures increased, with the final egg collection being made on 19 June.

Spawning Observations

Striped bass spawning was observed in fresh water (specific conductance = 55 μ mhos/cm, water temperature = 22. °C) approximately 7 km upstream from saline water on 9 June between 2130 and 2215 hours. The river in this region is about 30 m wide, of uniform depth (1.5-2.0 m) with a bottom composed mainly of sand interspersed between basalt and granite rocks and boulders.

Spawning behaviour was similar to that described in Woodhull (1947), Raney (1952), and Miller and McKechnie (1968). Groups of bass were observed spawning in all sections of the river. Each group consisted of one large female and more than 5 males, each considerably smaller than the female. The female quivered and rolled at the surface, vigorously splashing water with her tail while the males remained close, periodically striking her side with their snouts. This action occurred for several minutes, ceased for a few minutes during which time the fish milled around in the general area, and then resumed. A 0.6-m diameter plankton net held stationary just below the surface in the vicinity of spawning bass collected 5075 recently fertilized eggs in 10 min. Although anglers were fishing in the area no bass were caught by them, supporting the contention that striped bass do not feed during spawning (Trent & Hassler 1966), although they may feed within a few hours before and after.

Table I Striped bass egg and larvae collections made with drift nets, 1-19 June 1976. Numbers in parentheses indicate river distances above the Annapolis River Tidal Dam in km. (see Fig 2).

Date (June)	Drift net station no.	Time of day (hrs)	No. eggs collected	No. larvae collected	No. per hour	% of total
8- 9	2(25)	2140-1050	0	2	0.2	0.1
	3(29)	2220-1030	1419	0	116.6	53.9
13-14	3	2220-1050	1	0	0.1	0.0
16	5(35)	1129-2220	842	0	77.6	32.0
	6(38)	1229-2315	50	0	4.6	1.9
18-19	7(42)	1950-0922	317	0	23.4	12.1
Totals			2629	2	36.1	100.0

Table II Striped bass egg and larvae collections made with towed nets, 1-19 June 1976. Tow net station locations are given in Williams (1978). Numbers in parentheses indicate river distances above the Annapolis River Tidal Dam in km.

Date (June)	Tow net station no.	Time of day (hrs)	No. eggs collected	No. larvae collected	No. per minute	% of total
1	6(28)	0911-0921	9	0	0.9	1.1
	7(29)	0940-0950	6	0	0.6	0.7
7- 8	8(30)	2243-2253	410	0	41.0	49.1
	9(32)	2319-2329	36	0	3.6	4.3
	10(33)	0008-0013	5	0	1.0	0.6
	11(35)	0057-0107	4	0	0.4	0.5
10	5(25)	0815-0825	74	0	7.4	8.9
	6(28)	0920	145	0	14.5	17.4
	7(29)	1005-1015	135	0	13.5	16.2
	9(32)	1132-1142	1	0	0.1	0.1
	12(36)	1350-1400	8	0	0.8	1.0
12-13	5(25)	2010-2020	0	1	0.1	0.1
	10(33)	0000-0010	1	0	0.1	0.1
Totals			834	1	6.7	100.1

Table III Developmental stage, size, age, and estimated origin of striped bass eggs collected on 9 June 1976 while spawning was observed (see text).

Developmental stage	Mean dia. (mm)	Age (hours)	% of total ^a	Estimated origin ^b
pre-cleavage	2.59	1.1	29.8	0.0-2.2
2-16 cells	3.53	1.1-2.0	46.2	2.2-4.4
17-32 cells	3.74	2.1-3.0	19.0	4.4-4.6
32 cells	3.75	3.1-4.3	5.0	6.6-8.8

^aTotal = 1139 eggs (22% of 5075 eggs collected)^bin km. upstream from collection site

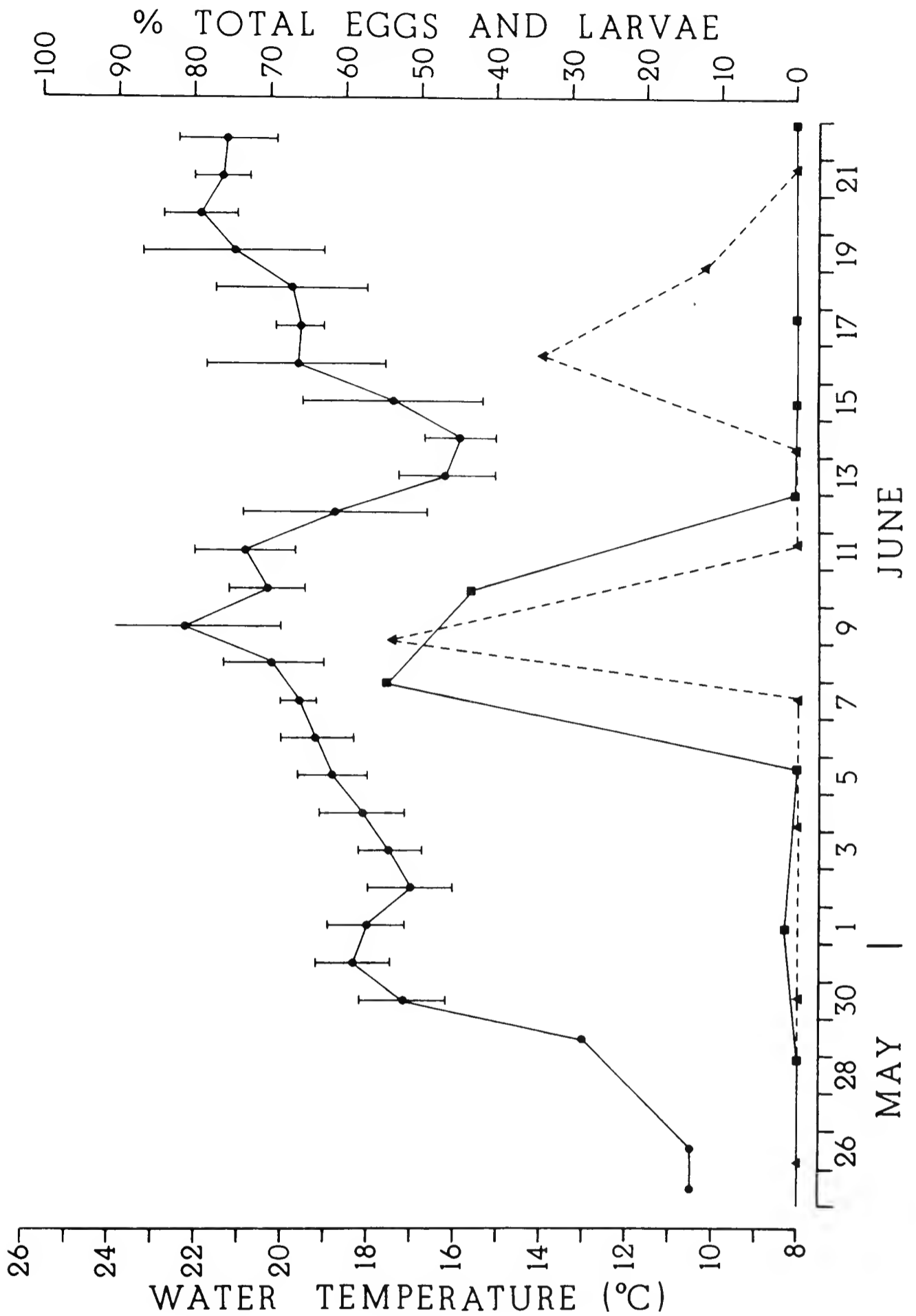


Fig 1. Relationships between water temperatures on the spawning grounds and the % of the total striped bass eggs and larvae collected in tow nets (■) and drift nets (▲) from the Annapolis River, 1976. Vertical bars indicate daily temperature ranges around means (•). Water temperatures prior to May 30 are single readings, taken with a telethermometer.

Spawning Area

All eggs were collected within the first 15 km above the head of the salt wedge (which fluctuated between km 20 and 27 during the spawning period) and with two minor exceptions the most downstream collections were made 4-5 km upstream from saline water.

According to drift and tow-net collections of eggs and larvae, striped bass spawned only in fresh water ($< 0.1\text{‰}$ salinity) along a 19 km stretch of river. A 9 km stretch from km 29 to 38 was apparently the most productive portion of the spawning grounds (Williams 1978). An estimate of how far upstream spawning had occurred on 9 June was made using the eggs collected during the spawning observations. Five subsamples of about 225 eggs each (22% of 5075) were aged and each egg was extrapolated to its spawning origin using water velocities upstream from the collection site. Eggs ranged in age from 1.1-4.3 hours; 76% were ≤ 2.0 hours old (Table III). Spawning on 9 June occurred primarily along a 9 km section between the collection site at km 32 and km 41 with the majority (76%) occurring within the lower 4 km section from km 32 to km 36 (Fig 2.).

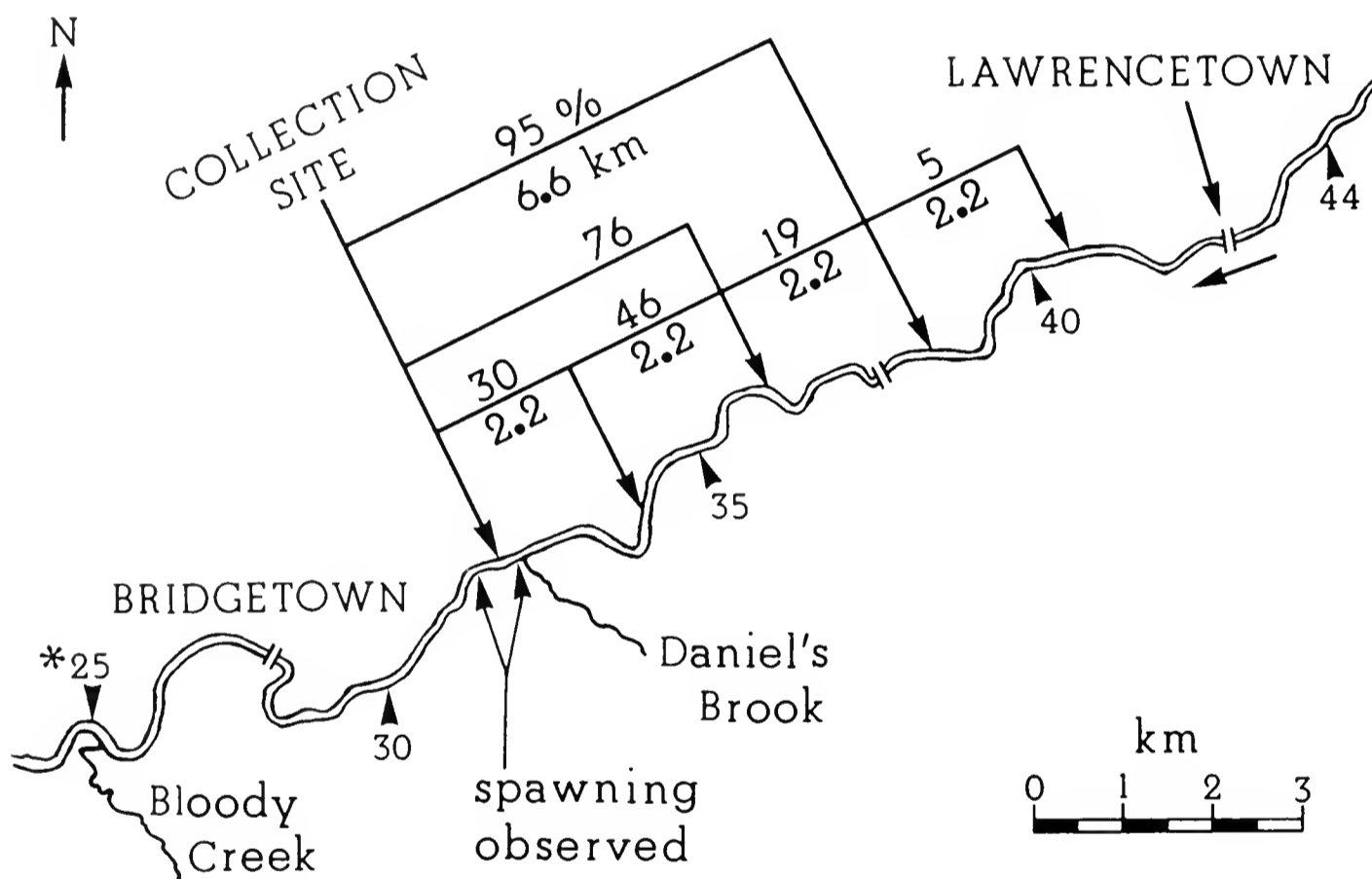


Fig 2. Map of the Annapolis River showing the estimated spawning area on 9 June 1976, determined by examination of eggs collected while spawning was observed (see text). The % eggs originating within each specific area is indicated. River distances (km) above the Annapolis River Causeway are indicated (beginning with *25).

Discussion

According to egg collections and spawning observations, striped bass spawned intermittently in the Annapolis River from 1-19 June in 1976. Striped bass in

Canadian waters usually spawn in June (Bigelow & Schroeder 1953; Scott & Crossman 1973) although Dadswell (1976) noted spawning from 13-19 May, 1975 in Belleisle Creek, a small tributary of the Saint John River, New Brunswick. He attributed this early spawning to the small size and consequent earlier warming of the creek. Most spawning in the Annapolis River occurred on relatively few days: 4 consecutive days (7-10 June) accounted for 64.6% of all egg and larvae collections (Table I). Similar restricted spawning periods have been noted elsewhere (Calhoun et al. 1950; May & Fuller 1962; Humphries 1966; Johnson 1973; Calif. Dep. Fish and Game et al. 1974).

Bass spawning in the Annapolis River was closely related to water temperatures on the spawning grounds (Fig 1). Apparently a rapid temperature increase above a minimum of approximately 18°C will initiate spawning. In 1976, temperatures rose >8°C between 26 May and 31 May, and the first eggs were collected on 1 June at 18.4°C. In American rivers other investigators have made initial collections at lower temperatures; usually 14.4-16.1°C (Calhoun et al. 1950; Scruggs 1957; McCoy 1959; May & Fuller 1962; Farley 1966).

Although water temperatures during the 1976 spawning period ranged from 15.0-24.4°C, most spawning occurred at temperatures $\geq 18^\circ\text{C}$ with peak collections being made between 19.0°C and 24.4°C. Similarly, Humphries (1966) and McCoy (1959) found peak spawning occurred at 18-22°C and 18-20°C in the Tar and Roanoke Rivers, respectively. Spawning did not occur at <15°C in the Tar River or <14°C in the Roanoke River. In contrast, spawning in the Sacramento, San Joaquin, and Hudson Rivers has occurred over much wider temperature ranges and peak collections made at lower temperatures (Farley 1966; Jensen 1969). Rapid temperature decreases (to 15-16°C) during the spawning period resulted in a temporary cessation of spawning in the Annapolis River. Apparently this is a common phenomenon (Calhoun et al. 1950; Farley 1966; Calif. Dep. Fish and Game et al 1974).

Although striped bass have been shown to spawn in the Annapolis River, recruitment into the population seems to be very low or nil. No larvae or juvenile bass were collected after the 1976 spawning season even though all areas of the river were sampled from June to August using a variety of techniques (towed plankton nets, bag seines, otter trawl) at all times of the day (Williams 1978). Renewed sampling in 1977 indicated (Williams, unpublished data) that more spawning occurred in 1977 than in 1976, although results may be biased because angling was banned on the spawning grounds in 1977. Sampling in the post-spawning period of 1977 (June-October) also produced no larval or juvenile bass (Daborn et al 1979a; Williams, unpublished data). The age-structure of angled bass in the Annapolis River has also changed radically since 1972 with ages 3-5 making up 54% of the catch in 1972, compared with 32% in 1975, 9% in 1976, and 2% in 1978 (Jessop 1980). This trend is probably primarily due to the failure to recruit young fish into the population. The reasons for this apparently poor recruitment are unknown. Earlier suggestions that it was due to high levels of DDT or PCB's (Jessop and Doubleday 1976) or to relatively low pH (6.0-7.0) during spawning (Williams 1978, Jessop 1980) appear to be unfounded (Dr. M. Wiles, Saint Mary's Univ., Halifax, pers. comm.). Nevertheless, angler catches of adult bass in the Annapolis River are still high (Jessop & Doubleday 1976; Jessop 1980), perhaps because part of the Annapolis River bass population is actually derived from others (see Jessop & Doubleday 1976), similar to that of the American shad (*Alosa sapidissima*) in the Bay of Fundy (Dr. M. Dadswell, St. Andrews Biol. Sta., New Brunswick, pers. comm.). If true, this migratory population may continue to provide a sport fishery indefinitely.

Acknowledgements

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ROCKY SHORE ZONATION AT NORTH RUSTICO AND PRIM POINT, PRINCE EDWARD ISLAND¹

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The vertical zonations of organisms on rocky shores are described for two sites. The principal study area, near North Rustico, is in the PEI National Park. The general pattern at this site was: (1) a zone of blue-green algae at the highest level in the intertidal zone; (2) a zone of *Fucus* at mean sea level; (3) a zone of leafy green algae, especially on rocks near sandy beaches; (4) a zone of *Chordaria flagelliformis* at mean lower low water. The subtidal zone was dominated by *Chondrus crispus* and vesiculate *Fucus vesiculosus*, with very little *Laminaria saccharina* except on steel surfaces of a breakwater. Details of four transects and a brief description of the horizontal distribution of algae are included. At the second study site, Prim Point on the south coast of PEI, the zonation pattern is similar except that the zone of *Chordaria* is replaced by a zone of *Chondrus* and *Fucus serratus*. The vegetation and fauna are denser at Prim Point. The results are compared to Stephenson & Stephenson's (1954a, b) study of shores of PEI and Nova Scotia.

Les zonations verticales des organismes sont décrites pour deux sites situés sur des rivages rocheux. Le site principal de l'étude est situé près de North Rustico, dans le parc national de l'Isle-du-Prince-Edouard. A ce site le patron général était: (1) une zone d'algues blue-vertes située au niveau le plus élevé de la zone intertidale; (2) une zone de *Fucus* au niveau moyen de la mer; (3) une zone d'algues vertes feuilles, située spécialement sur des roches près des plages sablonneuses; (4) une zone de *Chordaria flagelliformis*, au niveau moyen inférieure de la marée basse. La zone subtidale était dominée par *Chondrus crispus* et *Fucus vesiculosus* sans vésicules. *Laminaria saccharina* était très peu représentée dans cette zone sauf sur les surfaces d'acier des jetées. Sont aussi inclus les détails de 4 transects ainsi qu'une brève description de la distribution horizontale des algues. Prim Point, le second site de cette étude, est située sur la côte sud de l'Isle-du-Prince-Edouard. Le patron de zonation à ce site est semblable sauf que la zone de *Chordaria* est remplacée par une zone de *Chondrus* et de *Fucus serratus*. La végétation et la faune sont plus denses à Prim Point. Ces résultats sont comparés aux travaux de Stephenson et Stephenson (1954a, b) sur les rivages de l'Isle-du-Prince-Edouard et de la Nouvelle-Ecosse.

Introduction

The general features of rocky shore intertidal zonation are well known and can be fitted to a universal pattern (Lewis 1954, Stephenson & Stephenson 1972). However, the details at individual locations vary and are of local interest. The rocky shores along the north coast of Prince Edward Island were described by Stephenson & Stephenson (1954a) as among "the most barren and peculiar we have encountered on our travels". The Stephenson's brief visit has been the only work to date on the vertical distribution of intertidal organisms on rocky shores of PEI. Subtidal algal distribution in northeast PEI has recently been studied by Bird et al. (1983). The present study was undertaken for the Dept. Indian Affairs and

¹This work formed part of a BSc Honours Thesis submitted by CSL to Dalhousie University, and a report by LAH and CSL to the Dept. Indian Affairs and Northern Development, Historic Parks Branch, Ottawa (Project No. 05/1-14).

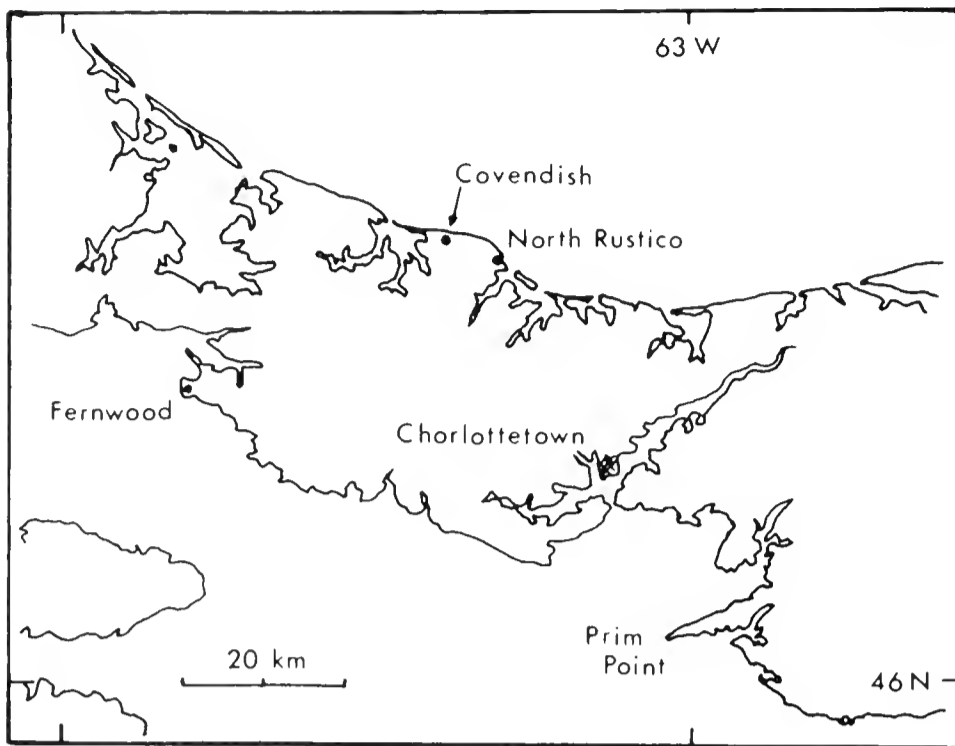


Fig 1. Map of central Prince Edward Island, showing locations of our two study sites at North Rustico and Prim Point, and those of the Stephensons.

Northern Development, National and Historic Parks Branch, to provide more detailed information on intertidal distribution of organisms in the PEI National Park, including observations throughout the year. In addition, we made a briefer comparative study at Prim Point on the south coast of PEI (Fig 1).

The study area in the National Park included the breakwater at the mouth of North Rustico Harbour and the shore for 4 km westward, as far as Doyle's Cove (Fig 2). The substratum, except for two sandy beaches, was rough, friable siltstone, underlain by harder sandstone which forms ledges in the intertidal and subtidal zones. Siltstone in the intertidal zone breaks along bedding planes to form ridges (see Fig 8). Tidal amplitude is 0.70 m (mean tide); tides are semidiurnal, except for a few days each fortnight when they become diurnal with an extended low tide. The shore at Prim Point is also siltstone, but the slope is very much less than at

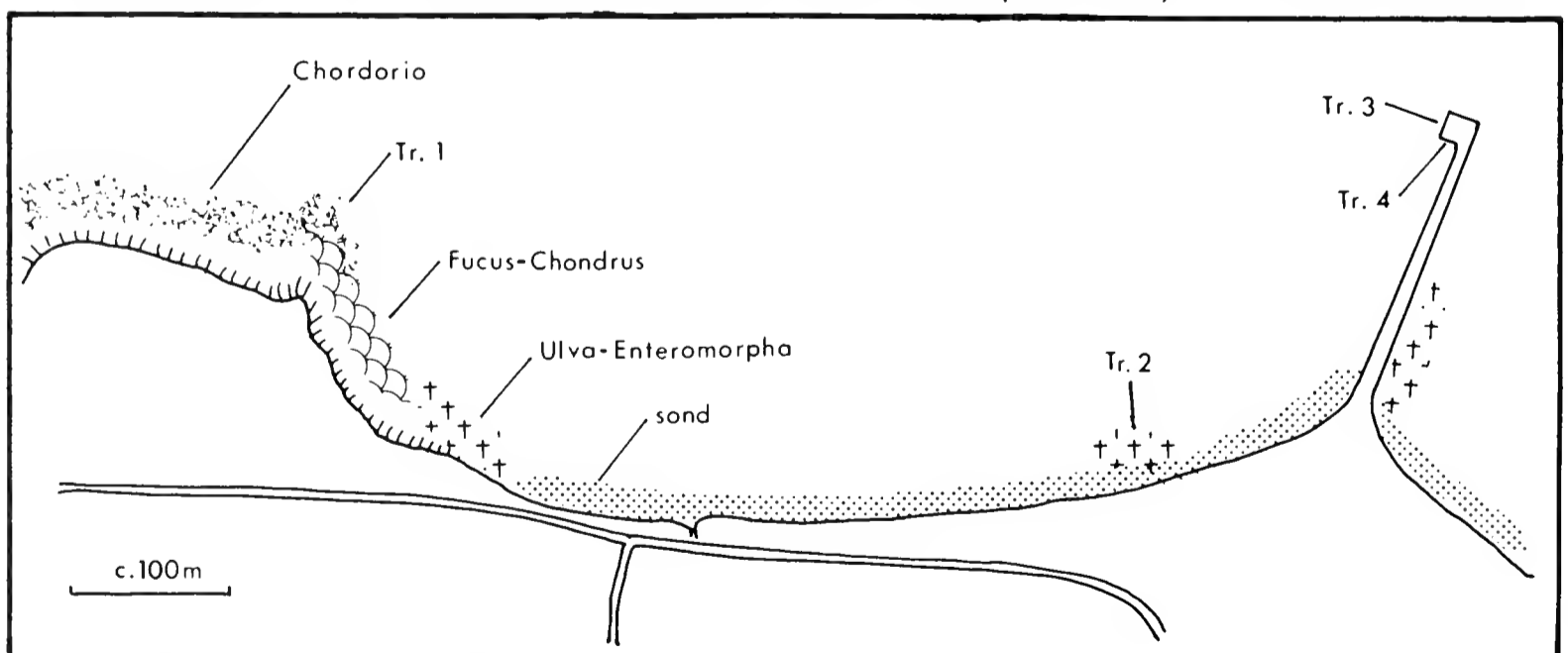


Fig 2. Map of the shore to the west of North Rustico Harbour breakwater, showing diagrammatically the characteristic features of horizontal distribution of major seaweeds, and locations of the four transects.

Rustico and the intertidal area is about 125 m wide. Tides there are semidiurnal with a mean amplitude of 1.83 m. Water temperature at both sites ranges from -1.8°C (freezing) in winter to $22-25^{\circ}\text{C}$ in summer. Salinities range up to 31‰ in winter, decreasing to $26-27\text{‰}$ in summer.

Methods

The field work was carried out at roughly monthly intervals from July 1970 to June 1971 (at Rustico) and to November 1970 (at Prim Point). Most data were collected 14-29 July 1970, subsequent trips serving to record changes in the flora and fauna and to prepare additional transects. The survey of horizontal distribution at Rustico was carried out in August 1970. Semipermanent steel benchmarks were placed in the rock above each transect and their heights determined with reference to recorded tide levels. The concrete deck of the North Rustico Harbour breakwater also served as a reference level, 3.23 m above zero tide at a Canadian Hydrographic Service scale at the end of the breakwater. Subtidal organisms were studied cursorily with SCUBA, glass-bottomed box and rake collections from a *Chondrus*-harvesting boat. Voucher specimens of the organisms and a large collection of photographs were deposited with the Parks Branch along with our final report. A collection of voucher specimens was also sent to the National Museum of Natural Sciences, Ottawa.

Results

Horizontal Distribution at Rustico

The shore consists of alternate sandy beaches and rocky headlands and can be divided into three floristic regions (Fig 2). Rocks in the sandy areas bore chiefly *Ulva lactuca*² and species of *Enteromorpha*, with some *Chordaria flagelliformis*. At the western ends of the beaches, toward the headlands, there was typically a transition from *Enteromorpha* to *Ulva* to *Scytosiphon lomentaria*. The rocky west side of each bay leading to the promontories had well-developed intertidal belts of *Fucus vesiculosus* and *Chondrus crispus*. Thirdly, the shores from the headlands west to the next bay were dominated by *Chordaria* and a lower belt of Ceramiales (*Ceramium* spp., *Polysiphonia* spp. and some *Rhodomela confervoides*). A high intertidal black zone of blue-green algae was generally distributed along the rocky shore. *Balanus balanoides*, *Mytilus edulis*, *Littorina littorea* and *L. saxatilis* occurred in the regions of *Fucus* (*Mytilus* in the intertidal zone only in crevices).

Vertical distribution at Rustico












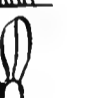


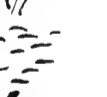

The general pattern of vertical zonation is shown in Fig 3, a composite of various transects. There was a black zone from HHWS³ down to a little below MHHW, passing into a barnacle zone (*Balanus balanoides*). This merged with a zone of *Fucus* which straddled MSL. A zone of *Ulva* and *Enteromorpha* lay between the *Fucus* and the top of a zone of *Chordaria flagelliformis* at MLLW. Below LLWS was an association of *Laminaria saccharina* and *Chondrus crispus*. The details of the transects are as follows (transect locations on Fig 2).




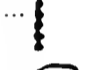


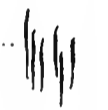







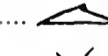

Transect 1. (July) (Fig 4a, 5). Because of the rather gentle slope of the shore, the zones were not sharply defined, but merged into one another. The black zone extended, albeit tenuously, to the limit of wave action, at the foot of the cliff, but was best developed between +0.61 m and +0.79 m, that is a little below MHHW. The upper part of this zone was *Calothrix*, the lower part *Rivularia*. It passed indistinctly into a "brown zone" of *Ralfsia verrucosa*. Although a few stunted plants of *Fucus*

² Authorities for the species names are given in the Appendix.

³ HHWS = highest high water of spring tides; MHHW = mean higher high water; MSL = mean sea level; MLLW = mean lower low water; LLWS = lowest low water of spring tides.

List for key symbols:

- Sand 
- Black zone blue-green algae 
- Tube-dwelling diatoms 
- Chondrus crispus* 
- Bonnemaisonia hamifera* tetrasporophytes 
- Crustose corallines 
- Ceramialean algae 
- Furcellaria fastigiata* 
- Devaleraea ramentacea* 
- Ahnfeltia plicata* 
- Corallina officinalis* 
- Sphacelaria* spp. 
- Ectocarpus* spp. 
- Fucus serratus* 
- Ralfsia verrucosa* 
- Chordaria flagelliformis* 

- Laminaria saccharina* 
- Scytosiphon lomentaria* 
- Chorda filum* 
- Chaetomorpha melagonium* 
- Ulva lactuca* 
- Enteromorpha linza* 
- Enteromorpha intestinalis* 
- Urospora* sp. 
- Cladophora sericea* 
- Littorina littorea* 
- Nucella lapilla* 
- Balanus balanoides* 
- Intertidal *Mytilus edulis* 
- Subtidal *Mytilus edulis* 
- Acmaea testudinalis* 
- Asterias vulgaris* 

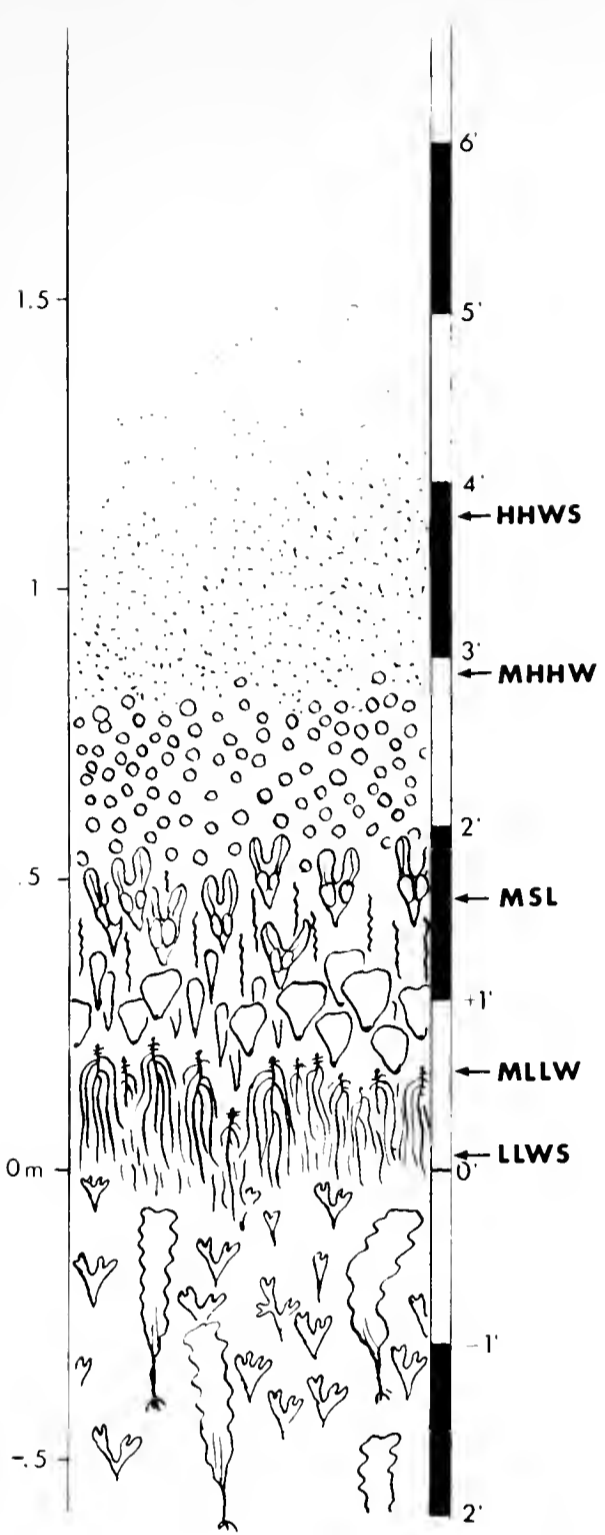


Fig 3. Generalized zonation scheme for North Rustico. (See key to symbols on page 28.)

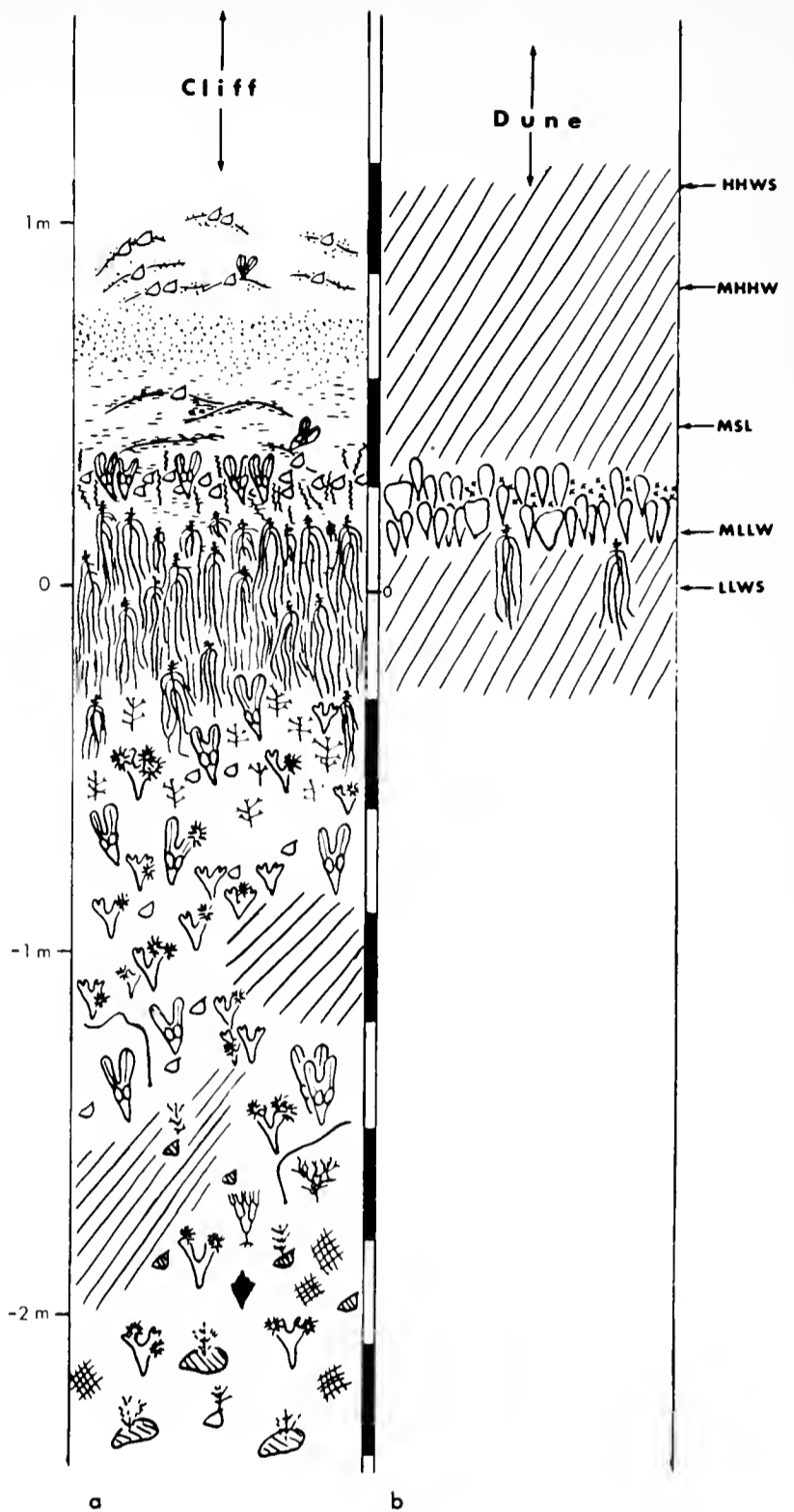


Fig 4. Zonation on Rustico shores. (a) Transect 1, a rocky headland. (b) Transect 2, a rocky outcrop on a sand beach.

vesiculosus occurred in the black zone, this species in the intertidal zone was at its best in a narrow zone between +0.24 m and +0.30 m, in association with *Scytosiphon lomentaria*. *Ralfsia* was also found in this zone. The dense mat of *Chordaria*, heavily epiphytized by *Dictyosiphon foeniculaceus*, straddled low water, from +0.24 m to -0.30 m. There was almost no *Balanus* on this transect, probably as a result of ice scour in winter.

There was a marked drop in the level of the rock under the transect from 0.0 m to -0.9 m. On the vertical face was a mixture of delicate red algae: *Polysiphonia* spp., *Ceramium* spp. and *Rhodomela confervoides*; plus *Chondrus* and *Fucus*. Subtidal



Fig 5. Photograph of the shore at Transect 1.

Fucus was well developed, highly branched, about 0.5 m long, and abundantly fertile, although the wings tended to be severely grazed. The *Chondrus* was heavily epiphytized by the tetrasporophyte phase of *Bonnemaisonia hamifera*, while *Fucus* was epiphytized by *Elachista fucicola*, *Pilayella littoralis* and sometimes *Ectocarpus* sp. The snail *Littorina littorea* was found all along the transect but in the intertidal zone sought shelter on the edges of the ridges (Fig 8) or under *Chordaria*. Below low tide these animals were randomly distributed and were covered by crustose coralline algae, *Corallina officinalis* and *Bonnemaisonia*. *Littorina saxatilis* was not seen on the transect in July or August but appeared in crevices in September. At other places along the shore it was found in pot holes or on *Fucus*. *Mytilus edulis* was common in the subtidal zone and the animals were larger than the intertidal individuals which grew in crevices. Clusters of subtidal mussels provided anchorage for *Fucus*, *Chondrus*, *Desmarestia aculeata*, crustose corallines, and the few *Laminaria*. *Chorda filum* and *Desmarestia* were fairly common from -1.2 m and from -3.0 m, respectively.

Transect 2. (July) (Fig 4b). This transect passed over a rock outcrop from +0.12 m to +0.34 m in the middle of North Rustico Beach. There were no major animals on the rock. The flora consisted of *Ulva lactuca*, *Enteromorpha linza*, *E. intestinalis* and some *Punctaria latifolia*. Tube-dwelling diatoms (*Navicula delognei* f. *elliptica* and

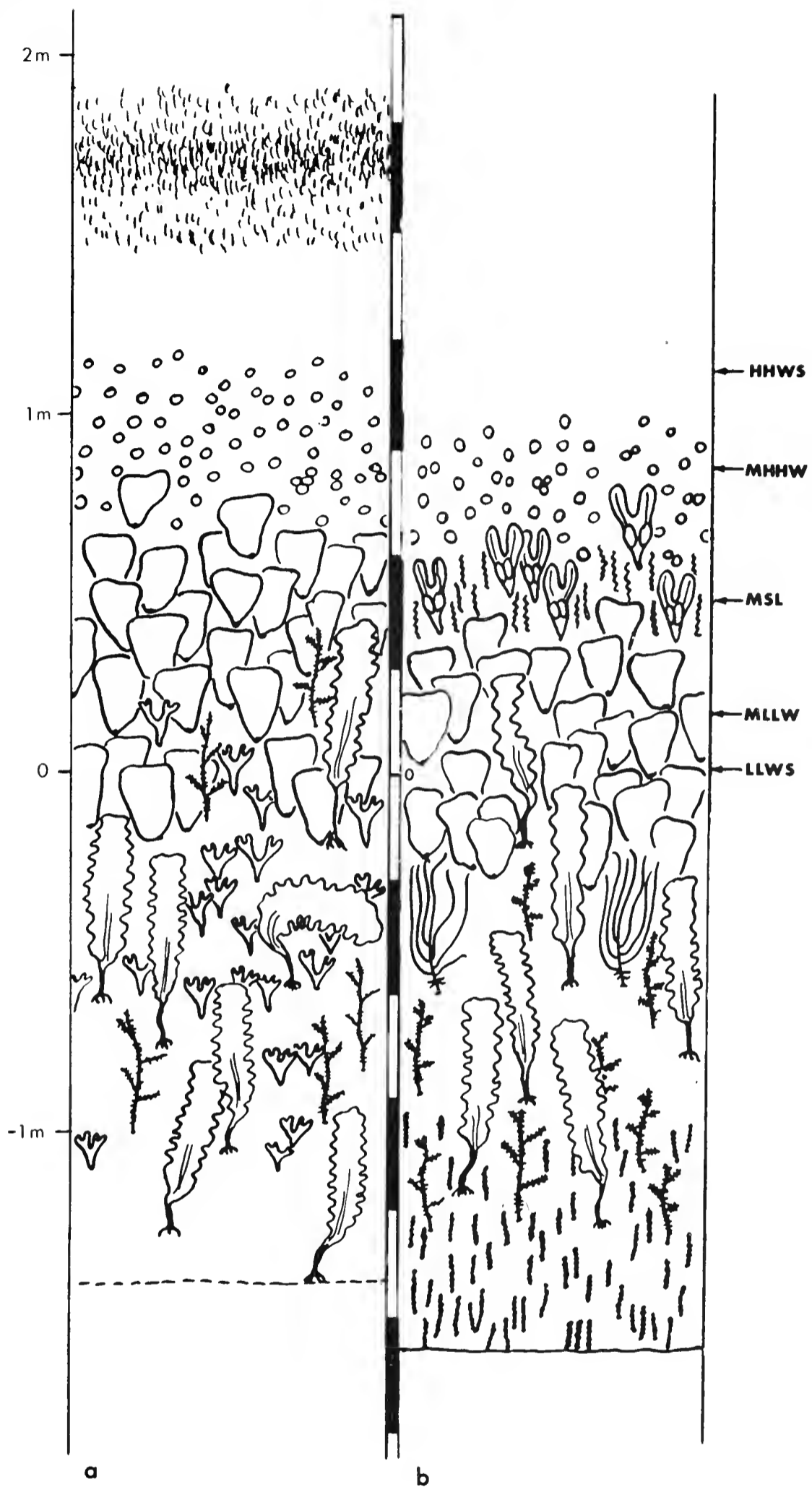


Fig 6. Zonation on Rustico breakwater. (a) Transect 3, west face. Dotted line represents a scour line below which there were no algae. (b) Transect 4, south face. Horizontal line represents the seabed.

Berkeleya rutilans) were found on the higher part of the outcrop. Some *Chordaria* (free of *Dictyosiphon*) grew at the lower edge. The *Ulva-Enteromorpha* association was typical of rocks surrounded by sand, occurring also at the west end of North Rustico Beach and on rocks in Doyle's Cove.

Transects 3 and 4. (November) (Fig 6a, b). These transects were on the west and south faces of the outer end of the breakwater. They differed from each other in two major environmental factors and in their floras. The west face receives less sunlight than the south face and is subject to more splashing by wave action. The zonation on these vertical faces, although not typical of the region, most closely resembled the generalized scheme shown in Fig 2.

The west face (Fig 6a) had a well-developed zone of *Urospora* sp. from above HHWS toward the limit of wave action (+1.46 m to +1.89 m), which was absent from the south face. The south face had a zone of *Fucus* and *Scytosiphon* straddling MSL (+0.40 m to +0.64 m). Both faces had *Laminaria saccharina* (-0.15 m to -1.37 m), *Devaleraea ramentacea* (ca. -0.3 m to -1.2 m) and *Balanus balanoides* (ca. +0.6 m to +1.1 m). The *Balanus* zone and the upper limits of *Ulva* and *Devaleraea* were both slightly higher on the west face. Neither face had a visible black zone.

Seasonal observations at Rustico

By October a marked and widespread zone of *Petalonia fascia* and *Scytosiphon lomentaria* had developed between the black zone and the zone of *Ulva* and *Chordaria-Dictyosiphon* had declined. During the winter the shore was scoured by ice between about +0.3 m and +0.6 m (Fig 7); *Fucus*, *Chondrus* and *Chordaria*, except behind boulders and under overhangs, were reduced to stumps or scraped away entirely (Fig 8, 9). For this reason growth of perennial algae, as well as barnacles, is largely confined to the lee of the siltstone ridges (Fig 8).

The first spring growth was dominated by *Ulothrix flacca*, *Urospora wormskiöldii* and species of *Enteromorpha*, with scarce patches of *Bangia atropurpurea*. These were followed by regrowth of *Fucus* and *Chondrus*, and by resettlement of *Chordaria*.

Vertical distribution at Prim Point

The intertidal biota on the south coast of the Island is rather richer, and the zonation is different in a number of respects (Fig 10). The black zone extended to the limit of wave action (ca +3.4 m) but was not well developed above +2.4 m. It reached its best growth between +1.5 m and +2.1 m. Between +2.0 m and +2.7 m, just above HHWS, it was mixed with a small, branching *Enteromorpha* sp. (?*Blidingia minima*) which was fairly well developed but patchy. *Balanus balanoides* extended to the foot of the cliff, +1.5 m, occasionally 0.3 m higher in crevices. Two generations of the animal were evident. The young dominated the open surfaces of the rock and extended a little higher than the older ones which were generally confined to the shelter of the siltstone ridges. The zone of *Balanus* extended from +0.15 m, just above LLWS, to +1.5 m. *Mytilus edulis* grew on open rock from +0.6 m to +1.0 m, and in crevices up to +1.5 m. A zone of *Fucus vesiculosus* lay between MLLW and MSL, from +0.6 m to +1.5 m. In some places along the upper shore the plants were very twisted. *Littorina littorea* was scattered throughout the zone of *F. vesiculosus*, and *L. saxatilis* was found from +1.2 m to about +1.4 m. *Nucella lapilla* extended from about +0.52 m to +0.73 m on open rock and to +0.79 m in hollows.

Cladophora sericea occurred up to +1.13 m on open rock, to +1.29 m in tide pools. It was not observed below +0.52 m, although it probably occurs in the sub-



Fig 7. Rustico shoreline in winter, showing ice foot encrusting the rocks and ice pans floating and beached.

tidal zone. *Chondrus* and *Scytosiphon* were found on open rock below +0.64 m and +0.61 m, respectively, occurring in the shallow tide pools as high as +0.91 m.

Fucus serratus and *Chorda filum* extended from just above MLLW at +0.85 m and were seen down to -0.3 m. *Sphacelaria* sp(p). was encountered from -0.15 m to +0.40 m. *Corallina officinalis* was fairly common below +0.70 m down to unknown depths, and between -0.60 m and -1.2 m there was a zone of *Furcellaria fastigiata* in which limpets (*Acmaea testudinalis*) were also noted. *Mytilus*, encrusted as at Rustico with crustose corallines and providing a holdfast for macrophytes, was found scattered throughout the subtidal region, as were *Ahnfeltia plicata* and the Ceramiales *Ceramium*, *Rhodomela* and *Polysiphonia*. *Palmaria palmata*, *Desmarestia aculeata* and *Laminaria saccharina* were occasionally found in the driftweed but were never seen attached. The starfish *Asterias vulgaris* was common on the edges of the bedding plane ridges, but they were rarely larger than 30 mm in diameter.

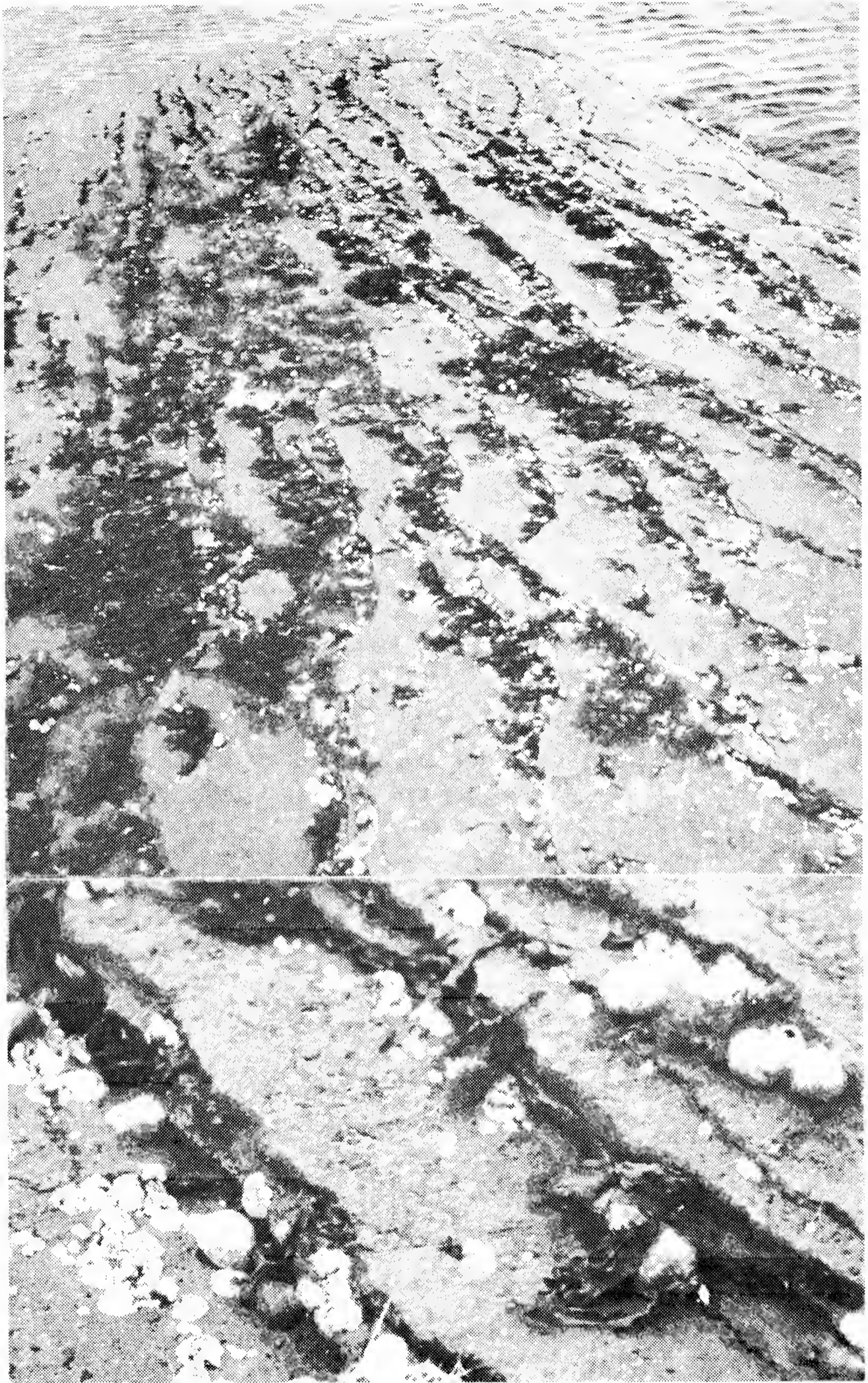


Fig 8. Distribution of fucoids and barnacles in the lee in siltstone ridges. Detail (below) ca. 0.75 x life size.



Fig 9. Appearance of rocky shore at Rustico in April, after winter ice scour (contrast with Fig 8).

Discussion

A comparison of the shores at Rustico and Prim Point reveals the following principal distinctions: (1) while both shores are of siltstone, Rustico slopes more steeply and is more exposed to wave and ice action; (2) the intertidal flora and fauna at Rustico are generally impoverished in comparison with those at Prim Point; (3) the zone of *Chordaria-Dictyosiphon* at Rustico was not present at Prim Point, being replaced by *Chondrus* and *Fucus serratus*; (4) *Chondrus* and *Fucus vesiculosus* were displaced into the subtidal zone at Rustico, and *F. serratus* was absent.

The vertical distribution of organisms in the intertidal zone described here is largely as the Stephenson (1954a, b) found it at Rustico and Fernwood. They, however, used *Littorina saxatilis* as a representative zone organism. Their "short orange-brown form of [*Pilayella*] *littoralis* growing directly on rock" was seen on some of the vertical sandstone faces during our study.

Stephenson and Stephenson (1954a) were not favourably impressed by the north coast of PEI, and it is therefore of interest to compare the zonation there with what they found at Peggy's Cove, Nova Scotia, which they considered to represent the fully developed zonation of the Maritime Provinces. The general paucity of the intertidal flora at Rustico and Prim Point is in stark contrast to the dense vegetation at Peggy's Cove. Another significant difference is the absence, at Rustico, of the *Chondrus* subzone: where *Chondrus* occurs in the intertidal zone it scarcely forms a zone. Its place is usually taken by *Chordaria flagelliformis*. The zone of *Chondrus*, although present at Prim Point, is much less dense than at Peggy's Cove, and partly replaced by barnacles.

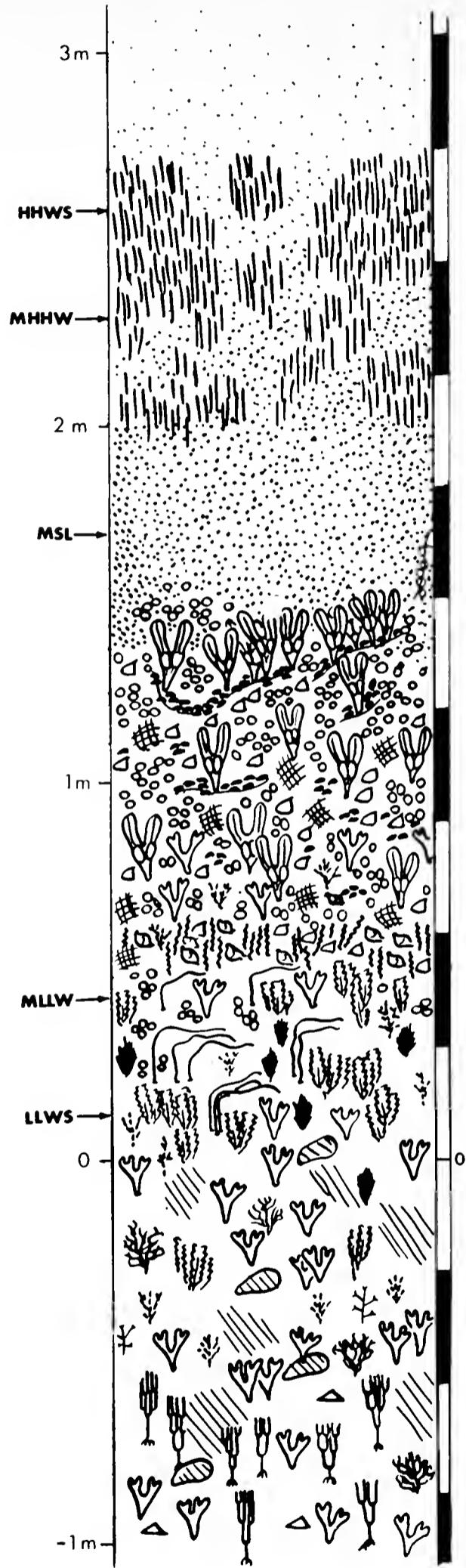


Fig 10. Zonation at Prim Point.

Three factors are probably of importance in the distribution of organisms at Rustico: ice scouring of the shore, leading to impoverishment of the zones of *Fucus* and *Chondrus*, sand scouring near beaches, and absence of competition from *Laminaria* in the shallow sublittoral zone. Sundene (1953) found that ice action in the Oslofjord, Norway, tended to be local and of brief duration—only part of the intertidal population being scoured off, over small horizontal distances. Removal was most often of the fucoids, and these were replaced by faster growing algae such as *Ulothrix*, *Urospora* and *Cladophora*. On the north coast of PEI *Chordaria* may replace *Chondrus* for the same reason. However, Sundene (1953) found that sporelings of *Fucus* often occurred and gradually took over, reestablishing the original zonation pattern if they survived the subsequent winter. This seems not to happen on the north shore of PEI, where, as also noted by Bird et al. (1983), perennial macrophytes are scarce. Wilce (1959, p. 36) gave a graphic first-hand account of the arrival of ice on the shore in Labrador, and said that ice masses there “devastate the algae of the intertidal zone”. In the Rustico area shore ice appears to protect the algae from the more severe grinding of pack ice, which remains off shore. The effects of ice on seaweed populations need closer study.

Rocks in or near the beach are subject to sand scour and even burial. The vegetation in these areas is dominated by ephemeral species. An effect of sand scour was also seen at the foot of Transect 3 (Fig 6a).

The scarcity of *Laminaria*, which again contrasts with Peggy's Cove, seems to be due to a combination of soft substratum and wave exposure. In shallow water, laminarians may be torn off the friable siltstone by storms (see Bird et al. 1983). They do not occur above about -4.6 m at Rustico or about -3.0 m at Prim Point. On the Rustico breakwater, however, which is made of steel at its northern end, *Laminaria* is found up to low water. The absence of *Alaria* is a feature of the region (Bell & MacFarlane 1933a).

The intertidal fucoid zone is different among Peggy's Cove, Prim Point and Rustico, becoming progressively more reduced in that order. At Rustico it is extremely depauperate and *Fucus spiralis* is absent. This species was not found by the Stephensons (1954a, b) at Rustico, nor in the sheltered St. Margaret's Bay near Peggy's Cove. *Ascophyllum* does not occur on open rocky shores at Rustico (although it is reported in sheltered bays and inlets along the north coast of PEI by Bell & MacFarlane 1933b). At Prim Point, *F. spiralis* and *F. vesiculosus* are found in the same zones as at Peggy's Cove, but there is also the species characteristic of the Northumberland Strait, *F. serratus*. This is found just below low tide, in the *Chondrus* zone. *Ascophyllum* is very scarce along the Northumberland Strait coast of PEI, although it is more common in very sheltered regions at Caribou, N.S., across the Strait from Prim Point (personal observations).

Our subtidal observations at Rustico were limited but corroborate data from Taylor (1975), showing abundance of *Chondrus* and evesiculate *Fucus vesiculosus*, and scarcity of *Laminaria*.

Although the rocky shores of PEI are “peculiar”, they merit further attention, particularly in winter, when they provide an easily accessible study area for the effects of pack ice and ice foot on intertidal organisms. Furthermore, there were indications of an interesting flora under fast ice, including *Phaeosaccion collinsii*, *Desmotrichum undulatum*, *Rhodophysema georgii*, and a rare foliose diatom *Navicula ulvacea*.

Acknowledgements

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APPENDIX: CHECKLIST OF LITTORAL ORGANISMS AT RUSTICO

(Additional species found only at Prim Point are marked*.)

RHODOPHYTA

Nemaliales

Nemalion helminthoides (Vell. in With.) Batt.

Bonnemaisonia hamifera Hariot

Gigartinales

Furcellaria fastigiata (L.) Lamour.

Gracilaria verrucosa (Huds.) Papenf.

Ahnfeltia plicata (Huds.) Fries

Chondrus crispus Stackh.

**Phyllophora truncata* (Pallas) A. Zin.

Cryptonemiales

Rhodophysema georgii Batt.

Hildenbrandia rubra (Sommerf.) Menegh.

Corallina officinalis L.

crustose corallines

Melobesia Lamour. sp.

Palmariales

Devaleraea ramentacea (L.) Guiry*Palmaria palmata* (L.) O. Kuntze

Ceramiales

Ceramium Roth spp.*Spermothamnion repens* (Dillw.) Rosenv.*Phycodryis rubens* (L.) Batt.*Polysiphonia* Grev. spp.*Polysiphonia nigrescens* (Huds.) Grev.*Rhodomela confervoides* (Huds.) Silva*Rhodomela lycopodioides* (L.) C. Ag.

Bangiales

Bangia atropurpurea (Roth) C. Ag.**PHAEOPHYTA**

Ectocarpales

Ectocarpus Lyngb. sp.*Giffordia* Batt. sp.*Pilayella littoralis* (L.) Kjellm.*Petroderma maculiforme* (Woolny) Kuck.*Ralfsia verrucosa* (Aresch.) J. Ag.*Elachista fucicola* (Vell.) Aresch.*Chordaria flagelliformis* (O.F. Müll.) C. Ag.*Sphaerotrichia divaricata* (C.A. Ag.) Kylin*Punctaria latifolia* Grev.*Dictyosiphon foeniculaceus* (Huds.) Grev.*Petalonia fascia* (O.F. Müll.) O. Kuntze*Scytosiphon lomentaria* (Lyngb.) Link

Desmarestiales

Desmarestia aculeata (L.) Lamour.

Laminariales

Chorda filum (L.) Stackh.*Agarum cribrosum* (Mert.) Bory*Laminaria saccharina* (L.) Lamour.*Sacchorhiza dermatodea* (Pyl.) J. Ag.

Sphacelariales

Sphacelaria Lyngb. sp.

Fucales

Fucus vesiculosus L.*Fucus distichus* subsp. *edentatus* (Pyl.) Powell**Fucus serratus* L.**CHLOROPHYTA**

Ulotrichales

Ulothrix flacca (Dillw.) Thur. in Le Jol.*Urospora wormskioldii* (Mert. in Hornem.) Rosenv.*Monostroma grevillei* (Thur.) Wittr.*Spongomorpha arcta* (Dillw.) Kütz.

Ulvales

Enteromorpha intestinalis (L.) Link.*Enteromorpha linza* (L.) J. Ag.*?*Blidingia minima* (Näg. ex Kütz.) Kylin*Ulva lactuca* L.

Cladophorales

- Chaetomorpha linum* (O.F. Müll.) Kütz.
Chaetomorpha melagonium (Web. et Mohr.) Kütz.
Cladophora sericea (Huds.) Kütz.

CHRYSOPHYTA

- Phaeosaccion collinsii* Farl.
Berkeleya rutilans (Trent.) Cleve
Navicula delognei van Heurck f. *elliptica* Lobban
Navicula rusticensis Lobban
Navicula ulvacea (Berk. ex Kütz.) Cleve

CYANOPHYTA

- Rivularia* (Roth) Ag. sp.
Calothrix Ag. sp.

MOLLUSCA

Gastropoda

- Littorina littorea* Linnaeus 1758
Littorina saxatilis Olivi 1792
Polinices heros Say 1822
 **Nucella lapilla* Linnaeus 1758
Acmaea testudinalis Muller 1776
Crepidula fornicata Linnaeus 1767

Bivalvia

- Mytilus edulis* Linnaeus 1758
Crassostrea virginica Gmelin 1792
Mya arenaria Linnaeus 1758

ANNELIDA

- Spirorbis borealis* Daudin 1800

ARTHROPODA: Crustacea

Cirripedia

- Balanus balanoides* (Linnaeus) 1758

Decapoda

- Homarus americanus* Milne-Edwards 1837
Cancer irroratus Say 1817
Pagurus longicarpus Say 1817
Pagurus sp.

Amphipoda

- Talorchestia* sp.
Orchestia sp.

ECHINODERMATA

Echinoidea

- Strongylocentrotus droebachiensis* (Muller) 1776

Stelleroidea

- Asterias vulgaris* Verrill 1866

RAISED BOGS ON THE CAPE BRETON PLATEAU

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An ecological study of five raised bogs on the Cape Breton Plateau was undertaken with the following objectives: to obtain qualitative and quantitative data on the vegetation and environment, and from these data to describe the plant associations and their ecological relationships. Single plots from each community were selectively chosen and the vegetation was analyzed using the phytosociological methods of the Zürich-Montpellier School. Environmental analysis involved the collection of data pertaining to edaphic and climatic factors. Based on the detailed study of 46 plots, seven associations are recognised. These include the aquatic *Nuphar variegatum*, the semi-aquatic *Eriophorum angustifolium* and *Rhynchospora alba* - *Drosera intermedia*, the bog meadow *Scirpus cespitosus* - *Sphagnum* spp. and *Scirpus cespitosus* - *Dicranum leioneuron*, and the drier *Picea mariana* - *Cladonia rangiferina* and *Picea mariana* - *Rhododendron canadense* Associations. The most commonly represented associations are the *Picea* - *Cladonia* and the *Scirpus* - *Sphagnum* while those of limited occurrence include the *Eriophorum* and the *Picea* - *Rhododendron*. Chemical analysis of the bog soils reveals a high degree of similarity between associations, with the peat having greater cation concentrations than the mineral substratum. This is because the bogs receive their entire nutrient and water supply from precipitation. The proximity of the study area to the sea causes an increase in the chlorides of magnesium and sodium in rain water resulting in a cation imbalance in the peat. The mineral substratum, because of its acidity and impermeability, creates favorable sites for raised bog development. Climatic data reveal that the Cape Breton Plateau has cooler summertime temperatures than the nearby lowland coastal areas. Minimum temperatures on the Plateau are low enough to become critical for plant growth as they approach freezing even during July and August. This ensures a slower rate of decomposition in the peat deposits. Precipitation on the Plateau appears to be adequate for raised bog development with amounts slightly exceeding those recorded at Ingonish Beach and almost double the amount at Cheticamp. Four dynamic processes occur in the raised bogs: development, cyclic succession, erosion, and regeneration. The associations are discussed in relation to these successional sequences. Examination of the ecological amplitudes of bog species reveals an increase in the complexity of the flora of the associations, proceeding from hydric to mesic habitats. The majority of the bog species are found in the drier associations. It is concluded that the raised bogs on the Plateau are dynamic self-sustaining units which will continue to grow through plant succession as long as the present edaphic and climatic conditions remain constant.

Une étude écologique de 5 tourbières surélevées situées sur le Plateau du Cap Breton fut entreprise avec les objectives suivantes: obtenir des données qualitatives et quantitatives sur la végétation et l'environnement et, à partir de ces données de décrire les associations végétales et leurs relations écologiques. Des parcelles de terrain de chacun des communautés furent sélectionnées. La végétation a été analysée à l'aide des méthodes phytosociologiques de l'Ecole de Zürich-Montpellier. L'analyse de l'environnement consistait à recueillir des données sur les facteurs édaphiques et climatique. Sept associations peuvent être distinguées et à partir de l'étude détaillée de 46 lots. Celles-ci incluent l'association aquatique à *Nuphar variegatum*, semi-aquatiques à *Eriophorum angustifolium* et *Rhynchospora alba* - *Drosera intermedia*, les associations de prairie marécageuse à *Scirpus cespitosus* - *Sphagnum* spp. et *Scirpus cespitosus* - *Dicranum leioneuron*, et les associations de terrains plus secs à *Picea mariana* - *Cladonia rangiferina* et *Picea mariana* - *Rhododendron*

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canadense. Les associations les plus communes sont celle à *Picea - Cladonia* et celle à *Scirpus - Sphagnum* alors que les associations à *Eriophorum* et à *Picea - Rhododendron* sont peu représentées. Les analyses chimiques du sol des tourbières ont révélé l'existence d'une grande similitude entre les associations, les concentrations en cations étant plus élevées dans la tourbe que dans le sous-sol minéral. Ceci peut être attribué au fait que les tourbières reçoivent leur approvisionnement en sels nutritifs et en eau des précipitations atmosphériques. La proximité du site étudié de la mer amène une augmentation des chlorures de magnésium et de sodium dans les eaux de pluie ce qui entraîne un déséquilibre cationique dans la tourbe. Le sous-sol minéral, à cause de son acidité et de son imperméabilité crée des sites favorables au développement des tourbières surélevées. Les données climatiques révèlent que les températures d'été du Plateau du Cap Breton sont plus fraîches que celles des terres basses côtières avoisinantes. Les températures minimum sur le plateau, en approchant le point de congélation pendant les mois de juillet et août sont suffisamment basses pour devenir critique pour la croissance des plants. Ceci assure une vitesse de décomposition plus lente des dépôts dans la tourbe. Les précipitations sur le plateau semblent adéquates pour le développement d'une tourbière surélevée. Elles excèdent faiblement celles d'Ingonish Beach et sont deux fois plus importantes que celles de Cheticamp. Quatre processus dynamiques se produisant dans les tourbières surélevées: développement, succession cyclique, érosion et régénération. Les associations sont discutées en relation avec ces successions. Un examen des amplitudes écologiques des espèces des tourbières révèle que la complexité de la flore de ces associations augmente des habitats hydriques vers les habitats mésiques. La majorité des espèces végétales des tourbières se trouvent dans les associations les plus riches. Il est conclu que les tourbières surélevées du Plateau sont des unités dynamiques autosuffisantes qui continueront leur croissance par les successions végétales aussi longtemps que les conditions édaphiques et climatiques actuelles resteront constantes.

Introduction

An ecological study of raised bogs from the interior of the Cape Breton Plateau was undertaken during 1970-71 with the following objectives: (1) to obtain qualitative and quantitative data on the natural vegetation, (2) to classify and describe the major associations found on the bogs, (3) to analyze the physical environment with emphasis on climatic and edaphic factors, and (4) to describe the ecological and successional relationships of the bog associations.

The study area, located inside the Cape Breton Highlands National Park, is situated between longitudes 46°41' and 46°44'N and latitudes 60°37' and 60°43'W, and at elevations ranging from 488 to 518 m above Mean Sea Level (Fig 1).

A review of the literature revealed that little ecological work had been done previously on the bogs of the Cape Breton plateau. Nichols (1918) divided the vegetation of Northern Cape Breton into two climax formations, the Deciduous Forest Formation of the lowland areas and the Northeastern Evergreen Coniferous Forest Formation of the Plateau. He considered the bogs on the Plateau to be an upward extension of the latter formation. Nichols did the only ecological study of the raised bogs in this region, recognizing three association-complexes, namely, a bog meadow, wet bog, and dry bog stage. He also described the successional relations between these stages, and speculated on how the bogs may have originated.

Any literature survey of important contributions to bog vegetation and ecology in eastern North America should include local studies by Ganong (1897), Nichols (1919), and Damman (1977) in New Brunswick and Maine; Pollett (1972), Pollett and Bridgewater (1973), and Wells (1980) in Newfoundland; Gauthier and Grandtner (1975), and Gauthier (1980) in Québec; and Allington (1961) in Labrador- Ungava. In central North America, important local studies are those of Sjors (1963), and Jeglum et al. (1974) in Ontario; Gates (1942) in Michigan; and Conway (1949), Janssen (1967), and Heinselman (1963, 1970) in Minnesota.

Early bog vegetation/ecology studies on a broader regional basis in North America include contributions by Transeau (1903), Rigg (1940, 1951), Dansereau and Segadas-Vianna (1952), and Osvald (1970). More recent works in this regard are studies by Fabiszewski (1975), Comeau (1977), and Damman (1979).

Some recent phytosociological studies have incorporated the techniques of the Zürich-Montpellier School as developed by Braun-Blanquet (1964) and used in this paper. These include the works of Pollett (1972), Pollett and Bridgewater (1973), Fabiszewski (1975), Gauthier and Grandtner (1975), Comeau (1977), Damman (1977), Gauthier (1980), Wells (1980), and Glaser et al. (1981).

Recent studies dealing with bog chemistry include contributions by Gorham (1967), Small (1972a), Damman (1978), and Waughman and Bellamy (1980).

Terminology

The term "bog" is one of several used in the English language to describe a waterlogged habitat. Ecologists recognize two classes of bog or peatland: minerotrophic types, dependent on an influx of terrestrial, nutrient-enriched water, and ombrotrophic (ombrogenous) types, dependent on atmospheric precipitation for water and nutrient supply (Gorham 1957a; Ratcliffe 1964).

Included within ombrogenous types are blanket and raised bogs. Blanket bogs, as the name implies, completely cover the ground in an unbroken mantle of peat. They usually occur on gently contoured land where precipitation is high. Raised bogs, occurring in cool, wet climatic regions, can be distinguished from blanket bogs by their characteristic convex surface, sloping from the center towards the edge (Ratcliffe 1964). Raised bogs become established once peat accumulation raises the surface above the influence of mineral soil water (Gorham 1957a; Ratcliffe 1964).

Description of the Study Area

Physiography

The Cape Breton Plateau rises steeply on its sides to heights of 300 m and more where it then levels off to form a broad flat tableland dissected by steep gorges. In the study area, the topography is gently undulating, consisting of low rounded hills and ridges surrounded by broad flat valleys. The area serves as the watershed for the Cheticamp, Mackenzie, and North Aspy Rivers as well as the Big Southwest, and Black Brooks.

Geology and Soils

The Cape Breton Plateau is underlain by resistant igneous and metamorphic rocks. Those in the study area belong to the George River Group of Precambrian time. This group is made up of undivided schist and gneiss intruded by granitic rocks (Roland 1982).

The soils of the Cape Breton Plateau are stony, and shallow, commonly occupying poorly drained sites. The parent material, from which these soils derive, is a stony sandy loam till, forming a thin layer over the bedrock. The thin glacial till covering the Plateau was deposited by ice approximately 10,000 years ago (Newman 1971). The impermeable nature of the bedrock covered by this till has led to the extensive development of peat bogs which are dependent on atmospheric precipitation for their water supply.

Climate

The climate of the Cape Breton region is influenced by two important factors: first, the region's proximity to the sea giving the area a wet maritime climate, and secondly, the Maritime Provinces lie in the direct path of storm systems leaving the North American Continent. Warm moist air from the south is constantly mixing with cold air flowing in from the northwest, and as a result, the Northern Cape Breton region can be characterized as having a wet, cool-temperate climate.

Table 1 Temperature and precipitation normals for Cheticamp and Ingonish Beach, Cape Breton. ⁺

Meteorological Station	Mean Annual Temp (°C)	No. Months with Mean Temp above 0°C	Mean Annual Temp (°C)		Mean Annual Rainfall (mm)	Mean Annual Snowfall (cm)	Total Mean Annual Precipitation (mm)
			Max	Min			
Cheticamp 46°39'N, 60°57'W Elevation 11 m	6.0	8	9.8	2.1	947.3	406.7	1362.7
Ingonish Beach 46°39'N, 60°24'W Elevation 5 m	6.2	8	10.6	1.9	1287.2	343.7	1630.7

⁺ Normals for Cheticamp are based on the period 1956-1980 and for Ingonish Beach from 1951-1980. (Data obtained from Atmospheric Environment Service, Environment Canada.)

The only long term climatic data available for the area are from coastal meteorological stations located at Cheticamp and Ingonish Beach. Climatic summaries for these two stations are presented in Table 1. Detailed weather information for the Cape Breton Plateau, recorded during the Summer of 1970, is included under Observation and Interpretation.

Vegetation

The Plateau is covered mainly by coniferous forest, wet peatlands, and dry barrens. There are two types of forest present, namely, *Abies balsamea* which occurs on well drained slopes and ridges, and *Picea mariana* which occurs in poorly drained sites and usually surrounds the bogs.

In the study area the bogs are mainly the raised type and are located where drainage is impeded. They vary in shape, some having a pronounced convex surface while others are generally flat with only slight elevations near their centers. They sometimes cover extensive areas and are broken up only by small streams and drainage gullies.

Dry barrens occupy the higher ridges where rock outcrops are common. Here, ericaceous plants make up a substantial part of the vegetation cover.

Methods

Initially, 17 raised and blanket bogs in the central part of Cape Breton Highlands National Park were located using aerial photographs and topographic maps. A reconnaissance of these was done in June 1970 and observations made on the composition and structure of the vegetation. From the reconnaissance, five bogs (designated by the capital letters A to E) were selected for detailed study (Fig 1) and a tentative list of plant associations based on dominance and physiognomy was prepared.

Nomenclature

Plant nomenclature generally corresponds with Fernald (1950) for the vascular flora, Crum et al. (1965) for the mosses, Schuster (1953) for the liverworts, and Hale and Culberson (1966) for the lichens.

Vegetational Sampling

The methods used are taken from Beil (1969). The communities to be sampled were located using the following selection standards: (1) a community had to be homogeneous in composition and structure; (2) it had to be large enough to permit a sample plot of a given size to be included; (3) a community had to occur commonly throughout the study area. A single plot method was used in sampling all communities.

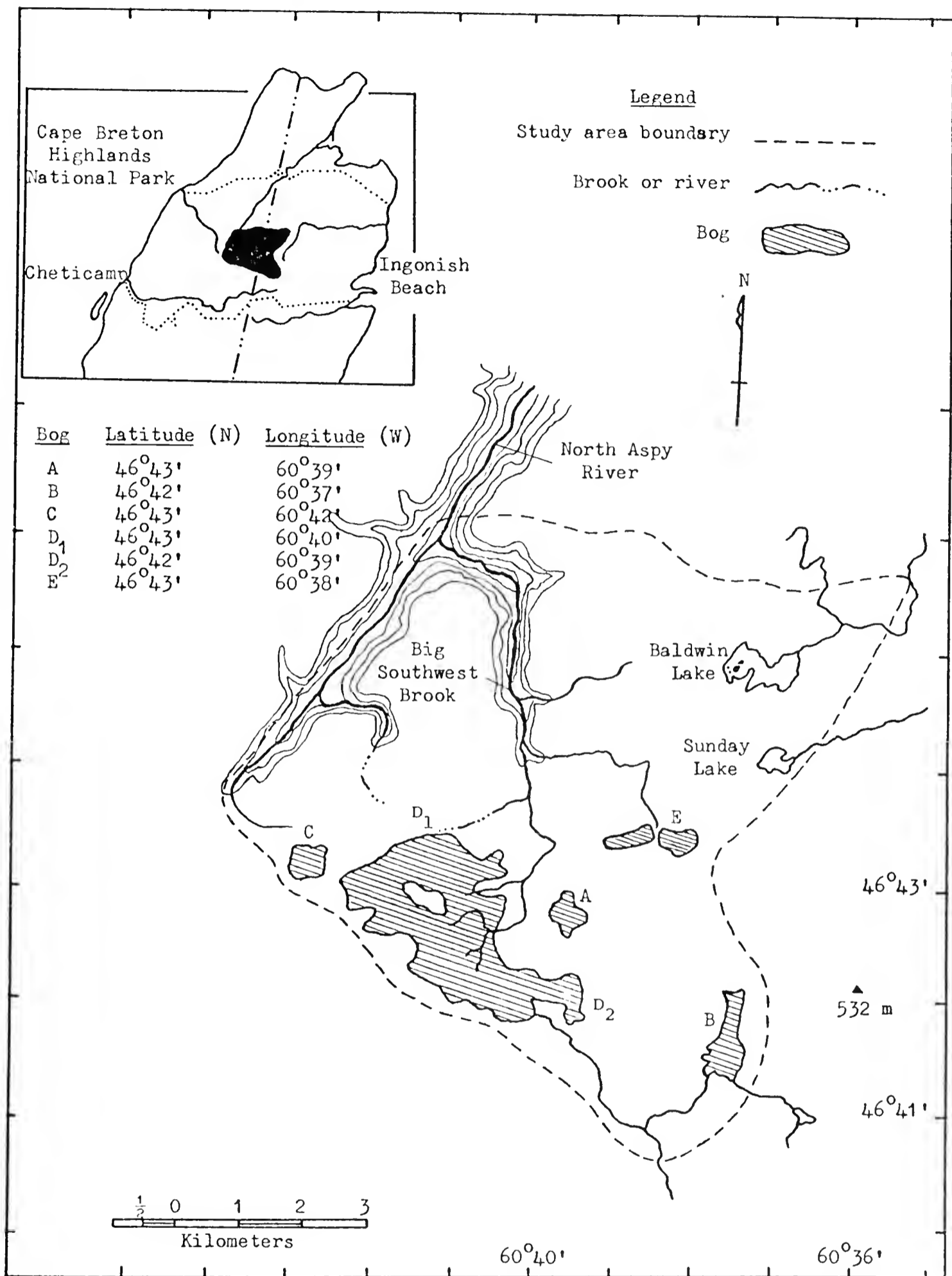


Fig 1. Map of the Sunday Lake, Baldwin Lake, Big Southwest Brook Study Area.

Communities were sampled with either 4 x 4 m (16 sq m) or 10 x 10 m (100 sq m) plots depending on the extent of the vegetation type. With the aid of a compass and metallic tape the plots were subjectively placed in the communities. This procedure permitted an accurate description of the associations to be made using as few sample plots as possible.

The phytosociological methods of the Zürich-Montpellier School were used in analyzing the vegetation (Becking 1957). Percentage cover was determined for the different vegetation layers. The parameters designated for these layers are given in the Appendix.

Species were listed according to strata, with the eleven-point Domin-Krajina scale (Krajina 1933) used to determine species significance for each. Estimates of sociability were also made for each species using an eleven-point Domin-Krajina scale (Becking 1957). These scales are presented in the Appendix. Unfamiliar species were given a descriptive name and collected for later identification.

Qualitative and quantitative data were collected for the following factors; slope gradient, exposure, latitude, longitude, elevation, landform type, pattern of topography, evidence of disturbance, degree of erosion, and percentage of ground surface covered by humus, litter, and decaying wood. Forty-six plots were analyzed.

Vegetation Synthesis and Classification

The methods are derived from Beil (1969). Based on floristic similarity, the sample plots were synthesized into associations. Constancy and average species significance were determined for each species. Constancy expresses how frequently a species will occur in an association provided all plots are of the same dimension. It was calculated by taking the number of plots in which a species occurred and expressing this as a percentage of the total number of plots. A five-class scale was used to express constancy percentages (see Appendix). Average species significance gives an indication of a species' importance in an association. It was determined by adding up the species significance values and dividing the total by the number of plots sampled in each association.

Dwarf Tree Analysis

The term "dwarf tree" was adopted to describe species of the B₁ and B₂ layers that under more favorable environmental conditions would attain normal tree size. These included *Picea mariana*, *Larix laricina*, *Abies balsamea*, and *Sorbus decora*.

In all plots the heights of dwarf trees were measured and the presence or absence of a dead top noted. Tree age was determined by felling representative individuals, removing a section of the stem near ground level and counting the growth rings.

Loose wood fragments, uncovered while digging peat pits, were collected. The wood was thoroughly dried, sectioned, and identified to family.

Soil Sampling and Analysis

The range of peat depth in each plot was determined using a Davis peat sampler. Peat pits were dug in 40 of the 46 plots and the profiles were described by layers distinguished on the basis of color and texture. Whenever possible the peat was excavated down to the underlying mineral substratum. Only a surface sample, to a depth of approximately 30 cm, was taken from the bottom of the ponds. The profile descriptions included: layer depth and thickness, type of boundary, layer color and structure, amount of moisture, root distribution, and presence of buried wood fragments.

A total of 214 samples (195 peat and 19 mineral soil) were collected; of these 151 were selected for analysis. These included one complete profile of samples from every association, except the aquatic one, plus samples from the alternate layers of the remaining peat pits.

The peat and soil samples were thoroughly dried, crushed, screened through a 2 mm sieve, and the fraction at less than 2 mm size was collected for chemical and textural analyses.

Textural analyses on the mineral soils was determined by the hydrometer method (Bouyoucos 1951) using a mechanical stirrer to agitate the soil suspension. The textural classification follows that of the United States Department of Agriculture (sand = 2.00 to 0.05 mm; silt = 0.05 to 0.002 mm; clay = less than 0.002 mm).

Chemical analyses were made on the fraction of less than 2 mm size for the peat and soil samples. Determinations of total nitrogen, total phosphorus, and organic matter were done at the Nova Scotia Agricultural College. The determinations of pH and exchangeable potassium, sodium, magnesium, and calcium were carried out in the Biology and Geology departments, Acadia University.

Total nitrogen and phosphorus determinations entailed a digestion in sulfuric acid and hydrogen peroxide followed by analysis on a Technicon Auto-analyzer. The nitrogen was expressed as a percentage and phosphorus as parts per million. Analysis of the samples for percent organic matter involved a "loss on ignition" determination by difference in weight upon ashing in a furnace. Percentages of organic carbon were estimated from percentages of organic matter found in the samples, by dividing each value for the organic matter (O.M.) by 1.7, as suggested by Buckman and Brady (1969). Then, from the estimated carbon (C) values and the appropriate nitrogen (N) values, the carbon-nitrogen (C/N) ratios were calculated.

To extract the exchangeable cations (potassium, sodium, magnesium, and calcium), the samples were soaked in 1 N ammonium acetate solution with the pH adjusted to 7, and then filtered. The concentrations of the cations were then determined from the filtrates using an atomic absorption spectrophotometer, with atomic absorption for calcium and magnesium, and flame emission for potassium and sodium. The results were expressed in meq/100 g of soil.

Peat and soil pH were determined with a pH meter on samples soaked in distilled water for a minimum of 24 hours.

Climatic Data

A central weather station was established in Bog A (46°43'N, 60°39'W). It consisted of a Stevenson screen situated on the ground, housing a thermograph and a maximum-minimum thermometer; a precipitation gauge; and a totalizing anemometer with cups positioned 2 m above the ground.

A continuous record of temperature, precipitation and total miles of wind was obtained for the period of June 14 to August 30. Spot readings of relative humidity, wind velocity and wind direction were taken. Observations were also made on the number of days of sunshine, overcast skies, and a combination of both.

Observation and Interpretation

Descriptions of the Associations

The descriptions of the bog associations are arranged according to a moisture gradient, proceeding from the wettest to the driest. The following moisture classes are used: hydric—the water level is always above the surface; hygric—the water level is at or near the surface with the upper peat layers being continually wet; mesic—the water level is well below the surface with the surface layers being moderately well drained.

Nuphar variegatum Association (Fig 2)

This Association is common in the ponds scattered on the bogs. These ponds are generally small, thus restricting the size of the communities. The water depths vary between 60 and 120 cm. The underlying peat has an average depth of 1.78 m. The

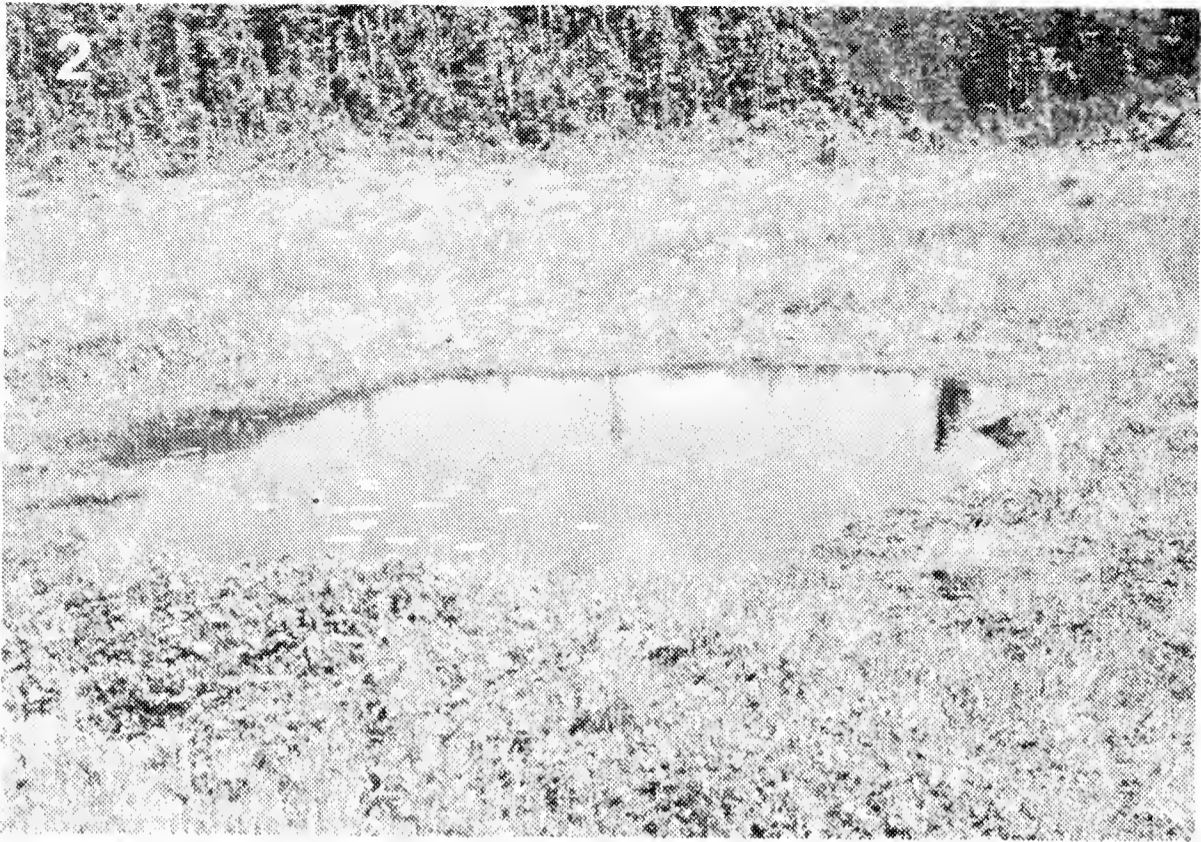


Fig 2. The species-poor *Nuphar variegatum* Association in a bog pond.



Fig 3. The *Eriophorum* Association (white bristles of inflorescence) along the edge of a drainage area.

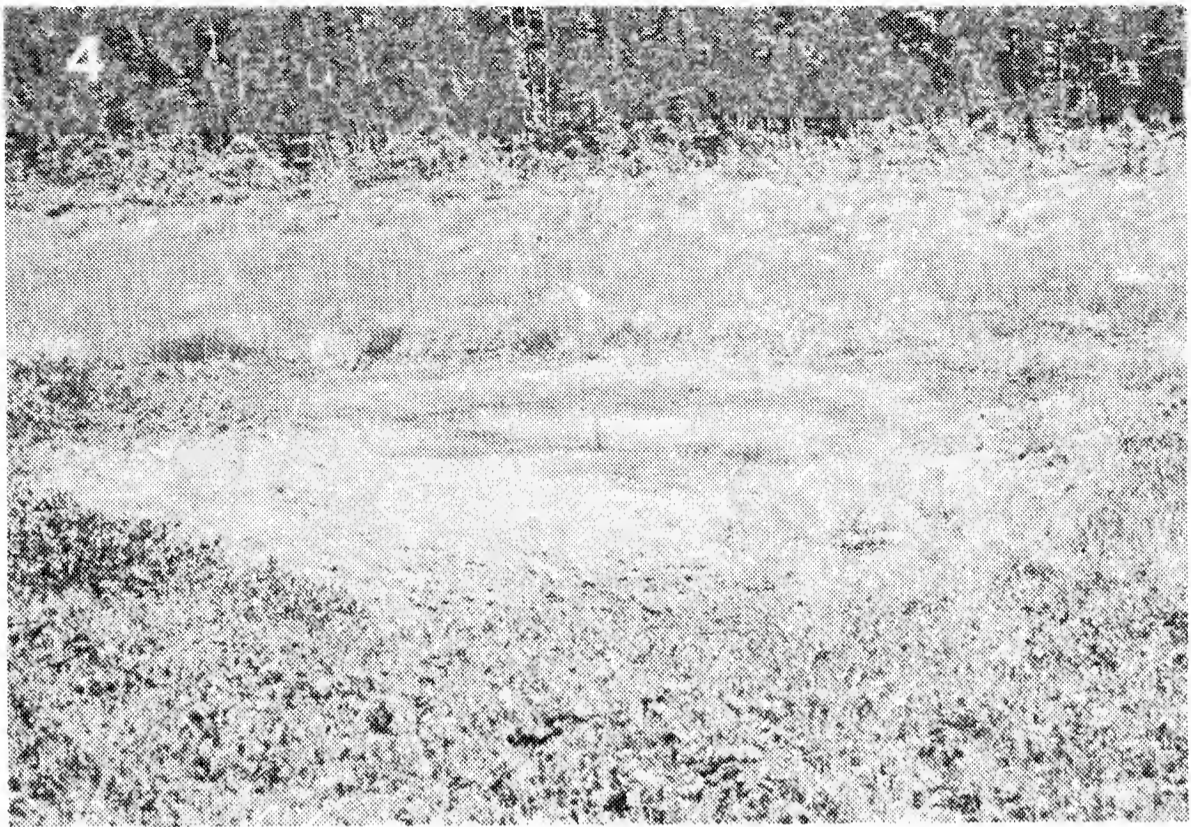


Fig 4. An early development stage of the *Rhynchospora* - *Drosera* Association with remnants of a pond.

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Fig 5. Extensive development of the hygric *Scirpus* - *Sphagnum* Association surrounding bog ponds.



Fig 6. The sub-hygic *Scirpus - Dicranum* Association at the bog's outer edge.



Fig 7. The mesic *Picea - Cladonia* Association (foreground).

water level in the ponds is controlled by precipitation and evaporation with little drainage or runoff occurring. The Association is rated as hydric.

The vegetation structure of the *Nuphar variegatum* Association is simple, consisting of a poorly developed C layer with a cover ranging from 5 to 15%. Except for algae, there is no apparent D layer. The Association is characterized by the presence of *Nuphar variegatum*, a constant dominant with an average species significance of 3.8. The large floating leaves are attached by long petioles to thick rhizomes on the mucky bottoms of the ponds. The only other species found is *Eriocaulon septangulare* having an average species significance of 1.5. It is considered characteristic because of its exclusiveness to this Association. *Eriocaulon*, when abundantly present, seems to play an important role in stabilizing the loose peat at the bottom of the ponds, due to its numerous basal leaves and dense root system. In one of the plots the basal leaves are estimated to cover from 50 to 60% of the surface of the underlying peat.

Table II *Eriophorum angustifolium* Association (5 plots).

Species (total: 19)	Constancy	Av. Species Significance
<i>C Layer</i>		
<i>Eriophorum angustifolium</i>	V	6.8
<i>Rhynchospora alba</i>	V	2.4
<i>Drosera intermedia</i>	IV	1.6
<i>Utricularia cornuta</i>	III	2.0
<i>Drosera rotundifolia</i>	II	0.6
<i>Nuphar variegatum</i>	II	0.4
<i>Kalmia polifolia</i>	II	0.2
<i>Utricularia geminiscapa</i>	II	0.2
<i>D Layer</i>		
<i>Sphagnum cuspidatum</i>	IV	4.6
<i>Sphagnum papillosum</i>	III	2.2
<i>Gymnocolea inflata</i>	III	1.2
<i>Cladopodiella fluitans</i>	II	3.2
Sporadics (with Species Significance values):		
<i>C Layer</i> — <i>Carex aquatilis</i> (4), <i>C. exilis</i> (1), <i>Vaccinium macrocarpon</i> (1), <i>V. oxycoccos</i> (+)		
<i>D Layer</i> — <i>Sphagnum pulchrum</i> (1), <i>S. recurvum</i> (7), <i>Sphenolobus minutus</i> (*)		

*only presence recorded

Eriophorum angustifolium Association (Table II)

The *Eriophorum angustifolium* Association (Fig 3) is not common and is restricted to the edges of shallow ponds in the expanded portions of gullies which dissect the bogs. The surface topography is flat, the exposure neutral, and the surface of the peat completely covered with humus and litter. The edge of the Association bordering the pond is submerged, thus some sedimentation of organic matter is occurring. There is no evidence of erosion, and both runoff and drainage are controlled by the water level of the adjacent pond. The average peat depth is 1.08 m, due to the shallowness of the organic deposits in the depressional areas. The Association is considered to be semi-aquatic and is rated as sub-hydric. Following periods of prolonged rainfall it becomes completely inundated, with the water reaching depths of 25 cm.

Structurally, the Association includes moderately developed C and D vegetation layers. The C layer has a cover ranging from 33 to 60% while the D layer has a cover range of 20 to 99%. The C layer is dominated by *Eriophorum angustifolium*, the characteristic species of the Association, growing best when partially submerged; only those individuals bordering the ponds flowered. *Utricularia geminiscapa* and

Carex aquatilis are exclusive to this Association. The former has a low average species significance while the latter was found in only one plot. Both are good indicators of the semi-aquatic habitat conditions. *Rhynchospora alba* and *Drosera intermedia* are constant non-dominants which occur only in the drier portions of the Association, where the peat surface is usually exposed. *Nuphar variegatum* always shows poor development, attaining importance only in the *Nuphar variegatum* Association. Other plants characteristic of drier areas but occurring here in a stunted form with a low species significance include: *Kalmia polifolia*, *Carex exilis*, *Vaccinium macrocarpon* and *V. oxycoccus*. *Utricularia cornuta* plays an important role in consolidating the surface of the peat through extensive rhizome development.

Sphagnum cuspidatum, dominating the D layer, is a good indicator of the sub-hydric nature of the Association as it usually grows under immersed conditions. It was absent from only one plot where *S. recurvum*, a sporadic, dominated the community with a species significance of 7. *S. papillosum* is present, forming fairly firm cushions which are the initial stages of hummock development. Three liverworts are found in this Association: *Gymnocolea inflata*, usually entangled with *Sphagnum*, *Cladopodiella fluitans*, which is abundant in two plots, and *Sphenolobus minutus*, found intermingled with *Cladopodiella*.

Rhynchospora alba - *Drosera intermedia* Association (Table III)

The *Rhynchospora alba* - *Drosera intermedia* Association (Fig 4) occurs commonly, but never in extensive communities. The size of the largest one studied was less than 200 sq. m. Nichols (1918) used the term "muck mat" to refer to these areas, an appropriate term, as the roots and rhizomes of the plants are so tightly interwoven in the mucky peat that a vegetation mat is formed. The surface topography is extremely flat and the exposure neutral. Humus and litter cover 100% of the peat surface. There is no evidence of erosion or runoff taking place. Drainage is impeded because of the total saturation of the underlying peat. Precipitation collecting on the surface is removed by evaporation and sub-surface drainage. The average peat depth is 2.19 m, ranging from a minimum of 1.8 to a maximum of 2.4 m. Traces of this Association are also found in depressions on shallow peat between the *Eriophorum angustifolium* Association (when it is present) and the *Nuphar*

Table III *Rhynchospora alba* - *Drosera intermedia* Association (6 plots).

Species (total: 19)	Constancy	Av. Species Significance
<i>C Layer</i>		
<i>Rhynchospora alba</i>	V	6.6
<i>Drosera intermedia</i>	V	2.6
<i>Utricularia cornuta</i>	V	1.5
<i>Eriophorum angustifolium</i>	V	1.1
<i>Vaccinium macrocarpon</i>	V	1.1
<i>Andromeda glaucophylla</i>	V	0.8
<i>Kalmia polifolia</i>	II	0.3
<i>Vaccinium oxycoccus</i>	II	0.3
<i>Chamaedaphne calyculata</i>	II	0.3
<i>Drosera rotundifolia</i>	II	0.3
<i>Sarracenia purpurea</i>	II	0.1
<i>D Layer</i>		
<i>Cladopodiella fluitans</i>	V	8.6
<i>Sphagnum pulchrum</i>	V	3.6
<i>Sphagnum cuspidatum</i>	IV	3.6
Sporadics (with Species Significance values):		
<i>C Layer</i> — <i>Calamagrostis pickeringii</i> (2), <i>Carex exilis</i> (+), <i>Picea mariana</i> (+)		
<i>D Layer</i> — <i>Drepanocladus revolvens</i> (4), <i>Orthocaulis gracilis</i> (3)		

variegatum Association. The Association can be considered sub-hydric to hygric as, after heavy rains, standing water collects on the surface to a depth of several centimeters.

Structurally, the vegetation of this Association is composed of a moderately developed C layer with a cover range of 28 to 60% and a well developed D layer with a coverage ranging from 60 to 100%. *Rhynchospora alba*, a characteristic species, dominates the C layer where it is commonly found in clumps with a sociability ranging from 1 to 3. *Drosera intermedia*, a subdominant, attains its highest average species significance in this Association. *Utricularia cornuta* and *Vaccinium macrocarpon* help to bind the fabric of the muck mat into a firm crust through their roots and trailing rhizomes. *Eriophorum angustifolium* has a low average species significance here, having its best development in associations formed in deep depressional areas. *Kalmia polifolia*, *Chamaedaphne calyculata*, *Andromeda glaucophylla*, and *Sarracenia purpurea* grow here in stunted form. They are all characteristic of more mesic habitats. *Vaccinium oxycoccos* and *Drosera rotundifolia* are present with low species significance and constancy. Both species are more abundant in drier associations where they grow entangled with the cushion-forming *Sphagnum*.

The dominant bryophyte of the D layer is *Cladopodiella fluitans*, a characteristic species and an important constituent of the vegetation mat. *Sphagnum cuspidatum* and *S. pulchrum* are the only *Sphagnum* present. The liverworts *Drepanocladus revolvens* and *Orthocaulis gracilis* occur as sporadics.

Scirpus cespitosus - *Sphagnum* spp. Association (Table IV)

This Association (Fig 5) is common on the raised bogs and can be described as a "wet" bog meadow. Conditions are favourable for the growth of cushion-forming *Sphagnum*. The surface topography is flat and the slope gradient varies from 0 to 2 degrees. The peat surface is totally covered in humus and litter. There is no evi-

Table IV *Scirpus cespitosus* - *Sphagnum* spp. Association (6 plots).

Species (total: 30)	Constancy	Av. Species Significance
<i>C Layer</i>		
<i>Scirpus cespitosus</i>	V	4.3
<i>Chamaedaphne calyculata</i>	V	3.5
<i>Andromeda glaucophylla</i>	V	3.1
<i>Kalmia polifolia</i>	V	2.6
<i>Vaccinium oxycoccos</i>	V	2.5
<i>Drosera rotundifolia</i>	V	2.1
<i>Carex exilis</i>	V	1.6
<i>Sarracenia purpurea</i>	V	0.6
<i>Eriophorum angustifolium</i>	IV	1.0
<i>Eriophorum spissum</i>	III	0.5
<i>Kalmia angustifolia</i>	II	0.3
<i>Ledum groenlandicum</i>	II	0.3
<i>D Layer (Bryophytes)</i>		
<i>Sphagnum tenellum</i>	V	4.8
<i>Sphagnum capillaceum</i> var. <i>tenellum</i>	V	3.3
<i>Sphagnum magellanicum</i>	V	3.3
<i>Dicranum leioneuron</i>	V	3.1
<i>Orthocaulis gracilis</i>	V	2.3
<i>Sphagnum papillosum</i>	IV	1.6
<i>Sphagnum fuscum</i>	IV	1.3
<i>Gymnocolea inflata</i>	IV	0.6
<i>Sphagnum pulchrum</i>	III	0.6
<i>D Layer (Lichens)</i>		
<i>Cladonia</i> sp. (alpestris?)	V	1.1
<i>Cladonia pleurota</i>	III	0.6
<i>Ochrolechia trigida</i>	II	0.5
<i>Cetraria islandica</i>	II	0.3
<i>Cetraria islandica</i> ssp. <i>crispa</i>	II	0.3
<i>Cladonia rangiferina</i>	II	0.3
Sporadics (with Species Significance values):		
<i>C Layer</i> — <i>Vaccinium macrocarpon</i> (2)		
<i>D Layer</i> — <i>Dicranum undulatum</i> (2), <i>Ptilidium ciliare</i> (1)		

dence of surface erosion, and runoff is retarded by the abundance of *Sphagnum*. The depth of the peat underlying the Association varies from 1 m in depressional areas to 2.5 m in the higher areas of a bog. The Association can best be described as hygric.

Structurally, the vegetation of the *Scirpus cespitosus* - *Sphagnum* spp. Association has a moderately developed C layer and a well developed D layer. The C layer has a cover varying from 25 to 35% while the D layer varies from 97 to 100%. The dominant species of the C layer is *Scirpus cespitosus* which is constantly present. It is a characteristic plant of the Association and is important in impeding the downward movement of water by consolidating the peat. The plants which attain their highest average species significance in this Association include: *Chamaedaphne calyculata*, *Andromeda glaucophylla*, *Vaccinium oxycoccos*, *Drosera rotundifolia*, and *Eriophorum spissum*. All are constant non-dominants with the exception of *E. spissum*. Both *V. oxycoccos* and *D. rotundifolia* are found growing with the *Sphagnum*.

Carex exilis, *Kalmia angustifolia*, *K. polifolia*, *Ledum groenlandicum* and *Sarracenia purpurea* which are characteristic of more mesic habitats occur here with low cover and poor vigor. *Eriophorum angustifolium* and *Vaccinium macrocarpon* are present with low species significance. These plants reach their ecological optima in more hydric habitats.

Sphagnum tenellum occurs largely in shallow depressions and is the most abundant bryophyte of the Association. *S. magellanicum* and *S. papillosum* are important cushion-forming species. Other *Sphagnum* found in the Association include: *S. capillaceum* var. *tenellum* (= *S. rubellum*), *S. fuscum*, and *S. pulchrum*. Entangled with the *Sphagnum* are the liverworts *Orthocaulis gracilis* and *Gymnocolea inflata*. The following lichens are present in the Association but with low cover and constancy: *Cladonia pleurota*, *C. rangiferina*, *Ochrolechia frigida*, *Cetraria islandica*, and *C. islandica* ssp. *crispa*. They are more abundant in the drier associations.

Scirpus cespitosus - *Dicranum leioneuron* Association (Table V)

The *Scirpus cespitosus* - *Dicranum leioneuron* Association (Fig 6) is confined to the outer edges of the bogs and is always found adjacent to the forest phase of the *Picea mariana* - *Rhododendron canadense* Association that surrounds most of the peatlands. The surface topography is flat with slope gradients varying from 0 to 2 degrees. The peat surface has a 100% cover of humus and litter. Surface runoff occurs and small erosional channels were found in two of the plots. Drainage is impeded because of the extremely compact underlying sedge peat. This peat is usually very shallow and has an average depth of 1.13 m. The Association is rated as sub-hygric.

Structurally, the vegetation consists of a moderately developed C layer with a cover ranging from 25 to 40% and a well developed D layer with a coverage of 95 to 99%. The C layer is dominated by the constant presence of *Scirpus cespitosus*. It is one of the characteristic species of the Association and is very important in consolidating the peat, making it almost impervious to percolation of water. This is an important step in initiating raised bog development.

The following plants attain their highest species significance in this Association: *Aronia prunifolia*, *Carex exilis*, *Sarracenia purpurea*, and *Calamagrostis pickeringii*. All are constant non-dominants. *Chamaedaphne calyculata*, *Kalmia polifolia*, and *Andromeda glaucophylla*, which have a wide tolerance for moisture conditions, occur in this Association with a high constancy. Species found here that are common in drier habitats include: *Coptis trifolia*, *Vaccinium boreale*, *Ledum groenlandicum*, and *Kalmia angustifolia*. In the damper hollows *Eriophorum angustifolium*,

Table V *Scirpus cespitosus* - *Dicranum leioneuron* Association (6 plots).

Species (total: 46)	Constancy	Av. Species Significance
<i>C Layer</i>		
<i>Scirpus cespitosus</i>	V	5.3
<i>Chamaedaphne calyculata</i>	V	3.0
<i>Aronia prunifolia</i>	V	2.8
<i>Kalmia polifolia</i>	V	2.8
<i>Andromeda glaucophylla</i>	V	2.5
<i>Carex exilis</i>	V	2.1
<i>Solidago uliginosa</i>	V	2.1
<i>Vaccinium oxycoccos</i>	V	1.8
<i>Sarracenia purpurea</i>	V	1.6
<i>Calamagrostis pickeringii</i>	V	1.5
<i>Eriophorum angustifolium</i>	V	1.5
<i>Coptis trifolia</i>	V	1.3
<i>Vaccinium boreale</i>	V	1.0
<i>Maianthemum canadense</i>	V	0.8
<i>Ledum groenlandicum</i>	IV	1.3
<i>Trientalis borealis</i>	IV	1.1
<i>Kalmia angustifolia</i>	III	1.1
<i>Drosera rotundifolia</i>	III	1.0
<i>Empetrum nigrum</i>	II	0.6
<i>D Layer (Bryophytes)</i>		
<i>Dicranum leioneuron</i>	V	5.5
<i>Sphagnum capillaceum</i> var. <i>tenellum</i>	V	3.0
<i>Sphagnum tenellum</i>	V	2.8
<i>Orthocaulis gracilis</i>	V	1.6
<i>Sphagnum magellanicum</i>	IV	2.5
<i>Dicranum undulatum</i>	III	1.1
<i>Sphagnum pulchrum</i>	III	0.5
<i>Sphagnum fuscum</i>	II	1.0
<i>Pleurozium schreberi</i>	II	0.6
<i>Ptilidium ciliare</i>	II	0.6
<i>Gymnocolea inflata</i>	II	0.5
<i>D Layer (Lichens)</i>		
<i>Cladonia</i> sp. (<i>alpestris</i> ?)	V	2.8
<i>Cladonia rangiferina</i>	V	1.6
<i>Cetraria islandica</i>	IV	1.1
<i>Cladonia pleurota</i>	IV	0.8
<i>Cladonia uncialis</i>	II	0.3
<i>Ochrolechia frígida</i>	II	0.3
Sporadics (with Species Significance values):		
<i>C Layer</i> — <i>Aster nemoralis</i> (1), <i>Eriophorum spissum</i> (1), <i>Rhynchospora alba</i> (1), <i>Schizaea pusilla</i> (1)		
<i>D Layer</i> — <i>Cetraria islandica</i> ssp. <i>crispa</i> (1), <i>Cladonia alpestris</i> (+), <i>C. pseudorangiformis</i> (1), <i>Microlepidozia setacea</i> (1), <i>Mylia anomala</i> (2), <i>Sphagnum papillosum</i> (2)		

Rhynchospora alba, and *Schizaea pusilla* occur. The latter two are sporadics. *Vaccinium oxycoccos*, *Drosera rotundifolia*, and *Empetrum nigrum* are always found associated with the cushion-forming *Sphagnum*. *Maianthemum canadense* and *Trientalis borealis* occur here with low cover and are species of forest affinity.

The dominant bryophyte of the D layer is *Dicranum leioneuron* with a sociability of 1 to 3. *Sphagnum capillaceum* var. *tenellum*, *S. fuscum*, *Dicranum undulatum*, *Pleurozium schreberi* and *Ptilidium ciliare* when present can be considered as indicators of the drier conditions that prevail. Species occurring in the damper hollows include: *Sphagnum tenellum*, *S. pulchrum*, and *Microlepidozia setacea*. The liverworts *Orthocaulis gracilis* and *Gymnocolea inflata* grow entangled with the *Sphagnum*. *S. magellanicum* is the most important cushion-forming species present but occurs with a low average species significance. *Cladonia rangiferina*, *C. uncialis*, *C. pleurota*, *Cetraria islandica*, and *Ochrolechia frígida* are some of the lichens found here, all being of low species significance.

Picea mariana - *Cladonia rangiferina* Association (Table VI)

This Association (Fig 7) is widespread in the bogs studied. The surface topography is hummocky with the slope gradients varying from 1 to 2 degrees. The hummocks range from 30 to over 120 cm in diameter and from a few to more than 30 cm in height. This increase in elevation above the wetter portions of the bog provides drier conditions allowing the establishment of more mesophytic species. Humus and litter cover 100% of the peat surface. Erosion was observed only in one plot where some of the *Cladonia* cover in the hollows had been washed away. The greatest accumulation of peat is under this Association with an average depth of 2.28 m. The Association is considered to be mesic.

Structurally, the *Picea mariana* - *Cladonia rangiferina* Association consists of three vegetation layers. These include, together with their cover ranges, a poorly developed B₂ layer (27 to 33%), a moderately developed C layer (15 to 53%), and a well developed D layer (90 to 99%). *Picea mariana*, characteristic for the Association, dominates the B₂ and C layers. It occurs in clumps up to 60 cm in height and has a sociability of 2 to 6. *Larix laricina*, also a characteristic species, is a constant non-dominant. It usually grows singly and attains heights of 120 cm. The tallest individuals of *Larix* frequently have dead tops. This may be the result of exposure of this part of the plant above the protective blanket of snow during winter.

Rhododendron canadense, *Ledum groenlandicum*, *Chamaedaphne calyculata*, *Kalmia angustifolia*, *K. polifolia* and *Vaccinium angustifolium* occur in the B₂ layer but are more common in the C layer. In the B₂ layer these species frequently are found growing alongside and intermingled with the *Picea* clumps. In some cases this seems to provide these species the support needed for their upright position.

In the C layer the following species are usually found growing on the hummocks: *Empetrum nigrum*, *Rubus chamaemorus*, *Cornus canadensis*, *Vaccinium boreale*, *Coptis trifolia* and *Trientalis borealis*. They all have high constancy. The presence of *Scirpus cespitosus*, *Calamagrostis pickeringii*, *Eriophorum angustifolium*, *E. spissum* and *Schizaea pusilla* in the hollows and depressions reflects the moist conditions that prevail between the hummocks. *Geocaulon lividum* and *Gaultheria hispidula*, on the other hand, are present only under the *Picea* clumps where shade is maximum. Two species which are able to tolerate both exposure and shade are *Sarracenia purpurea* and *Melampyrum lineare*. In well shaded areas they lack the purplish pigmentation in their leaves.

The dominant bryophytes are *Pleurozium schreberi* and *Sphagnum fuscum*, the latter being an important constituent in the development of hummocks. Other species which can be considered indicative of the mesic site include: *Ptilidium ciliare*, *Dicranum polysetum*, *Hylocomium splendens*, *Rhacomitrium lanuginosum* and *Ptilium crista-castrensis*. Species found between the hummocks in the damper hollows include: *Sphagnum tenellum*, *S. pulchrum* and *Microlepidozia setacea*. The liverworts *Orthocaulis gracilis* and *Mylia anomala* are found entangled with the *Sphagnum*.

The lichen cover is a conspicuous aspect of the Association. *Cladonia rangiferina* is the dominant species with a sociability of 3, while *C. alpestris* is a constant sub-dominant. Other *Cladonia* present include: *C. pleurota*, *C. uncialis*, *C. gracilis*, *C. pseudorangiformis*, *C. arbuscula*, *C. crispata*, *C. mitis* and *C. squamosa*. *Cetraria islandica* occurs with a high constancy and low average species significance.

Epiphytic lichens found on the dwarf *Picea* and *Larix* trees include: *Cetraria aurescens*, *Alectoria americana*, *A. ochroleuca*, *Ramalina miniscula* and *Usnea cavernosa*.

Table VI *Picea mariana* - *Cladonia rangiferina* Association (6 plots).

Species (total: 68)	Constancy		Av. Species Significance	
	C	B ₂	C	B ₂
<i>B₂ and C Layers</i>				
<i>Picea mariana</i>	V	V	4.3	3.5
<i>Larix laricina</i>	V	V	1.0	1.1
<i>Rhododendron canadense</i>	V	III	2.1	1.1
<i>Ledum groenlandicum</i>	V	III	3.3	0.8
<i>Chamaedaphne calyculata</i>	V	III	3.0	0.8
<i>Kalmia angustifolia</i>	V	II	3.5	0.6
<i>Kalmia polifolia</i>	V	II	2.8	0.6
<i>Vaccinium angustifolium</i>	V	II	2.0	0.5
<i>Scirpus cespitosus</i>	V		3.1	
<i>Empetrum nigrum</i>	V		3.0	
<i>Rubus chamaemorus</i>	V		2.6	
<i>Aronia prunifolia</i>	V		2.3	
<i>Cornus canadensis</i>	V		1.8	
<i>Vaccinium boreale</i>	V		1.6	
<i>Drosera rotundifolia</i>	V		1.5	
<i>Vaccinium oxycoccos</i>	V		1.5	
<i>Calamagrostis pickeringii</i>	V		1.3	
<i>Coptis trifolia</i>	V		1.3	
<i>Eriophorum angustifolium</i>	V		1.1	
<i>Solidago uliginosa</i>	V		1.1	
<i>Trientalis borealis</i>	V		1.1	
<i>Sarracenia purpurea</i>	V		1.0	
<i>Melampyrum lineare</i>	IV		0.8	
<i>Geocaulon lividum</i>	IV		0.5	
<i>Deschampsia flexuosa</i>	III		0.6	
<i>Andromedia glaucophylla</i>	III		0.5	
<i>Schizaea pusilla</i>	III		0.5	
<i>Eriophorum spissum</i>	III		0.5	
<i>Juniperus communis</i>	II		0.8	
<i>Maianthemum canadense</i>	II		0.6	
<i>Gaultheria hispidula</i>	II		0.3	
<i>D Layer (Bryophytes)</i>				
<i>Pleurozium schreberi</i>	V		4.5	
<i>Sphagnum fuscum</i>	V		4.0	
<i>Ptilidium ciliare</i>	V		2.5	
<i>Dicranum undulatum</i>	V		1.8	
<i>Hylocomium splendens</i>	IV		2.1	
<i>Orthocaulis gracilis</i>	IV		1.3	
<i>Sphagnum capillaceum</i> var. <i>tenellum</i>	IV		1.1	
<i>Sphagnum tenellum</i>	IV		0.8	
<i>Microlepidozia setacea</i>	IV		0.6	
<i>Rhacomitrium lanuginosum</i>	III		1.0	
<i>Ptilium crista-castrensis</i>	III		0.6	
<i>Dicranum leioneuron</i>	II		0.6	
<i>Cephalozia bicuspidata</i>	II		0.5	
<i>Sphagnum capillaceum</i>	II		0.3	
<i>Sphagnum pulchrum</i>	II		0.3	
<i>D Layer (Lichens)</i>				
<i>Cladonia rangiferina</i>	V		5.6	
<i>Cladonia alpestris</i>	V		4.1	
<i>Cladonia pleurota</i>	V		1.5	
<i>Cladonia uncialis</i>	V		1.5	
<i>Cetraria islandica</i>	V		1.3	
<i>Cladonia gracilis</i>	V		0.8	
<i>Cladonia</i> sp. (<i>alpestris</i> ?)	IV		1.8	
<i>Cladonia pseudorangiformis</i>	II		0.3	
<i>Ochrolechia frigida</i>	II		0.3	
Sporadics (with Species Significance values):				
<i>B Layer</i> — <i>Aronia prunifolia</i> (2)				
<i>C Layer</i> — <i>Abies balsamea</i> (1), <i>Amelanchier bartramiana</i> (1), <i>Carex exilis</i> (1), <i>Epigaea repens</i> (1), <i>Nemopanthus mucronata</i> (1)				
<i>D Layer</i> — <i>Cetraria islandica</i> ssp. <i>crispa</i> (1), <i>Cladonia arbuscula</i> (*), <i>C. crispata</i> (1), <i>C. mitis</i> (4), <i>C. squamosa</i> (1), <i>Dicranum polysetum</i> (1), <i>Gymnocolea inflata</i> (1), <i>Mylia anomala</i> (1)				

*only presence recorded

Picea mariana - *Rhododendron canadense* Association (Table VII)

This Association is limited to the banks of the drainage gullies dissecting the bogs (Fig 8). The surface topography is irregular and the slope gradients vary from 0 to 4 degrees. Humus and litter cover between 95 and 100% of the peat surface. There is no evidence of erosion and due to the topographic position there is a slight amount of runoff occurring. The average depth of peat is 1.69 m on the banks and 1.19 m in the gullies. The driest conditions within a bog occur in this Association which is considered to be submesic.

Structurally, the *Picea mariana* - *Rhododendron canadense* Association consists of four strata, a poorly developed B₁ layer with a cover ranging from 1 to 40% and moderately developed B₂, C and D layers. The coverages for these layers are: B₂ (15 to 85%), C (40 to 70%), and D (7 to 85%).

Picea mariana, one of the characteristic species with a sociability of 3 to 7, dominates the shrub layer. It occurs with only minor significance in the C layer. *Abies balsamea* and *Larix laricina* occur with low constancy and cover in the B₁, B₂ and C layers. Other shrubs characteristic of the B₂ sublayer include: *Amelanchier bartramiana*, *Nemopanthus mucronata*, and *Viburnum cassinoides*. *Betula papyrifera* and *Sorbus decora* occur in the B₂ sublayer only as sporadics.

Rhododendron canadense, a characteristic species and occurring in the B₂ sublayer, is the dominant species of the C layer. Other species found in the shrub layer but becoming more common in the C layer are *Ledum groenlandicum*, *Kalmia angustifolia*, *Vaccinium angustifolium*, *Aronia prunifolia* and *Myrica gale*.

The C layer contains forest species which in the bogs are exclusive to this Association. Included here are: *Clintonia borealis*, *Carex trisperma*, *Taxus canadensis* and *Linnaea borealis*. The following plants attain their highest average species significance values in this Association: *Cornus canadensis*, *Coptis trifolia*, *Vaccinium boreale*, *Epigaea repens*, *Melampyrum lineare*, *Gaultheria hispidula*, *Trientalis*

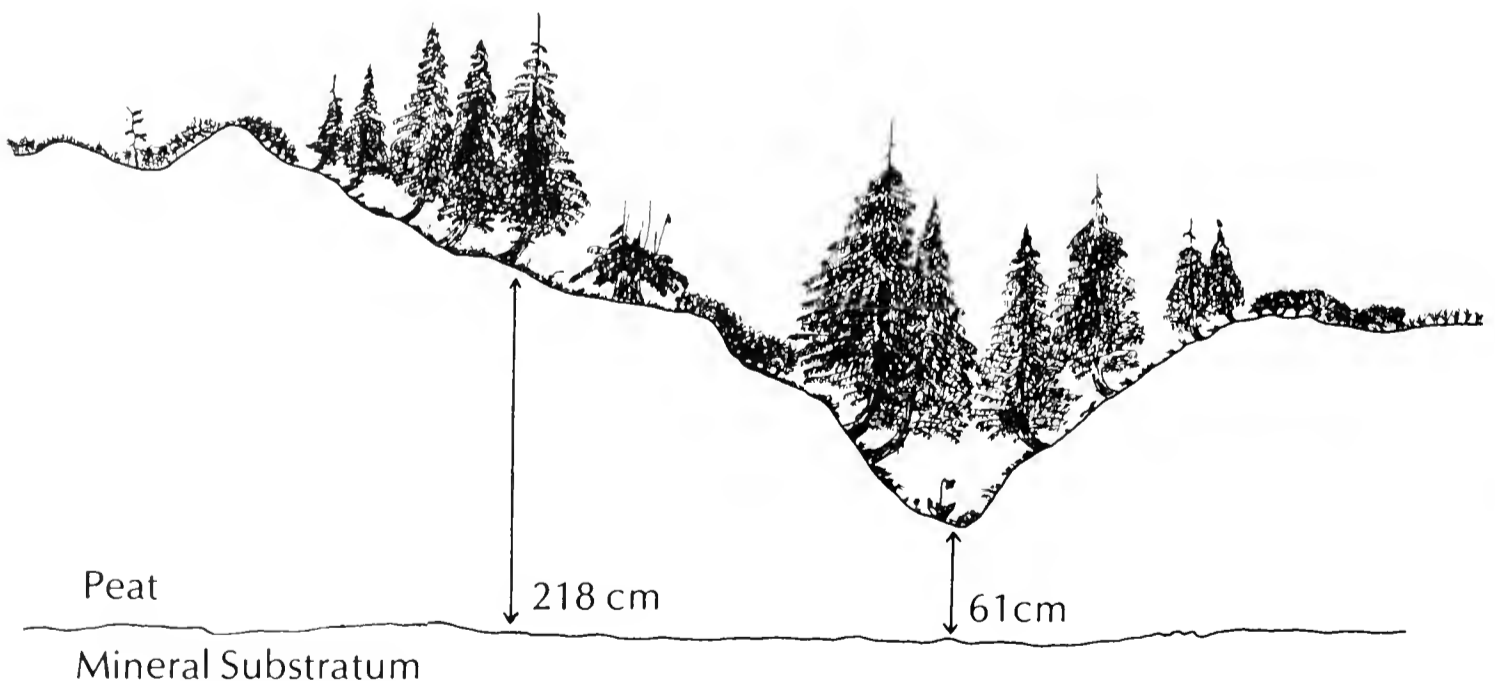


Fig 8. Profile of a drainage gully showing the *Picea mariana* - *Rhododendron canadense* Association.

Table VII *Picea mariana* - *Rhododendron canadense* Association (6 plots).

Species (total: 60)	Constancy			Av. Species Significance		
	C	B ₂	B ₁	C	B ₂	B ₁
<i>B and C Layers</i>						
<i>Picea mariana</i>	IV	V	V	1.1	5.8	3.3
<i>Abies balsamea</i>	II	III	III	0.5	0.3	0.3
<i>Larix laricina</i>		V	II		1.0	+.+
<i>Amelanchier bartramiana</i>	II	V		0.6	4.5	
<i>Nemopanthus mucronata</i>		V			2.3	
<i>Rhododendron canadense</i>	V	IV		4.1	2.8	
<i>Ledum groenlandicum</i>	V	IV		2.0	1.1	
<i>Kalmia angustifolia</i>	V	IV		1.8	0.8	
<i>Vaccinium angustifolium</i>	V	III		1.8	1.1	
<i>Myrica gale</i>	IV	III		1.3	1.1	
<i>Aronia prunifolia</i>	V	III		1.8	1.0	
<i>Viburnum cassinoides</i>		III			1.0	
<i>Kalmia polifolia</i>	V	III		2.0	0.6	
<i>Taxus canadensis</i>	III	III		0.6	0.3	
<i>Clintonia borealis</i>	V			3.0		
<i>Cornus canadensis</i>	V			2.8		
<i>Coptis trifolia</i>	V			1.8		
<i>Vaccinium boreale</i>	V			1.8		
<i>Epigaea repens</i>	V			1.5		
<i>Rubus chamaemorus</i>	V			1.5		
<i>Melampyrum lineare</i>	V			1.3		
<i>Calamagrostis pickeringii</i>	V			1.1		
<i>Eriophorum angustifolium</i>	V			1.1		
<i>Gaultheria hispidula</i>	V			1.1		
<i>Trientalis borealis</i>	V			1.1		
<i>Maianthemum canadense</i>	V			1.0		
<i>Carex trisperma</i>	IV			0.6		
<i>Sarracenia purpurea</i>	IV			0.6		
<i>Scirpus cespitosus</i>	IV			0.6		
<i>Deschampsia flexuosa</i>	III			0.5		
<i>Linnaea borealis</i>	III			0.5		
<i>Andromeda glaucophylla</i>	III			0.5		
<i>Empetrum nigrum</i>	III			0.5		
<i>Carex oligosperma</i>	II			0.3		
<i>Geocaulon lividum</i>	II			0.3		
<i>Solidago uliginosa</i>	II			0.3		
<i>D Layer (Bryophytes)</i>						
<i>Pleurozium schreberi</i>	V			4.8		
<i>Hylocomium splendens</i>	V			3.0		
<i>Dicranum scoparium</i>	V			2.8		
<i>Ptilidium ciliare</i>	V			2.1		
<i>Dicranum fuscescens</i>	V			1.3		
<i>Sphagnum subsecundum</i>	V			1.1		
<i>Sphagnum palustre</i>	IV			0.8		
<i>Orthocaulis gracilis</i>	II			0.6		
<i>Leucobryum glaucum</i>	II			0.3		
<i>Ptilium crista-castrensis</i>	II			0.3		
<i>D Layer (Lichens)</i>						
<i>Cladonia rangiferina</i>	V			1.3		
<i>Cladonia gracilis</i>	V			0.8		
<i>Cladonia pleurota</i>	V			0.8		
<i>Cladonia pseudorangiformis</i>	IV			0.5		
<i>Cladonia squamosa</i>	III			0.5		

Sporadics (with Species Significance values):

B₂ Layer—*Betula papyrifera* (1), *Chamaedaphne calyculata* (3), *Sorbus decora* (+)

C Layer—*Aster nemoralis* (1), *Carex exilis* (1), *Chamaedaphne calyculata* (3), *Larix laricina* (+), *Nemopanthus mucronata* (2)

D Layer—*Cladonia crispata* (1), *C. mitis* (2), *Dicranum polysetum* (3), *D. undulatum* (2)

borealis and *Maianthemum canadense*. All are constantly present and considered indicators of the drier habitat. Species occurring in areas receiving the maximum amount of light include: *Calamagrostis pickeringii*, *Scirpus cespitosus*, *Deschampsia flexuosa* and *Solidago uliginosa*. *Eriophorum angustifolium* and *Andromeda*

glaucophylla occur here but reach their optima in wetter associations. *Rubus chamaemorus*, a characteristic species of dry bog associations, is found here with a fairly high constancy.

The dominant species of the D layer is *Pleurozium schreberi* with a sociability of 1 to 3. The following constant species are all of forest affinity: *Hylocomium splendens*, *Dicranum scoparium*, *Ptilium crista-castrensis* and *Ptilidium ciliare*. Species found on the gully bottoms where damper conditions prevail include: *Sphagnum subsecundum*, *S. palustre* and *Leucobryum glaucum*.

The most abundant lichen is *Cladonia rangiferina*, occurring in the exposed areas on hummocks. *C. gracilis* and *C. pseudorangiformis* are found only in well shaded areas.

Cetraria aurescens and *Alectoria americana* are the most important epiphytes on the dwarf trees.

Description of the Bog Soils

The organic deposits underlying the bog associations can be classified under two categories, sedimentary and fibrous peat (Buckman and Brady 1969). The latter category includes sedge peat, and *Sphagnum* peat, with the distinction between the two based on the higher water-holding capacity of the *Sphagnum* peat. In some bog areas deposits composed mainly of one type of fibrous peat are found while in other sections both occur in the same profile. Sedimentary peat is deposited under long standing bodies of water and occurs in the lower sections of some profiles.

The average depth of peat in the communities sampled ranged from a minimum of 108 cm in the *Eriophorum angustifolium* Association, located in depressional areas, to a maximum of 228 cm in the *Picea mariana* - *Cladonia rangiferina* Association. The peat overlies a mineral substratum composed largely of granitic bedrock, often bare or thinly covered with a sandy loam soil (Table VIII). This substratum is practically impervious to the downward movement of water.

The profiles studied are composed of distinct layers which differ in physical and chemical characteristics, the degree of decomposition, and the nature of the original vegetation. The boundary between each layer is clear and smooth.

Table VIII Textural Analysis - Mineral Substratum.

Association	No. of Samples	Average % Sand	Average % Silt	Average % Clay	Textural Class
<i>Eriophorum</i>	1	79.2	19.3	1.5	loamy sand
	2	61.8	34.7	3.5	sandy loam
<i>Scirpus</i> - <i>Sphagnum</i>	1	75.2	22.3	2.5	loamy sand
	3	61.8	36.6	1.6	sandy loam
<i>Scirpus</i> - <i>Dicranum</i>	1	81.2	16.9	1.9	loamy sand
	4	64.2	32.5	3.3	sandy loam
<i>Picea</i> - <i>Cladonia</i>	1	66.0	30.3	3.7	sandy loam
<i>Picea</i> - <i>Rhododendron</i>	1	92.1	7.9	-	sand
	3	61.2	34.5	4.3	sandy loam

Physical Characteristics

The number of layers of peat found over the mineral substratum ranged from a minimum of three to a maximum of ten. The outer edges of the bog, drainage gullies, and depressions within the bog are the areas where the minimum number of layers occur. The former represents an immature phase in bog development while the latter two are mainly erosional areas. The maximum number of layers are found in those sections of the bog where hummocks are present.

The layers vary in thickness from 4 cm to 81 cm with the average being 21 cm. There is no apparent sequence in the thickness of layers in each profile, suggesting a differential rate of bog growth. No attempt was made to describe the various colors found in a peat profile as no color chart was available. It may be noted, however, that each layer is usually distinct in color from those adjacent to it.

The structure of the peat ranges from a loose mass to a compact fibrous substance. The former is found in the surface layers of the wetter associations where it is being deposited through sedimentation. Compact peat is found throughout the profiles of the *Scirpus cespitosus* - *Dicranum leioneuron* Association located at the bog's edge. The peat here has been formed by the continued presence of sedges, like *Scirpus cespitosus*, which consolidate the organic matter into a dense fibrous structure that is almost impervious to the downward movement of water. Other associations on the bog overlie peat which is intermediate between these two extremes, being composed of *Sphagnum* and sedge remains. This suggests the presence of different successional stages in the bog's history.

The moisture status of the peat is dependent upon precipitation and the nature of the organic matter. The *Sphagnum* peat is always wetter than the more compact sedge peat. Lateral seepage was observed in several profiles where a layer of *Sphagnum* peat overlies a layer of sedge peat. The former allows percolation of water while the latter is impervious to drainage. Precipitation water drains to the level of the sedge peat and then moves laterally. This phenomenon, together with the high water holding capacity of the *Sphagnum*, permits the water table to be maintained near the surface.

Root distribution is concentrated in the upper peat layers, the average rooting depth being around 45 cm. The dwarf trees on the mature hummocks and in the drainage gullies have shallow, spreading root systems. This suggests edaphic conditions are more favourable for root growth near the surface where better drainage results in improved aeration of the peat.

In all associations where peat pits were dug, buried wood fragments were found. In the peat underlying the ponds solid objects were often encountered in making depth determinations. It is probable that these objects were also buried wood fragments as no other solid objects were found in the peat. The significance of the buried wood is dealt with in the Discussion.

Chemical Analysis

The chemical properties of the peat and soil samples are very similar among the associations (Table IX). All peat samples showed an acidic reaction with pH ranging from 3.9 to 5.1. In the profiles, acidity always decreased from the surface to the underlying mineral substratum. This is possibly because acidity varies with the degree of oxidation and humification that is taking place. Drier, humified peats have lower pH values (Pearsall 1938) and occur in surface layers when an equilibrium has been established between accumulation and oxidation (Daubenmire 1968). Acidity also increased in the surface layers from the wettest to the driest associations. This is possibly because in drier peat sulfides are oxidized to sulfuric acid, thus lowering the pH (Gorham 1953). The soil collected from the surface layer of the mineral substratum ranged in pH from 4.4 to 5.6, indicating the acidic nature of the parent rocks. This would have enabled the substratum to be initially colonized by plants tolerant to acidic conditions (like *Sphagnum*), thus favoring bog development.

Percent carbon remains relatively constant in all the peat samples because there is no mineral soil incorporated in the organic matter. Total nitrogen is present in very small amounts. The nitrogen content of *Sphagnum* is low (Gorham 1953; Mal-

Table IX Chemical analysis of the bog soil samples (based on averages).

Association	Layer	pH	C(%)	Total N(%)	C/N	Total P(ppm)	Exchangeable Cations			
							K	Na	Mg	Ca
<i>Nuphar</i>	surface	4.4	57.68	1.84	31	237	0.37	3.12	13.28	3.56
<i>Eriophorum</i>	surface	4.2	57.18	1.56	36	174	0.09	1.40	10.79	5.04
	subsurface	4.7	56.33	1.63	34	390	0.08	1.25	5.83	4.92
	+ substratum	4.9	3.92	0.09	43	250	0.04	0.19	0.42	0.59
<i>Rhynchospora - Drosera</i>	surface	4.2	57.98	1.59	36	153	0.15	1.72	13.29	3.83
<i>Scirpus - Sphagnum</i>	surface	4.2	58.00	1.55	37	187	0.17	1.58	9.21	2.70
	subsurface	4.4	56.80	1.43	39	316	0.09	1.59	8.69	4.18
	substratum	4.8	4.16	0.08	52	191	0.04	0.22	0.51	0.44
<i>Scirpus - Dicranum</i>	surface	4.2	57.38	1.20	47	260	0.56	1.69	14.73	4.14
	subsurface	4.3	56.27	1.47	38	305	0.17	1.45	9.35	2.74
	substratum	4.7	4.02	0.11	36	220	0.03	0.22	0.21	0.29
<i>Picea - Cladonia</i>	surface	4.2	58.12	0.91	63	137	0.42	1.89	16.14	4.57
	*subsurface	4.9	54.67	1.90	28	375	0.08	0.97	4.23	2.00
	*substratum	5.1	1.50	0.06	25	145	0.02	0.22	0.14	0.19
<i>Picea - Rhododendron</i>	surface	3.9	56.87	1.13	50	131	0.09	1.54	15.66	3.56
	subsurface	4.5	56.75	1.05	54	225	0.11	1.43	8.36	7.73
	substratum	4.9	2.28	0.06	38	307	0.05	0.21	0.43	0.65

+ substratum = the mineral soil

*based on a single sample

mer and Sjörs 1955), and because these plants make up the bulk of the peat deposits, there will be little nitrogen available even after decomposition. The main source of nitrogen for bog vegetation comes from atmospheric precipitation (Gorham 1955; Eriksson et al. 1958-1962). The amount of nitrogen concentrated in rainwater is very small. Nitrogen, therefore, may become a severe limiting factor in raised bogs. Bog deciduous species compensate for this deficiency by reabsorbing greater amounts of nitrogen from their leaves prior to leaf fall than do non-bog plants (Small 1972b).

The carbon-nitrogen ratios are all very high, but they usually show a gradual decrease with increasing depth suggesting that some nitrogen is released in the lower layers through decomposition. The high ratios indicate that there is insufficient nitrogen available for microbial activity, and decomposition, therefore, proceeds slowly.

Phosphorus, present in low concentrations, is fairly constant within the same layers in different associations. Within the same association, however, there is always a pronounced increase in phosphorus in the sub-surface layers. This is probably due to leaching. Small amounts of phosphorus are added to the bog through atmospheric precipitation (Gorham 1957b; Sparling 1967). Available phosphorus in raised bogs is usually no greater than 16 ppm (Jasmin and Heeney 1960). Phosphorus, therefore, like nitrogen may become a limiting factor in these bogs.

Ombrogenous bogs, by definition, are removed from a nutrient-enriched water supply that has percolated through or run off the mineral soil. They are entirely dependent on atmospheric precipitation for nutrient supply, and thus enrichment of peat occurs. The peat samples contained concentrations of exchangeable cations up to 34 times as great as those of the underlying mineral substratum.

Magnesium is present in concentrations two to four times those of calcium in peat, while in the mineral substratum these cations occur in a 1:1 ratio. Magnesium is not as abundant in the lowest peat layers where the influence of precipitation decreases. Calcium, on the other hand, shows a slight increase in the lower peat layers. Next to hydrogen, calcium is the most important exchangeable cation and

is taken up readily by the plants, thus reducing its availability in the upper layers. As decomposition increases with increasing depth more calcium is released from the plant remains.

Sodium is present in concentrations ranging from three to 17 times those of potassium in the peat. In the mineral substratum sodium occurs in concentrations four to 11 times as great as those of potassium. Both these cations decrease in concentration with increasing depth.

The basic cation concentrations in the peat samples differed from most soils in that both magnesium and sodium were available in large amounts. The usual order of magnitude of the major cations in soils is as follows: $\text{Ca} \sim \text{Mg} > \text{K} > \text{Na}$ (Malmer and Sjörs 1955; Buckman and Brady 1969). In the analyzed peat samples these cations were available in the following order of abundance: $\text{Mg} > \text{Ca} > \text{Na} > \text{K}$. This change can be explained by the proximity of the Cape Breton Plateau to the sea, and the influence that the latter has in increasing the amounts of dissolved chlorides of magnesium and sodium in rain water. Sea spray, containing these chlorides, is picked up by the wind and transported inland where it becomes deposited on the bogs through precipitation. The details as to how this phenomenon takes place are described by Gorham (1957b). Large waves created by high winds develop foam patches containing numerous bubbles. These bubbles burst and create tiny droplets which are picked up by the wind and act as nuclei for the development of rain drops.

The concentrations of these chlorides in rain water vary with the distance from the sea. Sparling (1967) reports that these electrolytes have been transported over distances of up to 32 km with favorable winds. The bogs in the study area are approximately 19 km from the surrounding sea, well within the range of transport.

The cation imbalance found in the peat samples is strong evidence to suggest that sea spray is an important source of nutrients for the raised bogs of the Cape Breton Plateau. However, the overall nutritional status of the raised bogs is poor, with the low availability of nitrogen and phosphorus probably being important limiting factors. The chemistry of the peat and mineral soil samples does not show a significant difference between the bog associations so that other factors such as water level and topography probably control their distribution.

Climate

The weekly maximum temperatures for the summer of 1970 were lower on the Cape Breton Plateau than those of Cheticamp and Ingonish Beach (Fig 9). The average weekly maximum on the Plateau was 3.5°C cooler than Ingonish Beach and 1.6°C cooler than Cheticamp. The greatest difference in the maximum temperature between the Plateau and Ingonish Beach occurred during the two week period of August 16-29 when the Plateau was 5.6°C cooler, while the greatest difference between the Plateau and Cheticamp occurred during the weeks of August 2-8 and 23-29 when the former was 3.9°C cooler. The highest maximum temperature on the Plateau was recorded on July 26 at 30°C. The warmest weather for the three areas occurred during the week of July 26 to August 1.

The weekly minimum temperatures were also the lowest on the Plateau. Here the average weekly minimum temperature was 4.2°C cooler than Ingonish Beach and 2.9°C cooler than Cheticamp. The greatest difference in the minimum temperature between the Plateau and Ingonish Beach occurred during the week of June 14-20 when the Plateau was 8.8°C cooler, while the greatest difference between the Plateau and Cheticamp occurred during the week of August 2-8 when the former was 5.6°C cooler. The lowest minimum temperature on the Plateau was -0.5°C on June 14.

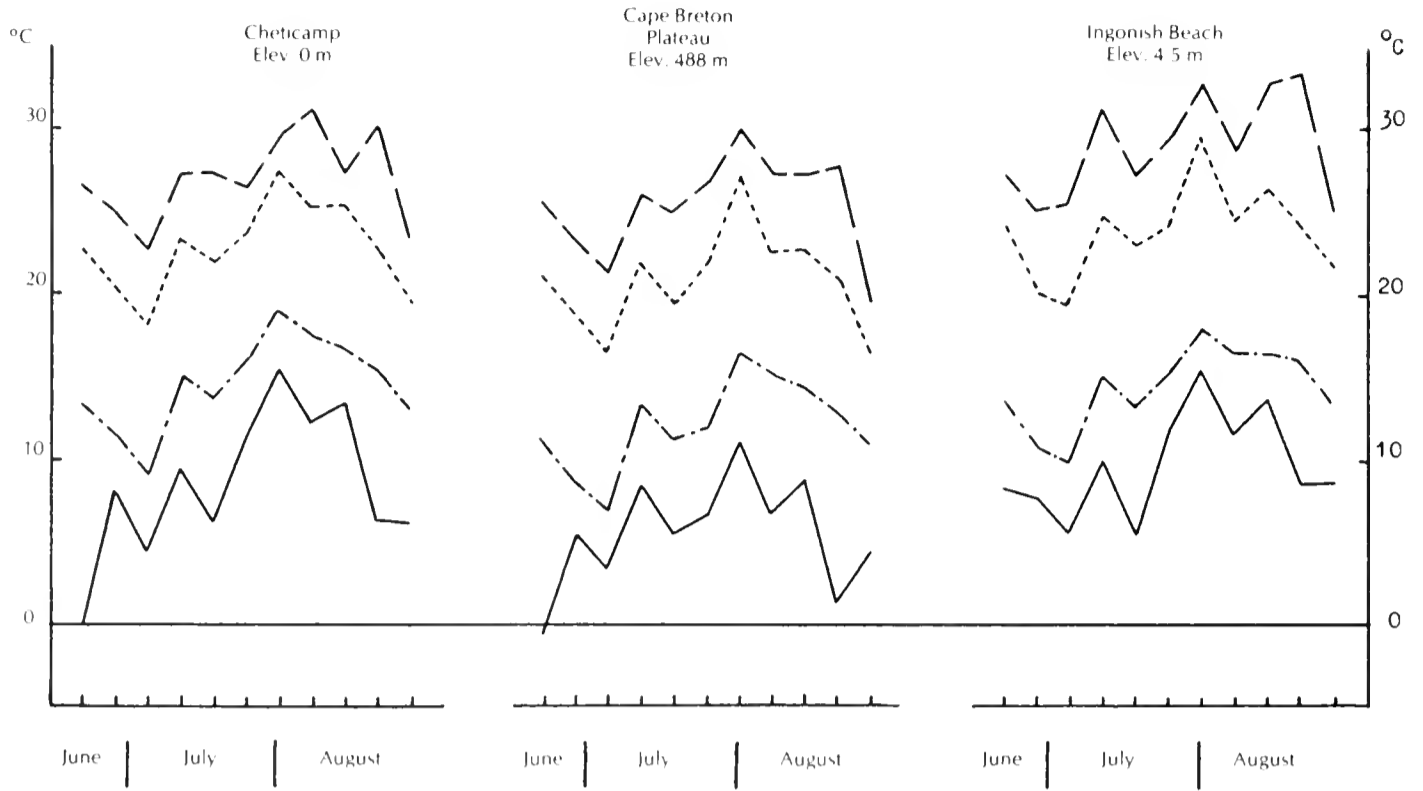
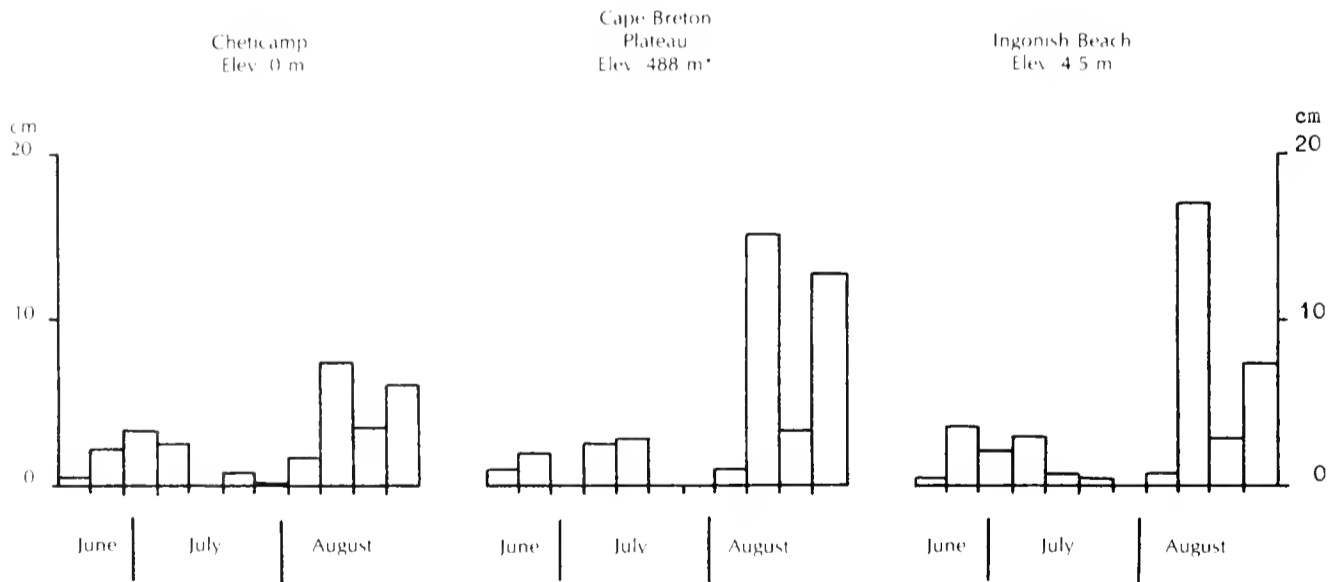


Fig 9. Weekly temperature summaries (June 14 - August 29, 1970) showing maximum (— —), mean maximum (— — — —), mean minimum (— · — ·), and minimum (— — — —).



*The total precipitation for the week of August 24-30 on the Plateau is not shown accurately because rain which fell on August 21 was collected with the total for the last week.

Fig 10. Weekly precipitation totals (June 15 - August 30, 1970).

There is no consistent significant difference between the three areas with regard to the daily temperature ranges. Approximately 60% of the summer days on the Plateau had a greater daily temperature range than those at Cheticamp, while only 41% had a greater temperature range than those at Ingonish Beach.

The data show that the Plateau is cooler during the summer than both of the coastal areas. The minimum temperatures appear to be the most critical on the Plateau with possibly only two months of the year being frost free. This may constitute an important limiting factor in the survival and growth of some of the plant species.

During the 77 day observation period 41.12 cm of rain were recorded at the Plateau Station (Fig 10). Ingonish Beach had almost as much rain with 38.53 cm recorded. Cheticamp was the driest site receiving only 28.15 cm. These results are consistent with the long range summaries presented for the two coastal stations in Table I. As the moisture-laden clouds, moving from west to east, reach the Plateau, the storm systems rise to higher elevations where cooler air temperatures prevail. This probably results in condensation, giving the region east of Cheticamp larger amounts of rainfall.

In all three areas August was the wettest month, accounting for 79% of the total summer's precipitation on the Plateau, 72% for Ingonish Beach, and 67% for Cheticamp. The average weekly rainfall for the summer period was 3.73 cm on the Plateau. This was the highest for the three areas with Ingonish Beach having an average of 3.50 cm, and Cheticamp only 2.55 cm. The largest amount of precipitation for a one week period was recorded during August 10-16, at all three stations. The Plateau received 15.27 cm, Ingonish Beach 17.12 cm, and Cheticamp only 7.59 cm. The largest amount of rainfall over a 24 hour period occurred in all three areas on August 12. The heaviest precipitation was recorded at Ingonish Beach at 14.37 cm, while Cheticamp had the least amount at 3.96 cm. On the Plateau 8.58 cm fell over the 24 hour period, with 5.09 cm of this total amount falling between 1045 hrs and 1745 hrs. These "cloudbursts" may aid in the erosion of a bog's surface. A large amount of runoff water results from heavy rainfall. This water creates small channels which may grow to become large erosional gullies. The exposed peat in these gullies remains in a very unstable condition until a vegetation cover can be re-established.

The results from the precipitation data indicate that the Plateau was slightly wetter than Ingonish Beach during the summer months of 1970, and that both of these areas were approximately one and a half times wetter than Cheticamp.

Precipitation data for Ingonish Beach, based on a 30 year period, show the rainfall to be abundant and evenly distributed throughout the year. The present study revealed that for the summer months the Plateau approximated Ingonish Beach in total precipitation. If this similarity in the precipitation data between the two areas extends throughout the entire year, then the long range summaries available for Ingonish Beach could be used to describe the conditions on the Plateau.

Spot readings of relative humidity were made at one of the bogs from June 18 to July 11, between 0830 hrs and 1830 hrs. Based on a total of 18 readings, the average relative humidity was 62.5%, ranging from a maximum of 100% to a minimum of 18%. Readings made in the morning showed a slightly higher average relative humidity than those made in the afternoon, 65.5% compared with 59.4%. It is not uncommon to have relative humidities in the range of 100% as low-lying cloud banks often rest upon the summit of the Cape Breton Plateau. However, humidity determinations were not made when these conditions prevailed.

Wind data were recorded from June 14 to August 30. The average wind velocity during daylight hours, based on 40 readings, was 15.9 km/hr, with the maximum

velocity recorded on June 19 at 28.9 km/hr. The average velocity during the mornings was 13.3 km/hr, as compared with an afternoon average of 18.9 km/hr. Wind gusts were reported up to 40.2 km/hr. The average wind velocity for the 78 day period was 12.1 km/hr based on the total kilometers of wind recorded (22631.6). Thus, there is a difference in wind velocity of 3.82 km/hr between the average for daylight hours and that for the total summer period, indicating that nocturnal wind velocities are lower than those recorded during the daytime.

Observations on wind direction showed that the wind blew mainly from the southwest and west. This is in agreement with Putnam (1940) who reported the direction of the prevailing winds in the region to be mainly from the northwest and west during the winter months, and from the southwest and west during summer.

During the period spent in the study area there were 25 days of sunshine, 23 days completely overcast during daylight hours, and 17 days partially overcast with sunny intervals. July had the most days of total sunshine (11), while August had the most completely overcast days (12).

The climatic features discussed become important when they are related to the widespread occurrence of raised bogs on the Cape Breton Plateau. Precipitation is in excess of amounts considered minimum for raised bog development, i.e., greater than 100 cm/year (Gorham 1957a). Even when it is not raining, a damp climatic condition will be maintained on the Plateau by the frequent occurrence of low-lying clouds causing high relative humidities.

Perhaps more significant is the fact that the Plateau is cooler than the coastal areas, having lower minimum temperatures. Conditions, therefore, become favorable for rapid peat accumulation on the bogs as low temperatures cause a reduction in evaporation and decomposition of the peat.

The climatic data indicate that the Plateau can be considered a distinct climatic region based on its cooler temperatures and abundant precipitation. This agrees with Putnam's (1940) classification of the area as the "Cape Breton Highlands" Climatic Region. This region corresponds to what Nichols (1918) called the "Northeastern Evergreen Coniferous Forest Formation" of the Plateau, in his vegetational study of Northern Cape Breton, and is also closely related to Loucks' (1960) "Cape Breton Plateau Ecoregion".

Discussion

There are four dynamic processes occurring in the raised bogs of the Cape Breton Plateau, namely, bog development, cyclic succession, erosion, and regeneration (Fig 11, 12).

Bog Development

The successional sequence for bog development probably begins on a gently undulating rocky substratum containing slight ridges and shallow depressions (Nichols 1918). The pioneer vegetation on the drier raised parts may consist of a thin covering of lichens and bryophytes. In the damper depressions *Sphagnum* may become established. As the layer of peat begins to accumulate, the surface vegetation of the depressions spreads laterally and coalesces, covering the slightly higher ridges.

The accumulation of organic matter produces a habitat that can support *Scirpus cespitosus*. Once this species becomes established the bog begins to develop. A layer of extremely compact sedge peat is deposited and impedes drainage. In this way the sub-hygic *Scirpus cespitosus* - *Dicranum leioneuron* Association is established (Fig 6). It approximates what Nichols (1918) called the "bog meadow association-type".

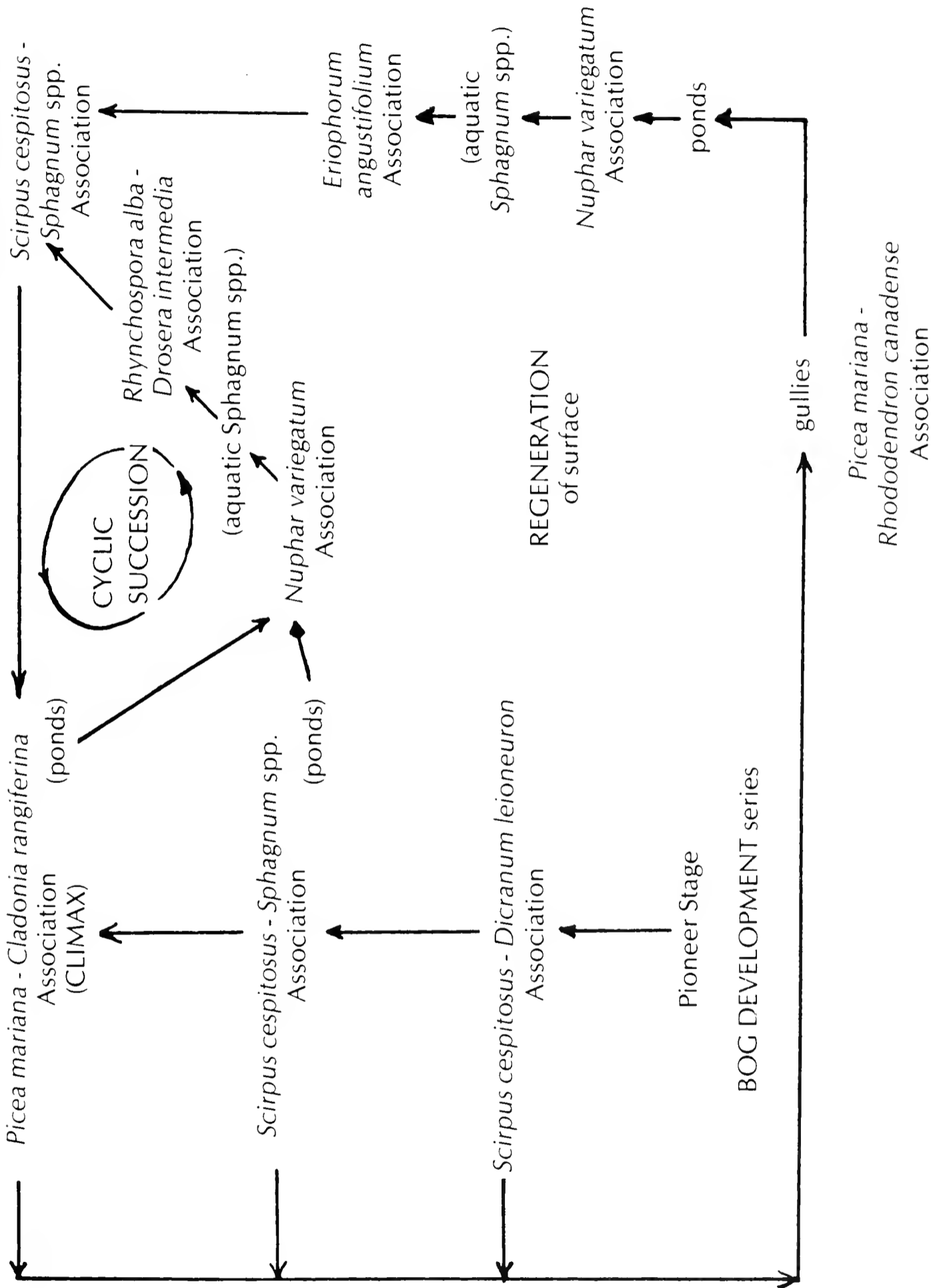


Fig 11. Successional relationships of raised bog associations.

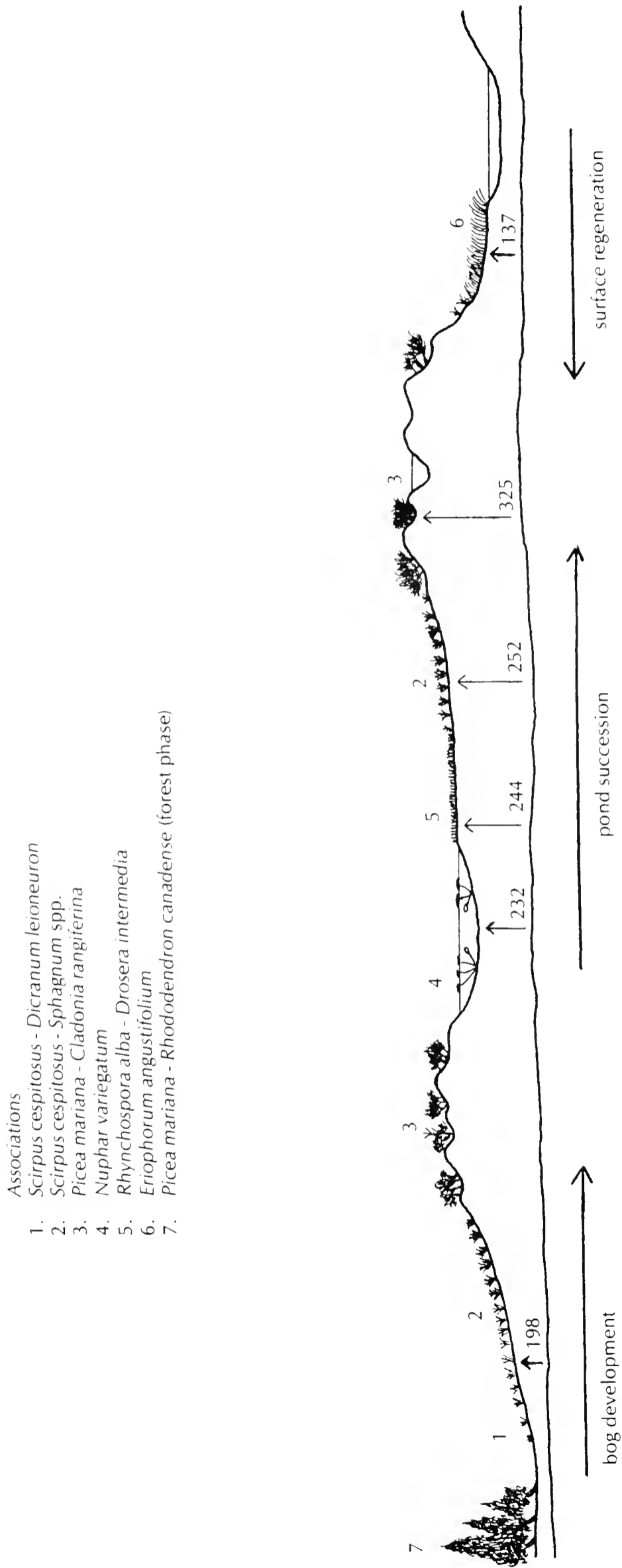


Fig 12. Topographic sequence of raised bog associations. Maximum recorded peat depths in centimeters are given under each association.

In well developed bogs the *Scirpus cespitosus* - *Dicranum leioneuron* Association occurs around the outer edges, sometimes covering extensive areas. This Association determines the size of a bog through its expansion into forested areas. Dwarf trees bordering a bog are subjected to severe winds which often cause small openings. Once the area is exposed to light it enables the shade intolerant *Sphagnum* and *Scirpus cespitosus* to become established. This in turn impedes the drainage causing further destruction of the forest and bog advancement. This process appears to be operative at different locations around the perimeter of bogs resulting in an irregular borderline.

The compact peat underlying the *Scirpus cespitosus* - *Dicranum leioneuron* Association is usually shallow (Fig 13) and has a low water holding capacity. Here, most of the precipitation is removed by runoff. As a result, surface conditions are relatively dry and a diverse vascular flora is supported. Damper conditions prevail only in the shallow depressions producing sites for the growth of *Sphagnum*. *S. tenellum* is one of the first plants to colonize. It is an erect slender species usually occurring in dense, loose masses and forming low lying mats. Successionally, it is soon followed by cushion-forming *S. capillaceum* var. *tenellum*, *S. magellanicum*, and to a lesser extent *S. pulchrum*. Once these are established the bog undergoes some important changes.

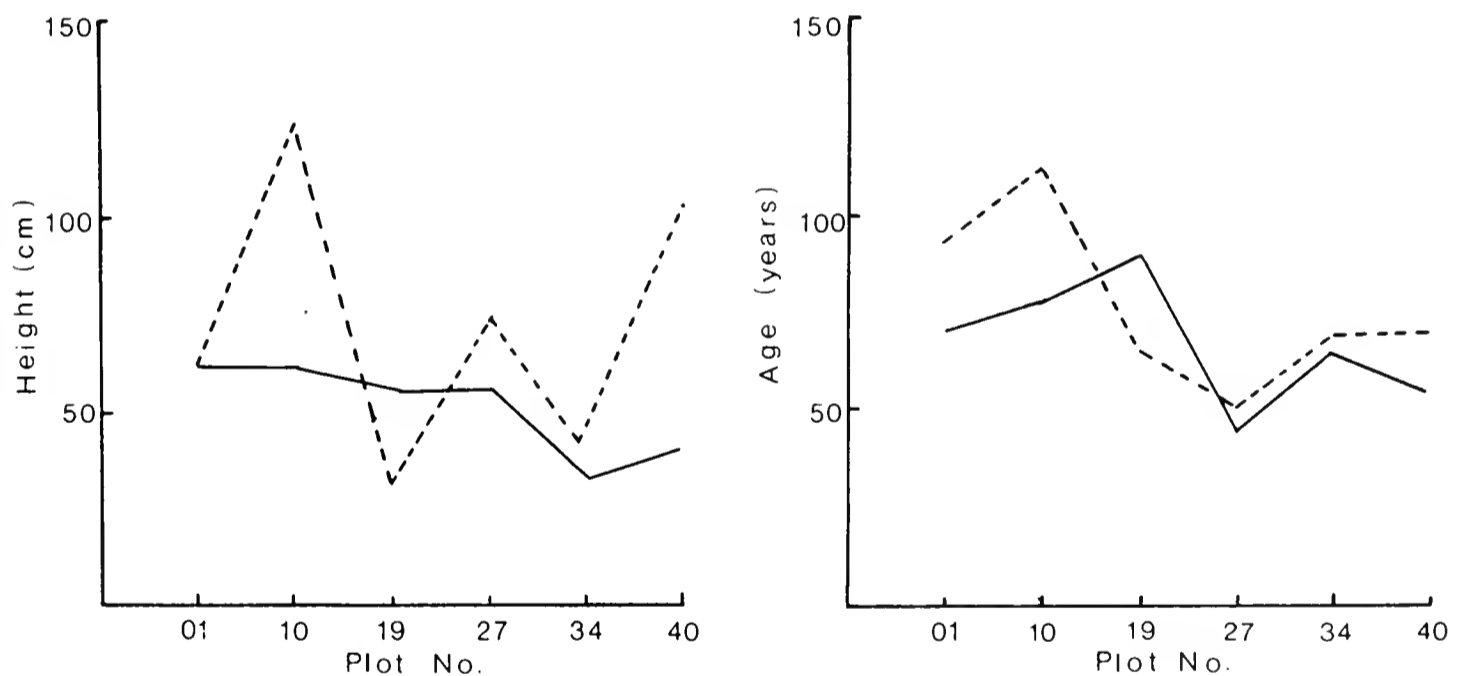


Fig 13. Height and age of dwarf *Larix laricina* (---) and *Picea mariana* (—) trees in the *Picea mariana* - *Cladonia rangiferina* Association. The data are based on one representative individual from each plot.

The new peat deposited becomes waterlogged which causes a restriction of air circulation and a depletion of the oxygen supply (Pearsall 1938; Armstrong and Boatman 1967). As a result the soil condition becomes anaerobic and dead plant remains decompose slowly. At this stage of development the peat accumulation is greatly accelerated and the *Scirpus cespitosus* - *Dicranum leioneuron* Association advances successionaly to the hygric *Scirpus cespitosus* - *Sphagnum* spp. Association (Fig 5). This Association is similar to what Nichols (1918) called the "wet bog association-type". All vascular plants found in this Association are also present in the *Scirpus cespitosus* - *Dicranum leioneuron* Association. However, only half as

many occur. This may be a result of the wetter surface conditions maintained by the abundance of cushion-forming *Sphagnum*. These species are robust, erect and rather rigid, forming dense widespread colonies. *S. magellanicum* and *S. papillosum* are the most important species, and are the most rapid peat-formers of all bog plants.

The six *Sphagnum* present in the *Scirpus cespitosus* - *Sphagnum* spp. Association (Table IV) have different growth rates and as a result the surface soon acquires an uneven topography of mounds and hollows. As the mounds are being built up there is a corresponding rise in the water table. Some mounds eventually coalesce and form ridges enclosing shallow depressions. The latter become filled with water and create bog ponds. The ridges are built higher by *Sphagnum*, strengthened by vascular plant remains and eventually become effective dams. With the underlying sedge peat impervious to drainage and the surrounding ridges maintaining the water table near the surface, the ponds become a permanent feature of the bog.

The bog surface is continuously raised by the growth of *Sphagnum* mounds until, eventually, it is above the water level of the ponds and is no longer influenced by seepage from them. At this stage drier surface conditions prevail and *S. capillaceum* var. *tenellum* becomes established followed by *S. fuscum*. These mesophytic species are erect, usually slender, and form very dense compact colonies. They replace the robust cushion-formers of the *Scirpus cespitosus* - *Sphagnum* spp. Association. As a result of this change in the bryophyte flora the bog advances to the mesic *Picea mariana* - *Cladonia rangiferina* Association (Fig 7). It can be regarded as the climax stage of bog development. This is equivalent to what Nichols (1918) called the "dry bog association-type".

In the earliest stages of this Association there is an increase in the number of vascular plants due to the mesophytic conditions that prevail. Dwarf trees of *Larix laricina* and *Picea mariana* become established. Age determinations and density data suggest that *Larix* is the first to colonize. Data based on representative individuals showed that this species, in every plot except one, was older than *Picea* by an average of about ten years. In one of the bogs a careful count of the dwarf trees showed a total of 54 individuals of *Larix* and only three of *Picea* per 100 sq. m.

Most of the woody plants reproduce vegetatively by layering. This is the prevalent mode of growth in the dwarf trees, especially in *Picea*. Hummocks are a distinguishing topographic feature of the *Picea mariana* - *Cladonia rangiferina* Association. Their growth is dependent on the combined presence of *Sphagnum* and woody vascular plants. The stems and branches of the woody species provide a framework which facilitates the upward growth of *Sphagnum* and gives a greater degree of firmness to the developing hummocks. *Picea* is the major vascular plant involved in hummock building. Once established, its upward growth corresponds with the upward growth of the hummocks. *Picea* branches are buried by *Sphagnum*, but through layering, branchtips turn upward and continue to grow above the surface. This forms characteristic *Picea* hummocks.

A common feature of these hummocks is the effect wind has on their development. Careful examination showed that at the windward end there were numerous dead branches, while on the leeward side actively growing branches occurred. Wind blowing almost continuously from the southwest causes the hummocks to become elongated in a southwest to northeast direction.

The continued upward growth of the hummocks results in further drying of the surface so that eventually *Sphagnum* is replaced by numerous lichens, especially *Cladonia rangiferina* and *C. alpestris*. Once the lichens are well established upward growth of the hummocks slows down. Evidence of the relative stability of the surface is suggested by the ages of the dwarf trees, some of which exceed 90 years.

The ponds formed in the *Scirpus cespitosus* - *Sphagnum* spp. Association are still present in the *Picea mariana* - *Cladonia rangiferina* Association. In addition new ponds are developed because of hummock growth. Older hummocks become senescent and are soon overtopped by younger actively growing ones. This results in the drainage restriction of older hummocks and surface accumulation of water. The numerous surface ponds are an important feature of the climax *Picea mariana* - *Cladonia rangiferina* Association.

The shape of the bog ponds is influenced by the topography of the bog. Flat bog surfaces lack orientation of relief features and contain ponds that have irregular or rounded shapes. On the other hand, convex bog surfaces have ridges and depressions formed at right angles to the slope. Elongated ponds, with steep downslope banks, are present in the depressions and often arranged in a step-like series. This type of alignment of ridge and depressional areas may be possibly the result of either "pressure-folding" (Pearsall 1956) or the nature of the drainage pattern affecting the bog (Boatman and Tomlinson 1973). It is possible also that the alignment may result from the tendency of the looser, saturated *Sphagnum* peat to creep over the more compact sedge peat. Often, active lateral seepage was observed at the base of the *Sphagnum* peat where it overlies the sedge peat.

Erosional forces can also change the shape of ponds, especially where the water level is almost flush with the surrounding bog. The surface of these ponds is subjected to continuous wind, blowing in a fairly constant direction. This produces small waves which scour the banks on one side of the pond resulting in expansion through erosion. Sometimes small ponds, located close together and at the same elevation, coalesce by erosion, thus creating a large single pond with a very irregular outline. In this process islands and small peninsulas are formed.

The water level in the bog ponds is controlled mainly by evaporation and precipitation. The ponds were never desiccated but the water level sometimes fluctuated markedly. Following periods of heavy and continuous rain the water level in some ponds was observed to increase as much as 15 cm.

Ponds are often found at different elevations in the same section of a bog. One of the ponds in which a plot was located, is in the middle of a series of ponds arranged in a step-like pattern. Its water level was approximately 76 cm higher than the water level in a pond only nine meters away. In another location, two ponds approximately three meters apart had a difference in water level of 106 cm. This marked change in the pond elevations demonstrates the water holding capacity of *Sphagnum* banks.

Cyclic Succession

In the ponds, a cyclic succession occurs resulting in a continued upward growth of the bog surface (Fig 11 and 12). The initial phase of the cycle involves the establishment of the *Nuphar variegatum* Association (Fig 2). The first plants to colonize are species of algae, which are found along the pond bottoms and edges. They are followed by *Nuphar variegatum* and *Eriocaulon septangulare*. These plants grow mainly in the deeper parts of the pond away from the surrounding banks. There is little change occurring in the Association until the aquatic *Sphagnum* become established. Once species like *S. cuspidatum* start to grow profusely around the edges, the filling-in process becomes greatly accelerated. Only in ponds of very small surface area was the *Sphagnum* cover complete. In the larger ponds there is greater exposure to the wind which appears to slow down the advancement of *Sphagnum* from the pond's edge. Here, shrub species have branches extending into the ponds which provide a framework supporting the aquatic *Sphagnum*. This results in the formation of vegetation mats, enabling *S. pulchrum* to become established on the surface.

These mats sometimes break loose and sink, accelerating the filling-in process. Some mats contain entrapped air enabling them to float freely or only become partly submerged. Air trapped in the peat underlying the ponds was demonstrated during depth determinations. When the sampler was removed, a steady stream of bubbles was often released.

Through the combined processes of sedimentation and the growth of vegetation mats the underlying peat is built up to the surface and eventually exposed. This exposed muck becomes the habitat in which the *Rhynchospora alba* - *Drosera intermedia* Association is established (Fig 4). This is equivalent to what Nichols (1918) termed the "muck mat".

Initially the surface remains semi-aquatic because of fluctuating water levels. The stabilization and consolidation of the muck is brought about by the growth and spread of a vegetation mat which provides a base upon which more mesophytic communities develop. The mat is firm, yet flexible, and when walked upon the surface quakes.

Among the first species to be established are *Cladopodiella fluitans* and *Utricularia cornuta*, the latter helping to stabilize the muck by binding together the loose peat through its extensive system of underground rhizomes. A firmer crust is produced through desiccation once the surface is continually exposed. On this crust *Drosera intermedia* is established followed by *Rhynchospora alba*. The latter species and the liverwort *Cladopodiella* eventually cover most of the mat.

The surface is not built up during this stage of succession and each community still retains the general outline of the former pond. After heavy rains the surface is inundated often to a depth of several centimeters. The only new *Sphagnum* established is *S. pulchrum*. The Association, therefore, occupies a unique position because of its paucity of *Sphagnum*. Apparently it is not wet enough to permit a greater intrusion of the aquatic *Sphagnum*, while on the other hand, it is still too wet to allow for the establishment of the cushion-forming species (Table XI).

Continuous organic matter deposition elevates the surface of the muck mat until it is no longer inundated. When this happens, the mat becomes populated by cushion-forming *Sphagnum*. The important vascular plants of the *Rhynchospora alba* - *Drosera intermedia* Association are replaced by *Scirpus cespitosus* and *Carex exilis*. This results in the successional advancement to the *Scirpus cespitosus* - *Sphagnum* spp. Association. This in turn is succeeded by the *Picea mariana* - *Cladonia rangiferina* Association in which new ponds may be formed thus completing the cycle.

Bog Erosion (Fig 11)

While the bogs are being continually built up through peat accumulation, wind and water erosion alter the surface. The vegetation covering a bog's surface has an important ecological function as a protective blanket, preventing the underlying peat from becoming desiccated. When this protection is removed, the surface peat will erode. Wind can loosen and remove dried out surface particles. Once this happens heavy runoff will create small erosional channels which can eventually expand to become gullies. Raised bogs, because of their slopes, are quite susceptible to gully erosion. Some gullies probably originate through subterranean channelling. Overlying peat layers are undermined and collapse creating an open gully. These gullies serve as drainage channels.

The banks of the gullies become stabilized by species like *Scirpus cespitosus* causing gully erosion to cease. Once this happens, the submesic *Picea mariana* - *Rhododendron canadense* Association comes into existence (Fig 8). This Associa-

tion is actually an extension into the bogs, via the drainage gullies, of an Association of the same name that surrounds the bogs. The bog phase of this Association has a very important ecological function as it completely stabilizes the gully, thus preventing further erosion.

A greater degree of protection is provided to plants growing in the gullies where the slopes and bottom are situated at much lower elevations than the surrounding bog. Thus, woody species are able to grow at a faster rate and attain greater heights than their counterparts on the exposed bog. The most striking example of this is seen in the different growth habits of *Picea mariana*. In the *Picea mariana* - *Cladonia rangiferina* Association one of these dwarf trees had a height of 61 cm and was aged at 77 years, while a *Picea* located in a drainage gully in the same bog had a height of 229 cm and an age of 65 years. The ages of the dwarf trees in the *Picea mariana* - *Rhododendron canadense* Association also reflect the stable nature of this community. A dwarfed *Picea* taken from one plot was aged at 139 years while that taken from another was approximately 144 years old.

Once the *Picea mariana* - *Rhododendron canadense* Association is well established in the gullies, shade-intolerant species, like *Sphagnum* and *Scirpus cespitosus*, are practically eliminated. Thus without the presence of cushion-forming *Sphagnum* there is little upward growth of the surface occurring.

Water movement in most drainage gullies is only noticeable after periods of rain. In the streams water varies from a few centimeters to over 40 cm in depth and usually overlies peat. Occasionally, however, the stream has eroded to the mineral substratum. When these streams are blocked, either through sedimentation or slumping, extensive flooding results. This causes the surrounding banks to be eroded and the vegetation cover is destroyed. Flooding may remove most of the eroded peat leaving behind only a shallow pond often lying on top of the mineral substratum.

These ponds belong to the drainage gully system as they receive water from undisturbed parts of the gully. They differ from the raised surface ponds by having drainage. The water level, therefore, fluctuates and the ponds vary from almost dry to completely flooded conditions. The water level recedes quickly following heavy rains. This was demonstrated from observations carried out over a period of 48 hours. Measurements were taken 24 hours apart in a depression which is usually exposed. The initial measurement showed a water depth of 21.6 cm, the second a depth of 19.0 cm, the third 3.8 cm. This decrease of 17.8 cm in water level illustrates the rapid and continuous drainage of the depression ponds.

Bog Regeneration

The regeneration of the bog surface begins when depressional ponds gradually become filled in through the continued influx of drainage water carrying organic sediments. Eventually conditions will become favorable for the establishment of the *Nuphar variegatum* Association. As the filling in process usually proceeds from the edges towards the center of these ponds, *Nuphar variegatum* becomes confined to a deep channel that dissects the depression.

Pond filling is aided by the presence of *Sphagnum cuspidatum*. Continued deposition finally results in the exposure of organic sediments above the surface. At this point the peat depth may vary from 89 cm to 137 cm. On the newly exposed peat *Utricularia cornuta*, *Drosera intermedia* and occasionally *Rhynchospora alba* become established. However, none of these plants ever become dominant here as they do in the raised sections of the bog. This may be due to the large fluctuations in the water level that still occur.

The stabilization of the mucky peat is dependent on the development of the *Eriophorum angustifolium* Association (Fig 3). *Eriophorum angustifolium* thrives best when partially submerged. Species like *Sphagnum cuspidatum* and *S. papillosum* aid in slowly building up the surface until it becomes suitable for the establishment of *Scirpus cespitosus*. As a result of these changes the *Scirpus cespitosus* - *Sphagnum* spp. Association is formed. Through continual upbuilding it is eventually replaced by the climax *Picea mariana* - *Cladonia rangiferina* Association, thus completing the regeneration of the bog surface (Fig 11 and 12).

Buried Wood Fragments and Peat Depth

Strong evidence in support of the continuous cycling of associations comes from the discovery of buried coniferous wood fragments. These were found beneath most of the associations. Out of 40 peat pits, 25 contained wood fragments, located at depths ranging from 31 cm to 180 cm. The wood was usually confined to a single level in each pit. In most cases the wood was well preserved and some samples still had bark present. The fragments were of various sizes and shapes, the largest being approximately 40 cm in length and from six to eight centimeters in diameter.

This evidence indicates that the *Picea mariana* - *Cladonia rangiferina* and the *Picea mariana* - *Rhododendron canadense* Associations existed earlier in the bog's history, as coniferous species occur only in these associations. Then through cyclic succession and regeneration the associations became submerged and with time eventually developed again on the bog's surface.

The depth of peat underlying each association can be correlated with the successional sequences occurring within the bog (Fig 14). Early pioneer stages, like the *Scirpus cespitosus* - *Dicranum leioneuron* and the *Eriophorum angustifolium* Associations, have the shallowest peat depths. In the former, occurring at the bog's edge, the thinnest peat deposits are found in those areas where lateral bog expansion has just recently taken place. In the latter Association, occurring in depressional areas, peat depth is determined by the amount of erosion or sedimentation that has taken place. Shallow peat depths also occur in the drainage gullies that dissect the bog's surface. The depth of peat underlying the *Picea mariana* - *Rhododendron canadense* Association varies a great deal as illustrated in Fig 8.

In the raised sections of a bog there is usually an increase in peat depth from the wettest to the driest associations, i.e., from the *Nuphar variegatum* to the *Picea mariana* - *Cladonia rangiferina*, reflecting a build-up of the bog's surface. Maximum peat depths are found in the oldest sections of a bog, provided that erosion has not altered the surface. In mature raised bogs, with a convex surface, the oldest sections occur at the center. In moving from the center towards the edges both peat depth and age decrease.

Successional Variations

The successional relationships of the bog associations are varied and complex and they do not always follow exactly the patterns previously discussed. Two variations occurred in the successional sequences which require brief descriptions.

The first occurs in the successional sequence that follows the *Scirpus cespitosus* - *Dicranum leioneuron* Association located at the bog's edge. This Association usually is succeeded by the wetter *Scirpus cespitosus* - *Sphagnum* spp. Association with its robust cushion-forming *Sphagnum*. In several locations it was observed that the former Association appears to be succeeded directly by an early phase of the *Picea mariana* - *Cladonia rangiferina* Association, bypassing the *Scirpus cespitosus* - *Sphagnum* spp. Association. The successional sequence which is followed is

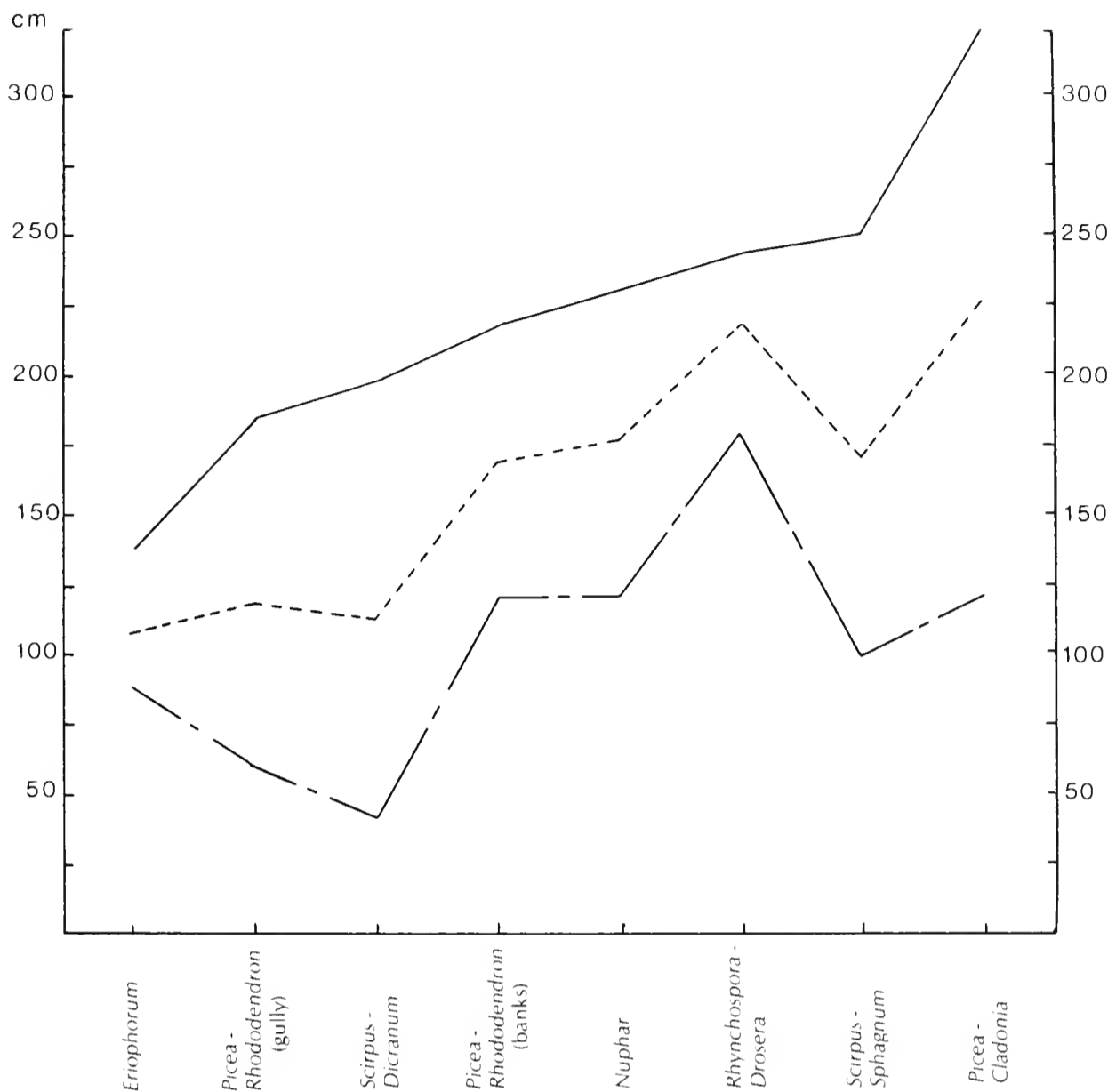


Fig 14. Peat depths for the bog associations showing maximum (—), average (---), and minimum (-·-).

probably dependent on the surface moisture status of the *Scirpus cespitosus* - *Dicranum leioneuron* Association. If the surface is too dry for the abundant growth of the hygric cushion-forming *Sphagnum*, then the mesic cushion-formers, such as *S. capillaceum* var. *tenellum* and *S. fuscum*, may become dominant and develop into small hummocks which are able to support dwarf trees and lichens.

The other variation occurs in the successional sequence that follows the *Nuphar variegatum* Association. This Association is normally succeeded by the *Rhynchospora alba* - *Drosera intermedia* Association in the raised bog sections, and by the *Eriophorum angustifolium* Association in the depressional areas. In some cases the filled-in pond appears to have proceeded directly to an early phase of the *Scirpus cespitosus* - *Sphagnum* spp. Association without going through either of the two Associations mentioned. The new Association still retains the outline of the old ponds. Here aquatic *Sphagnum*, such as *S. cuspidatum*, must have been largely responsible for filling in the pond with organic matter. As the water becomes shallow they would continue to thrive just beneath the surface while the semi-aquatic *S. pulchrum* would be established at the surface and soon dominate the emergent vegetation. This species would be able to build up the surface so that the hygric cushion-forming *Sphagnum* could become established.

Whether the regular successional processes or their variations predominate, raised bogs must be regarded as dynamic self-sustaining units whose survival is dependent on abundant atmospheric precipitation and cool temperatures. As long as these conditions remain constant the bogs will continue to grow.

Table X Ecological amplitudes of the vascular flora of raised bogs based on moisture tolerances as indicated by the average species significance values of each plant in the different associations. Sporadics are shown by the letter "S".

Species	Nuphar hydic ←	Eriophorum	Rhynchospora- Drosera	Scirpus- Sphagnum	Scirpus- Dicranum	Picea- Cladonia	Picea- Rhododendron → submesic
<i>Eriocaulon septangulare</i>	1.5	-	-	-	-	*	**
<i>Nuphar variegatum</i>	3.8	0.4	-	-	-	-	-
<i>Utricularia geminiscapa</i>	-	0.2	-	-	-	-	-
<i>Carex aquatilis</i>	-	S	-	-	-	-	-
<i>Utricularia cornuta</i>	-	2.0	1.5	-	-	-	-
<i>Drosera intermedia</i>	-	1.6	2.6	-	-	-	-
<i>Vaccinium macrocarpon</i>	-	S	1.1	S	-	-	-
<i>Rhynchospora alba</i>	-	2.4	6.6	-	S	-	-
<i>Drosera rotundifolia</i>	-	0.6	0.3	2.1	1.0	- 1.5	-
<i>Vaccinium oxycoccos</i>	-	S	0.3	2.5	1.8	- 1.5	-
<i>Eriophorum angustifolium</i>	-	7.2	1.1	1.0	1.5	- 1.1	- 1.1
<i>Carex exilis</i>	-	S	S	1.6	2.1	- S	- S
<i>Kalmia polifolia</i>	-	0.2	0.3	2.6	2.8	0.6 2.8	- 0.6 2.0
<i>Andromeda glaucophylla</i>	-	-	0.8	3.1	2.5	- 0.5	- - 0.5
<i>Sarracenia purpurea</i>	-	-	0.1	0.6	1.6	- 1.0	- - 0.6
<i>Chamaedaphne calyculata</i>	-	-	0.3	3.5	3.0	0.8 3.0	- S S
<i>Calamagrostis pickeringii</i>	-	-	S	-	1.5	- 1.3	- - 1.1
<i>Eriophorum spissum</i>	-	-	-	0.5	S	- 0.5	- - -
<i>Scirpus cespitosus</i>	-	-	-	4.3	5.3	- 3.1	- - 0.6
<i>Kalmia angustifolia</i>	-	-	-	0.3	1.1	0.6 3.5	- 0.8 1.8
<i>Ledum groenlandicum</i>	-	-	-	0.3	1.3	0.8 3.3	- 1.1 2.0
<i>Schizaea pusilla</i>	-	-	-	-	S	- 0.5	- - -
<i>Aster nemoralis</i>	-	-	-	-	S	- - -	- - S
<i>Solidago uliginosa</i>	-	-	-	-	2.1	- 1.1	- - 0.3
<i>Empetrum nigrum</i>	-	-	-	-	0.6	- 3.0	- - 0.5
<i>Aronia prunifolia</i>	-	-	-	-	2.8	S 2.3	- 1.0 1.8
<i>Vaccinium boreale</i>	-	-	-	-	1.0	- 1.6	- - 1.8
<i>Coptis trifolia</i>	-	-	-	-	1.3	- 1.3	- - 1.8
<i>Trientalis borealis</i>	-	-	-	-	1.1	- 1.1	- - 1.1
<i>Maianthemum canadense</i>	-	-	-	-	0.8	- 0.6	- - 1.0
<i>Juniperus communis</i>	-	-	-	-	-	- 0.8	- - -
<i>Rubus chamaemorus</i>	-	-	-	-	-	- 2.6	- - 1.5
<i>Deschampsia flexuosa</i>	-	-	-	-	-	- 0.6	- - 0.5
<i>Vaccinium angustifolium</i>	-	-	-	-	-	0.5 2.0	- 1.1 1.8
<i>Melampyrum lineare</i>	-	-	-	-	-	- 0.8	- - 1.3
<i>Larix laricina</i>	-	-	-	-	-	1.1 1.0	+++ 1.0 S
<i>Geocaulon lividum</i>	-	-	-	-	-	- 0.5	- - 0.3
<i>Rhododendron canadense</i>	-	-	-	-	-	1.1 2.1	- 2.8 4.1
<i>Picea mariana</i>	-	-	S	-	-	3.5 4.3	3.3 5.8 1.1
<i>Gaultheria hispida</i>	-	-	-	-	-	- 0.3	- - 1.1
<i>Epigaea repens</i>	-	-	-	-	-	- S	- - 1.5
<i>Cornus canadensis</i>	-	-	-	-	-	- 1.8	- - 2.8
<i>Amelanchier bartramiana</i>	-	-	-	-	-	- S	- 4.5 0.6
<i>Nemopanthus mucronata</i>	-	-	-	-	-	- S	- 2.3 S
<i>Abies balsamea</i>	-	-	-	-	-	- S	0.3 0.3 0.5
<i>Myrica gale</i>	-	-	-	-	-	- -	- 1.1 1.3
<i>Viburnum cassinoides</i>	-	-	-	-	-	- -	- 1.0 -
<i>Carex oligosperma</i>	-	-	-	-	-	- -	- - 0.3
<i>Linnaea borealis</i>	-	-	-	-	-	- -	- - 0.5
<i>Taxus canadensis</i>	-	-	-	-	-	- -	- 0.3 0.6
<i>Carex trisperma</i>	-	-	-	-	-	- *	- - 0.6
<i>Betula papyrifera</i>	-	-	-	-	-	- -	- S -
<i>Sorbus decora</i>	-	-	-	-	-	- -	- S -
<i>Clintonia borealis</i>	-	-	-	-	-	- -	- - 3.0
Totals: 54	2	12	14	13	23	36	41
Relative presence (%)	4	22	26	24	43	67	76

Note: Each column represents the C layer (herb and dwarf shrub) except for those columns designated by a single asterisk (*) representing the B₂ sublayer (low shrub), and that designated by two asterisks (**) representing the B₁ sublayer (high shrub).

Ecological Amplitudes of Bog Species

The distribution of bog species appears to be dependent on moisture requirements and topographic position (Table X and XI). Bog species can be placed in two groups according to their apparent tolerance to water.

Species with Narrow Moisture Tolerances

There are very few completely aquatic species. Included here are the vascular plants, *Eriocaulon septangulare* and *Nuphar variegatum*, the only species other than algae found in the *Nuphar variegatum* Association. *Nuphar* is also found in

Table XI Ecological amplitudes of the bryophytes and lichens of raised bogs based on moisture tolerances as indicated by the average species significance values for each plant in the different associations. Sporadics are shown by the letter "S".

Species	Nuphar hydris ←	Eriophorum	Rhynchospora- Drosera	Scirpus- Sphagnum	Scirpus- Dicranum	Picea- Cladonia	Picea- Rhododendron → submesic
Sphenolobus minutus	-	S	-	-	-	-	-
Sphagnum recurvum	-	S	-	-	-	-	-
Sphagnum cuspidatum	-	4.6	3.6	-	-	-	-
Cladopodiella fluitans	-	3.2	8.6	-	-	-	-
Sphagnum papillosum	-	2.2	-	1.6	S	-	-
Gymnocolea inflata	-	1.2	-	0.6	0.5	S	-
Sphagnum pulchrum	-	S	3.6	0.6	0.5	0.3	-
Drepanocladus revolvens	-	-	S	-	-	-	-
Orthocaulis gracilis	-	-	S	2.3	1.6	1.3	S
Sphagnum magellanicum	-	-	-	3.3	2.5	-	-
Sphagnum tenellum	-	-	-	4.8	2.8	0.8	-
Sphagnum capillaceum var. tenellum	-	-	-	3.3	3.0	1.1	-
Ochrolechia frigida	-	-	-	0.5	0.3	0.3	-
Cetraria islandica ssp. crispa	-	-	-	0.3	S	S	-
Dicranum leioneuron	-	-	-	3.1	5.5	0.6	-
Cetraria islandica	-	-	-	0.3	1.1	1.3	-
Sphagnum tuscum	-	-	-	1.3	1.0	4.0	-
Cladonia pleurota	-	-	-	0.6	0.8	1.5	0.8
Cladonia rangiferina	-	-	-	0.3	1.6	5.6	1.3
Dicranum undulatum	-	-	-	S	1.1	1.8	S
Ptilidium ciliare	-	-	-	S	0.6	2.5	2.1
Cladonia uncialis	-	-	-	-	0.3	1.5	-
Mylia anomala	-	-	-	-	S	S	-
Microlepidozia setacea	-	-	-	-	S	0.6	-
Cladonia alpestris	-	-	-	-	S	4.1	-
Pleurozium schreberi	-	-	-	-	0.6	4.5	4.8
Cladonia pseudorangiformis	-	-	-	-	S	0.3	0.5
Rhacomitrium lanuginosum	-	-	-	-	-	1.0	-
Cephalozia bicuspidata	-	-	-	-	-	0.5	-
Sphagnum capillaceum	-	-	-	-	-	0.3	-
Cladonia arbuscula	-	-	-	-	-	S	-
Cladonia crispata	-	-	-	-	-	S	S
Cladonia mitis	-	-	-	-	-	S	S
Dicranum polysetum	-	-	-	-	-	S	S
Ptilium crista-castrensis	-	-	-	-	-	0.6	0.3
Cladonia gracilis	-	-	-	-	-	0.8	0.8
Hylocomium splendens	-	-	-	-	-	2.1	3.0
Cladonia squamosa	-	-	-	-	-	S	0.5
Dicranum scoparium	-	-	-	-	-	-	2.8
Dicranum fuscescens	-	-	-	-	-	-	1.3
Sphagnum subsecundum	-	-	-	-	-	-	1.1
Sphagnum palustre	-	-	-	-	-	-	0.8
Leucobryum glaucum	-	-	-	-	-	-	0.3
Totals: 43	0	7	5	16	22	31	19
Relative presence (%)	0	16	12	37	51	72	44

Note: each column represents the D layer (bryophytes and lichens).

the *Eriophorum angustifolium* Association, but it only grows in those areas that are continually submerged. The most important aquatic species in bog development is *Sphagnum cuspidatum*. It grows abundantly around the edges of ponds and accelerates the filling-in process.

Species confined to habitats that are very wet but not continually submerged include *Utricularia cornuta*, *Drosera intermedia*, *Rhynchospora alba*, and *Cladopodiella fluitans*. All of these species are important in consolidating the loose peat of the *Rhynchospora alba* - *Drosera intermedia* Association.

Species confined to the driest sections of a bog are numerous. Some are of forest affinity and only occur in the *Picea mariana* - *Rhododendron canadense* Association of the drainage gullies, none of which are very important to bog development. The most important species in the driest sections are *Picea mariana*, *Rhododendron canadense*, and *Cladonia alpestris*. The first two are very important in stabilizing the banks of the drainage gullies. *Picea* is also important in the hummock stage of bog development, where together with *Cladonia* they constitute a dominant part of the vegetation cover.

Species With Wide Moisture Tolerances

Species with a wider tolerance to moisture conditions but occurring only in continually exposed areas, include *Scirpus cespitosus*, *Sphagnum magellanicum*, *S. tenellum*, *S. capillaceum* var. *tenellum*, *S. fuscum*, *Dicranum leioneuron*, and *Cladonia rangiferina*. All of these species affect surface conditions by controlling moisture and altering the topography.

There is a steady increase in the number of species in proceeding from the wettest to the driest associations. This is possibly because in waterlogged habitats anaerobic conditions prevail, imposing severe restrictions on plant growth, whereas, in drier habitats growing conditions improve. The *Picea mariana* - *Rhododendron canadense* Association has the largest number of vascular plants (41) and the most complex vegetation structure. The largest number of bryophytes and lichens (31) are found in the *Picea mariana* - *Cladonia rangiferina* Association. There is a sharp decline in the number of bryophyte and lichen species in the former Association where maximum shade conditions occur. As a result, the latter Association contains the largest number of species, having a total of 67 (excluding epiphytes).

The bogs are ecologically complex but floristically simple. Only 60 vascular species were found. These belong to 46 genera and 27 families. The most commonly occurring families are the Ericaceae (8 genera, 12 species) and Cyperaceae (4 genera, 10 species). There were 30 bryophytes and 18 lichen species found. The most common genera among the bryophytes were *Sphagnum* (11 species) and *Dicranum* (5 species), while the most common lichen was *Cladonia* (10 species).

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APPENDIX

SCALES USED IN THE VEGETATIONAL SAMPLING AND SYNTHESIS.

Parameters designated for the vegetation layers

Layer	Sublayer	Height Range
B—Shrub		0.3 m to 3.6 m
	B ₁ —High Shrub	1.8 m to 3.6 m
	B ₂ —Low Shrub	0.3 m to 1.8 m
C—Herb/Dwarf Shrub		0.3 m
D—Bryophyte/Lichen		
E—Epiphyte		

Domin-Krajina scale for species significance (after Krajina 1933)

+	solitary	only one plant
1	seldom	cover negligible
2	very scattered	cover negligible
3	scattered	cover to 5% of the plot
4	common	cover 5% to 10%
5	often	cover 10% to 20%
6	very often	cover 20% to 30%
7	abundant	cover 30% to 50%
8	abundant	cover 50% to 75%
9	abundant	cover 75% to 95%
10	abundant	cover 95% to 100%

Domin-Krajina scale for sociability (after Krajina 1933)

+	solitary	not touching others of the same species
1	2-3 plants	bryophytes, clumps
2	a few clumps	clumps one square meter
3	groups	0.09 to 0.36 sq m
4	groups	0.36 to 0.91 sq m
5	groups	0.91 to 1.84 sq m
6	groups	1.84 to 4.62 sq m
7	groups	4.62 to 9.24 sq m
8	groups	9.24 to 46.40 sq m
9	groups	46.40 to 929.0 sq m
10	groups	over 929.0 sq m

Scale for constancy percentages

Class	Percentage
I	0- 20
II	21- 40
III	41- 60
IV	61- 80
V	81-100

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The *Proceedings of the Nova Scotian Institute of Science* publishes the proceedings of the Institute and original articles, including notes, pertaining to the natural sciences of the Atlantic Provinces, especially in biology and geology. Manuscripts may be either in English or French, and acceptance for publication is based on recommendations of referees.

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
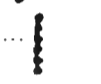







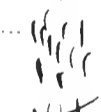



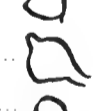



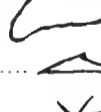








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ERRATUM

Page 28 of the Proceedings, Volume 34, Part 1, was in error. Please substitute this page.

List for key symbols:

Sand		<i>Laminaria saccharina</i>	
Black zone blue-green algae			
Tube-dwelling diatoms		<i>Scytosiphon lomentaria</i>	
<i>Chondrus crispus</i>		<i>Chorda filum</i>	
<i>Bonnemaisonia hamifera</i> tetrasporophytes		<i>Chaetomorpha melagonium</i>	
Crustose corallines		<i>Ulva lactuca</i>	
Ceramialean algae		<i>Enteromorpha linza</i>	
<i>Furcellaria fastigiata</i>		<i>Enteromorpha intestinalis</i>	
<i>Devaleraea ramentacea</i>		<i>Urospora</i> sp.	
<i>Ahnfeltia plicata</i>		<i>Cladophora sericea</i>	
<i>Corallina officinalis</i>		<i>Littorina littorea</i>	
<i>Sphacelaria</i> spp.		<i>Nucella lapilla</i>	
<i>Ectocarpus</i> spp.		<i>Balanus balanoides</i>	
<i>Fucus vesiculosus</i>		Intertidal <i>Mytilus edulis</i>	
<i>Fucus serratus</i>		Subtidal <i>Mytilus edulis</i>	
<i>Ralfsia verrucosa</i>		<i>Acmaea testudinalis</i>	
<i>Chordaria flagelliformis</i>		<i>Asterias vulgaris</i>	

BIOACTIVITIES IN MARINE GENERA OF ATLANTIC CANADA: THE UNEXPLORED POTENTIAL¹

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One hundred sixty genera of marine algae, invertebrates and tunicates represented in Atlantic Canadian waters are known to contain chemically uncharacterized bioactive metabolites of potential chemotherapeutic or marine-ecological interest. These include antiviral, antifungal, antibacterial, antitumor, cytotoxic, cardiovascular, hormonal, antifeedant, chemorecognition, chemoattractant, and ichthyotoxic principles.

Cent soixante genres d'algues marines, d'invertébrés et de tuniciers, représentés dans les eaux de l'Atlantique canadien, contiennent des métabolites bioactifs non caractérisés chimiquement. Ces métabolites ont un intérêt potentiel en chimiothérapie ou en écologie marine. On y retrouve des principes antiviraux, antimycophytes, antibactériels, antitumoraux, cytotoxiques, cardiovasculaires et hormonaux, des répresseurs alimentaires, des substances de reconnaissance et d'attraction chimiques ainsi que des toxines ichthyosspécifiques.

Introduction

At present marine organisms are being viewed as potential sources of new biologically active (bioactive) products. This interest is based on three areas of research:

Marine pharmacology

Fleming's discovery of penicillin (1929), and the subsequent successes of screening programs for novel systemic antibiotics in culture media of fungi and actinomycetes, inspired pioneering surveys for antibacterial principles in seaweeds, unicellular algae and marine animals (Pratt et al. 1951; Kamimoto 1955, 1956; Chesters & Stott 1956; Roos 1957; Allen & Dawson 1960; Li 1960; Jørgensen & Steemann Nielsen 1961). Such studies were eventually expanded to encompass more organisms and bioassays, and beginning in the 1960s gave rise to pharmacologically oriented reviews (Der Marderosian 1969a; Grant & Mackie 1977; Kaul 1979), monographs (Baslow 1969; Hashimoto 1979), and symposia (Nigrelli 1960, 1962; Freudenthal 1968; Youngken 1960; Webber & Ruggieri 1976; Kaul & Sindermann 1978; Hoppe et al. 1979; Fuhrmann & Jacobs 1981). It is probable that the recent appearance of literature on the traditional medicinal and religious utilization of marine plants and animals by indigenous cultures of China, Japan, southeast Asia, India, Hawaii and elsewhere (Anon. 1978; Diaz-Piferrer 1979; Hoppe 1979; Misra & Sinha 1979; Nisizawa 1979) will stimulate these investigations.

Marine biology and ecology

The production of antibacterial or autoinhibitory substances by phytoplankton has been known since the early days of culture studies (e.g. Waksman et al. 1937; Levring 1945; Harder & Oppermann 1953). A growing awareness that marine organisms face special biological problems (chemoreception, detoxification, predation, fouling, reproduction, nutrition, symbiosis, competition), and the development of

¹NRCC No. 23818

theories of response and adaptation which emphasize chemical mediators (Nigrelli 1958; Lucas 1961), have promoted ecologically oriented studies of bioactive marine natural products (Green 1977; Herring 1979; Bakus 1981).

Taxonomy and phylogenetics

Modern concepts of taxonomy and phylogenetics (Copeland 1938; Whittaker 1969; Ragan & Chapman 1978; Margulis & Schwartz 1982) are placing increasing emphasis on the great phyletic (hence, potentially, chemical: Phinney 1969) diversity of "lower" marine organisms which formerly were considered often as merely underdeveloped members of the two great (and largely terrestrial) kingdoms of Animals and Plants.

These parallel fields have motivated large-scale surveys for bioactive principles in marine organisms. Many diverse and chemically unique natural products exhibiting antiviral, antifungal, antibacterial, antitumor, cytotoxic, cardiovascular and other bioactivities have been characterized (Wright 1984). In addition, there exist numerous reports of biological effects produced by chemically uncharacterized metabolites of marine organisms.

The present paper reviews chemically uncharacterized bioactivities which have been reported in genera of marine organisms represented in Atlantic Canadian waters (Table I). Excluded were prokaryotes, vascular plants (see Harrison 1982), chordates (except tunicates), and complex assemblages of species such as the dinoflagellate-containing sea anemone *Zooanthus* (Welch 1962). The inclusion of phytoplankton genera occurring in the area in question was necessarily complicated by a number of hydrographical, physiological (e.g., salinity tolerance) and taxonomic variables. Therefore, all marine or saline-tolerant phytoplankton genera were included in the compilation, whether or not they have been reported specifically from the northwest Atlantic. Authorities consulted for lists of marine flora and fauna of Atlantic Canada include Lambe (1896), Whiteaves (1901), Taylor (1957), MacFarlane & Milligan (1965), Gosner (1971), Marine Research Associates (1973), South (1976), Caddy et al. (1977), Linkletter et al. (1977), and Wilson et al. (1979). A few important genera of benthic organisms represented in the Gulf of Maine but not reported from Atlantic Canada have also been included.

The bioactivities listed here include a wide range of antibiotic, pharmaceutical, allelopathic and ectocrine activities. All relatively unambiguous examples of hormones, internally active growth- or reproductive regulators, antigens (e.g., Yazykov 1966), vitamins, chelators, general nutrients, odor- or taste-factors, and enzyme activities were excluded. Also excluded, with some reservations, were the numerous cases in which a certain bioactivity has been "explained" by reference to a known compound or group of compounds; in many such instances the cause-and-effect relationship itself and/or the chemical identification of the compound(s) is incomplete or unconvincing. Finally, numerous ecological observations, such as the frequent association of *Polysiphonia lanosa* and *Ascophyllum nodosum*, or species succession in phytoplankton blooms, have been excluded for the most part owing to a lack of sufficiently specific information on the chemical mediators involved. Even after these exclusions, a lengthy list of uncharacterized bioactivities remains, and this undoubtedly represents only a small fraction of the largely untapped potential of marine bioactive compounds.

Table I Chemically uncharacterized bioactivities in marine organisms belonging to genera represented in Atlantic Canadian waters. Numbers denoting target organisms for antifungal and antibacterial bioactivities refer to species listed in Table II.

ALGAE	
CLASS RHODOPHYCEAE	
SUBCLASS BANGIOPHYCIDAE	
ORDER PORPHYRIDIALES	
<i>Goniotrichum</i> sp.	toxic to mice (Hashimoto et al. 1972)
<i>Porphyridium</i> sp.	antibacterial: 83 (two species) (Berland et al. 1972)
ORDER BANGIALES	
<i>Bangia atropurpurea</i>	<i>Ulva</i> morphogenetic factor (Provasoli & Pintner 1964) (as <i>B. fuscopurpurea</i>)
<i>Porphyra atropurpurea</i>	folk medicine: poultices (Hoppe 1979)
<i>P. coccinea</i>	folk medicine: goiter, throat diseases (Schwimmer & Schwimmer 1955)
<i>P. columbina</i>	antibacterial: 5, 12, 27, 32, 37-40, 53, 62, 63, 66, 71 (Maurer 1965); laxative (Hoppe 1979)
<i>P. crispata</i>	folk medicine: "cooling", "soothing", clearing the lungs, relieve tension and anxiety, pulmonary and lymphatic tuberculosis, goiter, toothache, high blood pressure, kidney and urinary problems (Anon. 1978)
<i>P. dentata</i>	folk medicine: goiter, coughing, bronchitis, edema, measles (Anon. 1978)
<i>P. haitanensis</i>	folk medicine: "cooling", "soothing", clearing the lungs, relieve tension and anxiety, pulmonary and lymphatic tuberculosis, goiter, toothache, high blood pressure, hypertension, kidney and urinary problems, scrofula, tonsillitis, bronchitis, asthma (Anon. 1978; Tseng & Zhang 1984)
<i>P. leucosticta</i>	antibacterial: 71 (Fassina & Berti 1962)
<i>P. suborbiculata</i>	folk medicine: "cooling", "soothing", clearing the lungs, relieve tension and anxiety, pulmonary and lymphatic tuberculosis, goiter, toothache, high blood pressure, kidney and urinary problems (Anon. 1978)

antifungal: 1, 2, 4-7, 10, 15, 18, 19, 21, 24, 28, 30, 36, 37, 45 (Sakagami et al. 1982); antibacterial: 5, 6a, 6b, 7, 7a, 12, 27, 31, 32aa, 32b, 48, 51, 53, 60a, 62, 68, 69a, 71 (Aubert et al. 1979; Sakagami et al. 1982); hypocholesterolemic (Tsuchiya 1969; cf. Nisizawa 1979); antioxidants (Fujimoto & Kaneda 1980); antiulcer (Sakagami et al. 1982)

antimitotic: *Helianthus* assay (Chénieux et al. 1980); antibacterial: 27, 31, 71 (Biard et al. 1980)

influences growth of *Melosira moniliformis* (Kucherova 1970); settling, attaching, and morphogenetic inducers for *Haliotis rufescens* (Morse & Morse 1984); folk medicine: goiter, scrofula (Tseng & Zhang 1984)

P. tenera

P. umbilicalis

Porphyra sp.

SUBCLASS FLORIDEOPHYCIDAE

ORDER NEMALIALES

Audouinella sp.

Bonnemaisonia asparagoides

B. hamifera

*Celidium amansii*¹

G. cartilagineum

G. cartilagineum var. *robustum*

G. crinale

G. divaricatum

G. filicinum

G. glandulaefolium

G. lingulatum

Ulva morphogenetic factor (Provasoli & Pintner 1964) (as *Rhodochorton* sp.)

antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)

antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)

antibacterial: 12, 39 (Kamimoto 1956; Ma & Tang 1984)

antiviral: influenza B, mumps (Gerber et al. 1958)

toxic to mice (Habekost et al. 1955)

folk medicine: "cooling" or "soothing", dysentery, blood platelet diseases (breaking up skin spots) (Anon. 1978)

folk medicine: "cooling" or "soothing", dysentery, blood platelet diseases (breaking up skin spots), stomach ailments, hemorrhoids (Anon. 1978; Tseng & Zhang 1984)

antibacterial: 5, 12, 27, 32, 37-40, 53, 62, 63, 66, 71 (Maurer 1965)

anti-inflammatory (Baker 1984)

antibacterial: 5, 12, 27, 32, 37-39, 53, 62, 63, 66, 70, 71 (Maurer 1965)

ORDER GIGARTINALES

- Chondrus crispus*
antifungal: 14, 47 (Biard et al. 1980); antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974); folk medicine: "consumption", coughs, diarrhoea, dysentery, gastric ulcer, pulmonary disorders (Schwimmer & Schwimmer 1955; Hoppe 1979); inhibits feeding by *Littorina littorea* (Geiselman & McConnell 1981); inhibits growth of marine diatoms (Khfaji & Boney 1979); weight gain and fertility enhancement in ewes (Brewer et al. 1979)
- Chondrus* sp.
antibacterial: 27, 63, 71 (Maurer 1965)
- Cystoclonium purpureum*
antifungal: 14, 47 (Biard et al. 1980); antibacterial: 12, 27, 31, 38, 61, 71 (Biard et al. 1980; Roos 1957 (as *C. purpurascens*)); antimitotic: *Helianthus* assay (Chénieux et al. 1980); agglutinin (Shiomi 1983)
- Furcellaria lumbricalis*
antifungal: 14 (Biard et al. 1980); antibacterial: 31, 61, 71 (Biard et al. 1980), 11 (Chesters & Stott 1956 (as *Furcellaria* sp.)); antimitotic: *Helianthus* assay, crown gall assay (Chénieux et al. 1980); cytotoxic: KB (Chénieux et al. 1980); stimulates growth of *Skeletonema costatum* (Levring 1945) (as *F. fastigiata*); agglutinin (Shiomi 1983) (as *F. fastigiata*)
- Gigartina acicularis*
antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- G. alveata*
antibacterial: 71, 76a (Reichelt & Borowitzka 1984)
- G. cranwellae*
antibacterial: 76a, 77 (Reichelt & Borowitzka 1984)
- G. stellata*
antifungal: 14, 47 (Biard et al. 1980); antibacterial: 27, 31, 38, 71 (Biard et al. 1980)
- G. teedii*
agglutinin (Shiomi 1983)
- Gigartina* spp.
antibacterial: 63, 71 (Maurer 1965)
- Gracilaria bursa-pastoris*
folk medicine: cooling effect, "soothing", goiter, cough, congestion (Anon. 1978)
- G. compressa*
antifungal: 8 (Biard et al. 1980); antibacterial: 38 (Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- G. confervoides*
antibacterial: 63, 71 (Maurer 1965)
- G. constricta*
folk medicine: cooling effect, "soothing", goiter, cough, congestion (Anon. 1978)

- G. corticata*
antibacterial: 8, 71 (Rao & Parekh 1981)
folk medicine: goiter, scrofula, stomach ailments, hemorrhoids (Tseng & Zhang 1984)
- G. eucheumoides*
antifungal: 8 (Biard et al. 1980); antibacterial: 31, 38, 61 (Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980); produces mitotic anomalies in human synovial (McCoý) cell culture (Starr et al. 1966)
- G. lichenoides*
antibacterial: 76a, 77 (Reichelt & Borowitzka 1984); activity against *Trichomonas foetus* (Reichelt & Borowitzka 1984); inotropic (Baker 1984); folk medicine: intestinal and bladder problems (Schwimmer & Schwimmer 1955)
- G. verrucosa*
antifungal: 1, 2, 4-8, 10, 14, 15, 18, 19, 21, 24, 28, 30, 36, 37, 45, 47 (Sakagami et al. 1982); antibacterial: 5, 6a, 6b, 7, 7a, 12, 27, 31, 32aa, 32b, 48, 49, 51, 53, 60a, 62, 68, 69a, 71, 77 (Hornsey & Hide 1974; Sakagami et al. 1982); *Helianthus* assay (Chénieux et al. 1980); antiulcer (Sakagami et al. 1982); folk medicine: "soothing", "cooling", "dysentery, urinary problems, dropsy, enteric fever, assist stomach functions, "reinforcing body fluids", "nourishing the blood", goiter, scrofula (Anon. 1978; Tseng & Zhang 1984)
- Gracilaria* sp.
antifungal: 20, 45 (Reichelt & Borowitzka 1984); antibacterial: 71, 76a, 77 (Reichelt & Borowitzka 1984)
- Gymnogongrus norvegicus*
antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- Phyllophora crispa*
antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974); agglutinin (Shiomi 1983)
- P. nervosa*
anticoagulant (Hoppe 1979); antilipemic (Hoppe 1979)
- P. pseudoceranooides*
antibacterial: 12, 27, 49, 71, 77 (Roos 1957; Hornsey & Hide 1974) (as *P. membranifolia*); agglutinin (Shiomi 1983)
- Polyides rotundus*
antimitotic: *Helianthus* assay (Chénieux et al. 1980) (as *P. caprinus*); agglutinin (Shiomi 1983)
- ORDER CRYPTONEMIALES
- Corallina chilensis*
antibacterial: 27, 63, 71 (Maurer 1965)
- C. officinalis*
antifungal: 8 (Biard et al. 1980); antibacterial: 8, 27, 31, 38, 71, 77 (Haas 1950; Biard et al. 1980; Rao & Parekh 1981); preferential settlement of *Spirorbis* larvae (Williams 1964)

<i>C. pilulifera</i>	antibacterial: 12 (Ohta 1979)
<i>C. squamata</i>	antibacterial: 27, 38 (Biard et al, 1980)
<i>Corallina</i> spp.	spasmogenic (Naqvi et al. 1980); folk medicine: burns, chronic gastritis, diarrhoea (Hoppe 1979); oxytotic (Naqvi et al. 1980); toxic to mice (Naqvi et al. 1980); vermifuge (Hoppe 1979)
<i>Dilsea carnosia</i>	antifungal: 14 (Biard et al. 1980); antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974); antimitotic: <i>Helianthus</i> assay (Chénieux et al. 1980)
<i>Dumontia contorta</i>	antimitotic: <i>Helianthus</i> assay (Chénieux et al. 1980); stimulates growth of <i>Skeletonema costatum</i> (Levring 1945) (as <i>D. incrassata</i>)
<i>Gloiosiphonia capillaris</i>	antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)
<i>Lithothamnion californicum</i>	settling, attaching, and morphogenetic inducers for <i>Haliotis rufescens</i> (Morse & Morse 1984)
<i>Jania rubens</i>	hypoglycemic (Hoppe 1979); fibrinolytic (Hoppe 1979); lipolytic (Hoppe 1979) (as <i>Corallina rubens</i>)
ORDER PALMARIALES	
<i>Palmaria palmata</i>	antibacterial: 8, 71 (Rao and Parekh 1981); antimitotic: <i>Helianthus</i> assay (Chénieux et al. 1980) (as <i>Rhodymenia palmata</i>); agglutinin (Shiomi 1983)
ORDER RHODYMENIALES	
<i>Halosaccion glandiforme</i> ²	antibacterial: 27, 53, 71 (Pratt et al. 1951)
<i>Lomentaria articulata</i>	antifungal: 14 (Biard et al. 1980); antibacterial: 27, 31, 71 (Biard et al. 1980); antimitotic: <i>Helianthus</i> assay (Chénieux et al. 1980)
<i>Rhodymenia indica</i> ³	vermifuge (Hoppe 1979)
<i>R. ordisoni</i>	antiviral: influenza A (Fassina & Berti 1962)
<i>Rhodymenia</i> spp.	antibacterial: 27, 63, 71 (Maurer 1965)

ORDER CERAMIALES

- Anthamnion cruciatum* antibacterial: 12, 27, 49, 71, 77 (Fassina & Berti 1962; Hornsey & Hide 1974)
- A. glanduliferum* *Ulva* morphogenetic factor (Provasoli & Pintner 1964)
- A. plumula* antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)
- A. sarniense* *Ulva* morphogenetic factor (Provasoli & Pintner 1964)
- Callithamnion arbuscula* antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)
- C. corymbosum* agglutinin (Shiomi 1983)
- C. tetragonum* antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)
- C. tetricum* antifungal: 14 (Biard et al. 1980); antibacterial: 12, 27, 31, 38, 49, 71, 77 (Hornsey & Hide 1974; Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- Callithamnion* sp. influences growth of *Melosira moniliformis* (Kucherova 1970)
- Ceramium acanthonotum* antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- C. boydenii* antibacterial: 37 (Kamimoto 1956); stimulates growth of bacteria: 36 (Kamimoto 1956)
- C. byssoideum* antibacterial: 27, 38, 71 (Burkholder et al. 1960)
- C. ciliatum* antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- C. diaphanum* antibacterial: 12, 71 (Roos 1957)
- C. kondoi* agglutinin (Shiomi 1983)
- C. loureirii* folk medicine: "chest diseases" (Hoppe 1979)
- C. nitens* stimulates growth of fungus: 5 (Welch 1962)
- C. rubrum* antifungal: 8, 14, 47 (Biard et al. 1980); antibacterial: 12, 27, 31, 38, 71 (Roos 1957; Biard et al. 1980; cf. Ikawa et al. 1973); stimulates growth of *Skeletonema costatum* (Levring 1945); agglutinin (Shiomi 1983)
- Ceramium* sp. hemolytic (Hashimoto et al. 1972); toxic to mice (Hashimoto et al. 1972)

- Chondria armata* antibacterial: 8, 71 (Rao & Parekh 1981); hypotensive (Naqvi et al. 1980); toxic to mice, LD₅₀ = 17.8 mg·kg⁻¹ (Naqvi et al. 1980)
- C. coerulescens* agglutinin (Shiomi 1983)
- C. dasyphylla* antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974); antimitotic: *Helianthus* assay (Chénieux et al. 1980); inotropic (Baker 1984)
- C. littoralis* antifungal: 8 (Burkholder et al. 1960; Olesen et al. 1964; Hoppe 1979); antibacterial: 27, 38, 71, 83 (four species) (Burkholder et al. 1960; Olesen et al. 1964; Hoppe 1979); antitumor: KB (Martinez Nadal et al. 1965); vermifuge (Michanek 1979)
- C. sanguinea* folk medicine: indigestion (Hoppe 1979); anthelmintic (Hoppe 1979; Michanek 1979)
- C. vermicularis* folk medicine: indigestion (Hoppe 1979); anthelmintic (Hoppe 1979; Michanek 1979)
- Chondria* sp. hemolytic (Hashimoto et al. 1972)
- Dasya baillouviana* *Ulva* morphogenetic factor (Provasoli & Pintner 1964) (as *D. pedicellata*)
- Griffithsia flosculosa* agglutinin (Shiomi 1983)
- Griffithsia* spp. antibacterial: 63 (Maurer 1965); hemolytic (Hashimoto et al. 1972); toxic to mice (Hashimoto et al. 1972)
- Membranoptera alata* antifungal: 14 (Biard et al. 1980); antibacterial: 12, 49, 71, 77 (Hornsey & Hide 1974); agglutinin (Shiomi 1983)
- Odonthalia dentata* antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)
- Phycodrys rubens* antibacterial: 12, 71 (Roos 1957); agglutinin (Shiomi 1983)
- P. sinuosa*⁴ stimulates growth of *Skeletonema costatum* (Levring 1945)
- Plumaria elegans* agglutinin (Shiomi 1983)
- Polysiphonia elongata* antibacterial: 12, 27, 49, 71, 77 (Roos 1957; Hornsey & Hide 1974)
- P. ferrulacea* antibacterial: 71 (Burkholder et al. 1960)
- P. fruticulosa* antifungal: 14 (Biard et al. 1980); antibacterial: 31, 38, 61, 71 (Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980)

- P. harveyi*
increases survival of vorticellids (Langlois 1975)
- P. kappannae*
antibacterial: 8, 71 (Rao & Parekh 1981)
- P. lanosa*
antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974; Biard et al. 1980); antimutotic: *Helianthus* assay, crown gall assay (Chénieux et al. 1980); increases survival of vorticellids (Langlois 1975); agglutinin (Shiomi 1983)
- P. nigra*
antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)
- P. nigrescens*
antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)
- P. subulifera*
increases serum lipolytic activity (Hoppe 1979)
- P. thuyoides*⁵
antifungal: 8, 14, 47 (Biard et al. 1980); antibacterial: 31, 38, 61, 71 (Biard et al. 1980)
- P. urceolata*
antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974; Ma & Tang 1984); *Ulva* morphogenetic factor (Provasoli & Pintner 1964)
- P. violacea*
antibacterial: 12, 71 (Roos 1957); stimulates growth of *Skeletonema costatum* (Levring 1945)
- Polysiphonia* spp.
antibacterial: 3 (two species), 11, 12, 27, 55, 57, 63, 70, 71, 76a, 77, 84 (two species) (Chesters & Stott 1956; Maurer 1965; Reichelt & Borowitzka 1984)
- Ptilota plumosa*
agglutinin (Blunden & Rogers 1976; Shiomi 1983)
- Rhodomela confervoides*
antifungal: 14 (Biard et al. 1980); antibacterial: 12, 31, 49, 71, 77, 80a (Hornsey & Hide 1974; Biard et al. 1980; Ma & Tang 1984); antimutotic: *Helianthus* assay (Chénieux et al. 1980)
- R. larix*
antifungal: 8, 42, 46 (Mautner et al. 1953); antibacterial: 5, 8, 27, 31, 36, 37, 39, 53, 61, 71 (Mautner et al. 1953)
- R. subfusca*
antibacterial: 10, 12 (two strains), 27, 33 (two strains), 37, 67, 70, 71 (twenty-three strains), 80 (Roos 1957); stimulates growth of *Skeletonema costatum* (Levring 1945)
- Spyridia filamentosa*
agglutinin (Shiomi 1983)

CLASS PHAEOPHYCEAE**ORDER ECTOCARPALES**

- Chordaria flagelliformis* antibacterial: 12, 49, 71, 77 (Hornsey & Hide 1974); anticoagulant (Hoppe 1979); agglutinin (Shiomi 1983)
- Colpomenia sinuosa* antibacterial: 5, 12, 27, 32, 37, 38, 40, 62, 63, 66, 71 (Maurer 1965)
- Dictyosiphon foeniculaceus* agglutinin (Shiomi 1983)
- Ectocarpus siliculosus* antibacterial: 12, 27, 71 (Roos 1957; Fassina & Berti 1962)
- Pilayella littoralis* antifungal: 47 (Biard et al. 1980); antibacterial: 27, 31, 38, 71 (Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980); stimulates growth of *Skeletonema costatum* (Levring 1945)
- Ralfsia spongiocarpa* antialgal: *Porphyrodiscus simulans*, *Rhodophysema elegans* (Fletcher 1975)
- Scytosiphon lomentaria* antifungal: 3, 4, 14, 31, 32 (Khaleafa et al. 1975; Biard et al. 1980); antibacterial: 31, 71 (Biard et al. 1980); folk medicine: dry coughs, laryngitis, lymphatic tuberculosis (Anon. 1978); antimitotic: *Helianthus* assay (Chénieux et al. 1980); stimulates growth of *Skeletonema costatum* (Levring 1945); decreases survival of vorticellids (Langlois 1975)
- Stictyosiphon tortilis* agglutinin (Shiomi 1983)
- ORDER DESMARESTIALES**
- Desmarestia aculeata* antibacterial: 12, 27, 49, 71, 77 (Roos 1957; Hornsey & Hide 1974); agglutinin (Shiomi 1983)
- D. ligulata* antifungal: 14 (Biard et al. 1980); antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974); agglutinin (Shiomi 1983)
- D. viridis* agglutinin (Shiomi 1983)
- ORDER LAMINARIALES**
- Alaria crassifolia* convulsive toxin (Shirahama 1937); paralytic toxin (Shirahama 1937)
- A. esculenta* antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)

- Chorda filum*
antibacterial: 12, 71 (Roos 1957)
- Laminaria angustata*
antibacterial: 12, 27 (Nisizawa 1979); antitumor: sarcoma-180, L-1210 leukemia, Meth-A, B-16 melanoma (Yamamoto et al. 1982)
- L. angustata* var. *longissima*
antitumor: L-1210 leukemia (Yamamoto et al. 1982)
- L. diabolica*
anticoagulant (Nisizawa 1979)
- L. digitata*
antifungal: 14 (Biard et al. 1980), antibacterial: 11, 12, 27, 38, 49, 71, 77, 84 (two spp.) (Chesters & Stott 1956; Roos 1957; Hornsey & Hide 1974; Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980); stimulates growth of *Skeletonema costatum* (Levring 1945)
- L. japonica*
antitumor: L-1210 leukemia (Yamamoto et al. 1982); anticoagulant (Nisizawa 1979); hypocholesterolemic (Nisizawa 1979); enhances activity of pancreatic lipase (Nisizawa 1979); stimulates growth of rats (Brekhman 1970); produces resistance in rats to low barometric pressure (Brekhman 1970); folk medicine: normalizing blood pressure, hyperthyroidism, "glandular weakness", "cleaning the blood", producing a "cooling effect", urinary problems, scrofula, stomach ailments, hemorrhoids (Hoppe 1979; Tseng & Zhang 1984), drowsies (Read & How 1927), high blood pressure (Anon. 1978)
- L. japonica* var. *ochotensis*
antitumor: L-1210 leukemia (Yamamoto et al. 1982); convulsive toxin (Shirahama 1937) (as *L. ochotensis*)
- L. longipedalis*
anticoagulant (Nisizawa 1979)
- L. religiosa*
anticoagulant (Nisizawa 1979); folk medicine: menstrual disorders (Read & How 1927); increases action of uterus during labour (Read & How 1927)
- L. saccharina*
antifungal: 8 (Biard et al. 1980); antibacterial: 12, 27, 38, 49, 71, 77 (Roos 1957; Hornsey & Hide 1974; Biard et al. 1980); antimitotic: *Helianthus* assay, crown gall assay (Chénieux et al. 1980); cytotoxic: KB (Chénieux et al. 1980); agglutinin (Shiomi 1983); folk medicine: skin diseases, goiter, syphilis, constipation, arteriosclerosis (Schwimmer & Schwimmer 1955; Hoppe 1979)
- Laminaria* spp.
inhibits viral and bacterial neuraminidases (Kathan 1965); folk medicine: skin diseases (Read & How 1927), high blood pressure and menstrual difficulties (Hoppe 1979)
- Saccorhiza polyschides*
antifungal: 14, 47 (Biard et al. 1980); antibacterial: 27, 31, 38 (Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980)

ORDER SPHACELARIALES

- Halopteris pseudospicata* antibacterial: 71, 76a, 77 (Reichelt & Borowitzka 1984)
- H. scoparia* antifungal: 47 (Chénieux et al. 1980); antibacterial: 27, 31, 38, 71 (Chénieux et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- Halopteris* sp. antibacterial: 76a (Reichelt & Borowitzka 1984)
- Sphacelaria* sp. *Ulva* morphogenetic factor (Provasoli & Pintner 1964)

ORDER FUCALES

- Ascophyllum nodosum* antibacterial: 5, 15, 27, 31, 33, 51, 53, 65, 71, 77 (Vacca & Walsh 1954; Biard et al. 1980); increases proliferation of soil bacteria (Nisizawa 1979); antimitotic: *Helianthus* assay (Chénieux et al. 1980); folk medicine: obesity, rheumatism, strains (Read & How 1927; Hoppe 1979) and glandular swellings (Read & How 1927); may reduce populations of red spider mites on apple (Booth 1969); various influences on seed germination (Senn & Skelton 1969); stimulates respiration in seeds, fruits and flowers (Senn & Skelton 1969); increases shelf life of peaches from treated trees (Skelton & Senn 1969); increases weight and heart diameter of lettuce, and curd diameter of cauliflower (Abetz & Young 1983); may increase hyoscyne content of *Duboisia* hybrid (Luanratana & Griffin 1982); toxic to fish larvae (Sieburth & Jensen 1969; cf. Jensen & Ragan 1978); stimulates growth of *Skeletonema costatum* (Levring 1945); promotes settling of larvae of *Alcyonidium polyoum* and *Flustrellidra hispida* (Crisp & Williams 1960); decreases survival of vorticellids (Langlois 1975); retards growth of rabbits (Hashimoto 1979); causes internal bleeding (Hashimoto 1979) and various other effects when fed to domestic animals (e.g. Bogen 1962; Jensen et al. 1968); agglutinin (Shiomi 1983)
- Fucus ceranoides* agglutinin (Shiomi 1983)
- F. esculentus* folk medicine: sclerosis, thyroid disturbances (Hoppe 1979)
- F. gardneri* hypocholesterolemic (Tsuchiya 1969; Hoppe 1979)
- F. helminthocorton* anthelmintic (Emerson & Taft 1945)

- F. serratus*: 10, 12 (two strains), 27, 33 (two strains), 37, 38, 53, 66, 67 (two spp.), 70, 71 (twenty-four strains), 76, 80, 85 (Roos 1957; Biard et al. 1980); promotes settling of larvae of *Alcyonidium polyoum*, *Flustrellidra hispida* and *Spirorbis borealis* (Crisp & Williams 1960; Williams 1964); agglutinin (Shiomi 1983)
- F. spiralis*: antimitotic: *Helianthus* assay, crown gall assay (Chénieux et al. 1980); cytotoxic: KB (Chénieux et al. 1980); decreases survival of vorticellids (Langlois 1975); agglutinin (Shiomi 1983)
- F. vesiculosus*: antibacterial: 12, 31, 71 (Roos 1957; Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980); cytotoxic: KB (Chénieux et al. 1980); folk medicine: obesity, goiter, Basedo's disease, scrofulosis (Hoppe 1979); stimulates growth of *Skeletonema costatum* (Levring 1945); promotes settling of larvae of *Alcyonidium polyoum* and *Flustrellidra hispida* (Crisp & Williams 1960); antifeedant for *Littorina littorea* (Geiselman & McConnell 1981); agglutinin (Shiomi 1983)
- F. virsoides*: antiviral: influenza A (Fassina & Berti 1962)

CLASS DINOPHYCEAE

ORDER GYMNODINIALES

- Amphidinium carterae*: antibacterial: 14, 24, 25, 29, 34 (three species), 71, 73, 76a, 77 (Duff et al. 1966; Reichelt & Borowitzka 1984); positively inotropic (Thurberg & Sasner 1973; cf. Hashimoto 1979); inhibits heart muscle activity (Thurberg & Sasner 1973; cf. Hashimoto 1979); toxic to mice and fish (Thurberg & Sasner 1979; Hashimoto 1979)
- Cochlodinium* sp.: antibacterial: 86 (Burkholder 1968)
- Gymnodinium alaskensis*: toxic (Kremer 1981)
- G. breve*: neurotoxic (Spiegelstein et al. 1973; Der Marderosian 1979; Kremer 1981); irritant to eyes and throat (Hashimoto 1979); hemolytic (Spiegelstein et al. 1973); blood anticoagulant (Doig & Martin 1973); ichthyotoxic (Hashimoto 1979)
- G. mikimotoi*: toxic (Kremer 1981)
- G. sanguineum*: toxic (Kremer 1981)
- G. veneficum*: neurotoxic (Kremer 1981); ichthyotoxic (Hashimoto 1979)

ORDER NOCTILUCALES

Noctiluca militaris ichthyotoxic (Hashimoto 1979)

ORDER PERIDINIALES

Coolia monotis inhibits growth of *Asterionella japonica* (Pincemin 1971)

Gonyaulax acatenella toxic (Nisizawa & Chihara 1979)

G. digitale toxic (Kremer 1981)

G. monilata toxic (Kremer 1981); ichthyotoxic (Nisizawa & Chihara 1979)

G. polyedra toxic (Kremer 1981)

G. tamarensis antifungal: 8 (Burkholder et al. 1960); antibacterial: 71 (Burkholder et al. 1960)

Heteraulacus sp. antifungal: 8, 12, 33, 39, 45 (Sharma et al. 1968); antibacterial: 86 (Burkholder 1968); ichthyotoxic (Sharma, Michaels & Burkholder 1968) (as *Goniodoma* sp.)

Protoperidinium polonium

ichthyotoxic (Der Marderosian 1979; Hashimoto 1979); inhibits growth and photosynthesis of algae (Hashimoto 1979) (as *Peridinium polonium*)

Pyrodinium phoneus toxic (Nisizawa & Chihara 1979)

Scrippsella trochoidea inhibits growth of *Asterionella japonica* (Pincemin 1971) (as *Peridinium trochoideum*)

CLASS DESMOPHYCEAE**ORDER PROROCENTRALES**

Prorocentrum micans inhibits growth of diatoms (Uchida 1981); stimulates antibiotic production by diatoms (Gauthier et al. 1978)

P. minimum stimulates growth of unidentified marine bacterium (Berland et al. 1972) (as *Exuviaella mariaelebouriae*)

Prorocentrum sp. neurotoxic (Nisizawa & Chihara 1979); toxic to mice (Hashimoto 1979); ichthyotoxic (Hashimoto 1979) (as *Exuviaella* sp.)

CLASS HAPTOPHYCEAE**ORDER ISOCHRYSIDALES***Emiliana huxleyi*

antibacterial: 4, 14 (two species), 25 (two species), 29, 34 (three species), 48, 71 (two strains), 73 (Duff et al. 1966) (as *Coccolithus huxleyi*)

Isochrysis galbana

antibacterial: 14 (two species), 25, 29, 34 (three species), 71 (two strains), 73, 75, 77 (Duff et al. 1966)

ORDER PAVLOVALES*Pavlova lutheri*

antibacterial: 14 (two species), 25 (two species), 29, 34 (three species), 71 (two strains), 73, 77 (Duff et al. 1966); vitamin B₁₂-binding factor (Droop 1968) (as *Monochrysis lutheri*)

ORDER PRYMNESIALES*Prymnesium parvum*

antibacterial: 12, 35, 43, 49, 66, 68, 71, 75 (Aubert et al. 1968; Aubert & Pesando 1969); cytotoxic: Ehrlich ascites, HeLa, FL amniotic, Chang liver (Shilo & Rosenberger 1960-1961); hemolytic (Shilo & Rosenberger 1960-1961); ichthyotoxic (Reich & Rotberg 1958; Shilo & Rosenberger 1960-1961; Reich & Parnas 1962); neurotoxic (Chapman 1979; Kremer 1981); toxic to molluscs and tadpoles (Shilo & Rosenberger 1960-1961)

CLASS CHRYSOPHYCEAE**ORDER OCHROMONADALES***Ochromonas danica*

ichthyotoxic (Reich & Spiegelstein 1964)

O. malhamensis

antibacterial: 8, 12, 27, 71 (Hansen 1973); ichthyotoxic (Reich & Spiegelstein 1964)

Olisthodiscus luteus

antialgal (Pratt 1966; cf. Tomas 1980); modifies larval development (Sieburth 1968)

ORDER PHAEOPALCALES*Stichochrysis immobilis*

antibacterial: 1, 3, 29, 82, 83 (two species) (Berland et al. 1972); enhances growth of bacteria: 59, 83 (Berland et al. 1972)

CLASS CRYPTOPHYCEAE**ORDER CRYPTOMONADALES***Cryptomonas* sp.

antibacterial: 14 (two species), 25 (two species), 29, 34 (three species) (Duff et al. 1966)

Hemiselmis virescens

antibacterial: 14, 24, 25 (two species), 26, 29, 34 (two species), 71 (two strains), 73, 75 (Duff et al. 1966)

Rhodomonas baltica

ichthyotoxic (Hashimoto 1979)

R. lens

antibacterial: 14 (two species), 27, 29, 34 (two species), 73 (Duff et al. 1966)

CLASS PRASINOPHYCEAE**ORDER PRASINOCCLADALES***Tetraselmis maculata*

antibacterial: 25, 71 (two strains), 73, 75 (Duff et al. 1966)

CLASS CHLOROMONADOPHYCEAE*Chattonella* spp.

ichthyotoxic (Nisizawa & Chihara 1979)

Heterosigma sp.inhibits growth of *Skeletonema costatum* (Honjo et al. 1978)**CLASS CHLOROPHYCEAE****ORDER VOLVOCALES***Dunaliella tertiolecta*

antibacterial: 24, 34, 73 (Duff et al. 1966); antihypertensive, bronchodilator, antiserotonin, antiwrithing, muscle relaxant, postsynaptic blocker, analgesic, antioedema (Baker 1984)

Dunaliella sp.antibacterial: 71 (Accorinti 1964); inhibits growth of *Chlorella stigmatophora* (Accorinti 1964)**ORDER CHLOROCOCCALES⁶***Chlorella pyrenoidosa*

antibacterial: 83 (Steemann Nielsen 1955); immunogenic (Bernstein et al. 1969)

*C. stigmatophora*antibacterial: 71 (Accorinti 1964); enhances growth of *Dunaliella* sp. (Accorinti 1964)

- C. vulgaris*
antibacterial: 64, 71 (Jørgenson & Steemann Nielsen 1961; Telitchenko et al. 1962); promotes growth of bacteria: 71 (Jørgenson & Steemann Nielsen 1961); immunogenic (Bernstein et al. 1969); reduces filtering rate of *Daphnia magna* (Ryther 1954)
- Protosiphon botryoides*
antibacterial: 9, 13, 57, 71 (Harder & Oppermann 1953)
- Scenedesmus basilensis*
immunogenic (Bernstein et al. 1969)
- S. obliquus*
antibacterial: 64 (Telitchenko et al. 1962)
- S. quadricauda*
reduces filtering rate of *Daphnia magna* (Ryther 1954)
- ORDER ULOTRICHALES**
- Monostroma nitidum*
hypocholesterolemic (Tsuchiya 1969)
- Spongomorpha arcta*
antibacterial: 12, 71 (Roos 1957)
- Stichococcus bacillaris*
antibacterial: 9, 13, 57, 71 (Harder & Oppermann 1953)
- ORDER ULVALES**
- Enteromorpha chaetomorphoides*
produces mitotic anomalies in human synovial (McCoy) cell culture (Starr et al. 1966)
folk medicine: relief from heat (Anon. 1978)
- E. clathrata*
antibacterial: 12, 27, 38, 71 (Roos 1957; Allen & Dawson 1960); hypocholesterolemic (Nisizawa 1979)
- E. compressa*
produces mitotic anomalies in human synovial (McCoy) cell culture (Starr et al. 1966)
- E. flexuosa*
antibacterial: 38, 71 (Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- E. hendayensis*
antifungal: 47 (Biard et al. 1980); antibacterial: 8, 27, 31, 38, 39, 63, 71 (Maurer 1965; Biard et al. 1980; Rao & Parekh 1981; Rao et al. 1982); antimitotic: *Helianthus* assay, crown gall assay (Chénieux et al. 1980); cytotoxic: KB (Chénieux et al. 1980); polysynaptic blocker (Baker 1984); agglutinin (Shiomi 1983); folk medicine: aphthae, back pain, paronychia, lymphatic swellings, goiter (Anon. 1978); stimulates growth of *Skeletonema costatum* (Levring 1945)
- E. intestinalis*

- E. kyllinii* antibacterial: 12, 38, 71 (Allen & Dawson 1960)
- E. lingulata* produces mitotic anomalies in human synovial (McCoy) cell culture (Starr et al. 1966)
- E. linza* antiviral: influenza A (Fassina & Berti 1962)
- E. prolifera* antibacterial: 12, 38, 55, 71 (Allen & Dawson 1960; Starr et al. 1962); produces mitotic anomalies in human synovial (McCoy) cell culture (Starr et al. 1966); folk medicine: aphthae, back pain, paronychia, nosebleeds, "sore-hand", lymphatic swellings, goiter, "cooling", cough, bronchitis, tonsillitis, asthma (Anon. 1978; Tseng & Zhang 1984); hypocholesterolemic (Tsuchiya 1969)
- E. ramulosa* antifungal: 14 (Biard et al. 1980); antibacterial: 38, 71 (Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- Enteromorpha* spp. antibacterial: 12, 27, 33, 37, 63, 71 (Katayama 1956-1957a; Roos 1957; Maurer 1965); influences muscle contraction in worms (Katayama 1956-1957c); diuretic (Naqvi et al. 1980); toxic to mice (Naqvi et al. 1980); influences growth of *Melosira moniliformis* (Kucherova 1970); folk medicine: goiter, scrofula, "cooling", cough, bronchitis, tonsillitis, asthma, nosebleeds, "sore-hand" (Tseng & Zhang 1984)
- Ulva arasakii* agglutinin (Shiomi 1983)
- U. conglobata* agglutinin (Shiomi 1983); folk medicine: sore throat, laryngitis, lymphatic tuberculosis, headaches, halitosis, goiter, "soothing" or "cooling" (Anon. 1978; Tseng & Zhang 1984)
- U. fasciata* hemolytic (Hashimoto et al. 1972); toxic to mice (Naqvi et al. 1980); folk medicine: sore throat, laryngitis, lymphatic tuberculosis, headaches, halitosis, goiter, "soothing" or "cooling" (Anon. 1978; Tseng & Zhang 1984)
- U. lactuca* antifungal: 14 (Biard et al. 1980); stimulates growth (5) and sporulation (18) of fungi (Welch 1962); antibacterial: 5, 12, 27, 31, 32, 37-40, 49, 53, 61-63, 66, 70, 71, 77 (Roos 1957; Fassina & Berti 1962; Maurer 1965; Hornsey & Hide 1974; Biard et al. 1980); antimitotic: *Helianthus* assay, crown gall assay (Chénieux et al. 1980); cytotoxic: KB (Chénieux et al. 1980); vermifuge (Michanek 1979); agglutinin (Shiomi 1983); folk medicine: gout, scrofula, "irritations" (Hoppe 1979), furuncles, sore throat, laryngitis, lymphatic tuberculosis, headaches, halitosis, urinary problems, dropsy, goiter, "soothing" or "cooling" (Anon. 1978; Tseng & Zhang 1984); influences growth of *U. lactuca* (cited in Levring 1945 and Kucherova 1970)

- U. linza* antibacterial: 27, 53, 71 (Pratt et al. 1951); folk medicine: heat stroke, goiter (Anon. 1978)
- U. penniformis* folk medicine: "medicinal preparation" (Hoppe 1979)
- U. pertusa* antibacterial: 12, 27, 36, 37, 80a (Kamimoto 1956; Nisizawa 1979; Ma & Tang 1984); influences muscle contraction in worms (Katayama 1956-1957c); hemolytic (Hashimoto et al. 1972); hypocholesterolemic (Tsuchiya 1969); anthelmintic (Katayama 1956-1957b); agglutinin (Shiomi 1983); folk medicine: fever (Hoppe 1979), heat stroke, edema, urinary problems, lymphatic swellings, goiter, high blood pressure, dropsy (Anon. 1978; Tseng & Zhang 1984)
- U. reticulata* hemolytic (Hashimoto et al. 1972)
- U. rigida* antibacterial: 76a, 77 (Reichelt & Borowitzka 1984)
- Ulva* spp. vermifuge (Hoppe 1979); stimulates growth of diatoms (Levring 1945)

ORDER CLADOPHORALES

- Chaetomorpha antennina* antifungal: 4, 9, 11, 26, 39 (Rao and Shelat 1982)
- C. brachygonia* produces mitotic anomalies in human synovial (McCoy) cell culture (Starr et al. 1966)
- C. capillaris* agglutinin (Shiomi 1983)
- C. linum* antiviral: TMV (Caccamese et al. 1981); antibacterial: 5, 12, 27, 32, 37, 38, 40, 53, 62, 63, 66, 70, 71 (Maurer 1965)
- C. minima* ichthyotoxic (Ohta 1979)
- Cladophora glomerata* folk medicine: burns (Hoppe 1979)
- C. gracilis* increases survival of vorticellids (Langlois 1975)
- C. monumentalis* antibacterial: 71 (Rao & Parekh 1981)
- C. pellucida* antifungal: 3, 4, 31, 32 (Khaleafa et al. 1975); antibacterial: 12, 49, 71, 77 (Hornsey & Hide 1974)
- C. pinnulata* toxic to mice, $LD_{50} = 8.25 \text{ mg} \cdot \text{kg}^{-1}$ (Naqvi et al. 1980)
- C. prolifera* antiviral: influenza A (Fassina & Berti 1962); antibacterial: 71 (Fassina & Berti 1962)

- C. rupestris* antibacterial: 31, 38, 71 (Biard et al. 1980); antimitotic: *Helianthus* assay (Chénieux et al. 1980); cytotoxic: KB (Chénieux et al. 1980); agglutinin (Shiomi 1983)
- Cladophora* spp. antiviral: murine meningopneumonitis virus (Starr et al. 1962); antibacterial: 38, 55, 63, 71 (Starr et al. 1962; Maurer 1965); cytotoxic: human synovial (Starr et al. 1962)
- Rhizoclonium riparium* antibacterial: 76a (Reichelt & Borowitzka 1984); beta-blocker, 5-hydroxytryptamine blocker (Baker 1984); folk medicine: wounds (Hoppe 1979)
- R. rivulare*⁷ vermifuge (Hoppe 1979); folk medicine: wounds (Hoppe 1979)
- Rhizoclonium* sp. antibacterial: 27, 63, 71 (Maurer 1965)
- ORDER CODIALES
- Bryopsis hypnoides* agglutinin (Shiomi 1983)
- B. pennata* produces mitotic anomalies in human synovial (McCoy) cell culture (Starr et al. 1966)
- B. plumosa* antiviral: influenza A (Fassina & Berti 1962); antibacterial: 12, 49, 71, 77 (Fassina & Berti 1962; Hornsey & Hide 1974)
- Codium adhaerens* antibacterial: 71, 76a, 77 (Biard et al. 1980; Reichelt & Borowitzka 1984); antimitotic: *Helianthus* assay (Chénieux et al. 1980); inotropic (Baker 1984); toxic to mice (Hashimoto et al. 1972)
- C. coralloides* antiviral: TMV (Caccamese et al. 1981); antifungal: 18a (Caccamese et al. 1981)
- C. dimorphum* antibacterial: 5, 27, 32, 37-40, 63, 66, 70, 71 (Maurer 1965)
- C. effusum* antiviral: TMV (Caccamese et al. 1981); antifungal: 18a (Caccamese et al. 1981)
- C. fragile* antibacterial: 12, 27, 37, 49, 71, 77 (Kamimoto 1956; Hornsey & Hide 1974); stimulates growth of bacteria: 36 (Kamimoto 1956); antimitotic: *Helianthus* assay (Chénieux et al. 1980); cytotoxic: KB (Chénieux et al. 1980); vermifuge (Tseng & Zhang 1984); folk medicine: urinary problems, dropsy (Tseng & Zhang 1984)
- C. fragile* subsp. *atlanticum* agglutinin (Shiomi 1983)
- C. fragile* subsp. *tomentoides* agglutinin (Shiomi 1983)

- C. intertextum* antibacterial: 7, 12 (Nuñez & Serpa Sanabria 1975)
 toxic to mice (Hashimoto et al. 1972)
- C. intricatum* stimulates sporulation of fungi: 3, 18 (Welch 1962); produces mitotic anomalies in human synovial (McCoy) cell culture (Starr et al. 1966); agglutinin (Shiomi 1983)
- C. isthmocladum* antibacterial: 12 (Ohta 1979); repels snail *Monodonta neritoides* (Ohta et al. 1978)
- C. latum* antibacterial: 71, 76a, 77 (Reichelt & Borowitzka 1984); antifungal: 9a (Reichelt & Borowitzka 1984)
- C. muelleri* antitumor: Ehrlich ascites, Ehrlich solid, Sarcoma-180 solid (Nisizawa 1979)
- C. pugniformis* antibacterial: 27, 71, 76a, 77 (Reichelt & Borowitzka 1984)
- C. spongiosum* antibacterial: 12, 27, 49, 71, 77 (Hornsey & Hide 1974)
- C. tomentosum* antimitotic: *Helianthus* assay (Chénieux et al. 1980)
- C. vermilaria* vermifuge, especially vs. *Ascaris lumbricoides* (Hoppe 1979); influences muscle contraction in worms (Katayama 1956-1957c)
- Codium* spp.

CLASS BACILLARIOPHYCEAE

SUBCLASS PENNATOPHYCIDEAE

ORDER DIATOMALES

- Asterionella japonica* antifungal: 14 (Pesando et al. 1979b); antibacterial: 12, 17-23, 43, 47, 66, 71, 72, 75, 81, 87 (eight species) (Aubert et al. 1968, 1979; Aubert & Pesando 1969; Gauthier et al. 1978)
- A. notata* antifungal: 2, 8, 14, 21, 33 (three species), 39, 43, 45, 49 (three species), 50 (six species) (Gauthier 1969; Pesando et al. 1979a,b); antibacterial: 6, 16, 27 (three strains), 30, 31, 41-45, 49-53, 60, 64, 66, 68, 69, 71 (three strains), 72, 75, 83 (seven species, Gram-negative) (Aubert & Pesando 1969; Gauthier 1969); inhibitory to phytoplankton: *Asterionella japonica*, *A. notata*, *Coccochloris elebens*, *Nitzschia ascicularis*, *Phaeodactylum tricornutum*, *Tetraselmis maculata*, *T. striata*, *T. tetra-thele* (Gauthier 1969)
- Fragilaria pinnata* antifungal: 8, 14, 21, 43, 45 (Pesando et al. 1979b)

- F. striatula* possible cause of contact dermatitis (Fraser & Lyell 1963; cf. Carlé & Christophersen 1980)
- Licmophora abbreviata* antibacterial: 43, 66, 71 (Aubert et al. 1968)
- Thalassionema nitzschioides* influences growth of *T. nitzschioides* (Kustenko 1975)
- Thalassiothrix frauenfeldi* antibacterial: 43, 66, 71 (Aubert et al. 1968)
- T. nordenskiöldii* antibacterial: 66 (Sieburth 1965)
- ORDER NAVICULALES
- Bacillaria paradoxa* antibacterial: 43 (Aubert et al. 1968)
- Gyrosigma fasciola* antifungal: 14 (Pesando et al. 1979b)
- G. spenceri* antibacterial: 43, 66, 71 (Aubert et al. 1968)
- Navicula incerta* antibacterial: 88 (Aubert et al. 1979)
- N. grevillei* inhibition or enhancement of growth of algal germings and sporelings (Huang and Boney 1983); production of morphological abnormalities in sporelings of *Ulva lactuca* and *Gigartina stellata* (Huang & Boney 1983)
- N. pelliculosa* reduces filtering rate of *Daphnia magna* (Ryther 1954)
- Navicula* sp. antibacterial: 71, 76a, 77 (Reichelt & Borowitzka 1984)
- Nitzschia ascicularis* antibacterial: 43, 66, 71 (Aubert et al. 1968)
- N. longissima* var. *closterium* antibacterial: 43, 66, 71 (Aubert et al. 1968)
- N. palea* antimutotic, autotoxic (Harder & Oppermann 1953)
- N. seriata* antibacterial: 43, 66, 71 (Aubert et al. 1968)
- Nitzschia* sp. growth inhibitor, autotoxic (Badour & Gergis 1965)
- Phaeodactylum tricornutum* antibacterial: 14 (two species), 25 (two species), 26, 29, 34 (three species), 75 (Duff et al. 1966); enhances growth of bacteria: 2, 28, 74, 82, 83 (two species) (Berland et al. 1972); antialgal: *Thalassiosira pseudonana* (Sharp et al. 1979)

Mixed culture of diatoms, including *Achnanthes longipes*, *Cocconeis scutellum*, *Grammatophora marina*, *Licmophora abbreviata*, *Navicula* sp., *Nitzschia* sp., and *Rhabdonema adriaticum*

stimulates growth of phytoplankton: *Nitzschia parvula*, *Prorocentrum micans*, *Synedra tabulata* (Kabanova 1959)

SUBCLASS CENTROPHYCIDEAE

ORDER BIDDULPHIALES

Chaetoceros affinis

antibacterial: 3, 29 (Berland et al. 1972); enhances growth of bacteria: 1, 2, 28, 56, 58, 78, 82, 83 (Berland et al. 1972)

C. lauderi

antifungal: 2, 14, 21, 43, 45 (Pesando et al. 1979b); antibacterial: 71, 72 (Gauthier et al. 1978; Pesando et al. 1979a)

C. peruvianus

antibacterial: 43, 66, 71 (Aubert et al. 1968)

C. pseudocurvisetus

antifungal: 14, 21, 45 (Pesando et al. 1979b)

C. socialis

antifungal: 14, 21, 45 (Pesando et al. 1979b); antibacterial: 71 (Aubert et al. 1968)

C. teres

antibacterial: 12, 43, 49-51, 66, 69, 71 (Aubert et al. 1968; Aubert & Pesando 1969)

ORDER COSCINODISCALES

Cyclotella nana

antibacterial: 5, 14, 25, 27, 34, 48, 64, 71 (two strains), 73 (Duff et al. 1966)

Skeletonema costatum

antifungal: 14 (Pesando et al. 1979b); antibacterial: 3, 14 (two species), 25 (two species), 27, 29 (two species), 34 (three spp.), 37, 66, 71 (three species), 73, 75, 77, 80a, 83 (three species) (Sieburth & Pratt 1961-1962; Sieburth 1965, 1968a; Duff et al. 1966; Aubert et al. 1968; Bell et al. 1974); influences growth of *S. costatum* (Kustenko 1975)

Thalassiosira decipiens

antibacterial: 71 (Aubert et al. 1968)

Thalassiosira sp.

antifungal: 14 (Pesando et al. 1979b)

ORDER RHIZOSOLENIALES

- Bacteriastrum elegans* antibacterial: 66, 71 (Aubert et al. 1968)
Dentonula confervacea antibacterial: 46, 66 (Sieburth 1965)
Lithodesmium undulatum antibacterial: 66, 71 (Aubert et al. 1968)
Rhizosolenia alata antibacterial: 43 (Aubert et al. 1968)

INVERTEBRATES**PHYLUM PORIFERA****CLASS CALCAREA**

- Scypha* sp. ichthyotoxic (Green 1977)

CLASS DESMOSPONGIAE**ORDER HAPLOSCLERIDA**

- Haliclona coerulea* cardiotoxic (Kaul et al. 1977); depresses blood pressure (Kaul et al. 1977)
H. doria ichthyotoxic (Green 1977)
H. erina cytotoxic: KB (Stempien et al. 1970); positively inotropic (Kaul et al. 1977); ichthyotoxic (Stempien et al. 1970); causes clumping of sea urchin eggs (Stempien et al. 1970)
H. hogarthi cardioactive (Kaul et al. 1977)
H. longleyi positively inotropic (Kaul et al. 1977); depresses blood pressure (Kaul et al. 1977)
H. magniculosa hypotensive (Baslow & Read 1968)
H. permallis positively inotropic (Kaul et al. 1977)
H. rosea antibacterial: 27 (Nigrelli et al. 1967)
H. rubens cytotoxic: KB (Stempien et al. 1970); cardiotoxic (Kaul et al. 1977); depresses blood pressure (Kaul et al. 1977); depolarizes muscle (Wang et al. 1973); ichthyotoxic (Stempien et al. 1970; Green 1977); causes clumping and parthenogenic development of sea urchin eggs (Stempien et al. 1970)

- H. subtriangularis*
antitumor: PS (Sigel et al. 1970)
cellular aggregation factor (Der Marderosian 1968)
- H. variabilis*
antifungal: 8 (Nigrelli et al. 1967); antibacterial: 5, 27, 40, 59, 71 (Nigrelli et al. 1967; Baslow & Read 1968); antitumor: Ehrlich ascites (Li et al. 1974); toxic to *Paramaecium*, sea urchin larvae, amphibia, fish, mice and other vertebrates (Jakowska & Nigrelli 1960-1961; Baslow & Read 1968; Green 1977); hypotensive (Baslow & Read 1968); causes developmental abnormalities in sea urchin eggs (Stempien et al. 1970)
- H. viridis*
antibacterial: 27 (Nigrelli et al. 1967)
- H. viscosa*
antibacterial: 12, 27 (Nigrelli et al. 1967; Nemanich et al. 1978); antitumor: Walker 256 (Burkholder & Sharma 1969); cytotoxic: KB (Nemanich et al. 1978); ichthyotoxic (Stempien et al. 1970; Green 1977; Bakus 1981)
- Haliclona* spp.
ichthyotoxic (Green 1977)
- Microciona parthena*
antifungal: 8 (Nigrelli et al. 1959; Jakowska & Nigrelli 1960-1961); antibacterial: 27, 40, 54, 57, 71, 89 (two species) (Nigrelli et al. 1959; Jakowska & Nigrelli 1960-1961); causes developmental anomalies in sea urchin eggs (Ruggieri et al. 1961)
- Mycale angulosa*
positively inotropic (Kaul et al. 1977); depresses blood pressure (Kaul et al. 1977)
- M. laevis*
causes developmental abnormalities in sea urchin eggs (Stempien et al. 1970)
- M. lingua*
ichthyotoxic (Green 1977)
- M. microstigmata*
antitumor: Walker M (Burkholder & Sharma 1969)
- Mycale* sp.
ichthyotoxic (Green 1977)
- ORDER HALICHONDRIDA**
Halichondria melanadocia
antibacterial: 27 (Stempien et al. 1970); positively inotropic and positively chronotropic (Kaul et al. 1977)

- H. panicea* antibacterial: 27, 89 (Jakowska & Nigrelli 1960-1961); ichthyotoxic (Green 1977)
- Halichondria* sp. cytotoxic: KB (Nemanich et al. 1978); ichthyotoxic (Green 1977)
- Pellina carbonaria* antifungal: 8 (Sharma, Vig & Burkholder 1968); cytotoxic: KB (Stempien et al. 1970); causes cytoplasmic abnormalities in KB tumor cells (Stempien et al. 1970)
- P. coela* cardiotoxic (Kaul et al. 1977)
- ORDER AXINELLIDA**
- Phakellia flabellata*⁹ antibacterial (Sharma, Vig & Burkholder, 1968)
- P. ventilabrum* antibacterial: 32a, 72 (Amade et al. 1982)
- ORDER HADROMEDA**
- Cliona caribboea* positively inotropic (Kaul et al. 1977); modifies coronary flow and blood pressure (Kaul et al. 1977)
- C. celata* antifungal: 8, 45 (Jakowska & Nigrelli 1960-1961; Amade et al. 1982); antibacterial: 27, 89 (Burkholder 1968); causes developmental anomalies in sea urchin eggs (Ruggieri et al. 1961)
- Suberites anastomosis* positively inotropic (Kaul et al. 1977)
- S. domunculus* toxic to dogs and rabbits (Hashimoto 1979); respiratory system, cardiovascular system and local activities (Der Marderosian 1969a)
- S. inconstants* causes itching and swelling in humans (Hashimoto 1979)
- PHYLUM CNIDARIA (COELENTERATA)**
- CLASS HYDROZOA**
- ORDER THECATA**
- Halecium beani* cardioactive (Kaul et al. 1977)

ORDER SIPHONOPHORA*Physalia physalis*

venom: dermatonecrotic, cardiotoxic, neurotoxic, musculotoxic to clam, fish, frog, mouse, rat, dog and man (Burnett & Calton 1977); depolarizes cell membranes (Hashimoto 1979); impedes binding of Ca^{2+} to muscle (Calton et al. 1973; Hashimoto 1979); folk medicine: ailments of blood vessels, nerves and muscles (Anon. 1978)

CLASS SCYPHOZOA*Aurelia aurita*

folk medicine: ailments of central nervous system (Anon. 1978)

A. labiata

antitumor: Ehrlich ascites, PS (Sigel et al. 1970; Tabrah et al. 1972)

Cyanea capillata

histamine-releasing factor (Uvnäs 1960-1961); dermatonecrotic, cardiotoxic, vasoconstrictive, spasmogenic to mouse, rat, guinea pig, rabbit, man (Walker 1977)

CLASS ANTHOZOA**ORDER ZOANTHIDEA***Epizoanthus* sp.

cytotoxic: KB (Nemanich et al. 1978)

ORDER ACTINIARIA*Metridium senile*

positively inotropic, positively chronotropic (Shibata et al. 1974); toxic to crayfish and barnacles (Hashimoto 1979)

Tealia coriacea

positively inotropic (Shibata et al. 1974)

T. felina

cytolytic toxin (Alsen 1983)

T. lofotensis

positively inotropic (Shibata et al. 1974); cytolytic toxin (Alsen 1983)

PHYLUM ECTOPROCTA (BRYOZOA)**ORDER CHEILOSTOMA***Bugula nerita*

antitumor: PS lymphocytic leukemia (Pettit et al. 1970)

- PHYLUM CTENOPHORA
Bolinopsis infudibulum inhibits murine erythrocyte proliferation *in vivo* (Premuzic et al. 1976)
- PHYLUM MOLLUSCA
 CLASS GASTROPODA
 ORDER MESOGASTROPODA
Littorina ziczac positively inotropic (Kaul et al. 1977); decreases coronary flow (Kaul et al. 1977)
- ORDER NEOGASTROPODA (STENOGLOSSA)
Buccinum undatum cardiotoxic (Emerson & Taft 1945); toxic to man (Hashimoto 1979); anemone attachment factor (McCauley 1969)
- ORDER NUDIBRANCHIA
Aeolidia papillosa predation signal (McCauley 1969)
- CLASS BIVALVIA (PELECYPODA)
 ORDER PTEROCONCHIDA
Crassostrea angulata antiviral: TMV (Limasset 1961)
Crassostrea spp. and/or *Ostrea* spp. antiviral: poliovirus (types I, II, III), influenza B (Li et al. 1961-1962); antibacterial: 71, 77 (Li 1960; Li et al. 1961-1962); can be toxic to humans (venerupin toxin) (Hashimoto 1979)
Mytilus edulis var. *galloprovincialis* antiviral: TMV (Limasset 1961)
M. viridis folk medicine: intestinal or uterine bleeding, dizziness, blurred vision, impotence, premature ejaculation, hypertension, high blood pressure (Anon. 1978)
- Ostrea denselamellosa*¹⁰ folk medicine: tranquilizing, neuroses, high blood pressure, promote salivation, stop coughing,
O. gigas lymphatic tuberculosis, stomach ache, stomach acidity and inflammation, night sweat, anal pro-
O. rivularis lapse, diarrhoea, seminal emission, kidney problems, scarlet fever, inflammations, tuberculosis, osteomalacia, erysipalis (Anon. 1978)

- O. spreta* antitumor: PS (Sigel et al. 1970)
- O. virginica* antibacterial: 71 (Li 1960); antitumor: Sarcoma-180 (Schmeer & Huala 1965); spawning promoter, filtering promoter (Emerson & Taft 1945)
- ORDER HETERODONTIDA**
- Mercenaria campechiensis* antitumor: Krebs-2 (Schmeer & Beery 1965)
- M. mercenaria* antiviral: Rous sarcoma, Moloney, Friend (Li et al. 1974); antibacterial: 71 (Li 1960); antitumor: Sarcoma-180, Krebs-2, Rous sarcoma, L1210 (Schmeer et al. 1966; Li et al. 1974); inhibits murine erythrocyte proliferation *in vivo* (Premuzic et al. 1976); chemical defensive cue *vis-à-vis* starfish (Doering 1982); inhibits growth of larvae of *Crassostrea virginica*, *M. mercenaria*, *Spisula solidissima* (Premuzic et al. 1976)
- Mercenaria* sp. antiviral: herpes simplex, adenovirus-12 (Li et al. 1965)
- Spisula solidissima* inhibits murine erythrocyte proliferation *in vivo* (Premuzic et al. 1976)

CLASS CEPHALOPODA

ORDER TEUTHIDIDA (TEUTHOIDEA)

- Loligo* sp. antitumor: Sarcoma-180 (Schmeer & Huala 1965)

ORDER OCTOPODIDA (OCTOPODA)

- Octopus dofleini* toxic to crayfish (Hashimoto 1979)
- O. macropus* toxic to crustaceans (Hashimoto 1979)
- O. maculosus* toxic to man (Der Marderosian 1969b)
- O. ochellatus* folk medicine: stimulate maternal milk production, treat malaria (Anon. 1978)
- O. vulgaris* cardiotoxic (Emerson & Taft 1945); toxic to crustaceans (Hashimoto 1979); folk medicine: stimulate late maternal milk production, treat malaria (Anon. 1978)

PHYLUM ENTOPROCTA*Pedicellina* sp.

antibacterial: 12, 27 (Nemanich et al. 1978); cytotoxic: KB (Nemanich et al. 1978)

PHYLUM ANNELIDA**ORDER TERESELLIDA***Pectinaria australis*

chemoattractant (McCauley 1969)

PHYLUM ARTHROPODA**CLASS CRUSTACEA****SUBCLASS CIRRIPIEDIA***Balanus balanoides*

hatching promoter (Crisp 1956)

B. eburneus

antitumor: PS (Sigel et al. 1970)

SUBCLASS MALACOSTRACA*Cancer borealis*

cardioacceleration (Belamarich 1963); neurotransmission blockers (Kravitz et al. 1963)

C. irroratus

cardioacceleration (Belamarich 1963)

Carcinus maenas

antiviral: TMV (Limasset 1961); cardioacceleration (Kerkut & Price 1964)

*Homarus americanus*neurotransmission blockers (Kravitz et al. 1963); inhibits murine erythrocyte proliferation *in vivo* (Premuzic et al. 1976)**PHYLUM ECHINODERMATA****CLASS HOLOTHUROIDEA****ORDER DENDROCHIROTIDA***Cucumaria echinata*

ichthyotoxic (Yamanouchi 1955)

C. japonica

ichthyotoxic (Yamanouchi 1955)

- C. miniata* antifungal: 8 (Constantine et al. 1975); antibacterial: 71 (Constantine et al. 1975)
- Cucumaria* spp. antifungal: 27, 39 (Nemanich et al. 1978); cytotoxic: KB (Nemanich et al. 1978); ichthyotoxic (Yamanouchi 1955)
- Pentacta australis* ichthyotoxic (Yamanouchi 1955)
- ORDER APODIDA**
- Leptosynapta ooplax* ichthyotoxic (Yamanouchi 1955)
- ORDER MOLPADIIDA**
- Caudina chilensis* ichthyotoxic (Yamanouchi 1955)
- CLASS ECHINOIDEA**
- ORDER ECHINOIDA**
- Strongylocentrotus dröbachiensis* toxins (cited in Frey 1951)
- Strongylocentrotus* sp. cardioactive (Kaul et al. 1977)
- CLASS STELLEROIDEA**
- ORDER PAXILLOSIDA**
- Leptychaster* sp. cytotoxic: KB (Kaul et al. 1977)
- ORDER VALVATIDA**
- Hippasteria spinosa* antifungal: 45 (Constantine et al. 1975); antibacterial: 71 (Constantine et al. 1975); predation signal (McCauley 1969)
- H. phrygiana* predation signal (McCauley 1969)
- Mediaster aequalis* antifungal: 8 (Constantine et al. 1975); antibacterial: 27, 71 (Constantine et al. 1975); cytotoxic: KB (Nemanich et al. 1978)

ORDER SPINULOSIDA

- Henricia leviuscula* cytotoxic: KB (Nemanich et al. 1978)
H. sanguinolenta muscle contractant (McCauley 1969)
Solaster papossus predation signal (McCauley 1969)

ORDER FORCIPULATIDA

- Asterias amurensis* toxic to fish, insects, earthworms (Yasumoto et al. 1964; Yasumoto & Hashimoto 1965; Hashimoto 1979); hemolytic (Hashimoto 1979); vomitory in cats (Yasumoto et al. 1964; Hashimoto 1979)
A. forbesi antiviral: influenza (Shimizu 1971); toxic to marine echinoderms and annelid (Chaet 1962); inhibits murine erythrocyte proliferation *in vivo* (Premuzic et al. 1976); delayed hypersensitivity (Li et al. 1974); macrophage inhibition (Li et al. 1974); induces autonomy in starfish (Chaet 1962); chemical signal to clams (Doering 1982)
A. pectinifera antiviral: influenza (Shimizu 1971); hemolytic (Yasumoto et al. 1966)
A. rollestoni cardiotoxic (Emerson & Taft 1945)
A. rubens muscle contractant (McCauley 1969); chemical signal (McCauley 1969)
A. vulgaris cytolytic (Owells et al. 1973)

VERTEBRATES (tunicates only)**PHYLUM CHORDATA****ORDER PLEUROGONA**

- Molgula manhattensis* inhibits murine erythrocyte proliferation *in vivo* (Premuzic et al. 1976)
M. occidentalis antitumor: PS lymphocytic leukemia (Pettit et al. 1970)

ORDER ENTEROGONA

- Ascidia mantula* antitumor: L1210, YC 8 MF 2S (Guyot & Morel 1978)
Ciona intestinalis oxytocic, pressor and melanophore-dilating activities (Emerson & Taft 1945)

Achnanthes	106	Dictyosiphon	93
Aeolidia	111	Dilsea	89
Alaria	93	Dumontia	89
Amphidinium	96	Dunaliella	99
Antithamnion	90	Ectocarpus	93
Ascidia	115	Emiliana	98
Ascophyllum	95	Enteromorpha	100
Asterias	115	Epizoanthus	110
Asterionella	104	Fragilaria	104
Audouinella	86	Fucus	95
Aurelia	110	Furcellaria	87
Bacillaria	105	Gelidium	86
Bacteriastrum	107	Gigartina	87
Balanus	113	Gloiosiphonia	89
Bangia	85	Goniotrichum	85
Bolinopsis	111	Gonyaulax	97
Bonnemaisonia	86	Gracilaria	87
Bryopsis	103	Grammatophora	106
Buccinum	111	Griffithsia	91
Bugula	110	Gymnodinium	96
Callithamnion	90	Gymnogongrus	88
Cancer	113	Gyrosigma	105
Carcinus	113	Halecium	109
Caudina	114	Halichondria	108
Ceramium	90	Haliclona	107
Chaetoceros	106	Halopteris	95
Chaetomorpha	102	Halosaccion	89
Chattonella	99	Hemiselmis	99
Chlorella	99	Henricia	115
Chondria	91	Heteraulacus	97
Chondrus	87	Heterosigma	99
Chorda	94	Hippasteria	114
Chordaria	93	Homarus	113
Ciona	115	Isochrysis	98
Cladophora	102	Jania	89
Cliona	109	Laminaria	94
Cocconeis	106	Leptosynapta	114
Cochlodinium	96	Leptychaster	114
Codium	103	Licmophora	105
Colpomenia	93	Lithodesmium	107
Coolia	97	Lithothamnion	89
Corallina	88	Littorina	111
Crassostrea	111	Loligo	112
Cryptomonas	99	Lomentaria	89
Cucumaria	113	Mediaster	114
Cyanea	110	Membranoptera	91
Cyclotella	106	Mercenaria	112
Cystoclonium	87		
Dasya	91		
Dentonula	107		
Desmarestia	93		

Metridium	110	Protosiphon	100
Microciona	108	Prymnesium	98
Molgula	115	Ptilota	92
Monostroma	100	Pyrodinium	97
Mycale	108	Ralfsia	93
Mytilus	111	Rhabdonema	106
		Rhizoclonium	103
Navicula	105	Rhizosolenia	107
Nitzschia	105	Rhodomela	92
Noctiluca	97	Rhodomonas	99
		Rhodymenia	89
Ochromonas	98	Saccorhiza	94
Octopus	112	Scenedesmus	100
Odonthalia	91	Scrippsiella	97
Olisthodiscus	98	Scypha	107
Ostrea	111	Scytosiphon	93
		Skeletonema	106
Palmaria	89	Solaster	115
Pavlova	98	Sphacelaria	95
Pectinaria	113	Spisula	112
Pedicellina	113	Spongomorpha	100
Pellina	109	Spyridia	92
Pentacta	114	Stichochrysis	98
Phaeodactylum	105	Stichococcus	100
Phakellia	109	Stictyosiphon	93
Phycodrys	91	Strongylocentrotus	114
Phyllophora	88	Suberites	109
Physalia	110		
Pilayella	93	Tealia	110
Plumaria	91	Tetraselmis	99
Polyides	88	Thalassionema	105
Polysiphonia	91	Thalassiosira	106
Porphyra	85	Thalassiothrix	105
Porphyridium	85		
Prorocentrum	97	Ulva	101
Protopteridinium	97		

Notes:

1. Despite one report, the occurrence of *Gelidium* in Atlantic Canada is doubtful.
2. *Halosaccion ramentaceum*, occurring in Atlantic Canada, has now been referred to *Devaleraea*, while *H. glandiforme* remains in *Halosaccion*.
3. *Rhodymenia palmata*, occurring in Atlantic Canada, has now been referred to *Palmaria*; *Rhodymenia*, in the current sense, may occur no closer than Massachusetts.
4. *P. sinuosa* may be identical with *P. rubens*.
5. *P. thuyoides* may be referable to the genus *Pterosiphonia*, which is not known from Atlantic Canada.
6. Chlorococcales are typically fresh-water, but many strains are halotolerant.
7. Fresh-water species.
8. *Codium* spp., although not reported from Atlantic Canadian waters, have now been reported in the Gulf of Maine.
9. *Phakellia* now referred to *Cladocroce* (Gosner 1971).
10. *Ostrea* has recently been introduced for aquaculture.

Table II Target organisms for antifungal and antibacterial bioactivities (numbers refer to Table I)**Fungi:**

1	<i>Alternaria kikuchiana</i>
2	<i>Aspergillus fumigatus</i>
3	<i>Aspergillus glaucus</i>
4	<i>Aspergillus niger</i>
5	<i>Aspergillus oryzae</i>
6	<i>Aspergillus parasiticus</i>
7	<i>Aspergillus sydowii</i>
8	<i>Candida albicans</i>
9	<i>Candida tropicalis</i>
10	<i>Colletotrichum gloeosporioides</i>
11	<i>Colletotrichum</i> sp.
12	<i>Bacillus subtilis</i>
13	<i>Bacterium coli</i> (= <i>Escherichia coli</i>)
14	<i>Brevibacterium</i> sp.
15	<i>Brucella melitensis</i>
16	<i>Citrobacter</i> sp.
17	<i>Clostridium botulinum</i>
18	<i>Clostridium chauvoei</i>
19	<i>Clostridium histolyticum</i>
20	<i>Clostridium oedematiens</i>
21	<i>Clostridium septicum</i>
22	<i>Clostridium sordellii</i>
23	<i>Clostridium tetani</i>
24	<i>Corynebacterium diphtheriae</i>
25	<i>Corynebacterium</i> sp.
26	<i>Diplococcus pneumoniae</i>
27	<i>Escherichia coli</i>
28	<i>Penicillium chrysogenum</i>
29	<i>Penicillium citrinum</i>
30	<i>Penicillium digitatum</i>
31	<i>Penicillium glaucum</i>
32	<i>Penicillium olivaceum</i>
33	<i>Penicillium</i> sp.
34	<i>Phoma tracheiphila</i>
35	<i>Pichia membranaefaciens</i>
36	<i>Piricularia oryzae</i>
37	<i>Rhizopus japonicus</i>
38	<i>Rhizopus oryzae</i>
39	<i>Saccharomyces cerevisiae</i>
40	<i>Saccharomyces pastorianus</i>
41	<i>Saccharomyces uvarum</i>
42	<i>Schizosaccharomyces pombe</i>
43	<i>Sporothrix schenckii</i>
44	<i>Trichoderma</i> sp.
45	<i>Trichophyton mentagrophytes</i>
46	<i>Trichophyton rubrum</i>
47	<i>Trichophyton tonsurans</i>
48	<i>Trichophyton</i> sp.

49	unidentified fungi
50	unidentified yeasts

Bacteria:

1	<i>Achromobacter parvulus</i>
2	<i>Achromobacter stationis</i>
3	<i>Achromobacter</i> sp.
4	<i>Achromobacterium</i> sp.
5	<i>Aerobacter aerogenes</i>
6	<i>Aerobacter cloacae</i>
6a	<i>Bacillus agri</i>
6b	<i>Bacillus anthracis</i>
7	<i>Bacillus cereus</i>
7a	<i>Bacillus licheniformis</i>
8	<i>Bacillus megatherium</i>
9	<i>Bacillus mycoides</i>
10	<i>Bacillus pseudodiphtheriae</i>
11	<i>Bacillus pumilis</i>
12	<i>Bacillus subtilis</i>
13	<i>Bacterium coli</i> (= <i>Escherichia coli</i>)
14	<i>Brevibacterium</i> sp.
15	<i>Brucella melitensis</i>
16	<i>Citrobacter</i> sp.
17	<i>Clostridium botulinum</i>
18	<i>Clostridium chauvoei</i>
19	<i>Clostridium histolyticum</i>
20	<i>Clostridium oedematiens</i>
21	<i>Clostridium septicum</i>
22	<i>Clostridium sordellii</i>
23	<i>Clostridium tetani</i>
24	<i>Corynebacterium diphtheriae</i>
25	<i>Corynebacterium</i> sp.
26	<i>Diplococcus pneumoniae</i>
27	<i>Escherichia coli</i>
28	<i>Flavobacterium aquatile</i>
29	<i>Flavobacterium</i> sp.
30	<i>Hafina</i> sp.
31	<i>Klebsiella pneumoniae</i>
32	<i>Klebsiella</i> sp.
32aa	<i>Micrococcus flavus</i>
32a	<i>Micrococcus luteus</i>
32b	<i>Micrococcus lysodeikticus</i>
33	<i>Micrococcus pyogenes</i>
34	<i>Micrococcus</i> sp.
35	<i>Moraxella bovis</i>
36	<i>Mycobacterium avium</i>
37	<i>Mycobacterium phlei</i>
38	<i>Mycobacterium smegmatis</i>

39	<i>Mycobacterium tuberculosis</i>	65	<i>Salmonella typhosa</i>
40	<i>Mycobacterium</i> sp.	66	<i>Sarcina lutea</i> (= <i>Micrococcus luteus</i>)
41	<i>Neisseria catarrhalis</i>	67	<i>Sarcina</i> sp.
42	<i>Neisseria caviae</i>	68	<i>Serratia marcescens</i>
43	<i>Neisseria flava</i>	69	<i>Shigella dysenteriae</i>
44	<i>Neisseria flavescens</i>	69a	<i>Shigella flexneri</i>
45	<i>Neisseria perflava</i>	70	<i>Staphylococcus albus</i>
46	<i>Pasteurella multocida</i>	71	<i>Staphylococcus aureus</i>
47	<i>Plectridium tetani</i>	72	<i>Staphylococcus epidermidis</i>
48	<i>Proteus mirabilis</i>	73	<i>Staphylococcus peoria</i>
49	<i>Proteus morgani</i>	74	<i>Staphylococcus</i> sp.
50	<i>Proteus rettgeri</i>	75	<i>Streptococcus faecalis</i>
51	<i>Proteus vulgaris</i>	76	<i>Streptococcus lactis</i>
52	<i>Providencia</i> sp.	76a	<i>Streptococcus pneumoniae</i>
53	<i>Pseudomonas aeruginosa</i>	77	<i>Streptococcus pyogenes</i>
54	<i>Pseudomonas aeruginospae</i>	78	<i>Vibrio alginosus</i>
55	<i>Pseudomonas fluorescens</i>	79	<i>Vibrio anguillarum</i>
56	<i>Pseudomonas putida</i>	80	<i>Vibrio finckler</i>
57	<i>Pseudomonas pyocyanea</i>	80a	<i>Vibrio</i> sp.
58	<i>Pseudomonas stereotropis</i>	81	<i>Welchia perfringens</i>
59	<i>Pseudomonas</i> sp.	82	<i>Xanthomonas</i> sp.
60	<i>Salmonella cholerae suis</i>	83	unidentified marine bacteria
60a	<i>Salmonella entitidis</i>	84	unidentified coryneform bacteria
61	<i>Salmonella gallinarum</i>	85	unidentified enterococci
62	<i>Salmonella pullorum</i>	86	unidentified Gram-positive bacteria
63	<i>Salmonella typhi</i>	87	unidentified pathogenic staphylococci
64	<i>Salmonella typhimurium</i>	88	unidentified soil bacteria
		89	unidentified "tubercule bacilli"

Envoi

The data presented above (Table I) illustrate some of the potential inherent in the marine biological resources of Atlantic Canada. Organisms from many genera contain antibacterial, antiviral, antitumor, cytotoxic or cardioactive metabolites whose chemical structures are currently unknown. Much less survey work has centered on neuroactive, immunopotentiating, anti-inflammatory, antifertility, mutagenic, anthelmintic and insecticidal principles, and other important bioactivities (e.g. antimalarial, antileprotic, antiarthritic, molluscicidal, memory-enhancing, tissue-regenerative, and most crop yield-related activities) have been totally ignored.

Chemical reinvestigation of the activities listed (Table I) would in all probability yield not only a lengthy list of novel bioactive natural products, but also data fundamental to answering broader questions central to the three areas of research described earlier. For example:

Are marine organisms employing certain adaptive strategies disproportionately rich or poor in specific types of bioactive compounds? The observations of Green (1977) and Bakus (1981) suggest that sessile, exposed, soft-bodied invertebrates in tropical ecosystems, where there is intense grazing pressure by fish, tend to be more ichthyotoxic than cryptic or hard-bodied invertebrates in the same ecosystems. Such toxicities may play an important role in maintaining species diversity in such ecosystems (Jackson & Buss 1975). It remains to be demonstrated whether these observations can be generalized to other ecosystems, adaptive strategies and bioactivities.

Are certain taxa of marine organisms disproportionately rich or poor in specific bioactive compounds? Weinheimer et al. (1978) screened 2252 species of marine organisms and found that 10.9% exhibited activity in the U.S. National Cancer Institute's P-388 murine leukemia bioassay; sponges, tunicates and fish yielded above-average "hit rates" (proportions of positive results), whereas the algae investigated were significantly below average (2.5%). Similarly, antiviral activities were more frequent among sponges, cnidarians, echinoderms, chordates, cyanobacteria, brown algae and red algae than among the other marine organisms examined by Rinehart et al. (1981). Multiple regression analysis (examining ecological, geographical and hydrographic as well as taxonomic variables) of such data might indicate whether the apparent correlations are in fact taxonomically based, and might provide a test for the relationship between phyletic and chemical diversities in "lower" organisms, as proposed in the Introduction.

Is there an independent geographical component in the distributional pattern of marine bioactivities? The fact that most investigations of marine bioactive substances have centered on tropical and subtropical species has reinforced the notion that the greatest potential for such compounds resides among the stereotypical flora and fauna of these regions: brightly coloured fishes and corals, toxic seaweeds, poisonous jellyfish, exotic sponges, venomous animals, and red tide plankton. By contrast, the colder-water flora and fauna are often assumed to be chemically uninteresting. This generalization has been supported for ichthyotoxicity of Pacific Ocean sponges (Green 1977), for antimicrobial activities of certain gorgonians (Burkholder and Burkholder 1958), and seems to be valid for many marine animal toxicities in general (Halstead 1965-1970). Large and taxonomically less restricted investigations (Weinheimer et al. 1978; J.T. Baker, pers. commun. 1981) have, however, revealed a more complex geographical distribution of activities "for which no ready rationalizations are apparent" (Weinheimer et al. 1978). Cold-water ecosystems typically exhibit less biological diversity than do tropical ecosystems (and thereby may be more amenable to biochemical analysis); nonetheless, individual colder-water organisms face the same types of biological challenges as do tropical ones (predation, fouling, etc.) and moreover do so in a physically changeable environment. Therefore, to the extent that bioactive natural products are of adaptive significance, there is no compelling reason to suspect *a priori* that individual colder-water organisms are unlikely to produce interesting bioactive compounds.

There have been disappointingly few examinations of bioactive compounds among colder-water organisms. Modest surveys, generally of only one activity, have been reported (e.g. Chesters & Stott 1956; Roos 1957; Hornsey & Hide 1974; Biard et al. 1980; Chénieux et al. 1980; Blunden et al. 1981), but most information has come from small, nonsystematic investigations which rarely have led to chemical characterization of the active metabolite.

Can an ecological approach help predict the occurrence of pharmaceutically or biomedically relevant bioactive compounds? Sieburth (1968b) conjectured the existence of such a predictive (positive) correlation. However, the few demonstrated relationships between ecotype and presence of bioactive metabolites (above) are restricted to toxins, and toxicity often limits the clinical utilization of otherwise efficacious compounds. Confirmation of a correlation, whether positive or negative, could greatly rationalize pharmaceutically oriented screening programs.

Do marine organisms constitute a promising source of novel pharmaceuticals, agrichemicals and other important bioactive compounds? All the conditions required for an optimistic response to this question appear to be in place. There is a well-recognized need for novel antibiotics, pharmaceuticals and agrichemicals (Meinhof 1979; Zak 1980; Anon. 1981a; Mitchell 1981; Shaw 1981; Weatherall 1982). Natural products are central to modern chemotherapeutics not only directly (Gosselin 1962; Farnsworth & Bingel 1977), but perhaps more importantly in the long term, by broadening our understanding of chemistry and biology. Not only do marine organisms synthesize a wide variety of novel natural products, but "hit rates" are often significantly higher with marine organisms than with terrestrial plants or microbiological fermentation broths (Weinheimer et al. 1978; Suffness & Douros 1982). Modern surveys can build on both traditional medicinal utilization and preliminary assay data (e.g. Table I). Despite the lengthy and difficult path from laboratory to market (Baker 1984), marine-derived anthelmintic, antitumor, analgesic and insecticidal agents are already in use (Der Marderosian 1979); other pharmaceuticals may be marketed commercially by the mid-1980s (Anon. 1981b), and still others are in advanced developmental stages (Suffness & Douros 1981, 1982; Suffness, pers. commun. 1984). Clearly, the potential of marine organisms as a source of novel pharmaceuticals, agrichemicals and other bioactive compounds, has yet to be fully realized.

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BIOLOGICALLY ACTIVE MARINE METABOLITES: SOME RECENT EXAMPLES¹

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In the last ten years or so the investigation of marine organisms for metabolites with biological activity has become an important aspect of natural product chemistry. This research has been rewarded with the discovery of some unique chemical structures possessing important biological activity. Some recent examples are reviewed.

Au cours des quelques dix dernières années, la recherche, chez les organismes marins, de métabolites bioactifs est devenue un aspect important de la chimie des produits naturels. Cette recherche a permis la découverte de structures chimiques uniques possédant d'importantes activités biologiques. Quelques exemples récents sont présentés.

Introduction

Nature has been found to be amazingly versatile in producing compounds with important biological activity. Often quite simple biosynthetic manipulations result in complex molecules with remarkable potency. Thus, natural product chemistry has provided us with many unusual and challenging structures, some of which are the basis of today's pharmaceutical industry. In fact, it is this search for biologically active compounds from natural sources that has, to a large extent, maintained the early momentum of natural product chemistry.

To date terrestrial microorganisms and plants have been the principal sources of biologically active materials. However, in the last 15 years or so, there has been a considerable increase in interest in marine natural products, fostered to a large extent by discoveries of a varied range of unique chemicals—many of which possess some form of biological activity.

Nevertheless, compared with studies of terrestrial organisms, progress in the chemistry of marine natural products has been slow. There is knowledge of biological activity among marine organisms which dates back to Biblical times (Halstead 1965), yet only in the last decade has significant progress been made in identifying the chemical agents. Several factors contributed to this slow start: (i) The success in dealing with natural products from microbes and land plants concentrated the major research thrusts in that direction, (ii) the comparative difficulty in locating and identifying marine species, (iii) our inability to mimic the high yielding laboratory cultivation of microorganisms using marine plants or animals, (iv) difficulties in purifying the lipophilic and often heavily pigmented extracts of marine organisms.

There is no clear-cut relationship between (a particular) biological activity and the type of organism. Consequently, there is no obvious guide that will lead a natural product chemist towards a source of bioactive metabolites. The most common approach is to establish a screen for the biological activity of interest, and examine groups of organisms displaying certain biological and ecological indicators. For example there is a belief that mollusks lacking protective shells, such as sea-hares and nudibranches, are prone to predation and thus likely to have adopted some form of chemical defense. This may also be true for algae which are able to flourish in an area of intense herbivorous pressure. Again, the symbiotic

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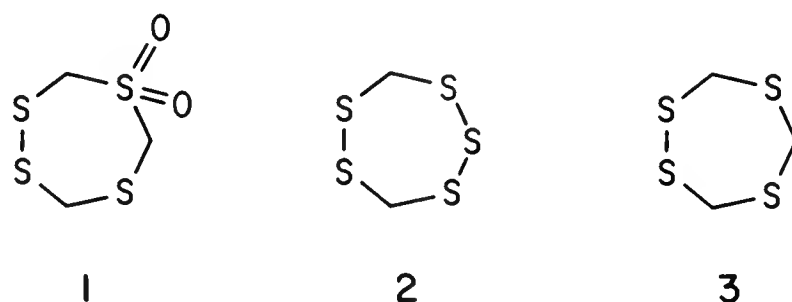
relationship between microorganisms and sponges may account for the isolation from sponges of several biologically active compounds which appear to be of microbial origin.

The variety of chemical structures and range of biological activities that have been reported from marine sources is remarkable and the aim of this review is to illustrate this with some fairly recent examples from the literature. Other pertinent reviews or accounts of the variety, structure, and biological activity of marine metabolites include those by Braslow (1969), der Marderosian (1969), Faulkner (1978), Fenical (1982), Glombitza (1979), Halstead (1965), Moore (1982), Scheuer (1973), Wells (1979), and Youngken (1969), as well as the excellent series of volumes edited by Scheuer (1978). The compounds reviewed here are separated into groups according to their effect upon mammalian cells or on organisms affecting mammalian cells.

Antimicrobial Agents

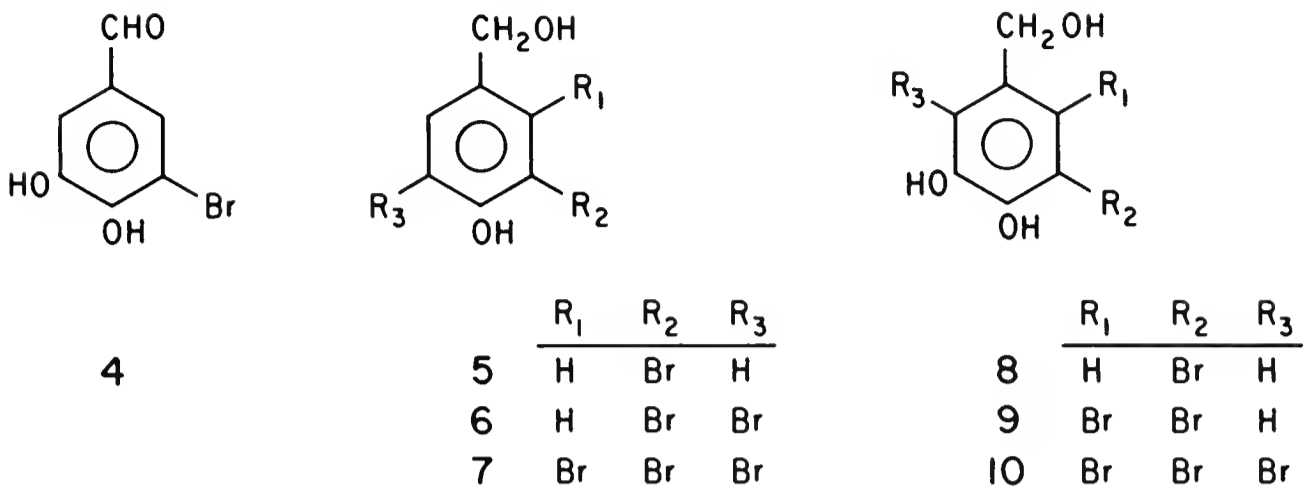
There are many reports of antimicrobial activity from marine plant and animal sources. Most likely this is because antimicrobial assays are relatively easy to perform and are often used as a preliminary screen for other pharmacological activity.

Since a crude extract of a plant or animal contains an enormous variety of compounds, an assay for bioactivity of any sort will often lead to the discovery of a metabolite that would otherwise have been overlooked: but for the antimicrobial activity of the cyclic polysulphides (1) - (3) from the brown alga *Chondria californica* (Wratten & Faulkner 1976) it is likely these compounds would have been overlooked as solvent impurities in the ^1H NMR spectrum of the extract. Curiously other species of *Chondria* which have been examined possess neither antimicrobial activity or cyclic polysulphides, though (2) and (3) have previously been isolated from the mushroom *Lentinus edodes*.



Several red algal genotypes produce antimicrobial metabolites containing halogen. Bromine is the most frequently encountered element despite the fact that the molar ratio of Cl^- to Br^- in seawater is approximately 60:1. The introduction of halogen is catalysed by peroxidase, and it has been proposed that the selectivity in halogen distribution among marine metabolites is based on oxidation-reduction potentials for a particular peroxidase as well as the intracellular halide concentration (Theiler et al. 1978).

Historically the presence of halo-organics in red algae has been known for many years (Augier 1953), and the first definite structure proof was presented for 3-bromo-4,5-dihydroxybenzaldehyde (4) a product of *Polysiphonia morrowii* almost three decades ago (Saito & Ando 1955). Some years later several di-bromophenols were described (Craigie & Greunig 1967; Katsui et al. 1967) and since then a considerable variety of brominated and sulphonated phenolics have been isolated, usually based on the 4-hydroxybenzyl alcohol and 3,4-dihydroxybenzyl alcohol skeleton (5 - 10) (Glombitza 1979).



Red algae of the family Bonnemaisoniaceae have a prodigious repertoire of non-aromatic halo-organic antiseptics (McConnell & Fenical 1979). Polyhalo-methanes, -acetic acids, -acetones -acrylic acids and -octenones containing various amounts of chlorine, bromine, and iodine, have been isolated (Fig. 1). These compounds

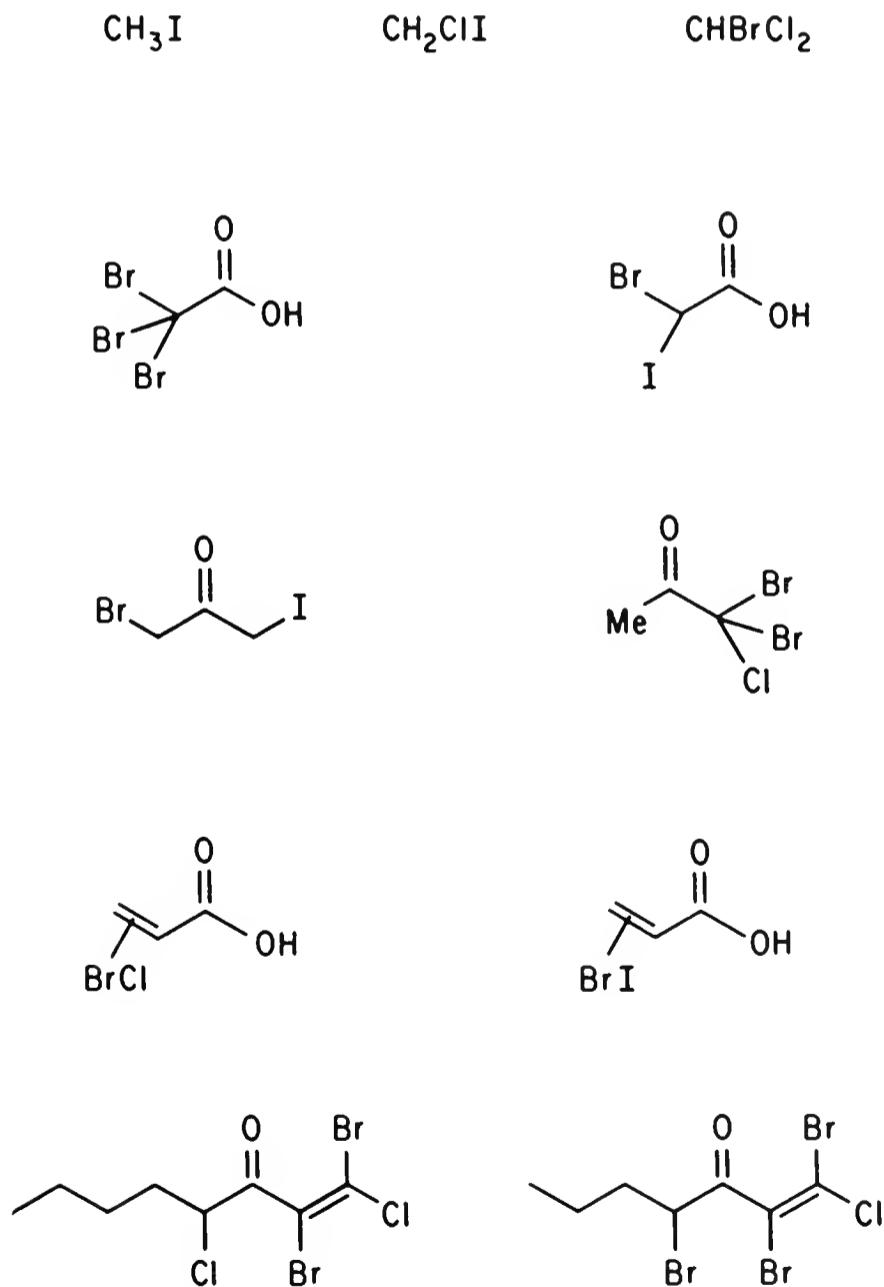
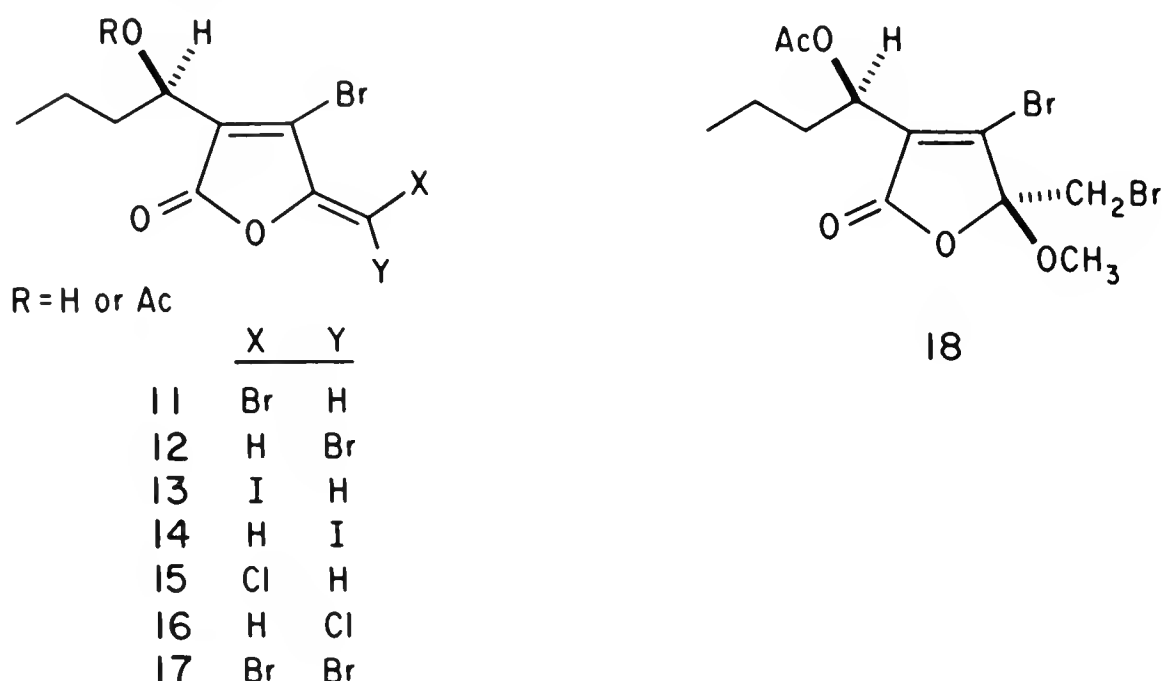
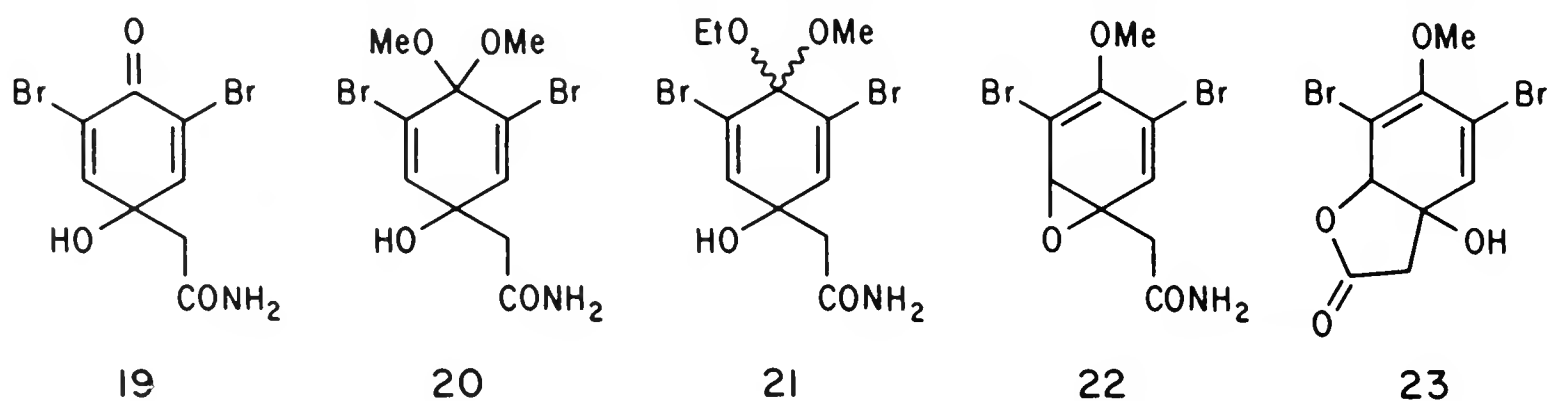


Fig 1. Halogenated polyketides of the family Bonnemaisoniaceae

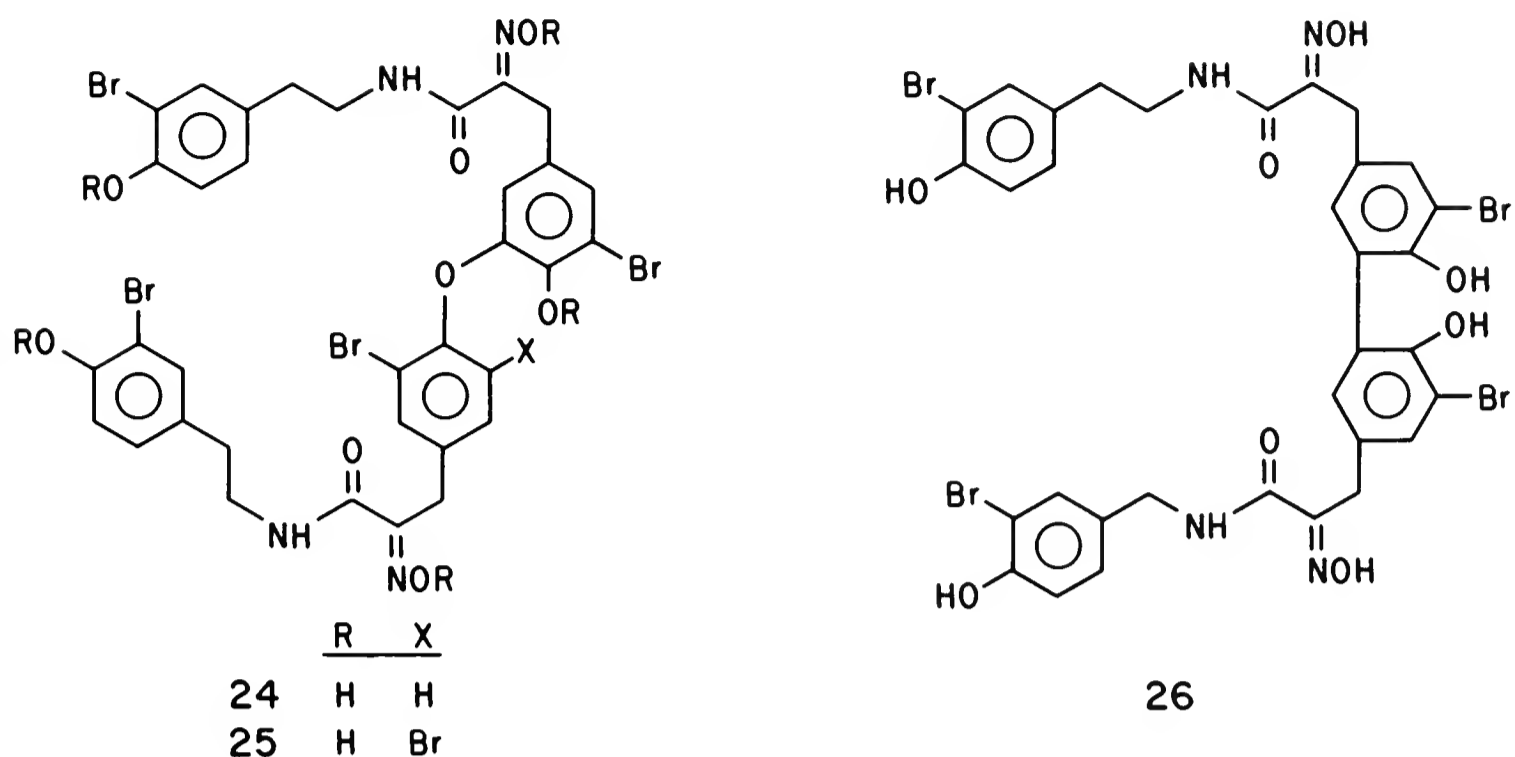
appear to be polyketide in origin and the polyhalo-1-octen-3-ones may share a common biosynthetic origin with the lactonic fimbrolides (11 - 17) from another red alga *Delisea fimbriata* (Kazlauskas et al. 1977a; Pettus et al. 1977). Over 60% of the dichloromethane extract was composed of these lactonic metabolites, as the acetoxy (major) and hydroxy (minor) derivatives. Conclusive structure proof came from an X-ray crystallographic analysis of the methanol adduct (18).



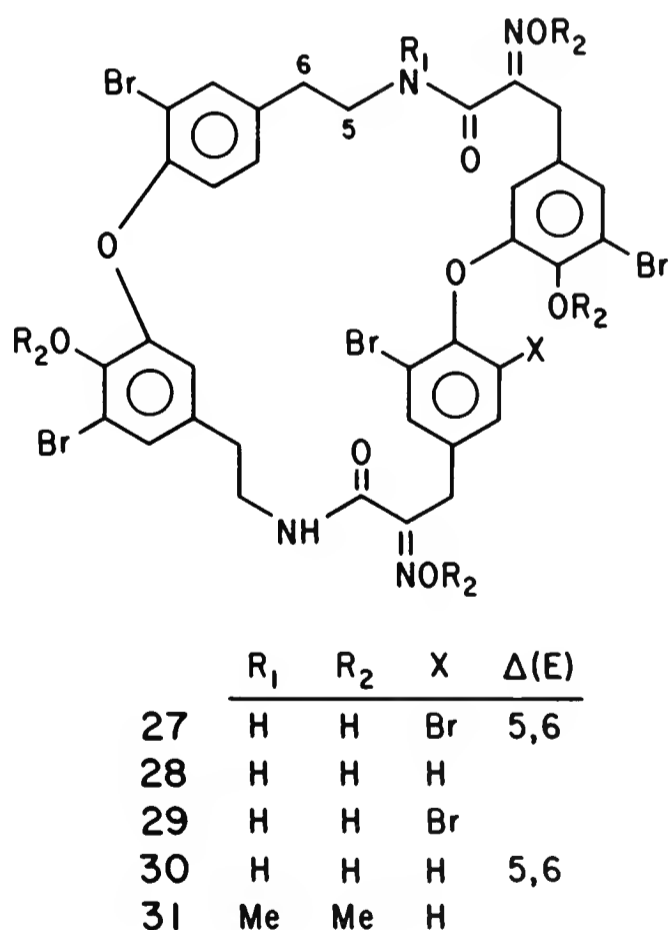
Algae are not the only marine source of halogenated metabolites. Sponges have a consistent record of yielding halogenated antibacterial substances and the genus *Verongia* is well known for its supply of bromo compounds. Sharma and Buckholder (1967) isolated the dienone (19) from *V. cauliformis*. The same authors subsequently reported (Sharma et al. 1970) the structure of another antimicrobial component as the ketal (20) which they assumed was a natural product. Later, however, the mixed ketal (21) was isolated from a species of *Verongia* following ethanol extraction (Anderson & Faulkner 1973). Even more significant was the discovery that (21) was a mixture of diastereoisomers suggesting that the dienone (19) and the ketals are all derived from a single intermediate [perhaps (22) or (23)]



by the addition of water, methanol, or ethanol. Another *Verongid* sponge *lanthella basta* has provided to date the most complex and varied source of bromotyrosine based metabolites (Kazlauskas et al. 1981). The methanol extract showed potent *in vitro* and some *in vivo* activity against Gram-positive bacteria and this was attributed to a series of related compounds which could be separated into two fractions. The most polar fraction contained bastadin-1 (24), bastadin-2 (25) and bastadin-3 (26). The less polar fraction contained bastadin-4 (27), bastadin-5 (28) [separated only as the tetramethyl ether (31)] bastadin-6 (29) and bastadin-7 (30). [The structures were assigned mainly on the basis of their spectral data.] It was thought that the biological activity of these cyclic compounds might be related to

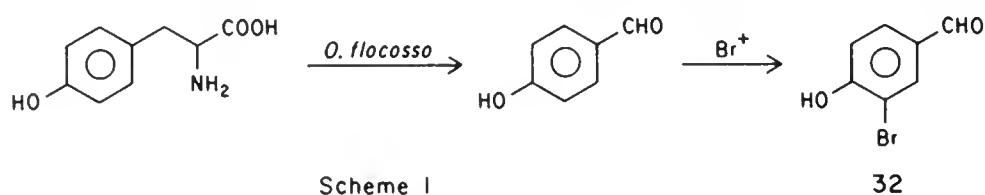


their ability to accommodate small mono- or di-valent metal cations. However, the X-ray crystal structure of bastadin-5 tetramethyl ether (31) revealed the central hole was blocked by one of the two methoxyimino groups and so it is improbable that these macrocyclic compounds can act as ionophores.

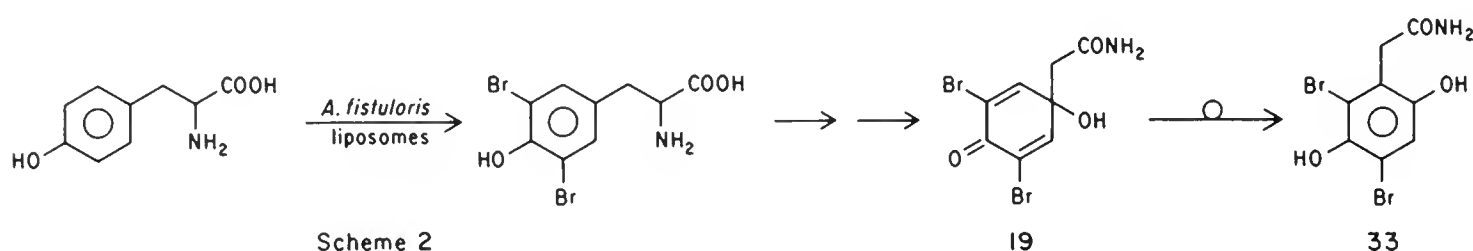


Clearly most of these halo-aromatics appear to be derived from tyrosine, but few biosynthetic studies have been performed to substantiate this. Manley and Chapman (1978, 1980) have shown that a cell-free homogenate of the red alga *Odonthalia floccosa* converts tyrosine to 3-bromo-4-hydroxybenzaldehyde (32). Bromin-

ation occurs after formation of p-hydroxybenzaldehyde (Scheme 1). Conventional biosynthetic studies with marine organisms are often hampered by very low incorporation of radiolabelled precursors. In a biosynthetic study of brominated phenols and quinones from the sponge *Aplysina fistularis* (*Verongia aurea*), Tymiak and Rinehart (1981) used liposome-enclosed precursors to improve incorporation levels. Both phenylalanine and tyrosine were converted to the dienone (19) as well as the rearrangement product dibromohomogentisamide (33) (Scheme 2).



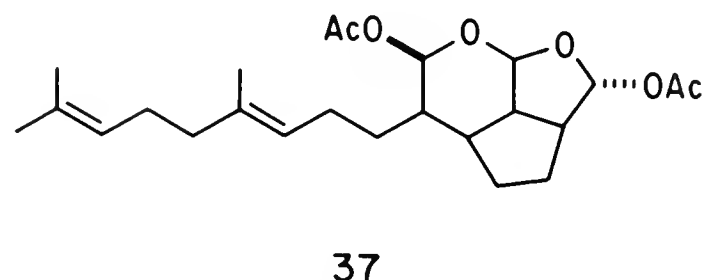
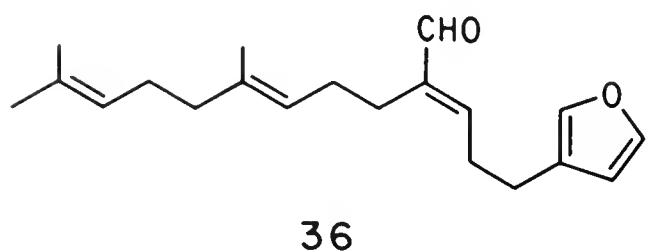
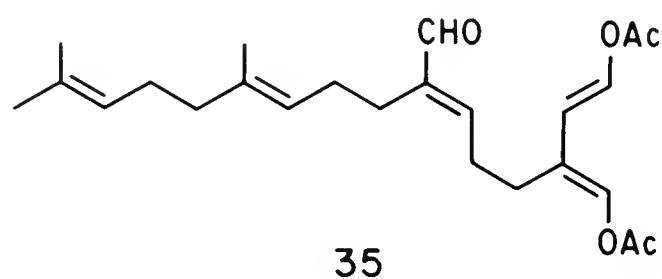
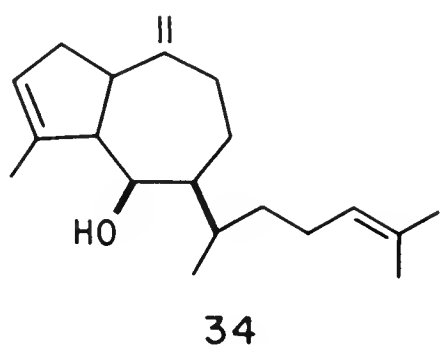
Scheme 1: Biosynthesis of 3-bromo-4-hydroxybenzaldehyde from tyrosine by the red alga *Odonthalia floccosa*



Scheme 2: Biosynthesis of the dienone (19) and dibromohomogentisamide (33) from tyrosine by the sponge *Aplysina fistularis*

Terpenoid antimicrobials containing halogen are common metabolites of certain red algae: most common are mono- or sesquiterpenoids all containing bromine and occasionally chlorine. Although the biosynthetic ability to produce such chemicals seems confined to a few genera, the variety and novelty of these terpenes is remarkable (Martin & Darias 1978; Erickson 1983). For example, the genus *Laurencia* provided at least six new terpenoid classes and several of these metabolites display antimicrobial activity (Fig. 2). In many cases their structures were established by X-ray crystallography.

In contrast, certain brown algal genera produce mainly diterpenes, usually containing no halogen. The antimicrobial pachydictyol A (34) from the Pacific seaweed *Pachydictyon coriaceum* was the first of a host of related metabolites to be



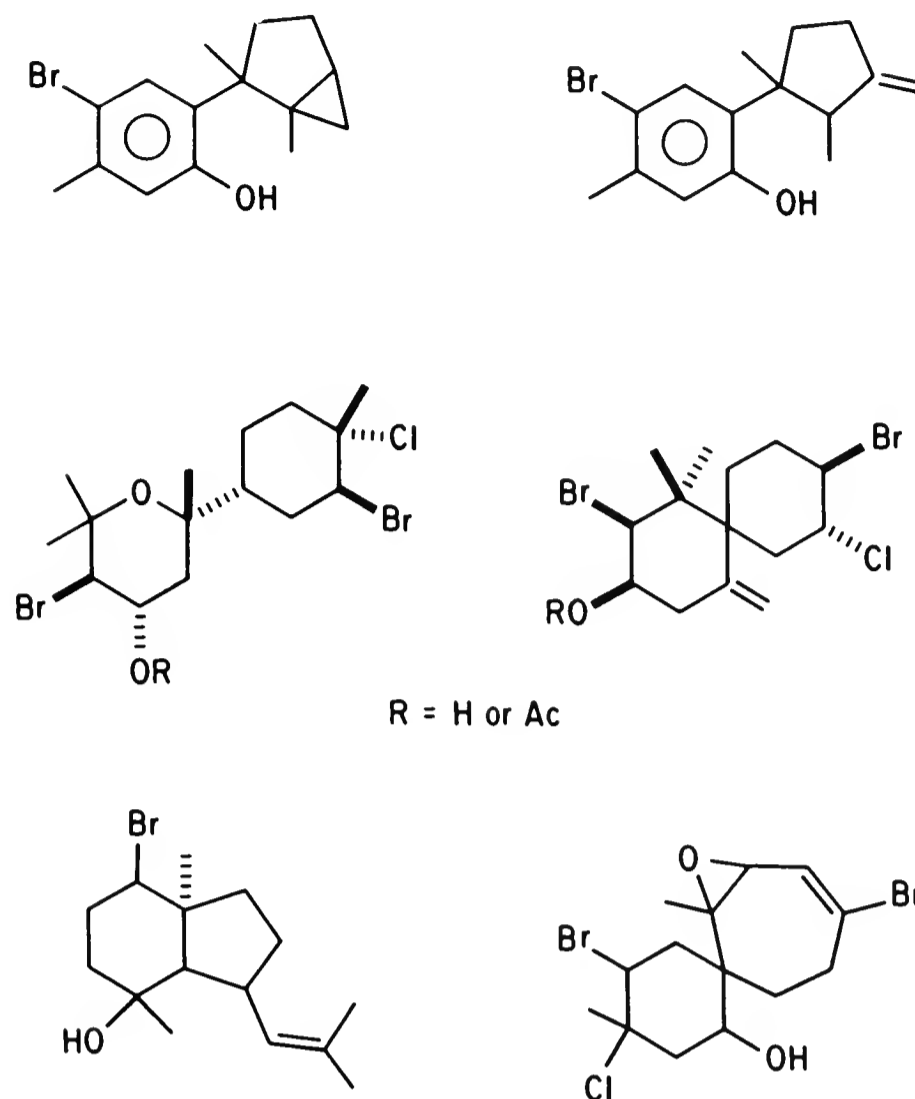
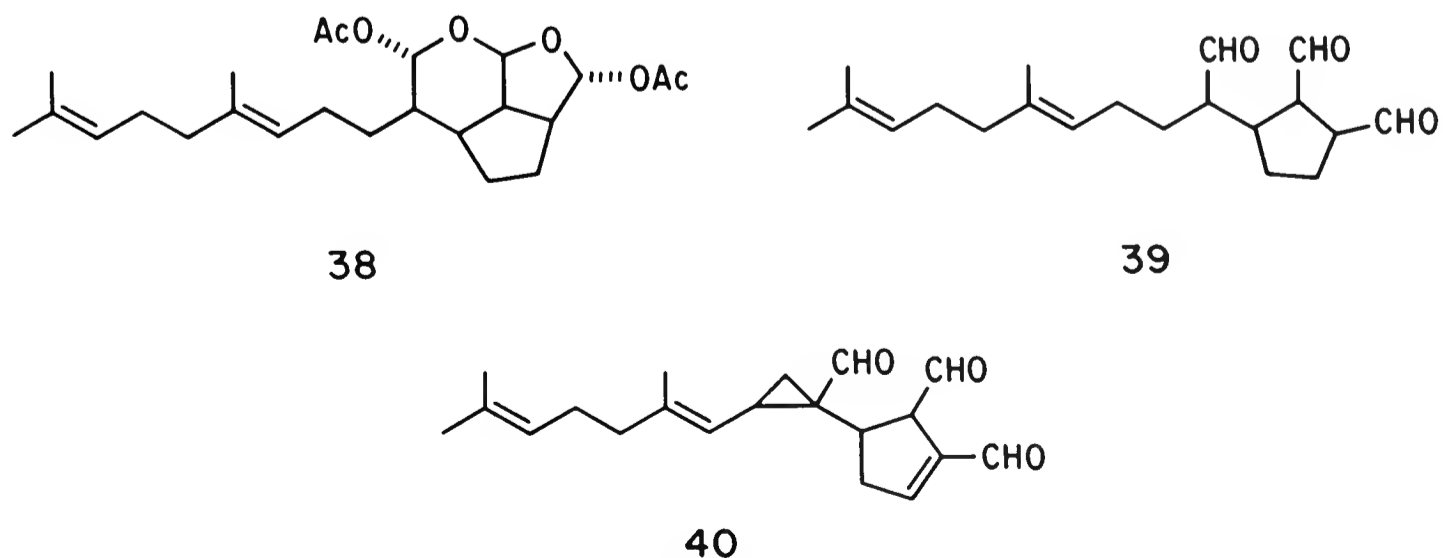


Fig 2. Halogenated terpenoids of *Laurencia* spp.

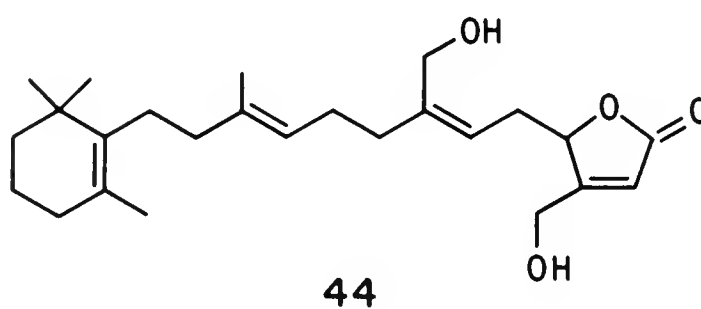
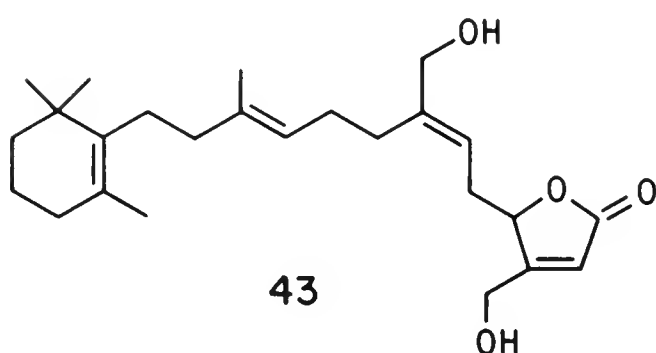
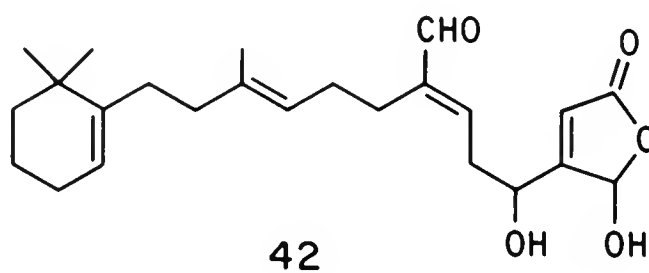
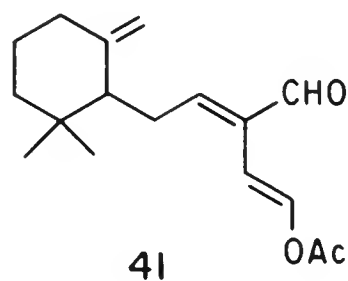
isolated from the biologically related plants *Pachydictyon*, *Dictyota*, *Dilophus* and others. Chemical and spectral studies (Hirschfield et al. 1973) led to the conclusion that (34) possessed a new terpenoid skeleton, confirmed by X-ray crystallography of the p-bromophenylurethane derivative.

Ethanol extracts of the calcareous green alga *Udotea flabellum* display moderate antimicrobial activity. The terpenoid constituent udoteal (35) was isolated from fresh extracts of the plant (Paul et al. 1982), but older ethanolic extracts contained udoteafuran (36) and a series of related cyclic compounds isolated as their acetates (37) - (38) (Nakatsu et al. 1981). All the acetates were optically active and are presumed to be derived from "udoteatrial" (39) which exists as an inseparable mixture of hydrates and ethanolates. Interestingly, a related calcareous alga of the

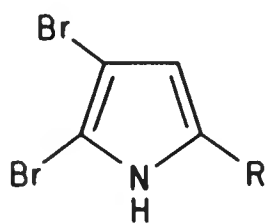


genus *Halimeda* produces a similar terpenoid trialdehyde (40) (Paul & Fenical 1983). In addition to antimicrobial activity this compound displays a range of deleterious biological effects and may offer relief to this macroalga from herbivores which inhabit the same area.

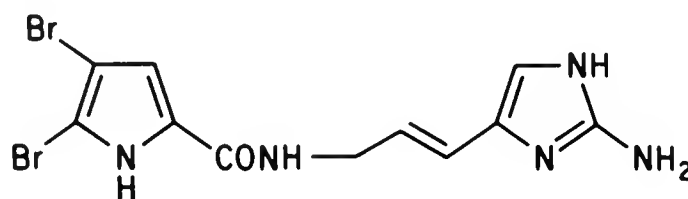
Similar metabolites containing the unsaturated aldehyde and enol acetate functions have been discovered in marine animals, though it is open to debate whether they are synthesized *de novo* or are simply dietary products. When irritated, the opisthobranch mollusc *Onchidella binneyi* secretes a white mucus containing the antimicrobial sesquiterpenoid enol acetate (41) (Ireland and Faulkner 1978). Similar functionality appears in the sesterterpenoid antibiotics (42), (43) and (44) which were isolated from the sponge *Luffariella variabilis* (deSilva & Scheuer 1981).



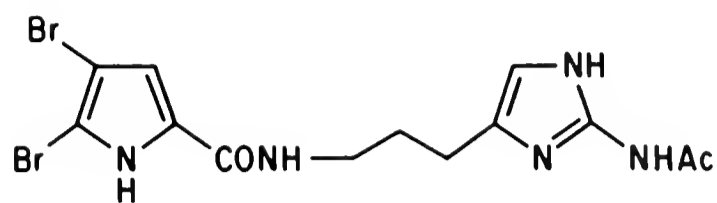
The sponge *Agelas oroides* contains 4,5-dibromopyrrole-2-carboxylic acid (45), the corresponding nitrile (46) and amide (47) as well as a fourth product, oroidin, containing the amide moiety linked to a substituted 2-aminoimidazole grouping (Forenza et al. 1971). This original structure proposed for oroidin was later revised to (48) based on comparison of the reduction product (49) with authentic synthetic material (Garcia et al. 1973). A separate study, by Faulkner's group, of *Agelas* sponges from the Caribbean area resulted in the isolation of sceptrin (50) a strong antimicrobial agent from *Agelas sceptrum* (Walker et al. 1981). The structure was established by X-ray crystallography. Sceptrin (50) is related to oroidin (48) by a



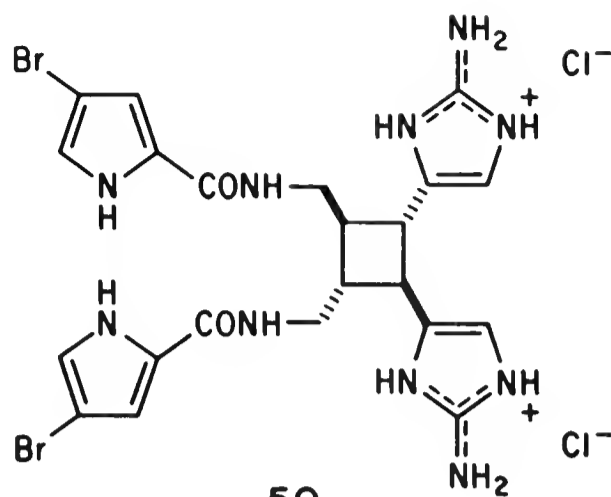
	R
45	COOH
46	CN
47	CONH ₂



48



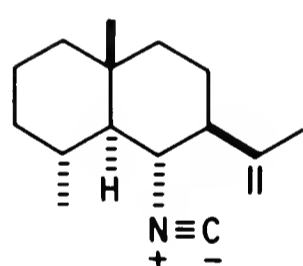
49



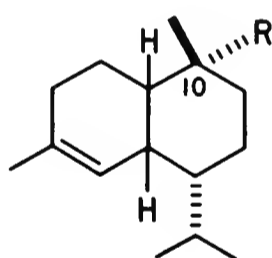
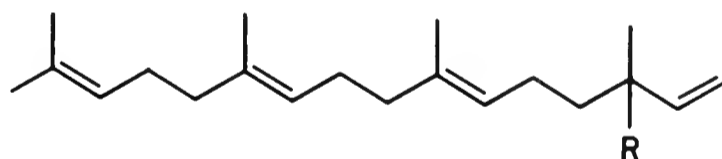
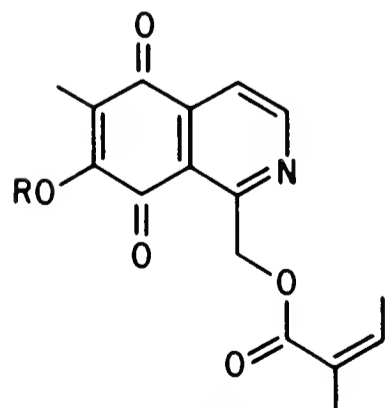
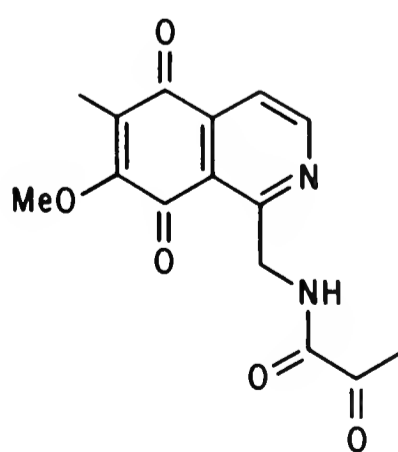
50

head-to-head [$\pi 2_s + \pi 2_s$] cycloaddition reaction. This is an allowed photochemical process but attempts in the laboratory to achieve the photodimerization of oroidin failed. The authors also point out that the biosynthesis of (50) cannot be regarded as a simple photodimerization of debromooroidin: there is insufficient light at the depth where *Agelas sceptrum* was found (from -20 to -30 m) and more significantly sceptrin is optically active while debromooroidin must be achiral.

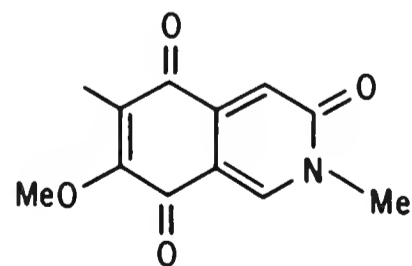
The antimicrobial activity of the sponge *Acanthella acuta* is due to the sesquiterpenoid isonitrile (51) (Minale et al. 1974). Although the isonitrile function is relatively rare in nature, several examples have been isolated from sponges. Another two terpenoid isonitriles are implicated in the antimicrobial activity of a different marine sponge *Halichondria* sp. (Burreson et al. 1975). The cyclic sesquiterpenoid derivative (52), based on the amorphane skeleton, is substituted at C-10 by an isocyanide group. The second isonitrile metabolite is the linear diter-



51


 52 $\frac{R}{\text{N} \equiv \text{C}^+}$
 54 NHCHO
 56 N=C=S

 53 $\frac{R}{\text{N} \equiv \text{C}^+}$
 55 NHCHO
 57 N=C=S

 58 $\frac{R}{\text{Me}}$
 64 H


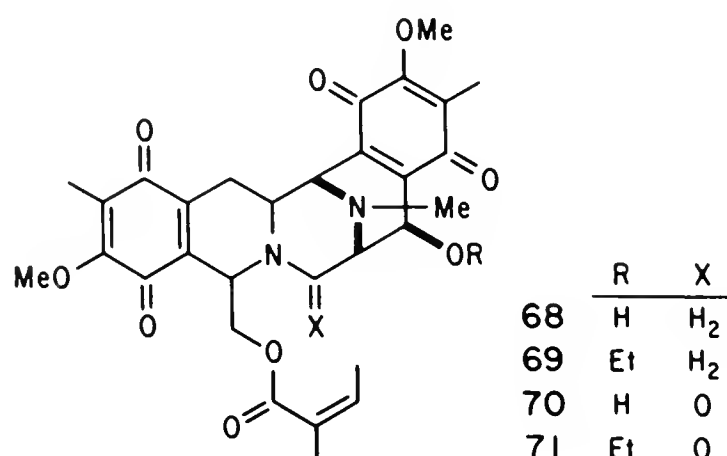
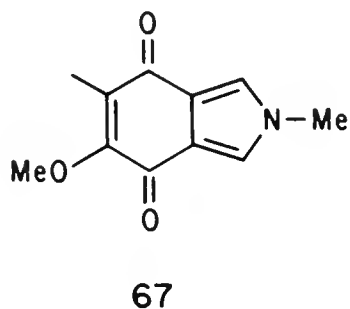
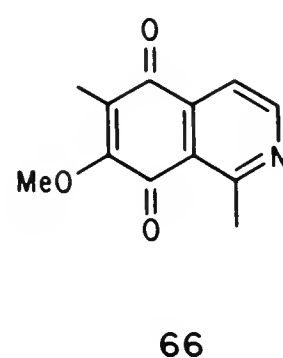
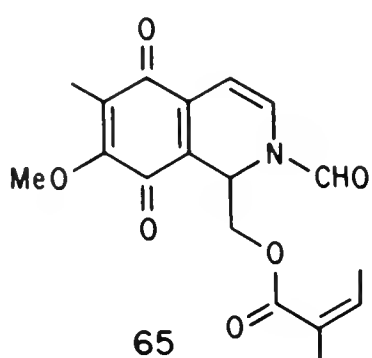
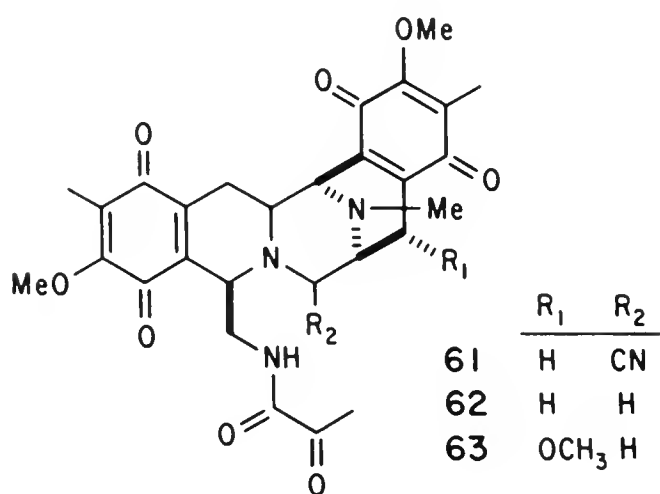
59



60

pene (53), an isocyanide analogue of the jasmine constituent geranylinalool. Interestingly both terpenoid isonitriles were accompanied by the corresponding formamides (54) and (55) and isothiocyanates (56) and (57), implying that the formamides are biosynthetic precursors of the isocyanides.

In the study of marine metabolites, there are several examples of products which are a likely consequence of symbiosis. This is most frequently encountered in sponges which are suspected of playing host to marine microorganisms and is beautifully illustrated by the recent isolation of several heterocyclic antibiotics from *Reniera* sp. a bright-blue sponge (McIntyre et al. 1979; Frincke & Faulkner 1982). The major antimicrobial agent was renierone (58), an orange-red pigment which bears a remarkable similarity to mimocin (59) a metabolite of *Streptomyces lavendulae* No. 314 (Kubo et al. 1980). This terrestrial microbe also produces the antibiotics mimosamycin (60) (Fukumi et al. 1978), saframycin A (61) (Arai et al. 1980), saframycin B (62) and saframycin C (63) (Arai et al. 1979). Remarkably, further examination of the metabolites of *Reniera* sp. (Frincke & Faulkner 1982) resulted in the isolation of a series of compounds including mimosamycin (60) and several other isoquinoline metabolites (64) - (66), the isoindole (67) and four "dimeric" metabolites called renieramycins A-D (68) - (71) which clearly are related to the saframycins.

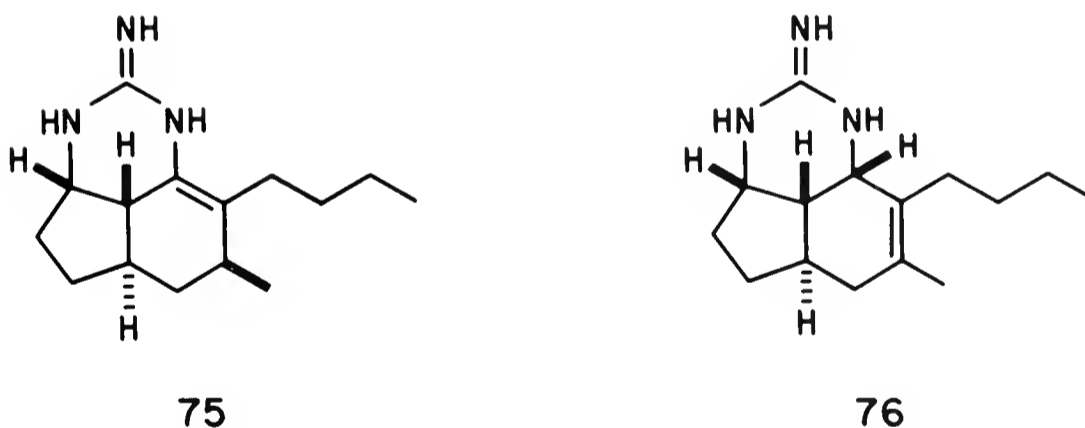
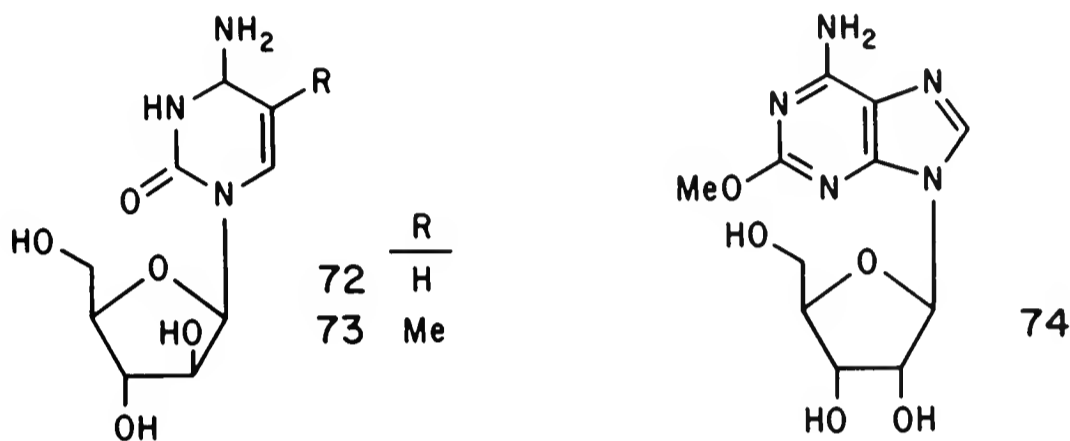


Antineoplastic and Antiviral Agents

As marine natural product chemistry developed, the discovery of unusual organic compounds, frequently very different from those found in terrestrial organisms, prompted the idea that new and effective anti-cancer drugs may be present among this assortment of structures. In fact preliminary results of the National Cancer Institute screening program have been encouraging (Suffness & Douros 1981) and several marine derived materials will be developed to clinical trials in the next few years.

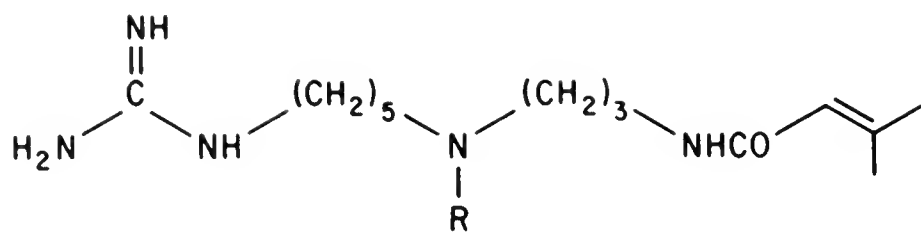
It is worth adding a cautionary note. Although *in vivo* testing for antineoplastic activity is more meaningful, it is slow and expensive. Consequently, in the interests of speed and convenience, researchers have often adopted an *in vitro* screen using cancer cell cultures. Since these assays only indicate cytotoxicity, and there is no clear correlation between cytotoxicity and antineoplastic activity, such measurements may be misleading unless correlated with animal testing data.

Very early work on marine natural products (Bergmann & Burke, 1955, 1956) led to the isolation of three new nucleosides, spongouridine (72), spongothymidine (73) and spongosine (74), from the sponge *Cryptotethia crypta*. The discovery and biological activity of these metabolites led, almost twenty years later, to the clinical use of the synthetic analogues adenine arabinoside (Ara-A) and cytosine arabinoside (Ara-C) as anti-viral and anti-cancer agents.

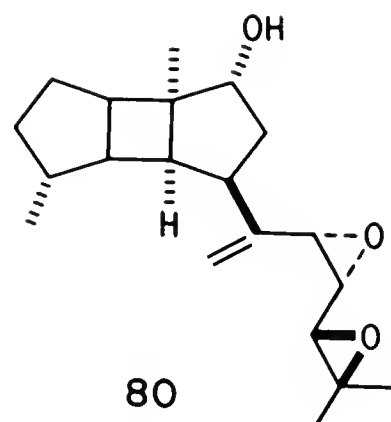


The potent cytotoxic and antimicrobial activity in crude extracts of another sponge, *Ptilocaulin* aff. *P. spiculifer*, was found to be associated with two cyclic guanidines, ptilocaulin (75) and isoptilocaulin (76) (Harbour et al. 1981). The guanidine function crops up again in the acarnidines (77) - (79) a novel group of sponge metabolites that display anti-viral and anti-bacterial activity (Carter & Rinehart 1978a). They have in common the unique substituted homospermidine skeleton and differ in the fatty acid substituent which is either isovalerate, laurate or myristate.

A variety of novel anti-viral and anti-tumor terpenoid metabolites have been isolated from marine plants and animals. The unusual diterpene spatol (80) a metabolite of the brown alga *Spatoglossum schmittii* inhibits cell division of sea-urchin



- R
- 77 $-\text{CO}(\text{CH}_2)_{10}\text{CH}_3$
 78 $-\text{CO}(\text{CH}_2)_3\text{CH} \overset{\text{cis}}{\text{=}} \text{CH}(\text{CH}_2)_5\text{CH}_3$
 79 $-\text{CO}(\text{CH}_2)_3(\text{CH} \overset{\text{cis}}{\text{=}} \text{CH}(\text{CH}_2)_3\text{CH}_3)$

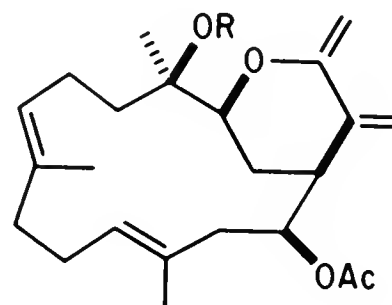


eggs in a manner similar to the antileukemic compounds, colchicine, vincristine and vinblastine (Gerwick et al. 1980). Following extensive chemical and spectroscopic investigations the final stereochemical details were obtained by an X-ray crystallographic study of the p-bromobenzoate derivative. A much simpler terpene, the linear derivative (81) was identified as the responsible agent from an extract of the marine tunicate *Aplidium* sp. which displayed inhibitory activity toward Gram-positive and Gram-negative bacteria, fungi and Herpes virus type I, as well as cytotoxicity towards tumor cells (Carter & Rinehart 1978b).

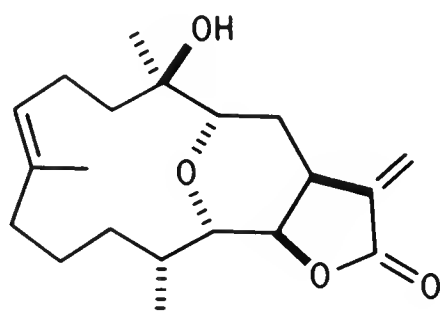
Soft corals and gorgonians have been a rich source of cembrane diterpenoids, many of which are cytotoxic to cancer cells *in vitro*. Investigations for biologically active metabolites in the Caribbean gorgonian *Plexaura crassa* yielded the first marine cembranolide crassin acetate (82) whose structure was established after extensive chemical studies and X-ray analysis of the corresponding p-iodobenzoate ester (83) (Hossain & van der Helm 1969). Investigations of other gorgonians has



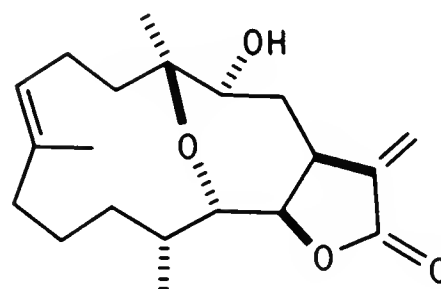
81



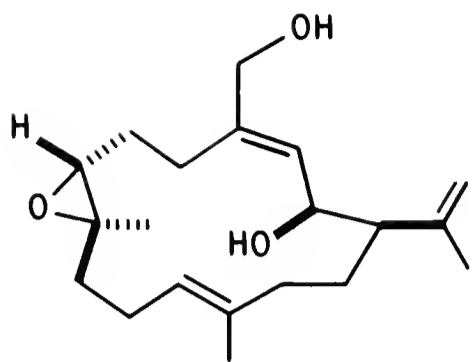
- R
- 82 H
 83 $\text{C}_6\text{H}_4\text{I}$



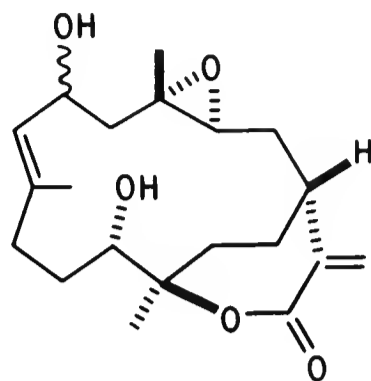
84



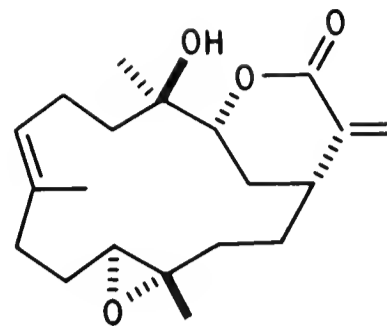
85



86



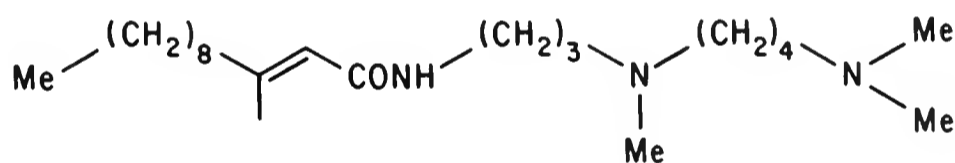
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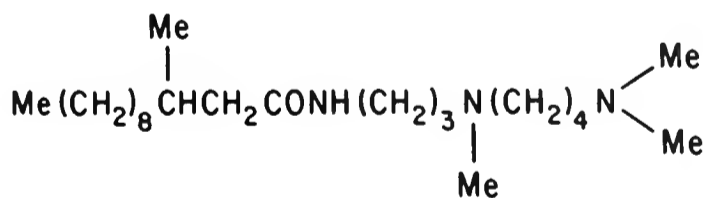
88

led to the discovery of a series of inter-related metabolites. Bahamian strains of *Euricea mammosa* contain the oxygen-bridged lactone eunicin (84) (Weinheimer et al. 1968; Hossain et al. 1968) whereas Caribbean samples of the same species contain the closely related cembranolide jeunicin (85) (van der Helm et al. 1976). Potent biological activity is often associated with the exomethylene lactonic ring but a new nonlactonic cembrane, asperdiol (86), isolated from two gorgonians *Eunicea aspenula* and *E. tourneforti*, displays significant *in vitro* anti-tumor activity in the N.C.I. test systems (Weinheimer et al. 1977).

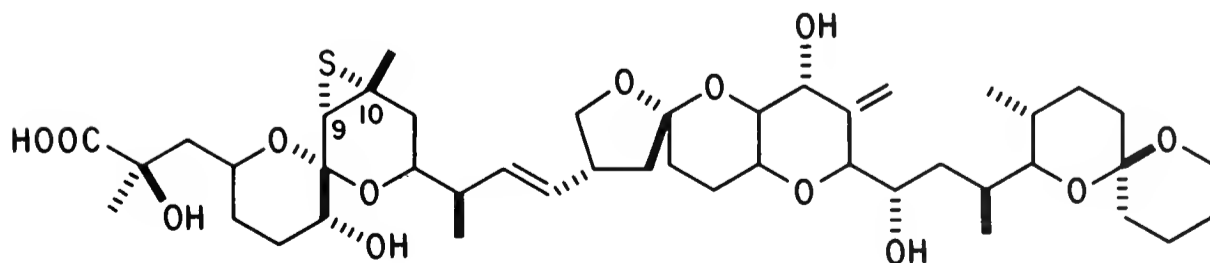
Soft corals have yielded even more cembrane derivatives than have gorgonians. For example, soft corals of the genus *Sinularia* from Hawaii, Indonesia and Australia have been examined by a number of independent groups (Fenical 1978) and typical structures are represented by sinulariolide (87) and flexibilide (88). Although the bioactivity of soft corals is often associated with these cembranolides,



89



90



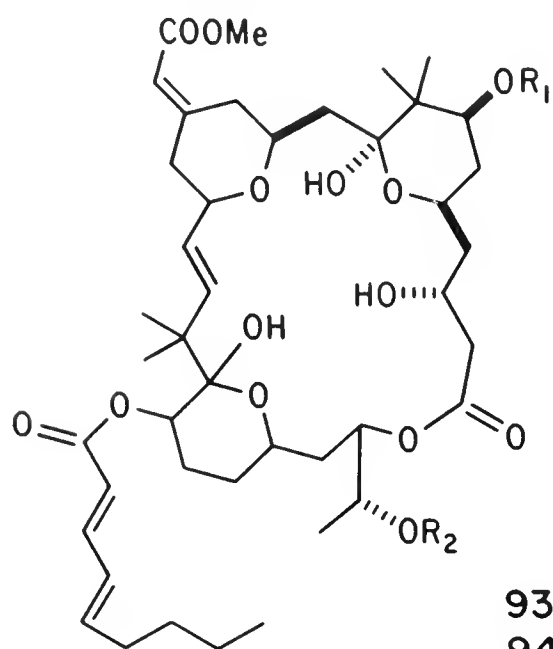
91

92 de-S, $\Delta^{9,10}$

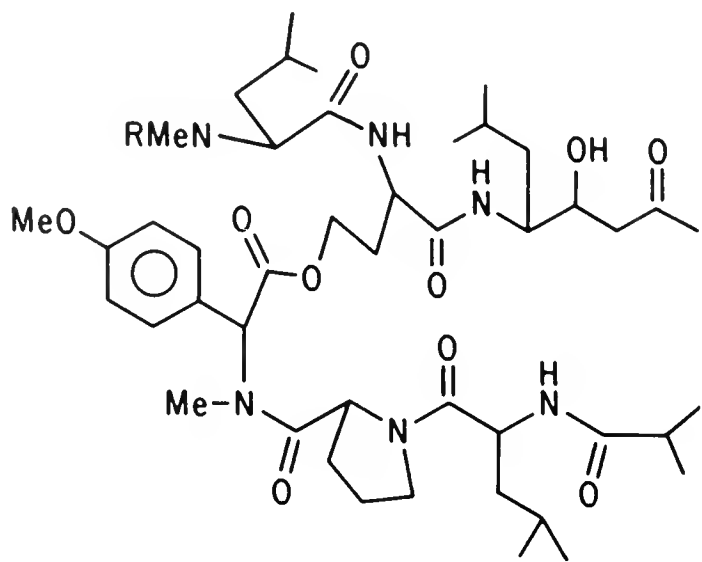
it was found that the cytotoxic activity of *Sinularia brongersmai* was due to the two spermidine derivatives (89) and (90) present as a 9:1 mixture (Schmitz et al. 1979). Catalytic reduction of the mixture yielded a single saturated amide which following acid hydrolysis and esterification gave methyl 3-methyldodecanoate.

Without a bioassay system to pinpoint activity, the novel anti-tumor agent ancanthifolicin (91) from the sponge *Pandaros acanthifolium* may have gone undiscovered. Antineoplastic activity in the lipid fraction is often associated with palmitoleic and oleic acids. However, in this case repeated purification revealed (91) as a very minor component (Schmitz et al. 1981). The structure of this novel episulphide-containing polyether was established by X-ray crystallography, and is clearly related to okadaic acid (92) isolated from two other sponges of the genus *Halichondria* about the same time (Tachibana et al. 1981). In fact, ancanthifolicin can be smoothly converted to okadaic acid using a Zn-Cu couple in refluxing ethanol. The structural features of these compounds class them as ionophores, which hitherto had not been isolated from a marine source. Very recently the structures of two related cyclic ionophores bryostatin 1 (93) and bryostatin 2 (94) from collections of the ubiquitous bryozoan *Bugula neritina* have been reported (Pettit et al. 1982a, 1983). These metabolites and as many as fifteen related, but very minor components, all display very potent antineoplastic activity. The structure of (93) was confirmed by X-ray analysis, and that of bryostatin 2 (94) by comparison of the high resolution ^1H nmr data with that of (93).

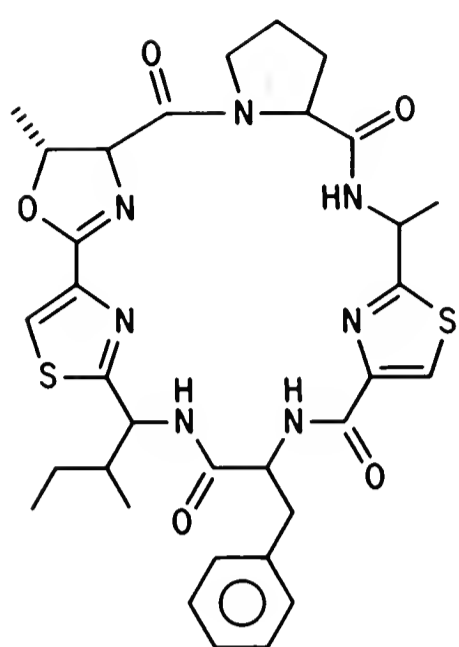
A number of novel peptides possessing considerable biological activity have been isolated from certain marine invertebrates. Initial extracts of the Caribbean tunicate *Didemnum* sp. showed significant cytotoxicity to monkey kidney cells and powerful anti-viral activity towards several DNA and RNA viruses (Rinehart et al. 1981). Purification of the active extract yielded three components, the major one didemnin A (95) and two minor ones, didemnins B (96) and C (97). Both A and C are anti-viral agents, whereas B has anti-cancer activity. The didemnins all contain an hydroxyisovalerylpropionyl (HIP) group, as well as statine, an amino-acid recently discovered in pepstatin a pepsin inhibitor of microbial origin (Morishima et al. 1970). Another marine tunicate *Lissoclinum patella* yielded the bioactive cyclic peptides ulicyclamide (98) and ulithiacyclamide (99) following MeOH extraction and purification (Ireland & Scheuer 1980). Threonine is masked as an oxazoline



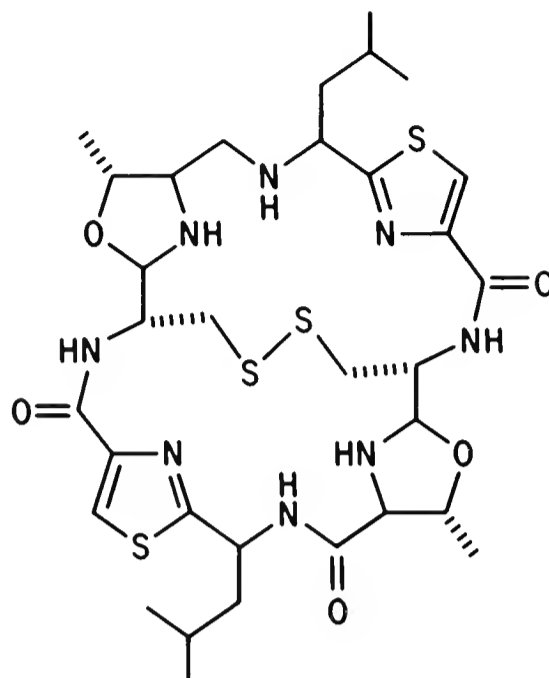
	R ₁	R ₂
93	COMe	H
94	H	H



	R
95	H
96	MeCH(OH)CO-Pro
97	MeCH(OH)CO

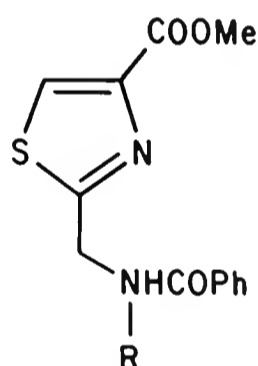


98



99

moiety and hydrolysis of (98) yielded five amino acids Pro, Phe, Thr and two thiazoles (100) and (101). The structural similarity of the second constituent (99) was indicated by the spectroscopic data and hydrolysis of this symmetrical peptide furnished cystine, threonine and thiazole (102) in a 1:2:2 molar ratio. Both ulithiacyclamide (99) and another symmetrical cyclic peptide (103) displaying

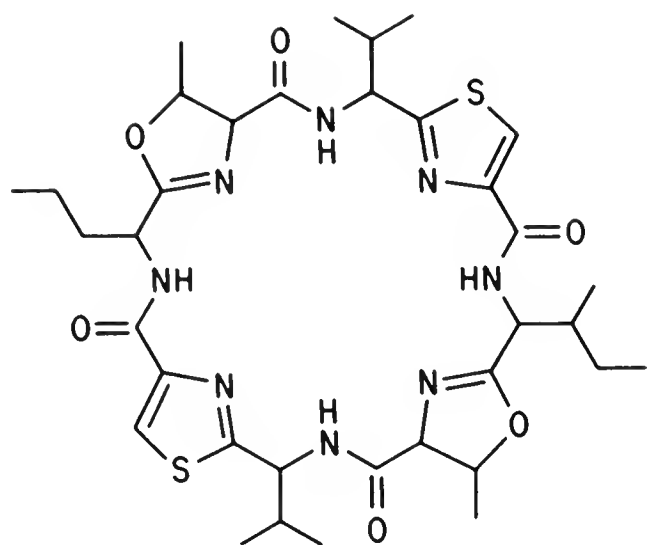


	R
100	Me
101	MeCH ₂ CHMe
102	Me ₂ CHCH ₂

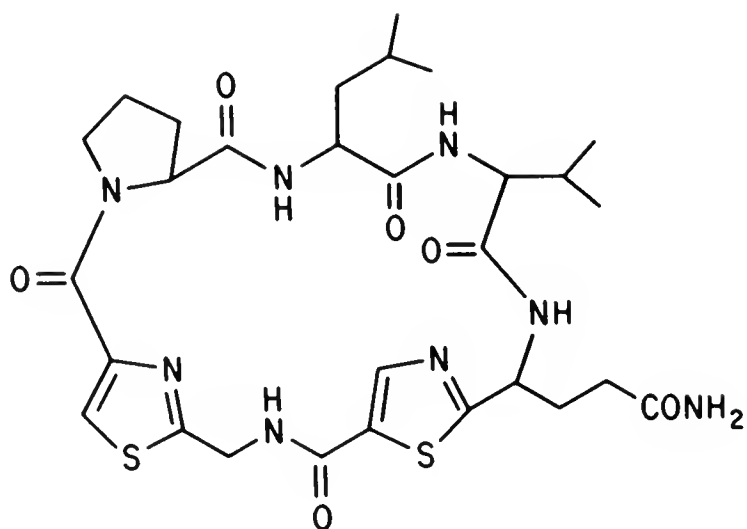
cytotoxicity were isolated from an unidentified ascidian (Hamamoto et al. 1983). In this case hydrolysis yielded leucine, threonine and a thiazole moiety containing a valyl side-chain. The cyclic peptide dolastatin 3 (104) is one of nine antineoplastic and/or cytotoxic substances isolated from the sea hare *Dolabella auricularia* (Pettit et al. 1982b). The similarity with the other tunicate-derived cyclic peptides is obvious. The structure of dolastatin 3 was established on the basis of extensive NMR and MS data.

Toxic Agents

The toxicity of certain marine organisms was probably the first and most widely known feature of their biological activity and dates back to Biblical times (Halstead



103

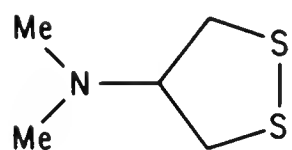


104

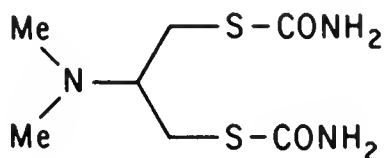
1965). However very few of the chemicals were identified until recently. This was due to difficulties in purifying the toxins, the often minute amounts produced by the organism, and the complex structures of the toxins themselves.

One of the first toxins to be characterized was isolated from the marine annelid *Lumbriconeris heteropoda*. Fishermen noted that flies landing on the worm quickly expired. From chemical extracts of the worm the cyclic disulphide nereistoxin (105) was identified as the responsible insecticide (Okaichi and Hashimoto 1962). Based on this lead, simpler synthetic analogues such as (106) (Konishi 1968) have been successfully employed as commercial insecticides.

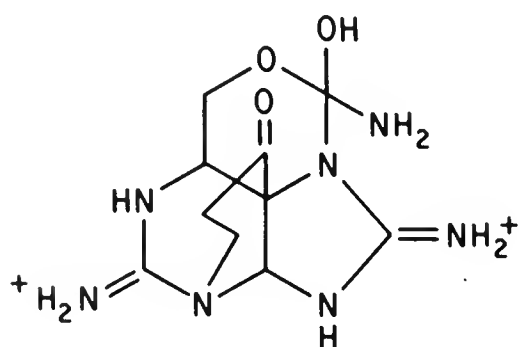
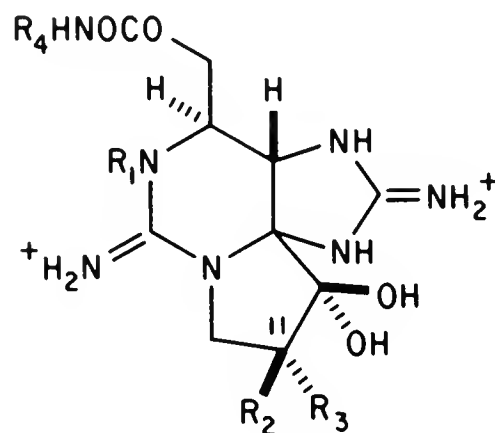
Saxitoxin (107) one of the so-called paralytic shell fish poisons (PSP) was originally isolated from the Alaskan butter clam *Saxidomus giganticus*. Although often sus-



105



106

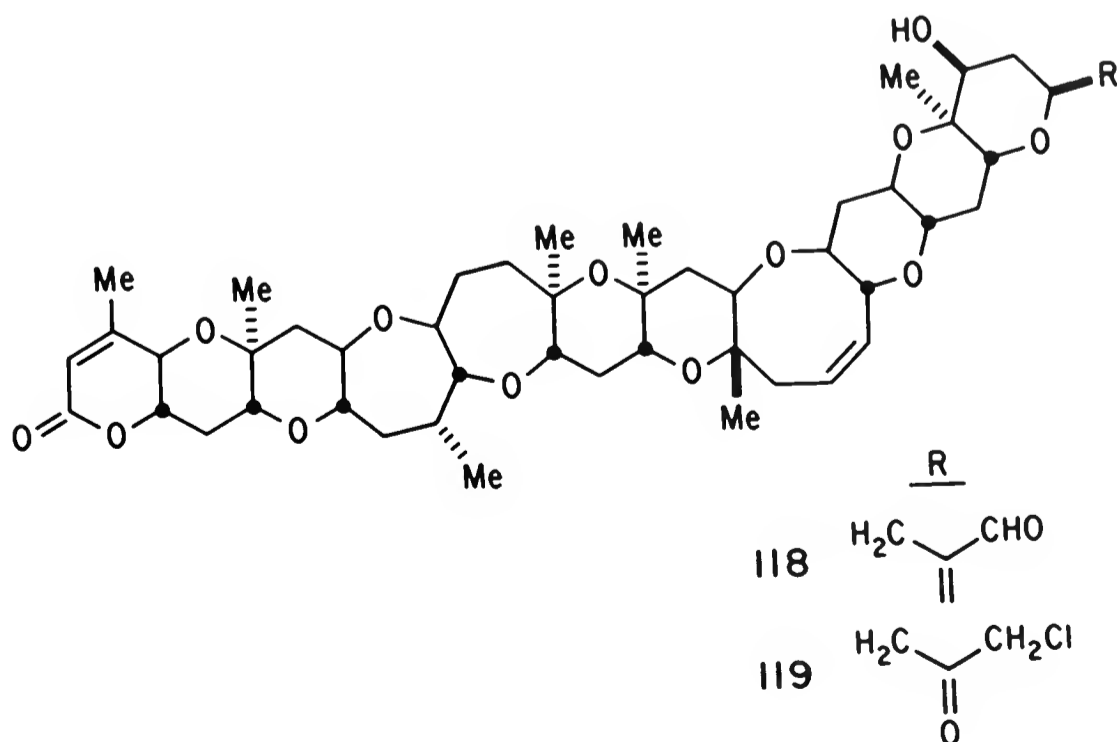


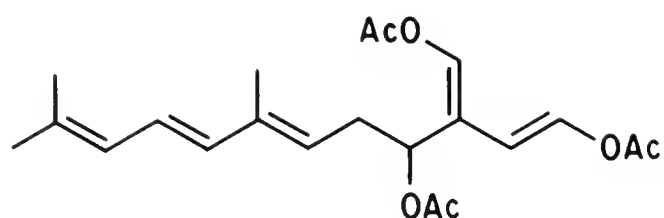
108

	R ₁	R ₂	R ₃	R ₄
107	H	H	H	H
109	OH	H	H	H
110	H	H	OSO ₃ ⁻	H
111	H	OSO ₃ ⁻	H	H
112	H	H	OSO ₃ ⁻	SO ₃ ⁻
113	H	OSO ₃ ⁻	H	SO ₃ ⁻
114	OH	H	OSO ₃ ⁻	H
115	OH	OSO ₃ ⁻	H	H
116	OH	H	OSO ₃ ⁻	SO ₃ ⁻
117	OH	OSO ₃ ⁻	H	SO ₃ ⁻

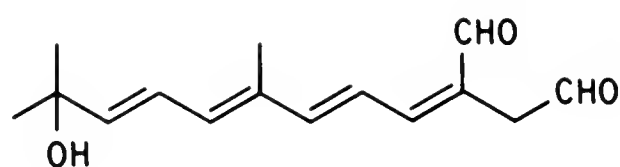
pected, it was some years before the toxin from the clam and the toxin from the dinoflagellate *Gonyaulax tamarensis* (Protogonyaulax)—responsible for the red tide—were shown to be the same chemical (cf. Shimizu 1978). After investigations spanning more than fifteen years, structure (108) was proposed to account for the spectroscopic data and most of the degradation products (Wong et al. 1971). However, this was changed a few years later when another group succeeded in preparing a crystalline di-p-bromobenzene sulphonate of the toxin (Schantz et al. 1975). The final structure is similar to that proposed earlier, the major difference being in the position of the propionyl group and the existence, in the crystalline form at least, of the hydrated ketone. Neosaxitoxin (109), an N-hydroxy derivative of saxitoxin, was first isolated as a minor constituent in the clam *S. giganteus*, but later it was discovered as a major component of the dinoflagellate *G. tamarensis* (Shimizu et al. 1978). Currently eight related toxins (110) - (117) have been isolated from a variety of sources including clams, mussels, and dinoflagellates (Alam et al. 1982). Structure variety is based on the saxitoxin and neosaxitoxin skeleton, and 11-OH epimers which occur as sulphate esters. The observation that brief exposure of a mixture of PSP toxins to acid resulted in enhanced toxicity, led to the discovery of a series of latent toxins containing the hitherto unreported sulphonatocarbamoyl function (Kobayashi & Shimizu 1981, Wichmann et al. 1981). The presence of this functional group considerably reduces the toxicity of the molecule but this returns following mild hydrolytic removal of the sulphate.

Another dinoflagellate *Ptychodiscus brevis* (*Gymnodinium breve*) has caused devastating red tide blooms in the Gulf of Mexico, resulting in massive fish kills. The toxicity is caused by a new group of compounds called the brevetoxins. Unlike the tetrodotoxin/saxitoxin group of paralytic shell-fish poisons which are water soluble and block sodium channels (Shimizu 1978) the brevetoxins are ether soluble neurotoxic shell-fish poisons which activate sodium channels (Risk et al. 1979). The crude ether-soluble toxin mixture from *P. brevis* contains 3 components: brevetoxin A (minor constituent, most potent) brevetoxin B (major component) brevetoxin C (minor component). An X-ray crystallographic study established the structure of brevetoxin B (118) and the structurally related toxins as large polycyclic molecules possessing contiguous trans-fused ether rings (Lin et al. 1981).

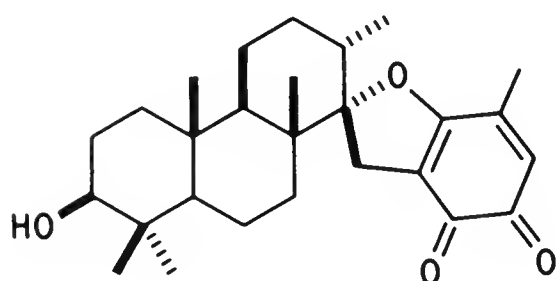




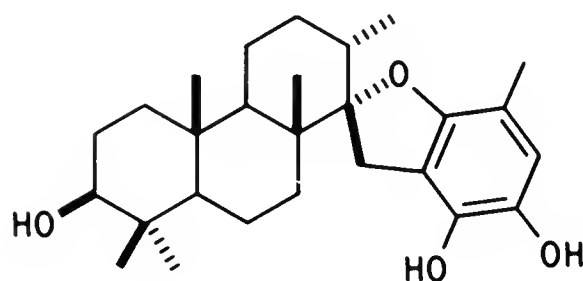
120



121



122

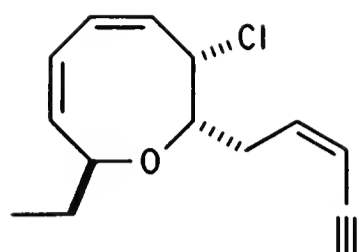


123

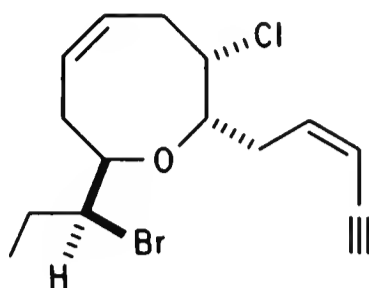
Shortly after, the structure of brevetoxin C (119) was elucidated by comparison of its spectral data with these of brevetoxin B (118) (Golik et al. 1982).

Several ichthyotoxins or fish repellants are produced by marine plants. A defensive role for these compounds seems obvious. For example, in an area subjected to predation by herbivorous fish the flourishing green alga *Rhypocephalus phoenix* produces two linear sesquiterpenoids rhipocephalin (120) and rhipocephenal (121) which induce pronounced feeding avoidance behaviour in the herbivorous fish *Eupomacentrus leucostictus* (Sun & Fenical 1979.) Another algal product which is both ichthyotoxic and cytotoxic is the novel terpenoid stypoldione (122) (Gerwick & Fenical 1981) from the brown alga *Stypodium zonale*, which produces stypoldione and several related ichthyotoxins. The o-quinone is found in the surrounding sea-water of the plant, and is in fact the air oxidation product of the more toxic stypotriol (123) the major intracellular toxin.

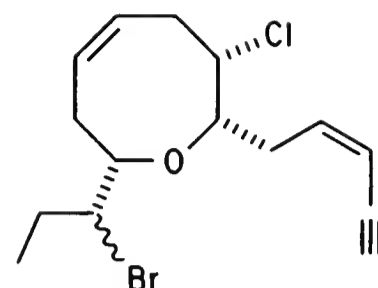
Antifeedants have also been found in marine animals, though frequently they are of algal origin. Sea hares are large slow-moving slug-like gastropod molluscs, that seem vulnerable to predation. However, when tested, sections of the mollusc *Aplysia brasiliensis* (eg. body wall, digestive gland, etc) were unpalatable to sharks. Chemical investigation of the digestive gland uncovered three halogenated cyclic ethers brasilenyne (124) *cis*-dihydrorhodophytin (125) and *cis*-isodihydrorhodophytin (126), all of which are produced by an alga which grows in an area inhabited by the sea-hare (Kinnel et al. 1979). Another example of sea hares accumulating noxious chemicals through their diet is illustrated by two recent reports from independent laboratories. From the brown alga *Dictyota crenulata*, Fenical's group isolated acetoxycrenulide (127) a major diterpenoid metabolite which is severely debilitating to the herbivorous fish *Eupomacentrus leucostictus* (Sun et al. 1983). The sea-hare *Aplysia vaccaria* is reported to feed on brown algae and from the digestive glands of these molluscs Sims' group isolated acetoxycrenulide (127) and three other crenulides (128) - (130) (Midland et al. 1983). The novel bicyclo [6.1.0] nonane skeleton of the crenulides, proposed following chemical investigation of the algal material, was confirmed by X-ray analysis of dihydroxycrenulide (129).



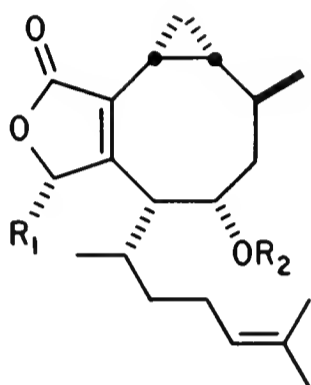
124



125



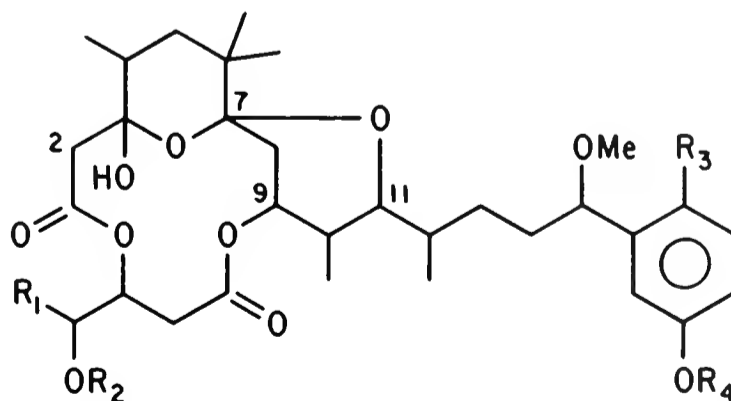
126



	R_1	R_2
127	H	Ac
128	H	H
129	OH	H
130	OH	Ac

A chemical examination of the toxic principles of another sea-hare *Stylocheilus longicauda* led to the isolation and identification of two toxins aplysiatoxin (131) and debromoaplysiatoxin (132) from an ether extract (Kato & Scheuer 1974). In a separate study Mynderse and co-workers (1977) identified debromoaplysiatoxin as the antineoplastic agent from a deep water variety of the blue-green alga *Lyngbya majuscula* upon which the mollusc *S. longicauda* was observed feeding. Somewhat surprisingly, aplysiatoxin (131) was not found in the alga, though shallow water varieties do generally contain both toxins. Debromoaplysiatoxin (132) and oscilla-toxin A (133) were identified as two of the compounds responsible for antineoplastic activity in two other blue-green algae *Schizothrix calcicola* and *Oscillatoria nigroviridis* (Mynderse and Moore 1978).

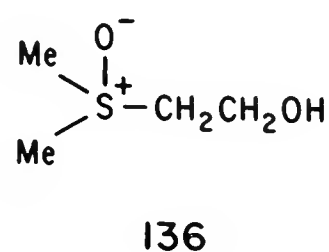
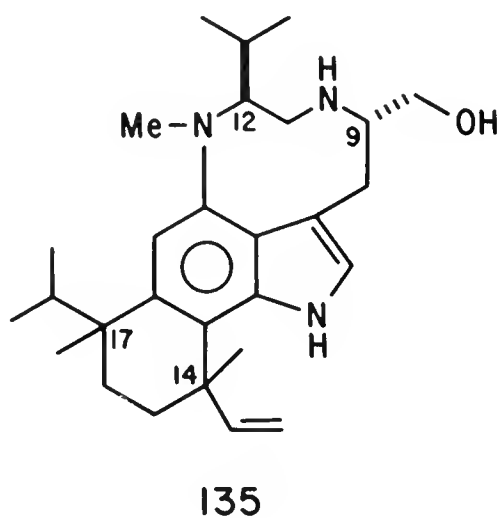
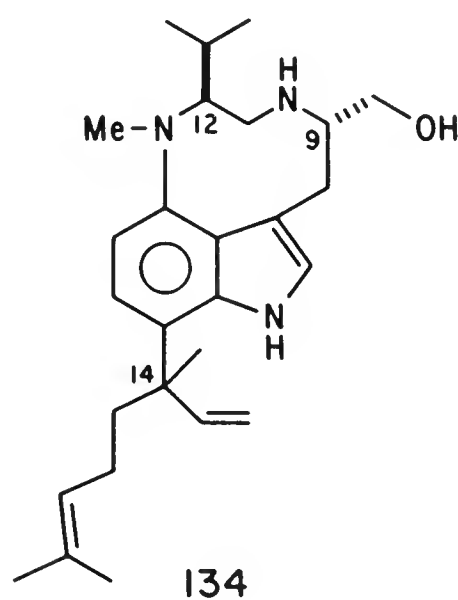
However, not all toxic strains of *L. majuscula* contain debromoaplysiatoxin or its congeners and another investigation of a shallow water variety revealed that the



	R_1	R_2	R_3	R_4
131	Me	H	Br	H
132	Me	H	H	H
133	H	H	H	H

marginal activity of this species was due to a completely different compound, lyngbyatoxin A (134) (Cardellina et al. 1979). The UV spectrum of the toxin was typical of an indole - a relatively rare structure in marine plant products - and other spectroscopic data established the nature and placement of a non-hydrolyseable N-methylvaline unit and a linalyl group. The algal toxin is identical with the C₁₄ epimer of teleocidin A, a metabolite of *Streptomyces mediocidicus* (Takashima et al. 1962). This bacterium also produces another toxin teleocidin B (135) which exists as a mixture of four C-14, C-17-diastereoisomers. Interestingly, only one epimer of lyngbyatoxin A has been found in the alga *L. majuscula*. Comparison of the ORD and CD measurements of the algal product and the teleocidin mixture indicated that the chirality at C-9 and C-12 in all the toxins is the same.

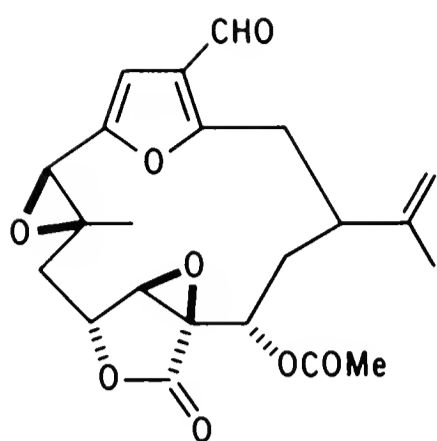
Contact with *Lyngbya majuscula* can result in severe dermatitis for swimmers in Hawaii during summer months, and debromoaplysiatoxin (132) aplysiatoxin (131) and lyngbyatoxin A (134) are each responsible for this effect. Not surprisingly, the teleocidin producer *S. mediocidicus* is responsible for a contact dermatitis which affects workers in the antibiotic industry (Moore 1982). A much simpler but no less unusual chemical that causes contact dermatitis—the so-called Dogger Bank itch—is the sulfonium ion (136) produced by the marine bryozoan *Alcyonidium gelatinosum* (Carlé & Christophersen 1980).



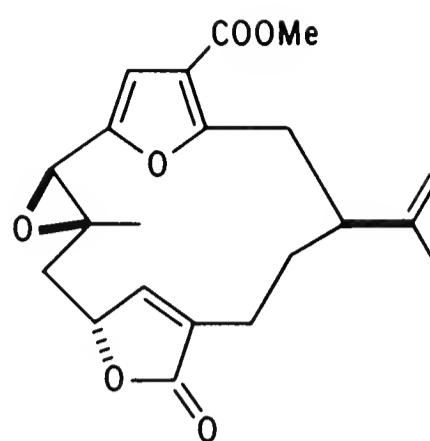
Considerable cytotoxic, ichthyotoxic and antibacterial activity was displayed by alcohol extracts of several gorgonians belonging to the genus *Lophogorgia*. From these extracts a powerful neuromuscular toxin, lophotoxin (137) was isolated (Fenical et al. 1981), which is another example of the cembrane class of diterpenes. We have seen that terpenes of this group frequently display biological activity but lophotoxin is unusual in that it contains furanoaldehyde and α, β -epoxy- γ -lactone functional groups, relatively rare features among natural products. Both functional groups seem important for the pharmacological activity of lophotoxin, and chemical modification of either group results in diminished toxicity. Along with lophotoxin, the extract also yielded a small amount of another cembrenolide, pukalide (138), an essentially inactive metabolite previously isolated from the soft coral *Sinularia abrupta* (Missakian et al. 1975).

Cardiovascular/Cardiotonic Agents

Few compounds displaying cardiotonic activity have been reported from marine organisms but this may be due to the fact that assays for such biological activity are less frequently performed.

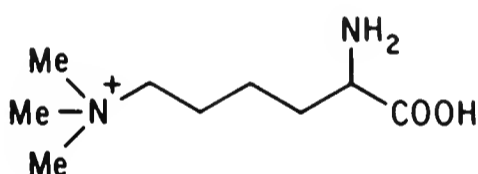


137

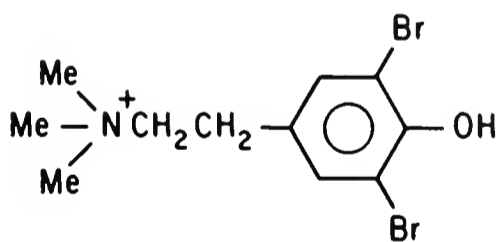


138

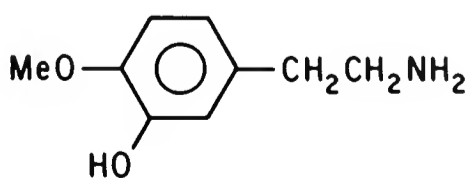
Laminine (139) a widely distributed metabolite of brown algae has long been known as a hypotensive agent. More recently another hypotensive agent, automonium (140), which also possesses a quaternary ammonium head group, was isolated from an aqueous-alcoholic extract of a sponge *Verongia fistularis* (Kaul 1981). The aqueous extracts of several holothurians (eg. *Pentacter arassa*, *Thelenota ananus* and *Stichopus chloronatus*) were found to possess hypotensive activity and in each case the causative agent was the known compound 5-hydroxytryptamine (Gregson et al. 1981b). An aqueous extract of the soft coral *Nepthea* sp. caused an increase in heart rate and blood pressure of test animals. A variety of aromatic amines including histamine, tyramine and dopamine were detected in the extract but none of these was responsible for the cardiovascular activity. Further



139



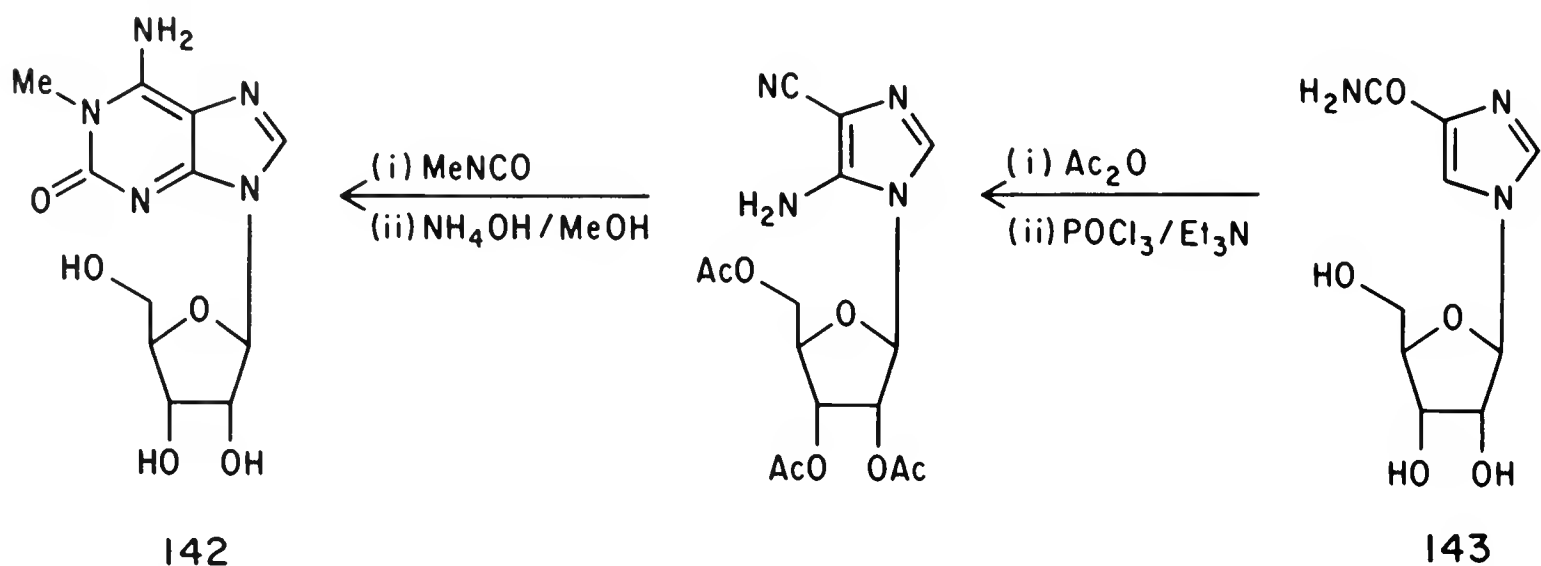
140



141

purification yielded a pure active fraction identified as 3-hydroxy-4-methoxyphenethylamine (141). Hitherto unreported from a marine source, this amine had already been found in cacti and human urine (Gregson et al. 1981a).

Free nucleosides are rare in nature but most possess some form of biological activity. An aqueous extract of the sponge *Tedania digitata* displayed muscle relaxant, antihypertensive, and anti-inflammatory properties, and all these pharmacological properties were eventually attributed to a single compound, 1-methylisoguanosine (142) (Quinn et al. 1980). Chemical degradation and spectroscopic evidence established the presence of D-ribose and 1-methylisoguanine, and a simple synthesis from the imidazole (143) (Scheme 3) yielded a product identical with the natural product. The same compound (named doridosine) was isolated by another group from extracts of the digestive gland of a nudibranch *Anisodoris nobilis* (Fuhrman et al. 1980).



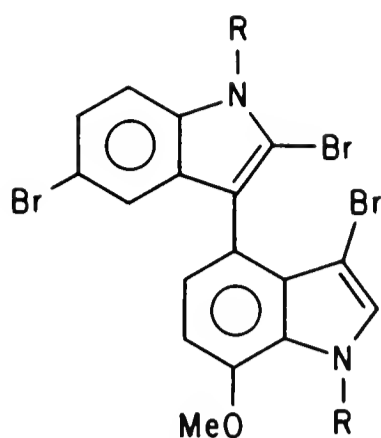
Scheme 3

Scheme 3: Chemical synthesis of 1-methylisoguanosine (142) from the imidazole (143)

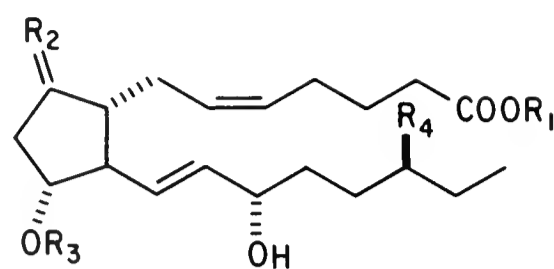
Anti-inflammatory Agents

Marine bi-indoles are extremely rare yet one of the most potent naturally occurring anti-inflammatory compounds ever discovered is the brominated bi-indole (144) isolated, together with several analogues, from a methylene chloride extract of the blue-green alga *Rivularia firma* (Norton & Wells 1982). The compound also displays anti-anaphylaxis properties which are enhanced by formation of the diacetate (145). An interesting feature of these bi-indoles is that despite their lack of a chiral centre most of them are optically active due to restricted rotation within the molecule.

A convincing case for serendipitous research was made by Weinheimers group following their isolation of unusually large concentrations of prostaglandins from the Caribbean gorgonian *Plexaura homomalla* (Weinheimer & Spraggins 1969). The excitement over this discovery stimulated activity in gorgonian fishery and raised the question as to the origin of these compounds since many of these primitive animals enjoy a symbiotic relationship with algae. Despite intensive searching it was ten years before another marine prostanoid was discovered and was in fact the first report of prostaglandins from a plant: the derivatives PGE₂ (146) and PGF_{2a} (147) were isolated from the red alga *Gracilaria lichenoides* (Gregson et al. 1979), and several others (148) - (151) from the soft coral *Lobophyton depressum* (Carmely et al. 1980).



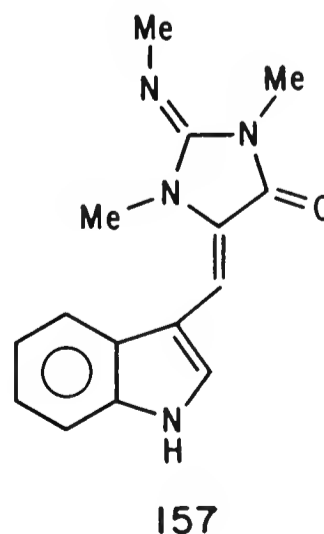
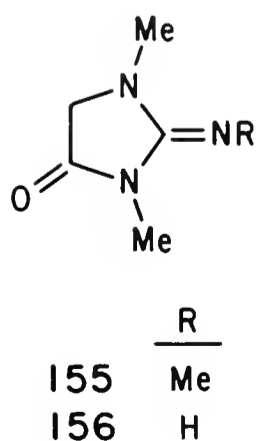
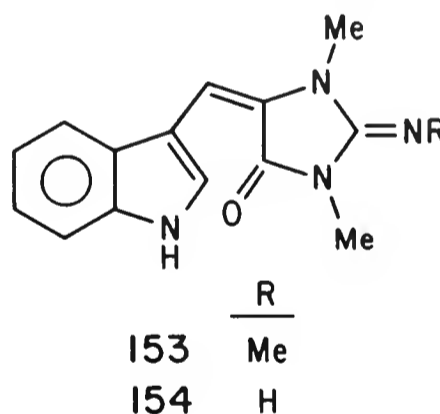
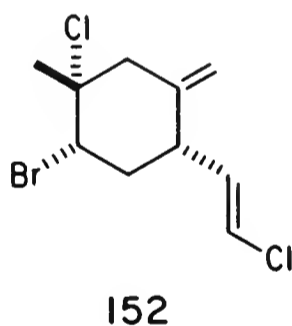
	R
144	H
145	Ac



	R ₁	R ₂	R ₃	R ₄
146	H	O	H	H
147	H	αOH, H	H	H
148	Me	αOH, H	Ac	H
149	Me	αOH, H	Ac	OAc
150	H	αOH, H	Ac	H
151	H	αOH, H	Ac	OAc

Central Nervous System (CNS) Agents

Many mono- and diterpenes isolated from marine organisms have non-specific depressant activity on the central nervous system (CNS) (Taylor et al. 1981). In contrast, the halogenated monoterpene plocamadiene A (152) isolated from the red alga *P. cartilagineum* (Higgs et al. 1977) causes an excitatory action on mouse behaviour. The effect is long-lasting and may have promise as a tool with which to study receptors of the CNS. Another drug with significant anti-depressant activity is methylaplysinopsin (153) a yellow crystalline metabolite isolated from the sponge *Aplysinopsis reticulata* together with the less active compound aplysinopsin (154)



(Kazlauskas et al. 1977b). Both natural products, and many analogues, were synthesized by piperidine catalysed condensation of indole-3-aldehyde with the requisite creatinine derivatives [(eg. (155) and (156)]. Both X-ray crystallographic analysis and nuclear magnetic resonance studies established the E configuration of the double bond in the natural products (c.f. Wells 1979.) The Z (157) isomer of methylaplysinopsin can be prepared but the antidepressant properties of this isomer are drastically reduced.

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NEW AND INTERESTING TAXA OF MYCENA PERS. OCCURRING IN NOVA SCOTIA

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This report includes ten taxa of *Mycena* Pers. occurring in Nova Scotia. *M. pteriphila*, *M. pelliculosa* var. *bryopsea*, *M. epipterygia* var. *sophia*, *M. insignis* var. *macrospora*, and *M. rubromarginata* var. *bulbosotipitata* are described as new. Five taxa are reported for the first time from Canada.

Ce rapport fort sur dix taxa de *Mycena* Pers. présents en Nouvelle-Ecosse. *M. pteriphila*, *M. pelliculosa* var. *bryopsea*, *M. epipterygia* var. *sophia*, *M. insignis* var. *macrospora*, and *M. rubromarginata* var. *bulbosotipitata* sont nouveaux. Cinq taxa sont mentionnés pour la première fois au Canada.

Species of *Mycena* Pers. occur abundantly in the forests of Nova Scotia where they often comprise a conspicuous part of the local flora, despite their small size. Species of *Mycena* included in this paper are either new or are reported for the first time from Canada.

Where descriptions exist that adequately cover our species, we provide references to the published accounts along with the summary of the general appearance of the fungus and remarks about our material. A full description is provided only for the species that is described as new. In the descriptions, color terms are cited from two sources. Terms from Ridgway (1912) are enclosed in quotation marks and those from the National Bureau of Standards (Kelly and Judd, 1955) are cited thus: (ISCC 56).

Collection numbers are designated ACAD and refer to fungi deposited in the E.C. Smith Herbarium, Acadia University. Camera lucida tracings were taken from the nomenclatorial type.

1. *Mycena rainierensis* Smith. *Mycologia* 42(1): 115. 1950. Fig. 9.

Pileus 6-22 mm broad, conic to broadly campanulate-convex to plano-convex with a depressed disc, margin incurved when young, often flaring in age; surface moist or subviscid when wet, becoming glabrous when dry; margin translucent striate, hygrophanous; color variable, pale brown at the disc and elsewhere pallid or "Snuff Brown" (ISCC 77) fading to watery gray-brown, often with yellow tints; flesh thin, pliant; taste slightly peppery, odor not distinctive. Lamellae close to subdistant, short-decurrent. Stipe 3-8 cm long, 1-4 mm thick, equal, hollow, fragile, surface pruinose at apex becoming glabrous below; color pallid or light gray. Spores 7-10 μm , globose, amyloid, smooth. Cheilocystidia 40-120 \times 9-17 μm , pyriform, avicular or more or less fusoid-ventricose with subacute to obtuse apices, sometimes with 2-3 small elongations at the top.

Our material agrees closely with the original description (Smith, 1950) with the exception that our specimens have a slightly peppery taste where Smith reported the taste as "not distinctive". We collected all our specimens growing scattered or gregarious on *Sphagnum* moss, a habit not reported by Smith for his Washington State material.

This is the first report of this species from Canada, and as far we can determine, the first report for its occurrence east of the west coast of N. America. It is common in Nova Scotia during the fall and may be locally abundant during rainy periods. *M. rainierensis* resembles *M. bisphaerigera* (Lange) Smith macroscopically, but differs in having a much darker pileus and shorter stipe (Favre, 1948). Favre's variety *M. bisphaerigera* var. *longicystis* Favre agrees more closely in coloration and stature, but differs microscopically by its greatly elongated cystidia.

Material examined: ACAD 14519, and 14520, Gifford Island, Mahone Bay, Lunenburg Co., N.S., 10 Oct. 82, leg. E. Hadjisterkoti; ACAD 14521, West Gasperaux, Kings Co., N.S., 21 Sept. 82, leg. E. Hadjisterkoti; ACAD 14517, and 14518, Port Hawkesbury, Richmond Co., N.S., 21 Sept. 82, leg. E. Hadjisterkoti.

2. *Mycena marginella* (Fr.) Quél. Champ. Jura et Vosges: 343. 1873. Fig. 7.

Pileus 6-12 mm broad, ovoid to subumbonate, umbo collapsing in age creating a depressed disc; margin translucent-striate, sometimes become rimose in age; surface moist, glabrous, sometimes appearing dry and velvety; color "Fuscous-Black" (ISCC 64) at center, elsewhere "Hair Brown" to "Fuscous"; flesh 1 mm thick at centre, oozing drops of hyaline liquid when cut, gray-pallid; taste mild or slightly acidic, odor mild. Lamellae broadly adnate, white with a blue component, edges brown. Stipe 1-5 cm long, 1-2 mm thick, equal hollow, surface pruinose when young becoming glabrous, base slightly enlarged, color dark bluish-brown at apex, elsewhere watery gray-brown, latex hyaline. Spores 6-7 x 4.5-5 μm , ellipsoid, smooth, weakly amyloid. Cheilocystidia (-10-40 (-75) x (-8) 11-15 μm , fusoid-ventricose with obtuse apices, abundant, intracellular contents sordid brown. Pleurocystidia similar to the cheilocystidia and present only near the lamellar edges. Pileal cuticle covered with irregularly arranged saccate cells, mostly 30-45 x 9-23 μm , intracellular contents dull-brown.

The most distinctive characters are its cuticular cells and cheilocystidia, both of which contain brown intracellular pigment. The above features in combination with the subumbonate pileal shape and velvety appearance characterize the species. Our material was collected only once on Blackman Is., Mahone Bay, and was growing in large troops on a rotten spruce log. This is the first report of its occurrence in Canada.

Material examined: ACAD 14516, Blackman Island, Mahone Bay, Lunenburg Co., N.S., 8 Aug. 1982; leg. E. Hadjisterkoti and D. Grund.

3. *Mycena rubromarginata* (Fr.) Quél. Champ. Jura et Vosges. p 435. 1875. var. *bulbosostipitata* Hadjisterkoti and Grund var. nov. Fig. 2.

Pileus 12-13 mm latus, conicus demum convexus, ad centrum depressus; glaber; ad marginem striatus; vinoso-bulbalinus ad brunneo-vinosus. Lamellae albridae, ad marginem rubra. Stipes basin bulbosus, lubricus. Sporae 10-13 x 5-8 μm , amyloideae, subglobosae; cheilocystidia 30-60 x 8-11 μm , fusoide ventricosa.

Typus ACAD 14515, in sylva convallis prope Universitatis Acadiae lectus; holotypus in herbario Universitatis Acadiae (ACAD) conservatus.

Pileus 12-13 mm broad, broadly conic to convex, centrally depressed, margin entire, striate, sometimes striatae reaching center, glabrous, moist and shiny when wet, hygrophanous; color "Vinaceous-Buff" to "Pale Brownish Vinaceous" (ISCC 7) at center, margin "Pale Vinaceous-Fawn"; (ISCC 32) flesh fragile. Lamellae adnate, narrow to moderately broad, subdistant, pallid, edges pinkish-red. Stipe 2.5-2.8 cm long, 1.5 mm thick, equal with a distinct bulbous base, bulb with scattered

mycelial hairs; surface lubricous, flesh elastic, firm, center hollow. Spores 10-13 x 5-8 μm , subglobose, amyloid.

Occurring gregarious on dead stick.

Material examined: ACAD 14515, on campus, Acadia University at location of physical plant buildings, Wolfville, Kings Co., N.S., 26 Sept., 1981, leg. E. Hadjisterkoti.

The distinctive feature of this new variety is the obvious bulbous base. Smith (pp. 211-212, 1947) discussed variations of *M. rubromarginata* that he examined from N. America, but did not mention the species having bulbous bases or a lubricous stipe surface. This is the first report of *M. rubromarginata* from Nova Scotia.

4. *Mycena galopus* (Fr.) Quél. Champ Jura et Vosges: 107. 1872. Fig. 10.

Pileus 6-15 mm broad, ovoid when young, becoming conic or conic-campanulate with a recurved margin, umbonate; margin entire, translucent, striate when moist; surface glabrous; color "Fuscous-Black" (ISCC 64) overall when young, margin becoming gray to "Hair Brown" (ISCC 64), umbo becoming blackish; flesh thin, fragile; odor slightly fruity, taste mild or sometimes slightly bitter. Lamellae subdistant, narrow, ascending-adnate, pallid. Stipe 4-6 cm long, 1-2 mm thick, equal, flexuous; surface glabrous; color "Olive-Brown" (ISCC 96), pallid at apex, blackish-brown at base, base white strigose; exuding white latex when broken. Spores 9-13 x 5-7 μm , smooth, ellipsoid, subpyriform, or rarely "heart-shaped", weakly amyloid.

Occurring gregarious on fronds of ferns (*Onoclea sensibilis* L.)

Material examined: ACAD 14468, in woodlot behind the E.K.M. Hospital, Wolfville, Kings Co., N.S., 5 Oct., 1982, leg. E. Hadjisterkoti.

This is the first report of this species in Canada, and also the first time it has been reported growing on ferns. Fresh specimens exude a milky white juice when the stipe is slightly cut with a razor blade.

5. *Mycena epipterygia* Fr. Syst., Myc. 1: 155. 1821. var. *eipipterygioides* (Pearson) Kühn. Encycl. Mycol. 10: 353. 1938.

Pileus 9-20 mm broad, ovoid to obtusely conic, becoming broadly conic or convex, nearly plane in age, umbonate; margin appressed against stipe when young; surface pruinose with young, becoming glabrous, viscid, pellicle separable; color "Pale Ochraceous-Buff" (ISCC 92) to "Tilleul Buff" (ISCC 31). Lamellae ascending and bluntly adnate, sometimes toothed, subdistant to close; concolorous with pileus. Stipe 4-7 cm long, 1 mm thick or less, equal, surface viscid; pallid with greenish-yellow component. Spores 9-11 x 4-5.5 μm , ellipsoid, smooth, amyloid.

Occurring gregarious on conifer needles and twigs among mosses.

Material examined: ACAD 14531, Port Hawkesbury, Richmond Co., N.S., 10 Oct., 1981, leg. E. Hadjisterkoti.

This is the first report for this taxon from Canada. Our collection was compared with Dr. A.H. Smith's collection (Mich 3446) and no microscopic differences were found. Spores from European material are reported to be wider (9-10 x 7.5-8 μm) and have two-spored basidia (Smith, p. 425, 1947). We did not observe red stains at the stipe base for the Nova Scotian material as reported by Smith for his Michigan specimens. The color of the stipe is pale yellow in dried material.

6. *Mycena insignis* Smith. Contrib. Univ. Mich. Herb. 5: 25. 1941. var. *macrospora* Hadjisterkoti and Grund var. nov. Fig. 3.

Pileus 8-10 mm latus, convexus, glaber; ad marginem striatus centrum fulvus ad marginem pallida. Lamellae adnatae, subdistantes, concolores. Stipes 25-33 mm longus, 1-1.5 mm crassus, aequalis, viscidus. Sporae 9-14 x 5-6 μm , ellipsoideae, amyloideae.

Typus ACAD 14454, in sylva convallis prope Universitatis Acadiae, Wolfville, N.S. lectus; holotypus in herbario Universitatis Acadiae (ACAD) conservatus.

Pileus 8-10 mm broad, convex to broadly convex, somewhat flattened at the center; surface subviscid to viscid and shiny when wet, dull when dry, striate; color yellowish-brown at center buff to light yellow on margins, "Cartridge Buff" (ISCC 89) to "Marguerite Yellow" (ISCC 104) overall in age; flesh thin, fragile, brown-gray. Lamellae with decurrent tooth, close to subdistant; "Cartridge Buff" (ISCC 89). Stipe 25-33 mm long, 1-1.5 mm thick, equal, cartilaginous, hollow; surface viscid; color "Ivory Yellow" (ISCC 104) at apex, darker towards base, base white-strigose. Spores 9-14 x 5-6 μm , ovoid to long ellipsoid, amyloid.

Growing solitary on humus under spruce.

Material examined: ACAD 14454, Acadia University woodlot, Wolfville, Kings Co., N.S., 27 Sept., 1981, leg. E. Hadjisterkoti.

This is the first report of this species from Canada. Smith's collections (paratype, MICH. 14471 and MICH 13101) were examined and the spores found to be 7-9 x 4 μm .; thus, the Nova Scotian material was much larger. In all other particulars our collection fits the description for the taxon growing on needle beds of Douglas Fir reported by Smith (Smith, p. 405, 1947).

7. *Mycena epipterygia* (Fr.) S.F. Gray. Nat. Arr. Brit. Plants. 1:619. 1821. var. *sophia* Hadjisterkoti and Grund. Fig. 6.

Pileus 8-13 mm latus, conicus vel campanulatus, ad marginem striatus, viscidus, olivaceo-brunneus. Lamellae eburneae, ad marginem viscidae. Stipes 3.3-5.5 (15) cm longus, 1-2 mm crassus, aequalis, viscidus. Sporae 10-12 x 6-7 μm vel 15-19 (21) x 5-7 μm , ellipsoideae.

Typus Acad 14502 in sylva convallis, Gifford Is. Mahone Bay, comitato Lunenburg, N.S. lectus; holotypus in herbario Universitatis Acadiae (ACAD) conservatus.

Pileus 8-13 mm broad, subovoid when young, umbonate, becoming conic-campanulate and retaining the umbo in age; translucent-striate; surface with a separable viscid cuticle; color "Olive Brown" (ISCC 86) to "Clove Brown" at the center becoming "Colonial Buff" (ISCC 86) at the margin; flesh thin, firm; odor not distinctive or slightly raphanoid; taste spicy, unpleasant and lingering. Lamellae subdistant, uncinatae, narrow, pallid to "Ivory Yellow" (ISCC 104), edges viscid. Stipe 3.3-5.5 (15) cm long, 1-2 mm thick, equal, cartilaginous, firm. Surface viscid; color "Lemon Chrome" to "Lemon Yellow" when older. Spores 10-12 x 6-7 μm , (four-spored), narrowly ellipsoid, cylindrical or pyriform.

Growing solitary or gregarious between mosses on fern and spruce debris, always under ferns (*Dennstaedtia* sp.).

Material examined: ACAD 14502, Gifford Island, Mahone Bay, Lunenburg Co., N.S., leg. S. Grund and E. Hadjisterkoti; ACAD 14503, Port Hawkesbury, Richmond Co., N.S., leg. E. Hadjisterkoti.

This new taxon is definitely one of the varieties of *M. epipterygia* because of its similarity in color, cystidia, viscosity of the stipe and cuticle, and the number of lamellae. It differs from the other varieties in having unusually large spores. *M.*

griseogilva Horak. (*M. epiterygia* var. *brunneola*) has spores [(10)11-15 x 6.5-7.5 μm ,] that are in the size range of our new variety, but differs in a number of other particulars. The large spores, lemon yellow stipe and the unpleasant taste distinguish this variety from others within the species.

8. *Mycena pelliculosa* (Fr.) Quél. Champ Jura et Vosges: 343. 1873. var. *bryopsea* Hadjisterkoti and Grund var. nov. Fig. 4.

Pileus 3-4 mm latus, conicus, umbonatus, ad centrum depressus; ad marginem striatus; fuscus et brunneus. Lamellae cineraceae vel pallide griseae; subdistantes, subdecurrentes. Stipes 23-40 mm longus, 0.8-1 mm crassus, aequalis, viscidus, pallidus. Sporae 5-10 x 4-5.5 μm , ellipsoideae, amyloideae.

Typus ACAD 14504, prope Port Hawkesbury lectus, holotypus in herbario Universitatis Acadiae (ACAD) conservatus.

Pileus 3-4.5 mm broad, conic hemispherical with an umbo, centrally depressed at maturity; margin entire, translucent-striate to the disc; surface glabrous to subviscid; "Fuscous" (ISCC 64) to "Drab" (ISCC 23) at center and on striations, lighter between striations; flesh thin, fragile; taste and odor not distinctive. Lamellae subdecurrent, distant to subdistant, gray. Stipe 23-40 mm long, 0.8-1 mm thick, equal, flexible, fragile, hollow; surface viscid, hygrophanous, translucent, pruinose at apex; watery white to pallid-gray; base attached to mosses and liverworts by white rhizoids. Spores 6-10 x 4-5.5 μm , smooth, amyloid, ellipsoid.

Growing gregarious on mosses and liverworts.

Material examined: ACAD 14504, Port Hawkesbury Community Park System (near highway), Richmond Co., N.S., 18 Oct., 1982, leg. E. Hadjisterkoti.

This taxon is similar to *M. pelliculosa* var. *pelliculosa*; however, hyphae of the pileipellis are rough where those in *M. pelliculosa* are described as gelatinous (Smith, 1947). Our collection was growing on mosses and liverworts whereas *M. pelliculosa* var. *pelliculosa* grows on humus under conifers. The gill edges gelatinize in both varieties. The pileus of this new variety has an umbo when young and then becomes depressed in older specimens, but Smith (loc. cit.) did not mention observing an umbo. The pileus of *M. pelliculosa* var. *bryopsea* is smaller than the typical variety (5-10 mm broad).

9. *M. pteriphila* Hadjisterkoti and Grund Sp. nov. Etymol: Gr.-pteris - fern; philo - fond of. Figs. 1, 5.

Pileus 4-13 mm latus, conicus demum plano-campanulatus, umbonatus, ad marginem rimosus et striatus; centrum fuscus, ad marginem bubalinus; odore farinaceus. Lamellae albae, subdistantes, latae. Stipes 2-6.5 cm longus, 0.8-2 mm crassus, aequalis, pruinosis demum glaber; fuscus demum pallidus. Sporae 8-11 x 6-7 μm , ovulatae vel ellipsoideae, non-amyloideae. Pleurocystidia et cheilocystidia 32-85 x 8-17 μm , subclavatae. Habitatio filices.

Typus ACAD 14505, prope Wolfville comitato Kings, N.S. lectus; holotypus in herbario Universitatis Acadiae (ACAD) conservatus.

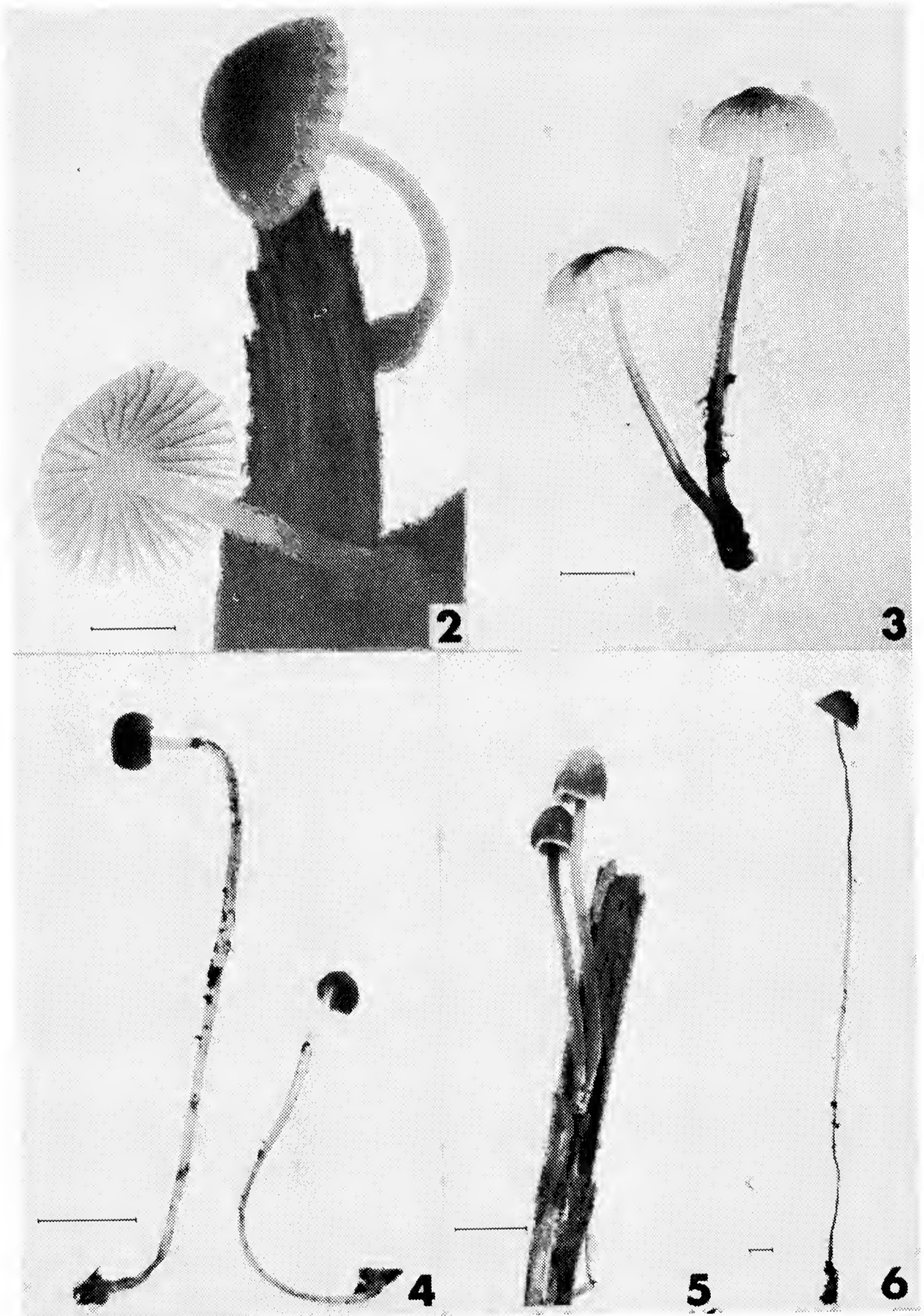
Pileus 4-13 mm broad, ovoid when young, becoming conic to broadly conic with an obtuse umbo, campanulate or plano-campanulate in age; margin at first appressed against stipe becoming straight-flaring in age, rimose, translucent-striate, sulcate in age; surface glabrous; color blackish-brown at center, fading to "Cream-Buffer" (ISCC 73) at margin, color generally variable; flesh thin, fragile; taste not distinctive or slightly acidic; odor farinaceous. Lamellae uncinatae, subdistant, rather broad; 18-23 reaching stipe, lamellulae in three series; pallid. Stipe 2-6.5 cm

long, 0.8-2 mm thick; equal, cartilaginous, surface covered at first with white pruina, later becoming polished, glabrous; color at apex "Fuscous-Black" (ISCC 64) when young, becoming concolorous with the lamellae or with a shade of "Old Gold" (ISCC 88) elsewhere pallid; base strigose, holding on fern fronds and rhizomes with several white mycelioid hairs. Spores 8-11 x 6-7 μm , ovoid to ellipsoid, smooth, nonamyloid, often thick-walled, sometimes granulated. Basidia 25-30(38) x 6-9(15) μm , subcylindric to clavate, 4, 5, 6, and sometimes 7-spored. Cheilocystidia 32-85 x 8-17 μm , subcylindric to subclavate, often with irregularities, abundant. Pleurocystidia similar to cheilocystidia, rare to scattered. Lamellar trama interwoven. Pileipellis interwoven, containing hyphae with short elongations or protruberances about 2 μm wide, hyphae often collapsing (gelatinizing) when examined in potassium hydroxide; subcutis with large, loosely arranged cells, some 40 μm wide; cuticle of stipe with cells similar to those in the pileipellis but larger, 2-5 μm wide and to 35 μm long.

Growing gregarious or clumped in pairs on the fronds and rhizomes of the fern *Osmunda cinnamomea* L.



Fig 1 *M. pteriphila* Hadjisterkoti and Grund. Symbols: Ch=cheilocystidia; Ca=caulocystidia; B=basidia and basidioles; S=spores; Pe=terminal cells in the pileipellis. All scale bars equal to 10 μm .



Figs 2-6 Fig 2—*M. rubromarginata* (Fr.) Quél. var. *bulbosostipitata* Hadjisterkoti and Grund; Fig 3—*M. insignis* Smth var. *macrospora* Hadjisterkoti and Grund; Fig 4—*M. pelliculosa* (Fr.) Quél. var. *bryopsea* Hadjisterkoti and Grund; Fig 5—*M. pteriphila* Hadjisterkoti and Grund; Fig 6—*M. epipterygia* (Fr.) S.F. Gray var. *sophia* Hadjisterkoti and Grund. All scale bars for Figs 2-6 equal 5.0 mm.



Figs 7-10 Fig 7—*M. marginella* (Fr.) Quél.; Fig 8—*M. speirea* (Fr.) Gill.; Fig 9—*M. rainierensis* Smith; Fig 10—*M. galopus* (Fr.) Quél. All scale bars for Figs 7-10 equal 1.0 cm.

Material examined: ACAD 14505, 26 May, 1982; ACAD 14506, 3 June, 1982, ACAD 14453, 20 Sept., 1982; near Wolfville train station, Wolfville, Kings Co., N.S., leg. E. Hadjisterkoti.

All three collections were taken from the same fern stand. Microscopically they were identical but the basidia varied in shape, size and number of sterigmata. Spores were often thick-walled and sometimes granulated. *Mycena pteriphila* is most closely related to *M. olida* var. *americana* Smith because of spore shape and size, cystidia similarities, and in the way the hyphae of the pileus gelatinize; however, its basidial characteristics, taste, odor, and habitat are definitely distinctive. *M. olida* var. *americana* Smith grows on humus and on old stumps (Smith, p. 153. 1947).

10. *Mycena speirea* (Fr.) Gillet. Les Hymen: 280. 1874. Fig. 8.

Pileus 3-13 mm broad; conic to convex, sometimes papillate, center depressed around papilla, papilla usually collapsing in older specimens, becoming plane; surface glabrous, translucent-striate, moist or appearing dry; margin rimose in age; color variable, center gray, "Isabella Color" (ISCC 94) to "Cream-Buff" (ISCC 73) becoming pallid at margin; flesh membranous but fragile; taste peppery and slightly acidic, odor not distinctive. Lamellae subdistant to distant, arcuate-decurrent, 12-17 reaching the stipe, in 2-series, lamellulae narrow to broad, usually intervenose; pallid to gray. Stipe 1-6 cm long, approximately 1 mm thick, filiform, equal, flexible, cartilagenous and firm, tubular; surface subpruinose becoming glabrous, often lubricous when young; color yellowish at apex grayish-yellow or "Cinnamon-Buff" (ISCC 72) to "Clay Color" (ISCC 74) below; base with white rhizoids.

Growing gregarious on bark of fallen trees.

Material examined: ACAD 14478, 26 Sept., 1982; ACAD 14479, 7 Oct., 1982, both collections taken behind E.K.M. Hospital, Wolfville, Kings Co., N.S., leg. E. Hadjisterkoti.

This is the first report of this species from Canada. Smith's collection (MICH 15227) was compared to our material. The yellow color in the apex of the stipe is a reliable character if young specimens are examined. Mature pilei must be used to examine microscopic details, especially cheilocystidia. Smith (p. 360, 1947) reported the odor and taste as non-distinctive or slightly farinaceous, but our specimens were definitely peppery-acidic.

Acknowledgement

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SEIROSPORA SEIROSPERMA (HARVEY) DIXON
(RHODOPHYTA, CERAMIACEAE)
—A FIRST RECORD FOR CANADA*

The marine red alga *Seirospora seirosperma* (Harv.) Dix. is reported for the first time in Canada. Although fairly widely distributed along the Atlantic coast of Europe (Rosenvinge 1923-24; Ardré 1969-70; Parke & Dixon 1976), *S. seirosperma* has been recorded from a much narrower range in the western Atlantic, from New Jersey to Massachusetts (Taylor 1957, as *S. griffithsiana* Harv.; Sears 1971). Further, within Massachusetts, the species is known only from south of Cape Cod, except for a single, early report of it from Salem (near Boston; Harvey 1853). Thus the present record of *S. seirosperma*, in Nova Scotia, is an apparent disjunction of some 650 km in its North American distribution.

Seirospora seirosperma (Figs 1, 2) was collected in October 1983 at Pauls Point (44°34'N, 64°56'W) and Mill Cove (44°35'N, 64°04'W), both in St. Margarets Bay on the Atlantic coast of Nova Scotia. Identification of the species was confirmed by reference to Feldmann-Mazoyer (1940), Taylor (1957) and Dixon (1971). Plants were rare to occasional, epiphytic usually on *Laminaria longicuris* Pyl. and *L. saccharina* (L.) Lamour., less frequently on *Cystoclonium purpureum* (Huds.) Batt., *Polysiphonia nigrescens* (Huds.) Grev. and *Chordaria flagelliformis* (O.F. Müll.) C. Ag. The species was found from 3 to 11 m depth, but plants were larger and more frequent in the 6- to 9-m depth range. Thalli were up to 6 cm tall and usually bore numerous seirosporangia (Fig 2). Even sparingly sporangiate or infertile smaller specimens were readily distinguishable from infertile *Callithamnion corymbosum*, abundant at this time at both sites, by their uninucleate cells, their most robust, pyramidal habit (Fig 1), and their coarser branching with ultimate divisions slightly appressed-corymbose. No reproductive structures other than seirosporangia were seen in material collected from the entire depth range over several weeks in October. Unfortunately, we were unable to follow the subsequent development and ultimate fate of this species in the field. However, in cultures derived from seirospores and apical segments of these plants (C.J. Bird, unpubl.), only an asexual cycle of seirosporangiate plants was obtained, at approximately 3-week intervals (cf. Plattner & Nichols 1977).

The occurrence of *S. seirosperma* in Nova Scotian waters is probably due primarily to supranormal inshore sea temperatures during summer and autumn of the past several years (Lauzier & Hull 1969; Scheibling & Stephenson 1984). The species has been observed in culture to require temperatures in the vicinity of 15°C or higher for growth and sporulation (Plattner & Nichols 1977; C.J. Bird, unpubl.). Sustained sea temperatures in excess of 15°C were noted during late summer and autumn of 1983 along the coast of Nova Scotia (R.E. Scheibling, pers. comm.), including subtidally to 9 m at the collection sites in St. Margarets Bay (C.R. Johnson, unpubl.). At the growth rates observed in cultures of *S. seirosperma*, these thermal conditions undoubtedly would support growth and reproduction of this species in nature, assuming the presence of viable propagules. Indeed, the occurrence of similar autumnal temperatures since 1980 suggests that *S. seirosperma* could have arrived here earlier and may now be more widespread in Nova Scotia than the present report indicates.

A second factor to promote the occurrence of *S. seirosperma* in this area is the recent mass mortality of sea urchins in St. Margarets Bay and elsewhere along the

Nova Scotian coast (Miller & Colodey 1983; Scheibling & Stephenson 1984). This event has reduced the severe grazing of the seafloor by these herbivores and allowed a subtidal algal macroflora to become re-established for the first time in about a decade. Urchin dieback was observed in 1980 at Pauls Point and 1981 at Mill Cove, and impressive recovery of the macroalgal flora has occurred in the ensuing 2-3 years.

Voucher specimens of *S. seirosperma*, NRCC 9618, 9619, 9673 and 9674, are deposited in the herbarium of the National Research Council of Canada, Halifax, N.S.

Acknowledgements

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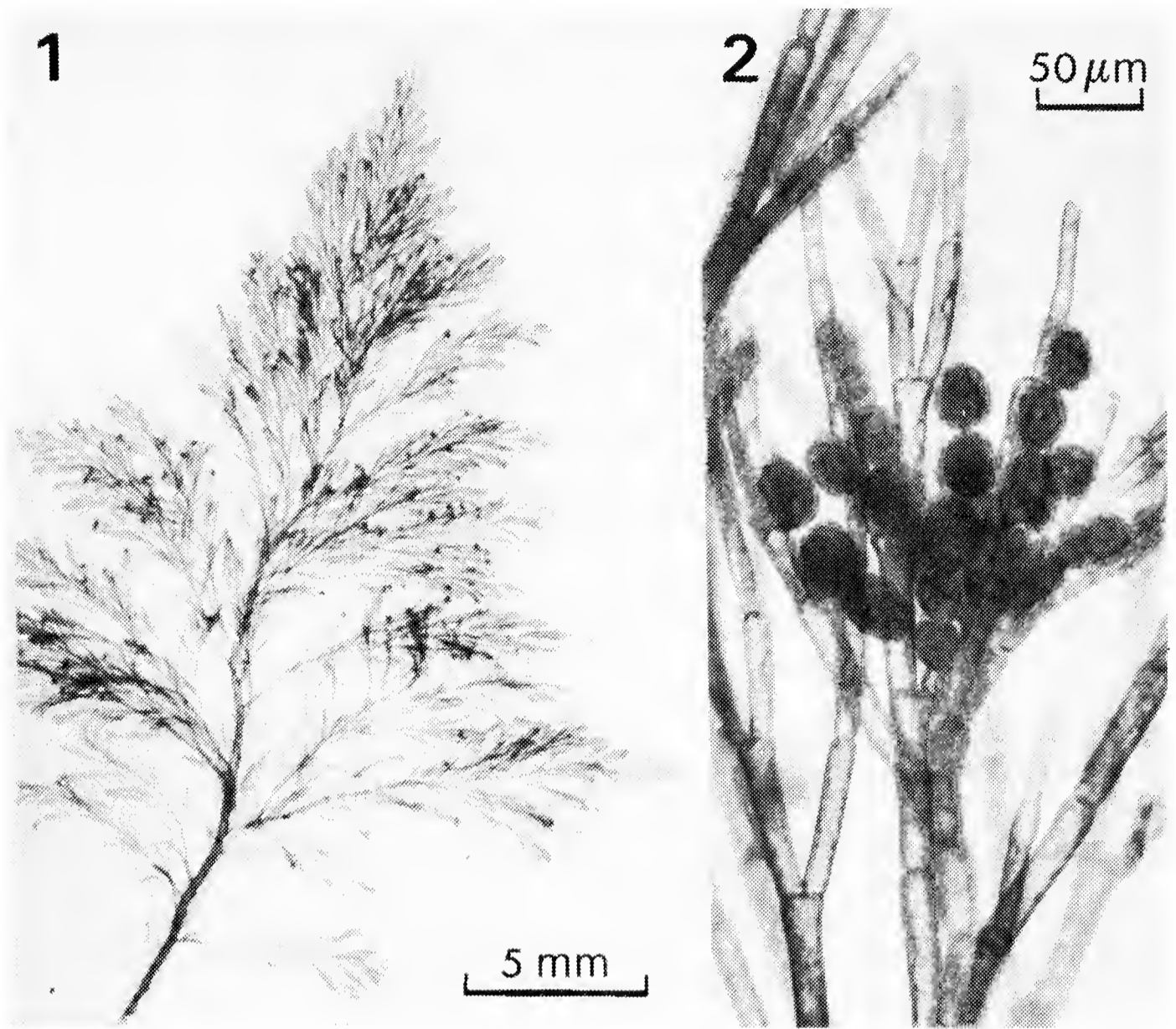


Fig 1: *Seirospora seirosperma*; habit, showing the characteristic pyramidal shape and distinct main axis. The dark spots at the apices of some of the branches are clusters of seirosporangia.

Fig 2: Detail of apical filaments and seirosporangia from the plant in Fig. 1.

THE CUBERA SNAPPER, *LUTJANUS CYANOPTERUS* (CUVIER) (PISCES: LUTJANIDAE) NEW TO NOVA SCOTIA AND CANADA

A large fish, 1.124 metres long, of a species and family previously unknown in Canada, was caught in a fish trap at Tuffin Island, off Ecum Secum, Nova Scotia, 17 September 1975 (Fig 1). This specimen is a cubera snapper, *Lutjanus cyanopterus* (Cuvier, in Cuvier and Valenciennes, 1828), originally described from Brazilian waters, but later reported from the Caribbean, the Gulf of Mexico and north to lower Chesapeake Bay, Virginia. The known range of the species is extended northward 1400 km. The description follows the format of Leim and Scott (1966).

There are several important reviews of the Lutjanidae of the western Atlantic. Guides and descriptive texts have been prepared (Anderson 1967; Hardy 1978; Vergara 1977).

The specimen is catalogued as NMC75-1962 in the National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario.

Family Lutjanidae

Snappers

A large family of bottom-associated predatory fishes, predominantly marine and tropical but frequently entering estuaries and temperate waters. They usually feed at night on crustaceans and fishes. The flesh of lutjanids, of a delicate taste, is highly esteemed, although some species have been reported to cause ciguatera poisoning. Several thousand tons are caught annually in the tropical Western Atlantic and north to Cape Hatteras, North Carolina. Small pelagic eggs and larvae are produced.

The family is composed of generalized predators often with elongate snout and many with large teeth, typically with 2 weak opercular spines, spinous and soft parts of dorsal fin united, three anal fin spines and ctenoid scales. The pelvic fins are thoracic with 1 spine and 5 soft rays, the caudal fin varies from truncate to deeply forked. The gill membranes are separate and free from the isthmus. The family includes about 17 genera and about 140 nominal species (excluding the Caesionidae).

The following description is based on our specimen with comparative notes from previous records.

Cubera Snapper

Vivaneau Cubéra

Lutjanus cyanopterus (Cuvier, 1828)

Description

Body robust, the greatest depth, at the beginning of the dorsal fin, 3 times in standard length (=SL), compressed; caudal peduncle deep, depth 9.5 in SL. Head large, 2.7 in SL, pointed, snout long, 2.5 in head length (=HL); upper limb preoperculum very finely serrated, coarser teeth at angle of preoperculum; mouth terminal, slightly angled, hind tip of upper jaw reaching to half way between posterior nostril and orbit (much further on smaller specimens, *fide* Dr. W. Anderson, at least to mid-orbit), length upper jaw 2.3 in HL; jaws with large canine teeth, 1 large and 1 small in upper jaw, 2 large and 4 moderate in lower jaw, v-shaped (frequently triangular *fide* Dr. W. Anderson) patch of villiform teeth on vomer without posterior extension; oval-shaped patch villiform teeth on tongue; lower jaw ex-

tends slightly beyond upper, but not always; orbit small, diameter 9.7 times in HL. Fins: Dorsal (1)X, 14, spinous and soft-rayed portions united but deeply notched, origin over base of pectoral fin; caudal fin large, emarginate; anal III, 8, soft portion distally rounded, not pointed; pectoral fins pointed, falcate, 17 rays, length 4.2 in SL; pelvic fins thoracic, 1.5, length 5.6 in SL. Lateral line present, complete, arched parallel to dorsum then descending to midline on caudal peduncle. There are about 52 rows of scales with approximately 43 with pores, and 8 rows above lateral line. Scales on bases of dorsal, caudal, anal and pectoral fins. Scales on opercle, subopercle and, in 8 rows, on cheeks. Gill rakers denticulate, 5 rudimentary on upper arch. 7 developed and 9 rudimentary on lower arch.

Colouration

In this preserved specimen head and body are dark brown above, lighter on abdomen, inter-radial membranes of soft dorsal and anal fins dark. No dark spots were observable elsewhere. Vergara (1977) reported colour of fresh specimens as dark grey with reddish tinges on back and upper sides; pectoral fins almost colourless, anal and pelvic fins somewhat reddish, and dorsal and caudal fins greyish. Walls (1975) included a colour photograph showing the dark inter-radials of the soft dorsal and anal fins, a dark caudal fin and silver-grey scales with dark edges.

Distinctive Characters

Distinguished from other fishes in the region that have united dorsals provided with soft and spinous rays by the long triangular snout, upper jaws that do not reach posteriorly to the eye (but at least to mid-orbit in small specimens) and slipping up under the preorbital bones when the jaws are closed, the large canine teeth in the jaws and the long pointed pectoral fins.

Size

Reported elsewhere to more than 1002 mm TL (Böhlke & Chaplin, 1968) and more than 45 kg, and to attain a maximum of 1600 mm (Vergara, 1977). Our specimen measured 930 mm SL, 1077 mm FL (fork length), 1124 mm TL, and weighed 19.1 kg.

Distribution

Known in the western Atlantic from Brazil (the type locality) north through the Caribbean, West Indies, Atlantic coast of Mexico (Castro-Aguirre 1978), rare in northern Gulf of Mexico (Moe 1968), from Florida (Rivas 1949) north to lower Chesapeake Bay, Virginia (Hardy 1978), and from Cape Lookout to Wrightsville, North Carolina (Schwartz 1972). Specimens were also reported off Charleston, North Carolina (Schwartz 1972). Specimens were also reported off Charleston, North Carolina and in Mill Pond, near Chatham, Massachusetts (clipping seen by Dr. W. D. Anderson, Jr., specimen not examined).

Canadian Distribution

Known only from the present record from Tuffin Island, Halifax County, 4.8 km south of Ecum Secum, Nova Scotia (44°55'N, 62°10'W).

Biological and Economic Notes

Vergara (1977) reported large specimens mainly along submarine ledges over rocky bottoms or around reefs, at depths usually of no more than 40 m; small specimens often inhabit mangrove-lined coasts. Vergara (1977) reported that it fed

mostly on fishes; Böhlke and Chaplin (1968) listed crustaceans and fishes. Juveniles are reported from estuarine areas in rivers, streams and canals or shallow turtlegrass beds at 3.7 - 37 ppt salinity and 24.5 - 31.0°C; nothing is known of spawning, eggs, larvae, or age and size at maturity (Hardy 1978).

The cubera snapper is caught mainly on hook and bottom longlines; also with gill nets and occasionally with bottom trawls, or with spears by skin divers. It is marketed fresh and frozen; its flesh is of good quality, although large individuals taken from toxic sectors of reefs may cause ciguatera poisoning when eaten (Randall 1968).

Several tropical fish species have been recorded less than half a dozen times on the Atlantic coast of Canada. These may be larvae or juveniles in which case the simplest explanation is northward expatriation through Gulf Stream currents, then shorewards to the Canadian coast by eddies from the Gulf Stream (Gilhen, Gruchy & McAllister 1975). This would also provide a mechanism for transport of adults of tropical pelagic fishes.

The explanation for occurrences of large benthic predatory fishes is less certain. Transport of eggs or larvae with development and maturation in Canadian waters is less probable given the tropical temperatures, approximately 24.5 - 31.0°C (Hardy 1978), at which juveniles of cubera snappers normally occur.

Robust fishes one metre long seem unlikely to be transported in ballast water from the tropics and discharged in Canadian waters since discharge pipes are commonly 15 cm in diameter. But on the other hand, the movement of large benthic fishes, some 2000 km northward unto unusual environments, is improbable. In this case, the fish would have either to cross the cold waters of the Bay of Fundy or those between Georges and Browns Banks to reach the outer coast of Nova Scotia. Perhaps the determination of growth rates from scale or otoliths will eventually help solve this enigma, although at present nothing is known of growth rates of the cubera snapper; a sudden slowing of the growth rate relative to tropical specimens might suggest at what age it moved into northern waters where its growth rate would presumably decrease because of lower temperatures.

Acknowledgements

Jadwiga Frank photographed and weighed the specimen. The specimen was caught by Bernell, Neil, Dennis, Harvey and Winston, all of the Jewers family, and saved by Jewers Fisheries Co-op. Jim Cameron, Fisheries Officer, recognized its rarity and advised the first author of its capture. The authors wish to warmly thank these persons. Dr. William D. Anderson, College of Charleston, Charleston, North Carolina, reviewed the manuscript and gave numerous helpful suggestions.

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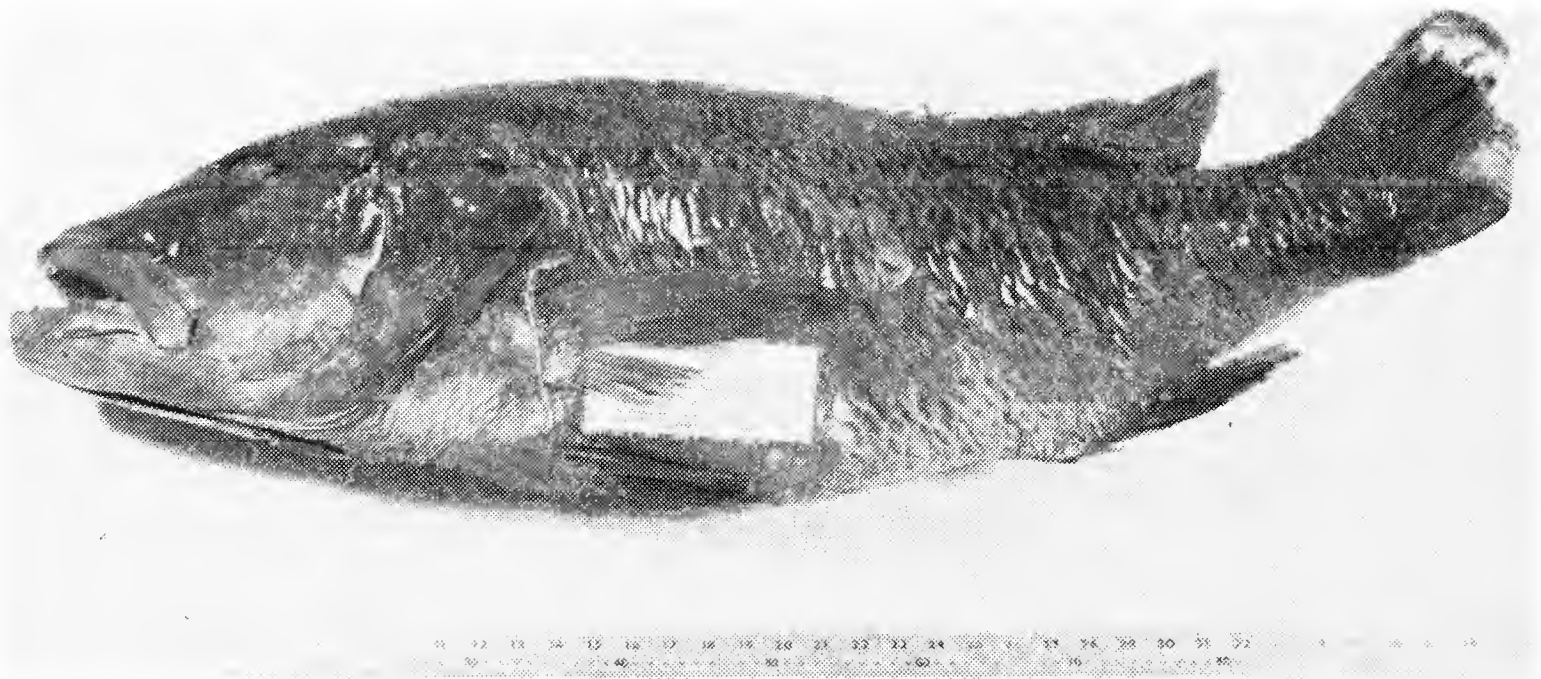


Fig 1 Cubera snapper, *Lutjanus cyanopterus* (Cuvier), caught at Tuffin Island, Halifax County, 4.8 km south of Ecum Secum, Nova Scotia, 17 September 1975, by Bernell, Neil, Dennis, Harvey and Winston Jewers.

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INSTRUCTIONS TO AUTHORS

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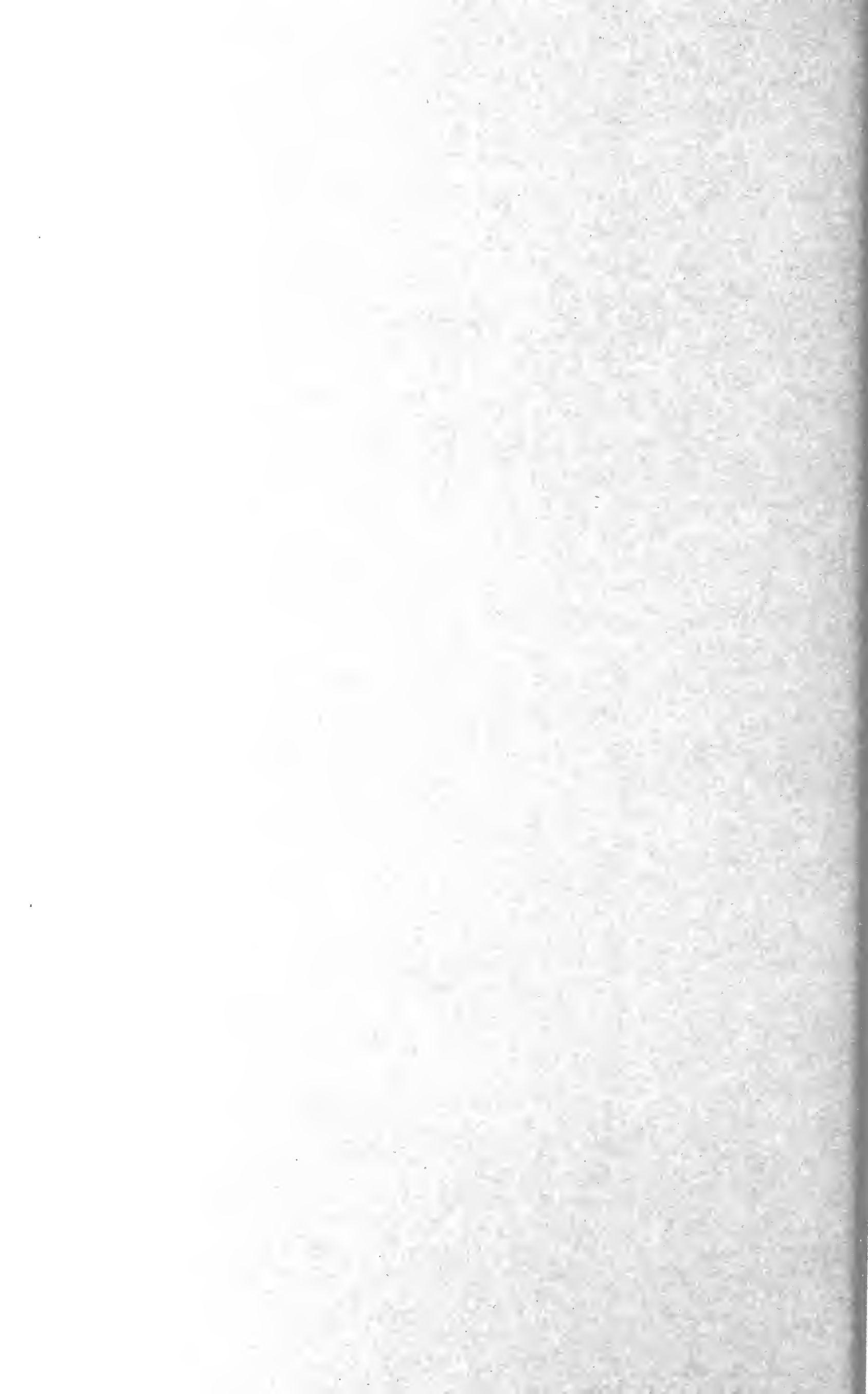
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THE VEGETATION AND PHYTOGEOGRAPHY OF SABLE ISLAND, NOVA SCOTIA

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Abstract

Sable Island is a crescent-shaped emergent sandbar 42.5 km long, 1.4 km wide, occupying 3400 ha and located about 160 km east of the Nova Scotia mainland. A 1981 field survey and literature search were undertaken to provide a more complete information base on vegetation and floristics of the island. The field work included the description and mapping of plant communities, soil and water analysis, and collection of plant specimens with a view to producing a current annotated list of vascular plants. Literature searches included the documentation of historical descriptions of vegetation, terrain, floristic composition, and phytogeography.

Since at least 1505, the island has been treeless with low herb and shrub cover, and with erosion and shifting sand. Substrates are alkaline or acidic sand, with very little organic matter and low levels of nutrients. Wetland and aquatic habitats are either acidic or brackish with high sodium levels. The climate is maritime and moderate, with relatively little snow cover, high average wind speeds, and less sunshine than on mainland sites.

It is possible that a larger precursor of Sable Island was unglaciated during the Wisconsin epoch, and acted as a refugium for flora and fauna. Introductions of livestock and settlement have undoubtedly influenced the vegetation, but the effects are not easily assessed. Other biotic factors including the occurrence of bird colonies and pollinator availability have probably also affected floristic composition. Erosion has apparently increased recently, and both the size of the island and the total area of vegetation have decreased. Periodic connections between many inland pools and the sea have resulted in changes favouring halophytes and/or depauperate vegetation.

The vegetated terrain of the island accounts for approximately 40% of the land surface of 3425 ha. Several distinctive plant communities were identified, described, and mapped. These include i) a community dominated by *Honckenya peploides* comprising 0.6% of the island surface; ii) Marram-Forb grasslands dominated by *Ammophila breviligulata*, *Lathyrus maritimus*, *Achillea lanulosa*, and *Solidago sempervirens* comprising 8.7% of the island; iii) sparse grasslands, comprising 22.5%, within which two types are readily discernable. Marram Grasslands are dominated by *Ammophila breviligulata*, while Marram-Fescue grasslands also have abundant *Anaphalis margaritacea*, *Festuca rubra*, *Fragaria virginiana*, *Myrica pensylvanica* and *Rosa virginiana*; iv) Shrub Heath vegetation is dominated by *Empetrum nigrum*, *Juniperus communis*, *Myrica pensylvanica*, *Rosa virginiana*, and *Vaccinium angustifolium*, with many other species as well as lichens and bryophytes also present; and v) Cranberry Heath communities dominated by *Vaccinium macrocarpon*. The two heath communities together cover 4.3% of the island. In terms of plant association these Heath communities appear quite different from mainland communities, and they deserve protection and further study.

Freshwater pools with pH 5.0-5.7 have *Potamogeton epihydrus*, *P. oblongus*, *Polygonum hydro-piperoides* var. *psilostachyum*, *Myriophyllum tenellum*, and *Fontinalis sullivantii*. Such ponds cover 0.8% of the island. Pond edge communities are dominated by a variety of forbs, graminoids and bryophytes. Brackish ponds cover 1.5% of the island surface. Characteristic submersed species include *Zostera marina*, *Ruppia maritima* and *Potamogeton pectinatus*. Shallower water and edges have dense swards of *Eleocharis parvula*. Various halophytic forbs and graminoids occur along the pool edges.

Circumstantial evidence based largely on the locations of different vegetation types, and patterns of sand deposition, suggests a succession from Marram-dominated communities to Marram-Fescue, and with lessening sand accumulation to Shrub Heath. This sere can be reversed by increased rates of sand deposition. It also appears that there is a succession from brackish to freshwater vegetation in ponds without recent influence of the sea.

Approximately 63% of the native island flora of 154 is characteristic of the general region, while 16% is boreal in affinity, 5% is southern, 2% is amphi-atlantic, and 9% is restricted. Three taxa are endemic. Of the restricted taxa, two (*Epilobium nesophilum* var. *sabulonense* and *Lathyrus palustris* var. *retusus*) were not found during our survey and are apparently extinct, while three (*Bartonia paniculata* var. *sabulonensis*, *Calopogon tuberosus* var. *latifolius*, and *Juncus pelocarpus* var. *sabulonense*) are rare on the island. Seventeen of the 19 significant (restricted or rare) taxa occur in vegetation types that together account for 5.8% of the island surface, including the heaths and freshwater pools.

The annotated list provides information on habitat, status and distribution on the island for 154 native and 69 introduced taxa. Comparison is provided with four previous botanical surveys.

L'île de Sable est une barre de sable émergente, en forme de croissant, d'une longueur de 42.5 km et d'une largeur de 1.4 km. Sa superficie est de 3400 ha et elle est située à environ 160 km à l'est de la côte de la Nouvelle-Ecosse. En 1981, une étude de terrain et une recherche bibliographique ont été entreprises dans le but d'obtenir une information de base plus complète concernant la végétation et la flore de l'île. Le travail de terrain a inclut la description et la cartographie des communautés de plantes, des analyses d'eau et du sol ainsi que la collecte de spécimens végétaux dans le but de produire une liste commentée des plantes vasculaires. Les recherches bibliographiques ont englobé la documentation historique décrivant la végétation, le terrain, la composition de la flore et la phytogéographie.

Depuis au moins 1505, l'île a été dépourvue d'arbres et caractérisée par un faible couvert végétal constitué d'herbe et d'arbustes, de l'érosion et des déplacements de sable. Les substrats sont des sables alcalins ou acides, pauvres en matière organique et à faible teneur en sels nutritifs. Les marécages et les habitats aquatiques sont ou bien acides ou soumates avec des concentrations en sodium élevées. Le climat est maritime et modéré avec un faible couvert de neige, des vitesses moyennes de vent élevées et avec moins d'émouillage que sur le continent.

Il est possible que, durant l'ère géologique du Wisconsin, un précurseur de l'île de Sable, de plus grande dimension, ne subit pas l'effet de la glaciation et servit de refuge à la flore et à la faune. La colonisation et l'introduction de chiptels ont sans doute influencé la végétation mais leurs effets ne sont pas faciles à déterminer. D'autres facteurs biotiques tel que la présence de colonies d'oiseaux et d'agents pollinisateurs ont probablement aussi influencé la composition floristique. L'érosion s'est apparemment accrue récemment et la taille de l'île ainsi que la surface totale du couvert végétal ont diminués. Des connections périodiques entre plusieurs étangs situés à l'intérieur de l'île et l'océan ont provoqué des changements favorisant les plantes halophytes et/ou un appauvrissement de la végétation.

Le couvert végétal de l'île représente environ 40% de la surface des terres (3425 ha). Plusieurs communautés distinctes de plantes furent identifiées, décrites et cartographiées. Celles-ci incluent: i) une communauté dominée par *Honckenya peploides* représentant 0.6% de la surface de l'île; ii) des prairies de type Marram-Ford dominées par *Ammophila breviligulata*, *Lathyrus maritimus*, *Achillea lanulosa*, et *Solidago sempervirens* représentant 8.7% de la surface de l'île; iii) des prairies clairsemées, comptant pour 25.5% de la surface, parmi lesquelles deux types peuvent être reconnus. Les prairies sont à oyat (Marram) dominées par *Ammophila breviligulata*, alors que dans les prairies à oyat et fétuque (Marram-Fescue) *Anaphalis margaritacea*, *Festuca rubra*, *Fragaria virginiana*, *Myrica pensylvanica* and *Rosa virginiana*; iv) La végétation arbustive des landes (Shrub Heath) est dominée par *Empetrum nigrum*, *Juniperus communis*, *Myrica pensylvanica*, *Rosa virginiana*, et *Vaccinium angustifolium*, avec plusieurs autres espèces ainsi que des lichens et des bryophytes; et v) Les communautés de landes à airelles (Cranberry Heath) sont dominées par *Vaccinium macrocarpon*. Ces deux communautés de lande combinées couvrent 4.3% de l'île. Du point de vue des associations de plantes, ces communautés diffèrent passablement de celles que se retrouvent sur le continent et elles méritent d'être protégées et étudiées plus à fond.

Potamogeton epihydrus, *P. oblongus*, *Polygonum hydropiperoides* var. *psilostachyum*, *Myriophyllum tenellum*, et *Fontinalis sullivantii* se retrouvent dans des étangs dont le pH varie de S.O. à 5.7. Ces étangs couvrent 0.8% de l'île. Les communautés des rives de ces étangs sont dominées par une variété de plantes herbacées de glaminées et de bryophytes. Les étangs saumâtres couvrent 1.5% de la surface de l'île. Les espèces submergées caractéristiques sont *Zostera marina*, *Ruppia maritima* et *Potamogeton pectinatus*. Les eaux peu profondes et les rives sont densément recouvertes d'*Eleocharis parvula*. On retrouve aussi le long des rives des étangs, une variété de plantes herbacées et graminées halophytes.

Des évidences indirectes basées sur la localisation de différents types de végétations et les patrons de dépôts du sable, suggèrent une succession des communautés dominées par le oyat (Marram) vois des communautés dominées par le oyat et la fétuque (Marram-Fescue), et avec une diminution des dépôts de sable vers les landes arbustives (Shrub Heath). Cette succession peut être renversée par une augmentation de la vitesse de dépôt du sable. Dans les étangs qui ne sont pas influencés directement par la mer, il semble y avoir une succession d'une végétation caractéristique des eaux saumâtres vers une végétation d'eau douce.

Approximativement 63% des 153 espèces endémiques de la flore de l'île sont caractéristiques de toute la région, 16% ont une affinité avec la flore boréale, 5% avec la végétation du sud, 2% est "amphi-atlantique" et 9% sont restreintes à l'île. Trois taxons sont endémiques. Des taxons restreints, deux (*Epilobium nesophilum* var. *sabulonense* et *Lathyrus palustris* var. *retusus*) ne furent pas trouvés lors de notre étude et sont apparemment éteints, alors que trois autres (*Bartonia paniculata* var. *sabulonensis*, *Calopogon tuberosus* var. *latifolius*, et *Juncus pelocarpus* var. *sabulonense*) sont rares dans l'île. Dix-sept des dix-neuf taxons importants (restreints ou rares) se retrouvent dans des types de végétations qui dans l'ensemble représentent 5.8% de la surface de l'île, en incluant les landes et les étangs d'eau douce.

Une liste commentée fournit de l'information sur l'habitat, le statut et la distribution, dans l'île des 154 taxons indigènes et 69 taxons introduits. Une comparaison avec quatre études botaniques antérieures est incluse.

INTRODUCTION

Sable Island is a partially-vegetated emergent sandbar, located at ca. 44°N and 60°W, ca. 160 km east of the Nova Scotia mainland. The island is part of a much larger, shallow, submerged sand bank. Sable Island presently has a length of ca. 42.5 km, a maximum width of 1.4 km, a surface area of 3400 ha, inland freshwater and brackish ponds totalling some 38 ha (not including Wallace Lake), and vegetated terrain comprising some 1300 ha, or 39% of the island's surface area.

The first botanist to collect plants on Sable Island was Macoun in 1899. He was followed by Gussow in 1911, St. John in 1913, Erskine in 1953, Keddy in 1975, and the present authors in 1981. Species lists were published as a result of some of these surveys (St. John 1921; Erskine 1953; Keddy 1975). Macoun (1900) did mention a collection of 191 species, but a list was not included in the article. Some of Macoun's Sable Island collections are noted later (Macoun 1901). Although the lists of Gussow and Macoun were unpublished, St. John (1921) apparently corresponded with both of them and included their records in his compilation. St. John's list was well annotated and included descriptions (and illustrations) of new taxa (see Chapter 5), as well as an excellent historical and ecological account making it the classic work on the flora and history of the island. St. John's annotated list appears to have provided the basis for separation of the Macoun and Gussow reports (Erskine 1953).

The floristic surveys of Macoun, Gussow, St. John, Erskine, and Keddy are supported by specimen vouchers, and only Gussow's list, based on miscellaneous collections in DAO (See Holmgren *et al.* 1981 for herbarium acronyms) was not fully supported. Specimens supporting Macoun's work are in CAN and MTMG, those of St. John in GH, those of Erskine in NSPM and DAO, those of Keddy at CAN, and ours are at DAO and MICH.

The vegetation of Sable Island was described generally by St. John (1921) and somewhat more briefly by Erskine (1953). Keddy (1975) made a detailed qualitative (species lists) survey of the vegetation of ponds near No. 3 Life Saving Station with a view to establishing the status of certain endemic taxa. McLaren (1968, 1972) and Welch (1975) published maps of the vegetation of the island. The map of Welch was relatively detailed and included the major plant communities, although the species composition was not described in detail (see also Stobo & McLaren 1975).

This previous botanical work on Sable Island provides a good background of botanical information, but it is nevertheless lacking in several respects. There has never been a detailed quantitative description of the plant communities. The available lists contain names that are out-of-date, and they require nomenclatural updating. Furthermore, the previous lists give little indication of the status, habitat or distribution of various taxa on the island. Various other aspects such as the factors affecting floristic composition, phytogeography, and rare and restricted taxa are also in need of more extensive discussion. By addressing all of these topics, we intend to provide a more complete information base on the vegetation and floristics of Sable Island.

Most of the information included here was collected during our field survey of 14-26 August 1981, with some additional work in 1982 and 1983. Preliminary reports have appeared (Freedman & Catling 1982; Freedman, Catling & Lucas 1982) and some of our information has been included in environmental impact studies conducted for Mobil Oil Ltd.

Methods

(a) *Soil Chemical Analysis*

Duplicate surface soil (0-5 cm) samples were collected at each of the terrestrial plant communities that we described quantitatively. These samples were combined by site, air-dried, sieved at 20 mesh, well-mixed, and then submitted for analysis to the Soils Lab, Soils and Crop Branch, Nova Scotia Department of Agriculture, Truro. The various analytical methods used were as follows:

- i) *Organic Matter*. Organic matter was measured by loss on ignition at 430°C of a 2.00 g soil sample. Combustions were made in a Luidbergh furnace.
- ii) *pH*. pH was measured in a 1:1 soil:water mixture. This was allowed to equilibrate for 30 min., and the concentration of H⁺ was then measured with a Corning 130 digital pH meter.
- iii) *Total Nitrogen, Phosphorus, Potassium, Calcium, and Magnesium*. Soil samples of 0.50 g were digested in a hot sulfuric acid-hydrogen peroxide mixture. Nitrogen and phosphorus concentrations were measured using an autoanalyzer. Potassium, calcium, and magnesium concentrations were measured by flame atomic absorption spectrophotometry.
- iv) *Exchangeable Potassium, Magnesium, and Calcium*. Soil samples of 2.5 g were shaken for 15 min. in N ammonium acetate (pH 5). The soil:extractant ratio was 1:25. The concentrations of these cations were then measured by flame atomic absorption spectrophotometry.
- v) *Available Phosphorus*. Soil samples of 2.5 g were shaken for 1 min. in 25 ml of 0.05 N ammonium fluoride and 0.1 N hydrochloric acid. Soluble phosphate was then measured using a Technicon Auto Analyzer.
- vi) *Water-soluble Nitrate and Ammonium*. Soil samples of 5 g were shaken for 30 min. in distilled water, and the nitrate and ammonium concentrations were then analyzed using Corning ion-specific electrodes.

(b) *Water Chemical Analysis*

All analytical techniques used in water analysis are described by Horwitz (1975). pH was measured directly using a Beckman Zeromatic II pH meter and conductivity was measured using a conductivity bridge. Sodium and calcium were determined by flame atomic absorption spectrophotometry. Chloride was measured by sodium thiosulphate titration.

(c) *Description of Plant Communities*

All field work was carried out over August 15-25, 1981. The various terrestrial plant communities of the island were subjectively divided into seven categories, on the basis of distinctive occurrences of dominant species or groups of species. These seven terrestrial communities were: Sandwort, Marram-Forb, Marram, Marram-Fescue, Shrub Heath, Cranberry Heath, and Pongedge Herbaceous. Additional aquatic plant communities occurred in or at the edges of the fresh and brackish-water ponds.

Quantitative descriptions were made at a total of 27 sites for the first six of the above terrestrial communities (Fig. 1). The seventh terrestrial community (Pongedge Herbaceous) and the aquatic communities were not sampled quantitatively due to their very heterogenous nature, but they were qualitatively described in terms of relative abundance and species composition.

Quantitative data were collected using 20 random placements per site of a 0.5 x 0.5 m quadrat. Visual estimations were made of the species-specific cover, and an attempt was made to take into account foliage overlap (i.e. leaf area index), so that total cover was more than 100% in some cases. Using these field data, calculations

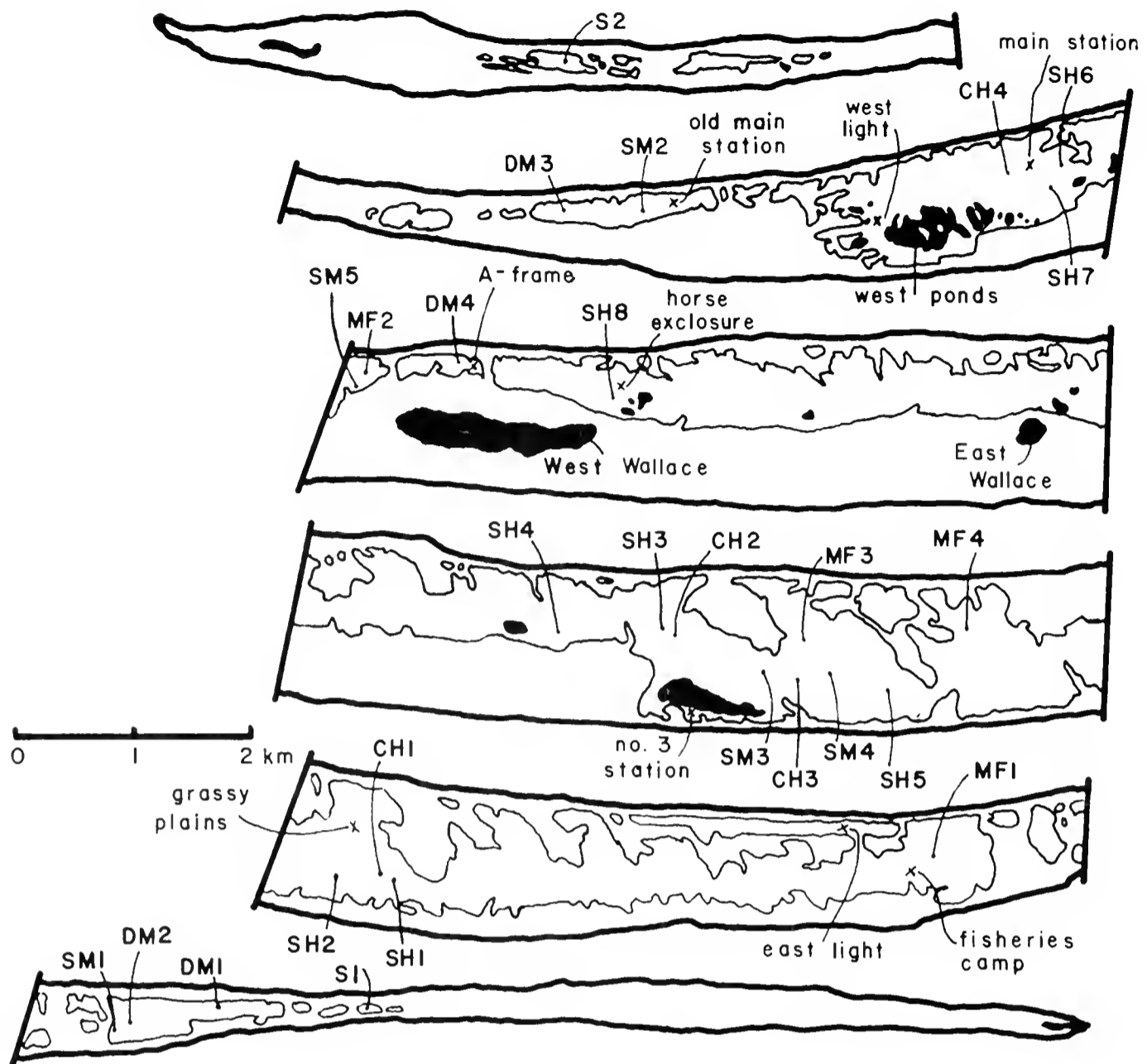


Fig 1. Locations of sites on Sable Island where quantitative descriptions of plant communities were made.

were made for each site of total and species-specific cover ($\%$, $\bar{X} \pm S.E.$), relative cover ($\%$), and frequency ($\%$) of each species, and community richness (\bar{X} species/quadrat) and diversity ($-\sum p_i \ln p_i$, where p_i = relative frequency). These methods are summarized in various standard references (Kershaw 1964; Goldsmith & Harrison 1976; Smith 1980).

(d) Mapping of Plant Communities

Plant community mapping was done using colour 1:20,000 scale photographs of Sable Island. The transect for these was flown at 3050 m above sea level on June 19, 1981, and the photos were taken with a Wild RC-8 camera fitted with a 15.2 cm lens. Mapping was done by tracing recognizable community boundaries onto clear plastic overlays under a binocular microscope or a stereoscope. This mapping process was aided by ground truthing done over August 15-25, 1981, in order to establish the locations of known community types for later comparison with air-photo interpretations. Not all community types could be recognized on the air-photos, so that the mapping was limited to the following vegetation types: Dense Grasslands (equivalent to the Marram-Forb community type); Sparse Grasslands (incorporating both the Marram and the Marram-Fescue communities); Heath (in-

corporating both the Shrub Heath and the Cranberry Heath communities); Pond-edge Herbaceous; Sandwort; Brackish Ponds; Freshwater Ponds; and Unvegetated. This is a somewhat more comprehensive treatment than that used in an earlier vegetation map of Sable Island (Welch 1975). The areas of each of these vegetation types were determined by cutting them out of the plastic overlays with fine scissors or scalpels, weighing the pieces, calculating area in cm² from the constant ratio of area: weight of the plastic overlays, and then converting these to terrain area by correcting for the 1:20,000 linear scale of the airphotos.

(e) *Annotated List*

Specimens documenting our list are at DAO and MICH and were collected from 14-26 August 1981 with a few additional collections in 1982. All identifications were made using the most recent available literature. Information from previous lists is incorporated. In some cases where names are brought up-to-date, the older generic or species name used in reference to the flora is listed in brackets following the current species name.

1. *EARLY DOCUMENTATION OF VEGETATION AND TERRAIN*

Many of the early explorers and other travellers recorded their impressions of Sable Island. The earliest probable reference to the island was contained in an ancient Icelandic saga describing the voyage of Biorn Heriulfson in 986 who, having passed Newfoundland and Nova Scotia (Helluland and Markland), came in sight of a barren sandy island (Oxley 1886). Much later, a Portuguese chart of 1505 recorded Sable Island, known to them as Santa Crus Island, and which was stocked with cattle and swine (Oxley 1886). Other early references were by the Frenchman Baron de Lery in 1538, and the Englishman Sir Humphry Gilbert in 1583 (Oxley 1886).

Later, Des Barres (1776-77) described Sable Island as having a length of some 45 km, a width of 2.4 km, and a large inland lake (Wallace Lake) having a length of 22 km. He named several distinctive topographic features, including the Naked Sand Hills, Mount Knight, Evans Cliff, Mount Luttrell, the Vale of Misery, and Ram Head. He described the island as having a ". . . broken face, and hove up in little hills, knobs, and cliffs, wildly heaped together, within which are hollows and ponds of freshwater, the skirts of which abound with cranberries, blueberries, juniper, etc.'" These place names and brief descriptions indicate that the sand dunes were shifting and dynamic at those times, as they are today, and that plant communities that exist today were also present in the late 1700's.

Morris (1802) provided some relatively detailed descriptions of the vegetation of Sable Island: ". . . the grass in general is tall thick and very strong. Three kinds—one spindling and soft, one long and flat-leaved also soft in some places thick, this I observed the sheep delight in along the valleys. From the lake westward are a variety mixed with the grass, bayberries, blueberries, strawberries, wild tansey, wild parsnip, running blackberry, Prince's pine . . . the soil in the valleys are about 4 inches thick, blackish mixed with black sand and decayed vegetables. The eastern valleys . . . horse paths in all directions, in some of those valleys lyes no end of cranberries . . . about the east end of the lake there is considerable clover grass, I expect the white kind. The grass at the east end is in general thicker and stouter than at the west end, but the peas are scarce . . . the lake or great pond is about 1/2 mile wide at the greatest width . . . and what I have sounded 1 to 4 fathoms deep. There is an abundance of manure around the pond, especially at the west end decayed eel and sea grass. In the lake there is a thick eel grass on the bottom which in high winds in the autumn comes on shore at the head of the lake. The water is shoal, the bottom is black rank and greasy composition, about 3 inches . . . I expect this will make good manure."

At about the same time Blunt (1806) described the face of Sable Island as broken, with little hills, knobs, and cliffs wildly heaped together. He also mentioned the presence of freshwater ponds, and noted that the "... south shore is, between the cliffs, so low that the sea breaks quite over in many places when the wind blows on the island." This obviously refers to the occurrence of eroded blow-outs, through which seawaters could flood inland during storm surges. Blunt (1806) described the Naked Sand Hills as being some 45 m high, and he mentioned another hill (the Ram's Head) that was higher (Scott (1902) referred to hills of up to 61 m in height in 1808). Today, the highest point on the island is only ca. 25 m (Welch 1975).

Other relatively detailed descriptions of the character of Sable Island were made by Gilpin (1858). He described the view from a high vantage point: "There it all lies spread like a map at my feet,—grassy hill and sandy valley fading away into the distance." He noted the presence of 30-40 species of "shrubs and plants". He also described the vegetation: "... tall coarse grasses cover the surface of the ground, alternating with sandy barriers and snowy peaks of blown sand ... the wild rose, blue lily, and wild pea enamel the valleys. Strawberries, blueberries, and cranberries are in abundance ... measured by bucketsful ... as autumn heats the luxuriant green, the tall, mallow, gay golden rods and wild China asters are swept by the heaving gales."

Gilpin (1858) also described the dynamic nature of the sand dunes: "... there are those still alive who once filled a happy hour where now the sea breaks five miles from dry land. The abrupt sandcliff rocks to a fall from the unceasing beat of the waves at its feet till a more than ordinary hurricane sweeps it into the lake or spreads it into a shallow bar. By this process five or six miles have gone at the west end, and changes the same are still going on. The winds, too, are perpetually sweeping the naked sand-hills into the lake or forming fantastic cones from the loose and shifting sand."

Similar observations were made at about the same time by Bayfield (1860). He described the topography of Sable Island as follows: "Sable Island seen from the north, at a distance of 9 to 10 miles presents the appearance of a long range of sand-hills, some of which are very white ... in some parts it is wholly or partially covered with grass, in others scooped out by the winds into crater-shaped hollows, or thrown up into sand-hills, not exceeding the height of 75 feet [23 m] above high water. Between these ridges a long pond, named Salt-water Lake [Wallace Lake], said to be gradually filling with blown sand, but still in some parts 12 feet deep, extends from the west end to the distance of 11 miles, and a low valley continues from it 6 1/2 miles more to the north-east end of the island ... many of the sand-hills are seen to have been partly removed by the waves, so as to have formed steep cliffs next to the sea. In other parts, they are covered by grass, and defended by a broad beach ... " Various other mid to late 19th century authors described the instability of Sable Island, and recorded changes in the length of the island, usually resulting from the removal of stretches of exposed sandbars at the west end (e.g. Howe 1850; Halleck 1866; MacDonald 1886).

Although these early reports clearly suggest that the island has changed little in character (although perhaps much in size and position) during historical times, the fact remains that no information is available for the period preceding the release of livestock in 1505.

2. FACTORS AFFECTING FLORISTIC COMPOSITION

Species and infraspecific taxa to a greater or lesser extent, are adapted to specific ecological conditions, both biotic and abiotic. The presence or absence of a particular species may be due to various interacting factors. Mainly, limiting factors include physical and chemical properties of the soil; chemical properties of water

and climate are discussed below. Other factors such as geological history (which involves migration, dispersal and isolation) and catastrophic events (including erosion, deposition, flooding and human impacts) are also briefly considered. Although these factors may not provide a complete explanation, they aid a great deal in gaining an understanding of the nature of the vegetation of Sable Island.

(a) *Soil and Water*

Both the chemical and physical composition of soil and the chemical composition of water affect floristic composition, since different taxa of plants are frequently adapted to different substrates. The chemical composition of soils collected from six terrestrial plant communities on Sable Island is summarized in Table I. These soils are of very poor nutritive quality, since they contain small quantities of organic matter and major nutrients. The best developed soils occur in the heath communities, but even these contain less than 4% organic matter within the surface 5 cm, and they have virtually no profile development below this depth.

Table I Chemical characteristics of surface soils (0-5 cm) on Sable Island.¹

Plant Community	pH	Organic Matter (%)	Total N (ppm)	Total P (ppm)	Total K (ppm)	Total Ca (ppm)	Total Mg (ppm)	NO ₃ -N (ppm)	NH ₄ -N (ppm)	Avail. P (ppm)	Exch. K (ppm)	Exch. Ca (ppm)	Exch. Mg (ppm)
Shrub Heath	5.7	2.5	1020	60	440	800	380	1.6	21	7.1	45	380	160
		1.8	410	20	210	160	80	0.7	14	3.0	22	160	71
Cranberry Heath	4.9	4.0	1020	62	600	790	440	2.0	10	9.2	28	178	105
		2.7	360	20	120	360	260	1.5	2	4.7	10	121	93
Marram-Forb	5.4	0.6	580	60	460	920	460	3.9	7	8.6	15	63	30
		0.2	15	30	150	360	180	1.4	5	1.1	1	18	4
Sparse Marram	6.0	0.5	450	40	350	580	280	2.2	7	7.8	11	41	19
		0.1	60	20	130	60	15	1.7	1	0.0	5	15	11
Marram-Fescue	5.4	0.8	560	40	280	590	280	2.5	9	5.9	14	84	36
		0.2	110	23	80	160	80	1.0	2	1.4	3	46	18
Sandwort	6.0	0.05	450	45	600	720	400	8.5	10	9.8	19	51	31
		0.03	150	7	280	90	30	1.7	1	2.8	2	1	1

¹ ±SD of five replicate samples per community type.

The shrub heath soils are relatively moist due to their higher content of organic matter. The Cranberry heath soils are also moist due to their low elevation. Both of these soils are relatively acid and nutrient-poor. The soils of the various other terrestrial communities are almost purely inorganic, and they tend to be drier.

With respect to mineralogy, the soils are comprised almost entirely of sand-sized particles, with ca. 84% of the bulk consisting of particles between 0.25 and 0.5 mm in diameter, and 99.8% between 0.13 and 1.0 mm (Willmore & Tolmie 1956). These sand grains are highly rounded in contour, as a result of long-term scouring by wind and wave action (Willmore & Tolmie 1956).

Aquatic and wetland habitats on Sable Island vary greatly in pH, sodium and chloride concentration (Table II). Lower pH, sodium, and chloride are characteristic of inland freshwater pools originating from rain and ground water table. Higher pH, sodium, and chloride are characteristic of brackish pools that are influenced by seawater, which can intrude as a result of storm surges. It is well known that differences between fresh and brackish water can create different plant associations (e.g. Moyle 1945).

Table II Chemical analysis of selected ponds on Sable Island

	pH	Na(mg/l)	Conductivity (µmhos)
Fresh Pools	5.0-7.3	13-38	76-320
Brackish Pools	27.1	1840-2100	1640

Table III Climatic data for Sable Island, compared with Halifax and Truro, N.S.¹

	Sable Island	Halifax	Truro
Temp. (°C) max.	10.1	11.5	10.9
Temp. (°C) min.	5.1	3.6	0.0
Temp. (°C) mean	7.7	7.6	5.5
Mean Precipitation (mm)	1270	1319	1101
Mean Snowfall (cm)	127.8	210.8	243.1
Sun (mean no. of hours)	1459	1883	1749
Average Wind Speed (km hr ⁻¹)	25.8	18.2	14.1

¹Data from Atmospheric Environment Service, Environment Canada.

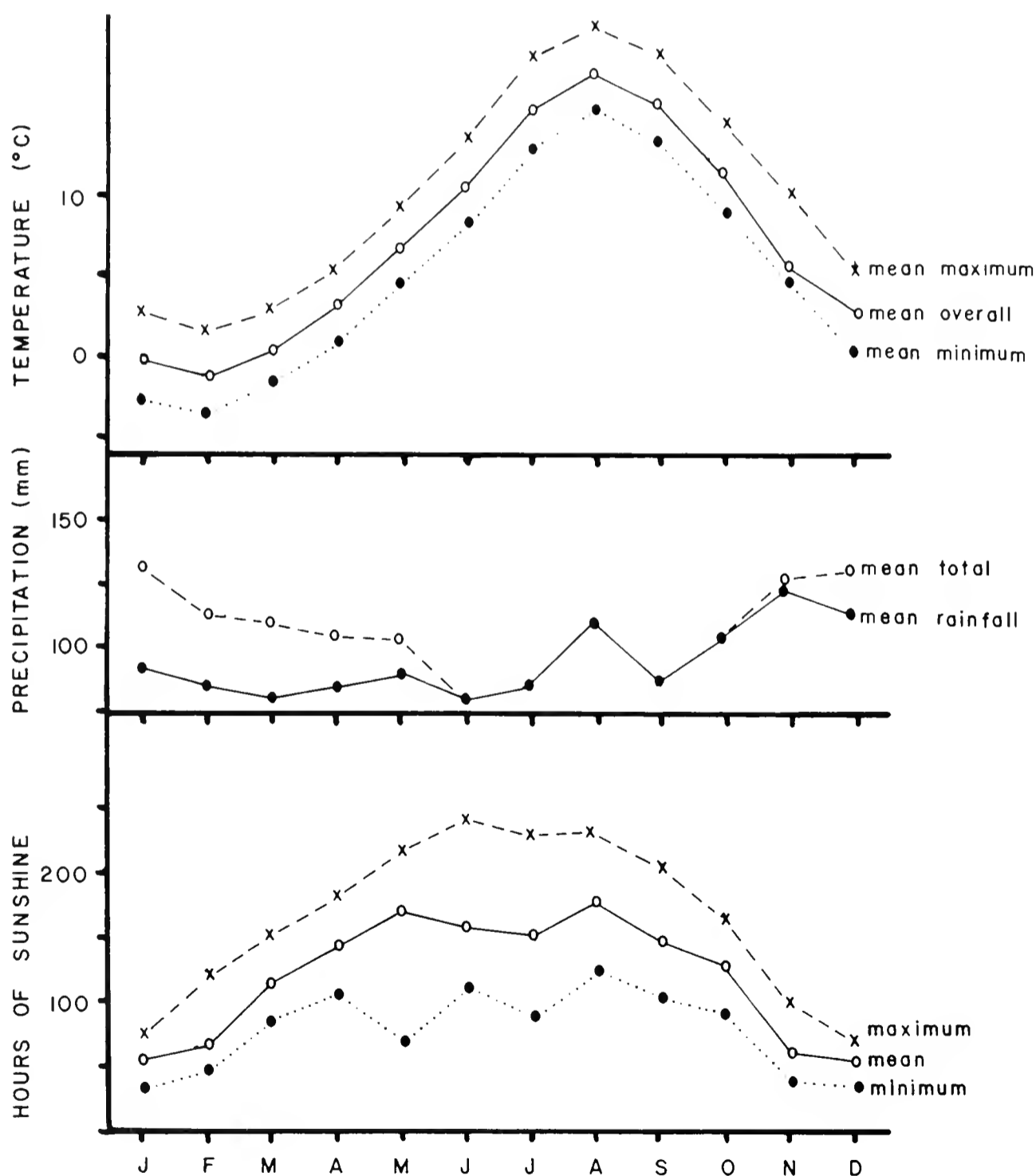


Fig 2. The seasonal course of temperature, precipitation, and sunshine at Sable Island. Data are from the Atmospheric Environment Service, Environment Canada.

(b) *Climate*

The climate of Sable Island is maritime and moderate for all variables except windspeed, as compared (Table III) with nearby locations that are coastal maritime (e.g. Halifax) or continental (e.g. Truro). The relatively moderate temperature regime includes a lower mean maximum, a higher mean minimum, and a similar or slightly higher mean annual temperature than either Truro or Halifax (Table III, Fig. 2). Mean precipitation is intermediate between that of Halifax and Truro, but a relatively small quantity is received as snow (Table III, Fig. 2).

The climatic characteristics of Sable Island have undoubtedly influenced the development of its vegetation. For example, the relatively lower temperatures during the growing season simulate the temperature regime to which certain boreal plant species are adapted. On the other hand, the higher minimum temperatures and less frequent frosts correspond to conditions in continental areas at lower latitudes, and are thus conducive to the presence of plants having a more southerly distribution. Thus, the moderate maritime climate of Sable and other islands may often result in an intermingling of typically northern and typically southern elements of flora and fauna (see Section 4). In addition, the relatively high average wind speeds (Table III) of Sable Island have an abrasive and desiccating effect, with a pronounced influence on floristic composition. Recent evidence for this is the fact that of the thousands of trees and shrubs planted on the islands (see Section 2(d)), the few survivors occurred in very protected places.

(c) *Recent Geological History*

Prests' (1970) glacial map of Canada indicates that Sable Island was glaciated, and the presence of subsea moraines suggests that glaciation extended well onto the present Nova Scotia shelf (James & Stanley 1968). However, Matthew (1979) has speculated that Sable Island may be a remnant of a broad emergent area of continental shelf that was unglaciated, although it may have been very near to the glacial edge. During the glacial period the emerged portion of the Nova Scotian shelf may have approximated the present 100 m depth contour, which would correspond to an island 240 km long and 80 km wide (Terasmae & Mott 1971).

Studies of existing ice-marginal sites in Iceland and elsewhere (Lindroth 1970) suggest that plants could have occurred quite near to the late Wisconsin glacial margins. Proof that Sable Island was a glacial refugium requires the discovery of fossil material dated from the glacial period. Since the oldest fossil material from Sable Island has been dated at about the time of deglaciation, *i.e.* 11,000 years ago, there is no paleoecological proof of the refugium theory (James & Stanley 1968; Terasmae & Mott 1971). However, the lack of older fossils does not require that the refugium concept be rejected. Older fossils may still be found, but even if they are not, their absence may have been caused by the eastward migration of the island over geological time (Terasmae & Mott 1971) which could have prevented older fossil material from accumulating. Thus, the possibility remains that there has been a continuity of land surface, and of habitats available on Sable Island, and its much larger pre- and postglacial precursors, which could have acted as a refugium. Both Howden (1975, discussing beetles) and Roland and Smith (1969, discussing vascular plants) considered a refugium on the Sable Island bank to be a reasonable possibility. The evidence, both for and against, is summarized by Holland (1981). Whether a result of evolution over the past 10,000 years or representing a relict from a much earlier time, the fact remains that there is some unique variation on Sable Island, in both flora and fauna.

An early postglacial climatic warm period is thought to have influenced Sable Island as evidenced by the presence of paleosoil and a fossil fauna characteristic of a

warmer climate than exists at present on the island (Medcof *et al.* 1965). However, the palynological work of Terasmae and Mott (1971) suggests that the vegetation on the island over the last 11,000 years has always been very similar to that which exists now. The lack of woody peat on the island and palynological evidence suggests that widespread forests did not exist, and this is also suggested by the earliest historical accounts (see section 1, also St. John 1921, p. 33). The increasing penetration of the Labrador current along the Atlantic coast resulted in gradual cooling (Holland 1981), and by 6,000 B.P. the Atlantic coastline of Nova Scotia was washed by summer-cold water.

(d) *Livestock, Cultivation and Settlement*

The grazing of pigs, cattle, sheep, or horses can be a significant factor determining the composition of plant communities. Likewise, cultivation of the soil and the effects of settlement (including buildings and waste disposal) can have effects on vegetation. These factors have influenced the floristic composition of Sable Island for several hundred years, as is indicated by the following historical account.

Various old maps and charts indicate that by the early 1500's Sable Island was familiar to Old World fishermen and traders, including the Spanish, Portuguese, and later, the French (Patterson 1894). These travellers had a policy of introducing livestock to offshore islands of the Americas (Campbell 1974), and in 1552 "... did put into this same island neat (sic) and swine to breed, which were since exceedingly multiplied." (Patterson 1894). The 1552 introductions were reported by a Portuguese fisherman to Sir Humphrey Gilbert's expedition of 1583. Gilbert's flagship was subsequently wrecked on Sable Island, and the survivors reported that the introduced cattle had greatly multiplied. There were no reports of horses at that time (Patterson 1894).

Between 1598 and 1603, French settlers were placed on Sable Island by de la Roche (St. John 1921). They lived off the land, presumably exploiting the Portuguese cattle and growing vegetables, and in addition they were supplied once a year with wine and clothing from the homeland. The survivors were evacuated in 1603 (Campbell 1974), although some of them apparently returned for a brief time to continue a trade in furs (Gilpin 1858), probably seal and perhaps the occasionally reported black fox.

In 1633, John Rose of Boston, returning from Sable Island following a shipwreck, reported foxes and 800 head of cattle, which survived by grazing on pastures of dune grass and beach pea (Halleck 1866; Patterson 1894). His reports prompted an exploitation of the stock by Acadians and New Englanders, and by 1668 Nicholas Denys reported that there was no livestock left on Sable Island (Christie 1980).

The return of livestock to Sable Island and the commencement of cultivation appears to have come with settlers sent to the island by le Mercier in 1738. Horses, sheep, cattle, and pigs were imported, and for fifteen years the settlers farmed and raised livestock. The le Mercier venture was abandoned in 1753, but livestock was left on the island (Campbell 1974).

Between 1753 and 1801 several attempts were made to live on Sable Island. Finally, the rumoured presence of wreckers who lured helpless ships onto the shoals by showing false navigation lights, the continuing cattle raids, and several high-profile shipwrecks prompted the establishment of life-saving stations by the Nova Scotia government (Campbell 1974). This began the settlement and agricultural exploitation of the island that continued until the mid-1900's. During this period livestock was kept, the feral horse population was controlled, subsistence farming was carried out, and numerous introductions of flora and fauna occurred.



Fig 3. A gang of 11 wild horses grazing on Beach Pea (*Lathyrus maritimus*) and Marram (*Ammophila breviligulata*) near Main Station.



Fig 4. A decumbent Scots Pine (*Pinus sylvestris*). This one is a recent planting and not a survivor of the great afforestation attempt of 1901.

The mandate of the government-appointed superintendent of the island was to “. . . carefully preserve and diligently encourage the growth and increase of all cattle, horses, and other livestock found on the island or sent by the commissioners . . . and not to suffer any to be exported upon any account or pretense whatever without license from this government first hand and obtained . . . report quality of stock and whatever measures may be useful for its preservation and increase . . .” (Morris 1802). Early reports from the superintendent stated the belief that there was sufficient forage on the island to support about 250 head of cattle, 2200 sheep, and 150 goats (Morris 1802). These predictions were probably optimistic, and they undoubtedly overestimated the carrying capacity of the island. In any case, over the years approximately 60-90 head of cattle and some sheep, hogs, and mainland horses were kept, while the feral horse population ranged between about 70 to 250 (miscellaneous superintendents’ reports on file in the Public Archives of Nova Scotia). During the summers, these animals grazed the Sable Island grasslands. In winter, the diets of the cattle and the domestic horses were supplemented by harvested hay. Island fodder mainly consisted of dune grasses and beach pea, in addition to cultivated hays. Roughly 120 tonnes of hay would be collected in the autumn, most of which was made of wild forage. To some extent, these supplies were supplemented by feed shipments from the mainland (misc. superintendents’ reports).

In addition to the cultivation of hay, some of the Sable Island terrain was used for growing vegetables for the residents. Root crops were especially successful, with a combined annual harvest of about 300 bushels of potatoes, carrots, beets, parsnips, and turnips, (Fig. 5). Each of the five stations had its own garden plot, with the largest being at main station. In total, perhaps 4 hectares were under cultivation for vegetables (misc. superintendents’ reports; Christie 1980).

The vegetable crops were raised in plots where cattle manure and eelgrass were used to enhance the tilth and nutrient content of the soils. One early report from the superintendent suggested that the muck from the bottom of Wallace Lake would make a good soil conditioner and fertilizer (Morris 1802). Drought, very wet seasons, and plagues of locusts were occasionally blamed for crop failures (Boutilier 1884-1912).

In addition to cultivated crops, wild cranberries were harvested and shipped to the mainland. Reports indicate that shipments ranging from 100 to 300 barrels of berries had been systematically harvested, cleaned, and sorted in the late autumn. The area of harvest appears to have been towards the east, possibly in the vicinity of the grassy plains (Howe 1850; Boutilier 1884-1912).

There were occasional attempts to grow exotic plants on the island, either to provide fodder or to stabilize the dunes. A tussock-forming grass was introduced from the Falkland Islands, but the attempt failed. Several plantings of trees and shrubs occurred, the most impressive of which was the great afforestation attempt of 1901, in which about 69,000 conifer seedlings of 25 species, 14,000 hardwood seedlings of 79 species, and 20 kg of pine seeds were planted, as were hundreds of shrubs and 1,000 willow cuttings (Saunders 1902, 1903). By 1913 there were only 13 surviving plants (St. John 1921; Boyce 1953).

Since no studies were ever conducted, it is impossible to know what the effects of livestock, cultivation and habitation have been. However, several authors referred to the loss of large areas of vegetation during the latter part of the 1800’s (Patterson 1894; Macoun 1901). Other studies have suggested that an accelerated destabilization of dune systems occurred during this period of intensive agriculture, and that sands from unstabilized dunes advanced over considerable areas (Patterson 1894; Willmore & Tolmie 1956; Cameron 1965; Terasmae & Mott 1971).



Fig 5. Turnips, potatoes and squash grown at Main Station, Sable Island in 1921. (Illustration from a photograph in the Thomas H. Raddall papers, Dalhousie University Archives).

The effect of the feral horses is not yet clear. However, it seems likely that excessive grazing in certain areas has increased erosion, and this would be especially important during years of peak population. Of course the horses recycle nutrients and minor disturbance probably creates habitat for certain species. Thus, the erosion damage may be fully or partly compensated for. The horse population has varied from 200 to 300 in a cyclic pattern over the past 20 years and is apparently under natural control (Lock 1971). Ongoing studies, including exclosure plots are attempting to clarify the relationship between horses, vegetation, and erosion.

The feral horses may have had other effects. Keddy (1975) suggested that the trampling and grazing of the wild horses on Sable Island has reduced the number of species which some ponds and their border areas can support. Decumbent and low-growing species are prevalent around the most used pools and aquatics are sometimes absent. In addition, differential grazing could have a very direct affect on species composition. The introduction of domestic animals which are allowed to run wild has severely impacted the vegetation of many islands, leading to both the extinction of species and habitats, and severe erosion (e.g. Melville 1979; Van der Werf 1979).

The existing vegetation of Sable Island is remarkable and valuable, but it is likely that it was even more diverse and interesting prior to its first visitation and exploitation by European man in the early 1500's.

(e) *Erosion and Deposition*

Continual erosion and deposition of sand on Sable Island probably results in relatively short-lived plant communities (as compared with mainland sites) and the island has apparently been continuously changing over the past several thousand years (St. John 1921; Terasmae & Mott 1971). There have been major changes in the island during historical times (see also Section 1 and Macoun 1900). An entire vegetated dune ridge that formerly occupied the seaward side of Wallace Lake has

been eroded away, and in one period of rapid erosion the western end of the island was disappearing at a rate of 1.5 miles/year requiring the continuing relocation of the lighthouse. MacDonald (1886) cited an instance when thousands of tons of sand were carried from the beach and strewn over the island, smothering vegetation, so that hundreds of horses died for want of food (St. John 1921, p. 20). Surveys made in the late 1700's indicate that Sable Island was 48 km long and 3 km wide, whereas now it is 32 km long and less than 1 km wide. It appears that erosion has dominated in the recent history of Sable Island.

Changes in water chemistry (see 2(a)) have been caused by the loss of dunes, with subsequent periodic connections developing between the sea and the inland pools or Wallace Lake. For example, the presently brackish pools at No. 3 station were fresh during St. John's survey in 1913, and had freshwater plant communities (St. John *loc. cit.*; Keddy 1975). This complex of pools was the only known station for *Epilobium nesophilum* var. *sabulonense* and other wetland species (St. John 1921, p. 90). The former and some other taxa were eliminated from the flora when the pond complex was inundated by the sea and made brackish (Keddy 1975).

(f) *Bird Colonies*

Large and dense colonies of gulls and terns may affect vegetation mechanically (trampling, displacement plucking, etc.) or by guano deposition, to the extent that a distinct flora can be associated with bird colonies (Gillham 1961; Sobey & Kenworthy 1979; Hogg and Morton 1983). Colonies are local on Sable Island, but they may move with time, since certain types of vegetation may provide optimal nesting habitat. However, this may change through time as a consequence of succession or the birds' presence. The effects of bird colonies on Sable Island vegetation have not yet been studied.

(g) *Other Factors*

The occurrence of plant species can be limited by pollinator availability. The diversity of pollinators on Sable Island is very low, with the abundant leaf cutting bee *Megachile melanophaea* acting as the principal pollinator of many plants.

3. PRESENT VEGETATION

Vegetated terrain accounts for ca. 39.1% of the total Sable Island area of 3425 ha (Table IV). This is considerably smaller than that reported in earlier studies (57% in 1952 and 47% in 1972, according to Welch (1975)). These differences reflect differences in the methods that were used to delimit plant communities, and/or real declines in vegetated areas due to inundations of established plant communities by sand.

Table IV Surface areas of the major vegetation types on Sable Island.

Community	Area (ha)	Percent of Total
Sandwort	20.3	0.6
Marram-Forb	299.4	8.7
Sparse Grasslands	772.1	22.5
Heath	147.0	4.3
Lakeside Herbaceous	23.6	0.7
Freshwater Ponds	26.3	0.8
Brackish Ponds —Lake Wallace	39.7	1.1
—others	12.1	0.4
Unvegetated	2084.5	60.9
Total	3425.0	

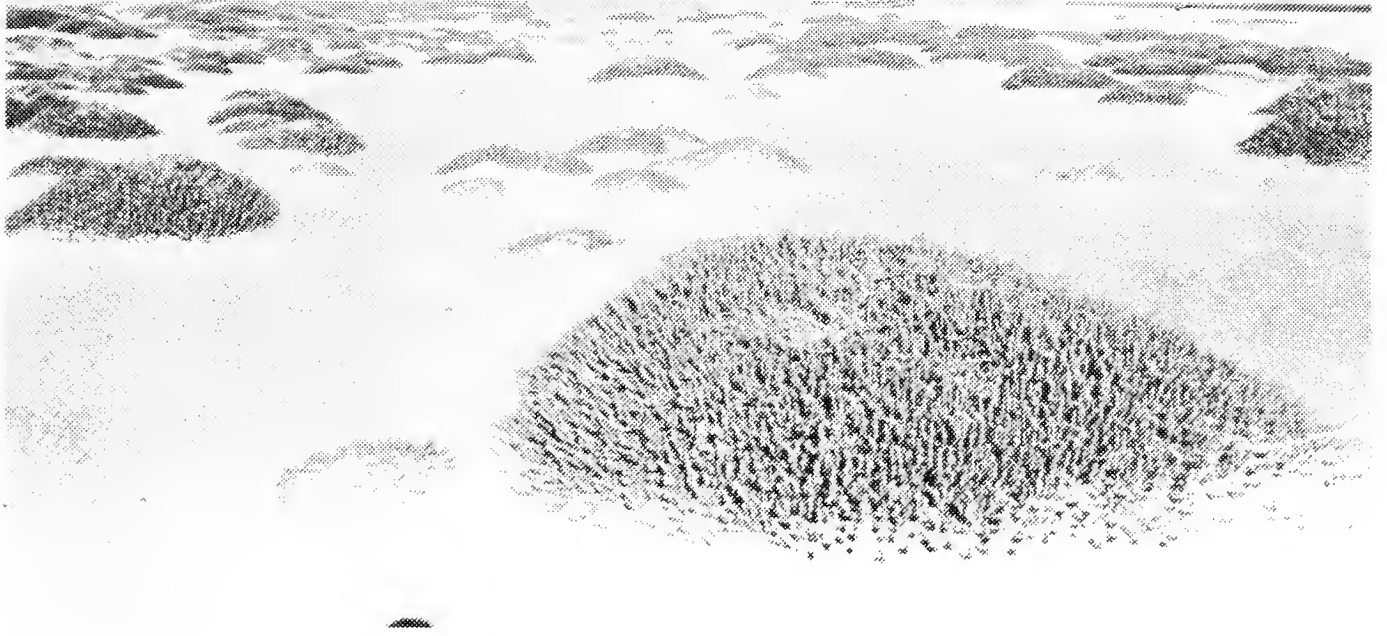


Fig 7. Sandwort (*Honckenya peploides*) stabilizing drifting sand in mounds to 1 m high, West Spit.



Fig 8. Marram-Forb Grasslands with *Ammophila breviligulata*, *Achillea lanulosa*, *Lathyrus maritimus* and *Solidago sempervirens*.



Fig 9. Marram grasslands on Grassy Plain, dominated by *Ammophila breviligulata*.



Fig 10. Marram-Fescue grassland dominated by *Ammophila breviligulata*, *Festuca rubra* and *Anaphalis margaritacea*. Near Grassy Plain.

A total of seven terrestrial plant communities has been recognized in this study. These are: Sandwort, Marram-Forb, Marram, Marram-Fescue, Shrub Heath, Cranberry Heath, and Pondedge Herbaceous. Additional aquatic plant communities occurred in the fresh and brackish water ponds. Each of these communities is described briefly below.

(a) *Sandwort*. This community type develops on raw sand (Table I), and covers ca. 20.3 ha, or 0.6% of the island (Table IV). Major occurrences are at the extreme east and west ends of the island (Fig. 6). These are very exposed locations (Fig. 7), and it is likely that occasional catastrophic declines in these communities occur as a result of severe storms. For example, St. John found *Honckenia peploides* to be very common in 1913, whereas Erskine recorded it as scarce in 1952 (St. John 1921, Erskine 1953). These differences may reflect variations in recent storm activity, with subsequent effects on the Sandwort community. Total cover in two established Sandwort communities averaged 118 and 178% respectively (Table V). Virtually all the cover in these species-poor communities is contributed by *Honckenia peploides* (Table VI).

(b) *Marram-Forb*. This community type (Fig. 8) covers ca. 229 ha, or 8.7% of the island (Table IV). It occurs throughout, but particularly along the oceanic edges of the vegetated terrain (Fig. 6). The rate of sand accumulation is apparently high. To-

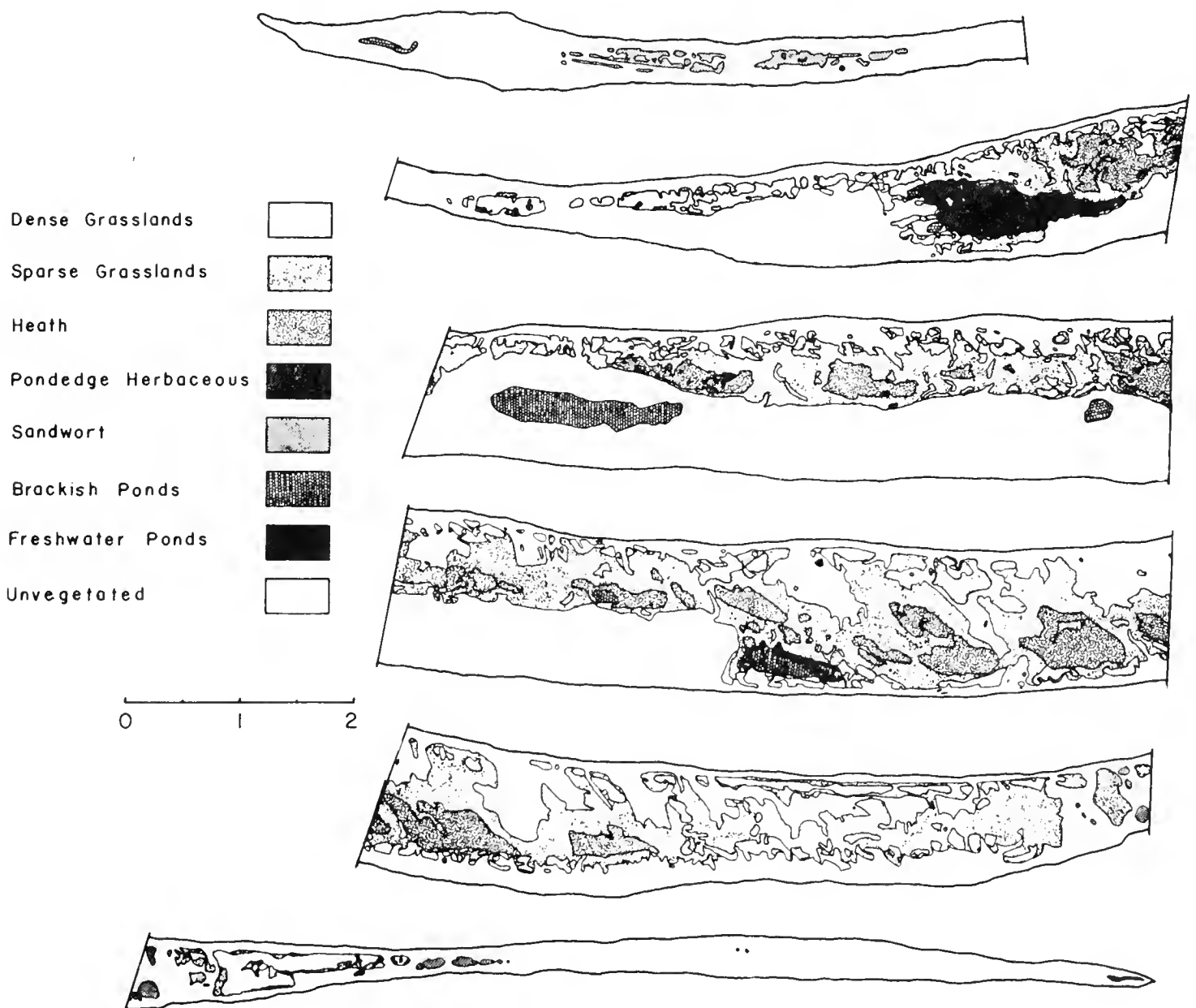


Fig 6. The plant communities of Sable Island.

Table V Summary of total cover, richness, and diversity of the quantitatively sampled plant communities.

Vegetation Type	Total cover (%)	Richness species/quadrat	Diversity
Sandwort	100-200	1.3	0.6
Marram-Forb	200-425	3.2	1.2
Sparse Marram	20-130	1.7	1.0
Marram-Fescue	20-120	4.4	2.0
Shrub Heath	100-330	11.2	2.9
Cranberry Heath	190-230	6.3	2.8

tal plant cover in the four Marram-Forb communities that were examined ranged from 173% to 400% ($\bar{x} \pm SD$ was 250% \pm 105%), and the community was moderately rich, averaging 3.2 species per quadrat (Table V). The most important species in the Marram-Forb community are *Ammophila breviligulata*, *Lathyrus maritimus*, and *Achillea lanulosa*, with lesser contributions by *Solidago sempervirens* and other species (Table VII). *Poa pratensis* is also important in some sites, although not in those quantitatively sampled.

Table VI Summary of the vegetation of the Sandwort communities.¹

Species	Site S-1			Site S-2		
	Cover (%), $\bar{x} \pm S.E.$	Rel. Cover (%)	Frequency (%)	Cover (%), $\bar{x} \pm S.E.$	Rel. Cover (%)	Frequency (%)
<i>Ammophila breviligulata</i>	0.4 \pm 0.1	0.8	30	0.2 \pm 0.2	0.1	15
<i>Cakile edentula</i>	P ¹	P	P	2.5 \pm 1.4	1.4	15
<i>Honckenya peploides</i>	118 \pm 23	99.2	100	175.3 \pm 29.0	98.5	100
<i>Solidago sempervirens</i>	P	P	P	P	P	P

¹P = present

²Data are based on twenty random 50 cm x 50 cm quadrats per site.

(c) *Marram*. Sparse grasslands (Figs. 9 & 10) ca. 772 ha, or 22.5% of the island (Table IV, these figures include both the Marram and Marram-Fescue communities, since they could not be reliably separated in the airphotos). Total plant cover in the five Marram communities that were examined ranged from 18% to 116% ($\bar{x} \pm SD$ was 58% \pm 40%; Table V). These communities are relatively species-poor, averaging only 1.6 species per quadrat (Table V). The most important species in the

Table VIII Summary of the vegetation of the Sparse Marram communities.¹

Species	Site SM-1			Site SM-2		
	Cover (%), $\bar{x} \pm S.E.$	Rel. Cover (%)	Frequency (%)	Cover (%), $\bar{x} \pm S.E.$	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	P ¹	P	P	0.0	0.0	0
<i>Ammophila breviligulata</i>	81.0 \pm 4.1	89.0	100	115.3 \pm 12.4	99.2	100
<i>Anaphalis margaritacea</i>	0.0	0.0	0	0.0	0.0	0
<i>Cakile edentula</i>	0.0	0.0	0	0.2 \pm 0.2	0.2	10
<i>Festuca rubra</i>	0.0	0.0	0	0.0	0.0	0
<i>Honckenya peploides</i>	1.5 \pm 1.0	1.6	35	0.2 \pm 0.2	0.2	5
<i>Lathyrus maritima</i>	8.6 \pm 4.8	9.4	20	0.5 \pm 0.5	0.4	5
<i>Myrica pensylvanica</i>	0.0	0.0	0	0.0	0.0	0
<i>Poa pratensis</i>	0.0	0.0	0	0.0	0.0	0
<i>Rosa virginiana</i>	0.0	0.0	0	0.0	0.0	0
<i>Solidago sempervirens</i>	0.0	0.0	0	P	P	P

¹P = present; data are based on twenty random 50 cm x 50 cm quadrats per site.

Table VII Summary of the vegetation of the Marram-Forb communities.¹

Species	Site DM-1			Site DM-2		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	38.1±9.1	22.0	90	65.9±9.6	26.9	90
<i>Agropyron repens</i>	0.1±0.1	0.1	5	0.0	0.0	0
<i>Ammophila breviligulata</i>	54.2±10.5	31.3	100	67.3±7.3	27.5	100
<i>Cakile edentula</i>	0.0	0.0	0	0.0	0.0	0
<i>Honckenya peploides</i>	0.0	0.0	0	0.1±0.1	0.1	5
<i>Lathyrus maritimus</i>	70.6±9.9	40.7	100	106.7±6.5	43.6	100
<i>Rosa virginiana</i>	0.1±0.1	0.1	5	0.0	0.0	0
<i>Solidago sempervirens</i>	10.0±10.0	5.8	5	5.0±4.7	2.0	10

Species	Site DM-3			Site DM-4		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	50.0±13.9	12.5	70	16.9±3.4	9.3	75
<i>Agropyron repens</i>	0.0	0.0	0	1.4±0.5	0.8	30
<i>Ammophila breviligulata</i>	164.4±27.9	41.0	95	68.4±6.7	37.7	100
<i>Cakile edentula</i>	0.0	0.0	0	0.5±0.5	0.3	5
<i>Honckenya peploides</i>	0.0	0.0	0	0.0	0.0	0
<i>Lathyrus maritimus</i>	186.0±16.9	46.5	100	72.0±6.9	39.6	100
<i>Rosa virginiana</i>	0.0	0.0	0	0.0	0.0	0
<i>Solidago sempervirens</i>	P ¹	P	P	22.4±9.0	12.3	55

¹P = present; data are based on twenty random 50 cm x 50 cm quadrats per site.

Marram community is *Ammophila breviligulata*, with lesser contributions from *Lathyrus maritima*, *Solidago sempervirens*, and several other species (Table VIII). In a successional sense, it appears that the Marram community is an early seral stage that establishes on newly-available sand following a decline in rate of accumulation. On sites that remain stable over the longer term, Marram-Fescue communities may develop, or ultimately, heath-dominated communities (see 4. Successional Trends).

(d) *Marram-Fescue*. These sparse grasslands (Fig. 10) are found throughout the vegetated parts of the island, and they make up much of the 772 ha that are classi-

Cover (%, $\bar{x} \pm S.E.$)	Site SM-3		Cover (%, $\bar{x} \pm S.E.$)	Site SM-4		Cover (%, $\bar{x} \pm S.E.$)	Site SM-5	
	Rel. Cover (%)	Frequency (%)		Rel. Cover (%)	Frequency (%)		Rel. Cover (%)	Frequency (%)
0.0	0.0	0	0.2±0.2	0.4	3	0.0	0.0	0
21.2±3.1	74.6	100	36.3±2.3	83.1	100	14.1±1.3	79.7	100
1.9±1.3	6.7	15	3.0±1.5	6.9	20	1.1±0.8	6.2	10
0.0	0.0	0	0.0	0.0	0	P	P	P
0.6±0.3	2.1	35	0.1±0.1	0.2	3	0.8±0.4	4.5	30
0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
0.0	0.0	0	2.1±2.0	4.8	7	0.0	0.0	0
0.1±0.1	0.4	5	0.0	0.0	0	0.0	0.0	0
0.0	0.0	0	1.4±0.8	3.2	10	0.0	0.0	0
4.6±1.9	16.7	35	0.6±0.6	1.4	7	1.7±0.8	9.6	30

fied as sparse grasslands (Fig. 6, Table IV). Total plant cover in the four Marram-Fescue communities that were sampled ranged from 26% to 103% ($\bar{x} \pm SD$ was $58\% \pm 33\%$), and the communities are relatively rich, averaging 4.4 species per quadrat (Table V). The most important species in the Marram-Fescue communities are *Ammophila breviligulata*, *Anaphalis margaritacea*, *Festuca rubra*, *Fragaria virginiana*, *Rosa virginiana*, and *Myrica pensylvanica* (Table IX).

Table IX Summary of the vegetation of the Marram-Fescue communities.¹

Species	Site MF-1			Site MF-2		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	1.1±0.4	2.4	32	P ¹	P	P
<i>Ammophila breviligulata</i>	2.9±1.0	6.4	76	4.8±0.8	18.6	100
<i>Anaphalis margaritacea</i>	1.4±1.1	3.1	8	3.7±1.5	14.3	35
<i>Arenaria lateriflora</i>	0.1±0.1	0.2	4	0.0	0.0	0
<i>Aronia prunifolia</i>	0.0	0.0	0	0.0	0.0	0
<i>Aster novi-belgii</i>	0.0	0.0	0	0.0	0.0	0
<i>Carex silicea</i>	0.0	0.0	0	<0.1	<0.1	5
<i>Empetrum nigrum</i>	P	P	P	0.0	0.0	0
<i>Festuca rubra</i>	10.4±1.4	23.1	100	5.8±1.3	22.5	100
<i>Fragaria virginiana</i>	19.9±3.4	44.1	92	3.9±1.4	15.1	50
<i>Juncus balticus</i>	0.0	0.0	0	0.2±0.2	0.8	10
<i>Juniperus communis</i>	0.0	0.0	0	0.1±0.1	0.4	5
<i>Myrica pensylvanica</i>	0.7±0.7	1.6	4	5.3±2.9	20.5	20
<i>Oenothera cruciata</i>	0.1±0.1	0.2	8	0.0	0.0	0
<i>Poa pratensis</i>	0.0	0.0	0	<0.1	<0.1	5
<i>Potentilla tridentata</i>	0.0	0.0	0	0.0	0.0	0
<i>Rosa virginiana</i>	8.1±1.9	18.0	64	0.3±0.2	1.2	10
<i>Rumex acetosella</i>	0.1±0.1	0.2	8	0.1±0.1	0.4	10
<i>Smilacina stellata</i>	P	P	P	0.0	0.0	0
<i>Solidago sempervirens</i>	0.3±0.3	0.7	4	1.6±0.9	6.2	35
<i>Trientalis borealis</i>	0.0	0.0	0	0.0	0.0	0
<i>Vaccinium angustifolium</i>	0.0	0.0	0	0.0	0.0	0

Species	Site MF-3			Site MF-4		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	0.1±0.1	0.2	5	5.8±1.1	5.7	75
<i>Ammophila breviligulata</i>	1.9±0.4	3.3	55	23.7±2.3	23.2	100
<i>Anaphalis margaritacea</i>	7.8±2.7	13.4	55	18.0±5.2	17.6	65
<i>Arenaria lateriflora</i>	0.0	0.0	0	0.0	0.0	0
<i>Aronia prunifolia</i>	0.0	0.0	0	0.8±0.8	0.8	5
<i>Aster novi-belgii</i>	0.6±0.6	1.0	5	1.8±1.0	1.8	25
<i>Carex silicea</i>	0.3±0.2	0.5	10	0.0	0.0	0
<i>Empetrum nigrum</i>	1.3±1.1	2.2	10	0.0	0.0	0
<i>Festuca rubra</i>	19.1±1.9	32.8	100	4.2±1.1	4.1	75
<i>Fragaria virginiana</i>	11.7±2.7	20.1	80	0.3±0.3	0.3	5
<i>Juncus balticus</i>	P	P	P	0.0	0.0	0
<i>Juniperus communis</i>	0.0	0.0	0	0.0	0.0	0
<i>Myrica pensylvanica</i>	11.5±4.0	19.8	40	9.2±3.6	9.0	35
<i>Oenothera cruciata</i>	P	P	P	0.0	0.0	0
<i>Poa pratensis</i>	0.0	0.0	0	0.2±0.2	0.2	10
<i>Potentilla tridentata</i>	0.4±0.3	0.7	10	0.0	0.0	0
<i>Rosa virginiana</i>	2.8±1.6	4.8	20	21.7±8.1	21.3	70
<i>Rumex acetosella</i>	0.4±0.4	0.7	15	0.0	0.0	0
<i>Smilacina stellata</i>	P	P	P	0.0	0.0	0
<i>Solidago sempervirens</i>	0.3±0.2	0.5	10	3.6±1.1	3.5	45
<i>Trientalis borealis</i>	0.0	0.0	0	0.1±0.1	0.1	5
<i>Vaccinium angustifolium</i>	P	P	P	12.6±7.3	12.4	35

¹P = present; data based on twenty random 50 cm x 50 cm quadrats per site.



Fig 11. An old sand-road through Shrub Heath vegetation dominated by *Empetrum nigrum*, *Juniperus communis* var. *megistocarpa*, *Myrica pensylvanica*, *Rosa virginiana*, *Juniperus horizontalis*, *Vaccinium angustifolium* and *Aster nova-belgii*.



Fig 12. Shrub Heath vegetation with *Juniperus communis* var. *megistocarpa*, *Juniperus horizontalis*, *Myrica pensylvanica* and *Empetrum nigrum*.



Fig 13. Cranberry Heath vegetation dominated by *Vaccinium macrocarpon*, *Juncus balticus*, *Myrica pensylvanica* and *Aster nova-belgii*. Near No. 3 Life Saving Station.

(e) *Shrub Heath*. The Shrub Heath community type (Figs. 11 & 12) is found in certain locations in interior parts of the island (Fig. 6). The soil is acidic (pH 5.7) and sandy but with relatively higher organic matter content and nutrients (Table I). In total, heath communities cover ca. 147 ha, or 4.3% of the surface of the island (Table IV). Most of this is Shrub Heath, with lesser contributions of Cranberry Heath (discussed next). Total plant cover in the eight Shrub Heath communities that were examined ranged from 105 to 325% ($\bar{x} \pm SD$ was 190% \pm 71%), and the communities are quite rich, averaging 10.2 species per quadrat (Table V). The most important species in the Shrub Heath communities are *Empetrum nigrum*, *Juniperus communis*, *Myrica pensylvanica*, *Rosa virginiana*, and *Vaccinium angustifolium*, with a relatively large number of associated species (Table X). Lichens were prevalent in some areas, including *Cladina stellaris*, *Cladina rangiferina* and *Coelocaulon aculeatum*. Occasionally important mosses included *Polytrichum commune* and *Dicranum condensatum*. The various Shrub Heath communities were rather variable in relative species composition, and at any location any of the aforementioned species could assume dominance. An extreme example of this occurred at site SH-3, where the introduced heath *Calluna vulgaris* contributed 92.4% of the relative cover. This species was not present at any of the other seven Shrub Heath communities that were sampled. In terms of succession, the Shrub Heath community type represents the climax seral stage on well-drained sites on the island.

An interesting aspect of the Shrub Heath and perhaps the Cranberry Heath vegetation on the island is that it differs from similar communities on the mainland. For example, several species that are important constituents of mainland heath, e.g. *Myrica asplenifolia*, *Pteridium aquilinum*, *Solidago bicolor*, *S. puberula*, *Kalmia angustifolia*, and *Arctostaphylos uva-ursi* are altogether lacking on the island. In terms of plant associations, the Heath communities on the island may be unique.

(f) *Cranberry Heath*. The Cranberry Heath community (Fig. 13) is found in intermittently wet locations in interior parts of the island, usually in association with Shrub Heath or Lakeside Herbaceous communities. Soil pH is relatively low (4.9) and organic matter is relatively high (Table I). Total plant cover in the four Cranberry Heath communities ranged from 197% to 227% ($\bar{x} \pm SD$ was 215% \pm 13%), and the communities were quite rich, averaging 7.0 species per quadrat (Table V). The most important species in the Cranberry Heath communities is *Vaccinium macrocarpon*, with lesser contributions of *Juncus balticus*, *Myrica pensylvanica*, *Aster novi-belgii*, *Viola lanceolata*, and *Calopogon tuberosus*, plus many minor associates (Table XI).

Important mosses of some Cranberry Heaths include *Aulacomium palustre*, *Cladopodiella fluitans*, *Sphagnum imbricatum* and *S. palustre*.

(g) *Freshwater Pools and Borders*. Because of the great heterogeneity in the composition and distribution of these plant communities, they were not sampled quantitatively using quadrats. However, they were carefully observed, and the following subjective descriptions illustrate the nature of the plant communities.

In total, freshwater pools (Figs. 14, 15, and 16) covered some 26.3 ha, and their bordering Pondedge Herbaceous communities covered some 23.6 ha, for a combined 1.5% of the island's surface area (Table IV). These freshwater pools and their associated wetlands are common over much of the interior parts of the island (Fig. 6). Most of the pools have a pH of 5.0 to 5.7, and there is relatively little variation in other aspects of water chemistry (numbers 1-4 in Table II). In a physical sense, the ponds represent surface exposures of the large rainwater-fed freshwater lens that underlies Sable Island (Hennigar 1976).

Table X Summary of the vegetation of the Shrub Heath communities.
 P = present; data based on twenty random 50 cm x 50 cm quadrats per site.

Species	Site SH-1			Site SH-2		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	0.1±0.1	<0.1	5	0.4±0.2	0.2	15
<i>Ammophila breviligulata</i>	2.7±0.7	2.2	70	0.6±0.3	0.3	35
<i>Anaphalis margaritacea</i>	12.4±3.2	10.0	80	2.6±1.0	1.5	55
<i>Anthoxanthum odoratum</i>	0.0	0.0	0	0.1±0.1	<0.1	10
<i>Arenaria lateriflora</i>	0.3±0.1	0.2	20	0.7±0.2	0.4	45
<i>Aronia prunifolia</i>	0.0	0.0	0	P	P	P
<i>Aster novi-belgii</i>	4.3±0.8	3.5	35	4.4±0.8	2.5	100
<i>Calluna vulgaris</i>	0.0	0.0	0	0.0	0.0	0
<i>Carex emmonsii</i>	0.0	0.0	0	0.0	0.0	0
<i>Carex silicea</i>	0.1±0.1	0.1	10	0.0	0.0	0
<i>Cerastium vulgatum</i>	0.0	0.0	0	0.0	0.0	0
<i>Coptis trifolia</i>	0.0	0.0	0	0.0	0.0	0
<i>Danthonia spicata</i>	0.0	0.0	0	0.0	0.0	0
<i>Empetrum nigrum</i>	26.0±6.5	20.9	70	96.8±11.7	54.5	95
<i>Euphrasia randii</i>	0.0	0.0	0	0.0	0.0	0
<i>Festuca rubra</i>	6.6±1.6	5.3	100	2.0±0.4	1.1	100
<i>Fragaria virginiana</i>	4.4±1.7	3.5	50	0.5±0.2	0.3	25
<i>Gnaphalium obtusata</i>	0.0	0.0	0	0.0	0.0	0
<i>Hieracium pilosella</i>	0.1±0.1	<0.1	10	0.0	0.0	0
<i>Hieracium scabrum</i>	0.3±0.2	0.2	10	0.1±0.1	0.1	10
<i>Juncus balticus</i>	0.3±0.2	0.2	15	0.1±0.1	<0.1	5
<i>Juniperus communis</i>	3.4±3.2	2.7	10	2.5±1.8	1.4	30
<i>Juniperus horizontalis</i>	0.0	0.0	0	P	P	P
<i>Leontodon autumnalis</i>	0.0	0.0	0	0.0	0.0	0
<i>Linnaea borealis</i>	0.0	0.0	0	0.0	0.0	0
<i>Luzula campestris</i>	0.0	0.0	0	0.2±0.1	0.1	15
<i>Lycopus uniflorus</i>	0.0	0.0	0	0.0	0.0	0
<i>Mitchella repens</i>	0.1±0.1	<0.1	5	0.0	0.0	0
<i>Myrica pensylvanica</i>	25.1±3.3	20.3	95	42.5±4.8	23.8	100
<i>Plantago lanceolata</i>	0.0	0.0	0	0.0	0.0	0
<i>Platanthera clavellata</i>	0.0	0.0	0	0.1±0.1	<0.1	5
<i>Platanthera lacera</i>	0.0	0.0	0	0.1±0.1	<0.1	5
<i>Platanthera viridis</i>	0.0	0.0	0	0.0	0.0	0
<i>Poa pratensis</i>	0.0	0.0	0	0.0	0.0	0
<i>Potentilla tridentata</i>	21.6±5.4	17.3	70	7.8±2.3	4.4	65
<i>Prenanthes trifoliolata</i>	0.0	0.0	0	0.0	0.0	0
<i>Rhinanthus crista-galli</i>	P	P	P	0.0	0.0	0
<i>Rosa virginiana</i>	4.8±1.4	3.8	60	3.2±1.1	1.8	70
<i>Rubus hispidus</i>	0.0	0.0	0	0.0	0.0	0
<i>Rumex acetosella</i>	0.5±0.2	0.4	50	0.8±0.6	0.4	25
<i>Sisyrinchium angustifolium</i>	0.0	0.0	0	0.0	0.0	0
<i>Smilacina stellata</i>	0.9±0.7	0.7	10	0.1±0.1	<0.1	5
<i>Solidago sempervirens</i>	0.7±0.4	0.6	15	0.0	0.0	0
<i>Spartina pectinata</i>	0.0	0.0	0	0.0	0.0	0
<i>Spiranthes romanzoffiana</i>	0.1±0.1	0.1	5	P	P	P
<i>Thalictrum polygamum</i>	0.0	0.0	0	0.0	0.0	0
<i>Trientalis borealis</i>	0.2±0.1	0.2	15	0.7±0.2	0.4	60
<i>Trifolium repens</i>	0.0	0.0	0	0.0	0.0	0
<i>Vaccinium angustifolium</i>	7.6±2.4	6.1	50	12.1±3.0	6.8	75
<i>Vaccinium macrocarpon</i>	2.1±1.8	1.7	10	0.1±0.1	<0.1	5
<i>Viburnum cassinoides</i>	0.0	0.0	0	0.0	0.0	0
<i>Viola lanceolata</i>	0.0	0.0	0	0.0	0.0	0
<i>Viola septentrionalis</i>	0.0	0.0	0	P	P	P
unidentified	0.0	0.0	0	0.0	0.0	0

Species	Site SH-3			Site SH-4		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	0.0	0.0	0	0.1±0.1	0.1	5
<i>Ammophila breviligulata</i>	0.2±0.2	0.1	10	1.0±0.6	0.4	15
<i>Anaphalis margaritacea</i>	0.0	0.0	0	0.1	0.1	10
<i>Anthoxanthum odoratum</i>	0.4±0.2	0.1	15	3.3±1.5	1.4	70
<i>Arenaria lateriflora</i>	0.1±0.1	0.1	10	0.9±0.3	0.4	40
<i>Aronia prunifolia</i>	2.9±1.3	0.9	45	0.4±0.4	0.2	5
<i>Aster novi-belgii</i>	0.3±0.1	0.1	20	4.9±0.5	2.1	95
<i>Calluna vulgaris</i>	300.0±20.6	92.4	100	0.0	0.0	0
<i>Carex emmonsii</i>	0.0	0.0	0	P	P	P
<i>Carex silicea</i>	0.0	0.0	0	0.0	0.0	0
<i>Cerastium vulgatum</i>	0.0	0.0	0	0.4±0.2	0.2	25
<i>Coptis trifolia</i>	0.0	0.0	0	2.3±2.3	1.0	5
<i>Danthonia spicata</i>	0.0	0.0	0	0.0	0.0	0
<i>Empetrum nigrum</i>	0.0	0.0	0	77.6±14.7	33.0	95
<i>Euphrasia randii</i>	0.0	0.0	0	0.0	0.0	0
<i>Festuca rubra</i>	0.4±0.2	0.1	20	2.9±0.5	1.2	95
<i>Fragaria virginiana</i>	0.0	0.0	0	0.8±0.3	0.3	45
<i>Gnaphalium obtusata</i>	0.0	0.0	0	0.0	0.0	0
<i>Hieracium pilosella</i>	0.0	0.0	0	0.0	0.0	0
<i>Hieracium scabrum</i>	0.0	0.0	0	0.0	0.0	0
<i>Juncus balticus</i>	4.3±0.7	1.3	85	0.0	0.0	0
<i>Juniperus communis</i>	0.0	0.0	0	104.5±21.5	44.5	90
<i>Juniperus horizontalis</i>	0.0	0.0	0	0.4±0.3	0.2	10
<i>Leontodon autumnalis</i>	0.0	0.0	0	0.0	0.0	0
<i>Linnaea borealis</i>	0.0	0.0	0	0.0	0.0	0
<i>Luzula campestris</i>	0.1±0.1	0.1	5	0.4±0.2	0.2	30
<i>Lycopus uniflorus</i>	0.2±0.1	0.1	10	0.0	0.0	0
<i>Mitchella repens</i>	0.0	0.0	0	0.5±0.4	0.2	15
<i>Myrica pensylvanica</i>	10.5±3.6	3.2	65	7.1±2.6	3.0	65
<i>Plantago lanceolata</i>	0.0	0.0	0	0.0	0.0	0
<i>Platanthera clavellata</i>	0.2±0.1	0.1	10	P	P	P
<i>Platanthera lacera</i>	0.1±0.1	0.1	10	0.6±0.2	0.1	25
<i>Platanthera viridis</i>	0.0	0.0	0	0.0	0.0	0
<i>Poa pratensis</i>	0.0	0.0	0	0.4±0.2	0.2	20
<i>Potentilla tridentata</i>	0.5±0.4	0.2	15	1.8±1.7	0.8	10
<i>Prenanthes trifoliolata</i>	0.0	0.0	0	0.3±0.2	0.1	20
<i>Rhinanthus crista-galli</i>	0.0	0.0	0	0.0	0.0	0
<i>Rosa virginiana</i>	0.9±0.4	0.3	25	4.3±1.6	1.8	55
<i>Rubus hispidus</i>	0.0	0.0	0	1.9±1.1	0.8	20
<i>Rumex acetosella</i>	0.1±0.1	0.1	5	0.0	0.0	0
<i>Sisyrinchium angustifolium</i>	0.0	0.0	0	0.1±0.1	0.1	5
<i>Smilacina stellata</i>	0.1	0.1	5	0.2±0.2	0.1	5
<i>Solidago sempervirens</i>	0.0	0.0	0	0.0	0.0	0
<i>Spartina pectinata</i>	0.0	0.0	0	0.0	0.0	0
<i>Spiranthes romanzoffiana</i>	0.0	0.0	0	P	P	P
<i>Thalictrum polygamum</i>	0.4±0.2	0.1	25	2.3±1.4	1.0	30
<i>Trientalis borealis</i>	0.5±0.2	0.2	45	0.6±0.2	0.3	40
<i>Trifolium repens</i>	0.0	0.0	0	0.0	0.0	0
<i>Vaccinium angustifolium</i>	1.1±0.5	0.3	35	14.9±4.1	6.3	90
<i>Vaccinium macrocarpon</i>	1.5±1.2	0.5	20	0.0	0.0	0
<i>Viburnum cassinoides</i>	0.0	0.0	0	0.0	0.0	0
<i>Viola lanceolata</i>	0.0	0.0	0	0.0	0.0	0
<i>Viola septentrionalis</i>	0.0	0.0	0	0.1±0.1	0.1	5
unidentified	0.1	0.1	5	0.0	0.0	0

Table X (continued)

Species	Site SH-5			Site SH-6		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	0.4±0.2	0.2	20	0.6±0.4	0.2	15
<i>Ammophila breviligulata</i>	1.1±0.5	0.5	35	1.8±0.8	0.9	60
<i>Anaphalis margaritacea</i>	2.8±1.3	1.3	30	0.7±0.3	0.3	25
<i>Anthoxanthum odoratum</i>	3.2±0.7	1.5	75	4.1±1.1	2.0	85
<i>Arenaria lateriflora</i>	2.1±0.6	1.0	75	1.9±0.4	0.9	85
<i>Aronia prunifolia</i>	14.6±4.0	6.9	65	5.3±1.8	2.6	55
<i>Aster novi-belgii</i>	7.8±1.5	3.7	100	8.0±1.4	3.9	95
<i>Calluna vulgaris</i>	0.0	0.0	0	0.0	0.0	0
<i>Carex emmonsii</i>	0.0	0.0	0	0.0	0.0	0
<i>Carex silicea</i>	0.0	0.0	0	0.0	0.0	0
<i>Cerastium vulgatum</i>	0.2±0.1	0.1	15	0.6±0.3	0.3	30
<i>Coptis trifolia</i>	0.0	0.0	0	0.0	0.0	0
<i>Danthonia spicata</i>	0.0	0.0	0	0.1±0.1	0.1	10
<i>Empetrum nigrum</i>	54.9±20.6	26.1	50	57.3±11.1	27.7	70
<i>Euphrasia randii</i>	0.0	0.0	0	2.6±2.0	1.3	25
<i>Festuca rubra</i>	3.6±0.4	1.7	95	3.4±0.4	1.7	100
<i>Fragaria virginiana</i>	5.4±1.7	2.6	60	4.6±1.4	2.2	70
<i>Gnaphalium obtusata</i>	0.0	0.0	0	0.0	0.0	0
<i>Hieracium pilosella</i>	0.4±0.3	0.2	15	0.0	0.0	0
<i>Hieracium scabrum</i>	0.0	0.0	0	0.0	0.0	0
<i>Juncus balticus</i>	0.5±0.3	0.2	15	2.1±0.7	1.0	55
<i>Juniperus communis</i>	P	P	P	14.6±5.4	7.1	40
<i>Juniperus horizontalis</i>	0.0	0.0	0	12.7±5.1	6.2	45
<i>Leontodon autumnalis</i>	P	P	P	P	P	P
<i>Linnaea borealis</i>	0.0	0.0	0	13.5±4.5	6.6	65
<i>Luzula campestris</i>	0.4±0.2	0.2	20	0.5±0.2	0.2	35
<i>Lycopus uniflorus</i>	0.0	0.0	0	0.2±0.1	0.1	15
<i>Mitchella repens</i>	5.6±3.2	2.7	20	5.9±2.0	2.9	35
<i>Myrica pensylvanica</i>	40.0±5.3	19.0	100	13.4±2.8	6.5	90
<i>Plantago lanceolata</i>	0.0	0.0	0	0.4±0.4	0.2	5
<i>Platanthera clavellata</i>	0.1±0.1	0.1	5	P	P	P
<i>Platanthera lacera</i>	0.0	0.0	0	0.0	0.0	0
<i>Platanthera viridis</i>	0.0	0.0	0	0.2±0.2	0.1	10
<i>Poa pratensis</i>	0.0	0.0	0	0.4±0.2	0.2	40
<i>Potentilla tridentata</i>	5.5±2.8	2.6	35	0.0	0.0	0
<i>Prenanthes trifoliolata</i>	P	P	P	P	P	P
<i>Rhinanthus crista-galli</i>	0.3±0.3	0.1	15	0.8±0.5	0.3	25
<i>Rosa virginiana</i>	16.2±2.7	7.7	95	7.8±1.5	3.8	100
<i>Rubus hispidus</i>	P	P	P	1.4±0.9	0.7	15
<i>Rumex acetosella</i>	0.1±0.1	<0.1	5	0.2±0.1	0.1	15
<i>Sisyrinchium angustifolium</i>	0.2±0.1	0.1	20	0.1±0.1	0.1	5
<i>Smilacina stellata</i>	6.8±2.7	3.2	40	7.7±2.1	3.7	70
<i>Solidago sempervirens</i>	0.0	0.0	0	0.0	0.0	0
<i>Spartina pectinata</i>	P	P	P	0.0	0.0	0
<i>Spiranthes romanzoffiana</i>	P	P	P	0.0	0.0	0
<i>Thalictrum polygamum</i>	8.7±1.9	4.1	70	4.7±2.1	2.3	35
<i>Trientalis borealis</i>	1.4±0.3	0.7	85	1.1±0.3	0.5	65
<i>Trifolium repens</i>	P	P	P	0.3±0.2	0.2	20
<i>Vaccinium angustifolium</i>	26.3±5.0	12.6	100	26.6±6.0	12.9	100
<i>Vaccinium macrocarpon</i>	0.2±0.1	0.1	20	0.2±0.1	0.1	20
<i>Viburnum cassinoides</i>	0.0	0.2	0	0.1±0.1	0.1	5
<i>Viola lanceolata</i>	0.4±0.2	0.2	20	0.0	0.0	0
<i>Viola septentrionalis</i>	1.3±0.6	0.6	40	0.1±0.1	<0.1	5
unidentified	0.0	0.0	0	0.0	0.0	0

Species	Site SH-7			Site SH-8		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	0.0	0.0	0	1.4±0.6	1.3	45
<i>Ammophila breviligulata</i>	0.8±0.2	0.6	45	0.8±0.3	0.8	55
<i>Anaphalis margaritacea</i>	0.7±0.4	0.5	20	0.7±0.3	0.7	35
<i>Anthoxanthum odoratum</i>	0.2±0.1	0.1	10	9.7±2.6	9.3	95
<i>Arenaria lateriflora</i>	<0.1	<0.1	5	0.3±0.1	0.3	45
<i>Aronia prunifolia</i>	0.1±0.1	0.1	5	P	P	P
<i>Aster novi-belgii</i>	1.1±0.6	0.8	40	2.5±0.8	2.4	65
<i>Calluna vulgaris</i>	0.0	0.0	0	0.0	0.0	0
<i>Carex emmonsii</i>	0.0	0.0	0	0.0	0.0	0
<i>Carex silicea</i>	0.1±0.1	<0.1	5	0.8±0.3	0.8	25
<i>Cerastium vulgatum</i>	0.0	0.0	0	0.3±0.1	0.3	40
<i>Coptis trifolia</i>	0.0	0.0	0	0.0	0.0	0
<i>Danthonia spicata</i>	0.0	0.0	0	0.0	0.0	0
<i>Empetrum nigrum</i>	29.8±8.8	22.0	55	2.3±2.0	2.2	15
<i>Euphrasia randii</i>	0.0	0.0	0	0.0	0.0	0
<i>Festuca rubra</i>	4.0±1.5	3.0	90	3.1±1.1	3.0	100
<i>Fragaria virginiana</i>	0.5±0.4	0.4	15	5.0±2.0	4.8	80
<i>Gnaphalium obtusata</i>	0.0	0.0	0	P	P	P
<i>Hieracium pilosella</i>	0.0	0.0	0	0.0	0.0	0
<i>Hieracium scabrum</i>	P	P	P	<0.1	<0.1	10
<i>Juncus balticus</i>	0.0	0.0	0	0.4±0.2	0.4	15
<i>Juniperus communis</i>	21.2±14.2	15.7	25	0.2±0.2	0.2	5
<i>Juniperus horizontalis</i>	15.9±4.6	11.8	50	P	P	P
<i>Leontodon autumnalis</i>	0.0	0.0	0	P	P	P
<i>Linnaea borealis</i>	P	P	P	0.0	0.0	0
<i>Luzula campestris</i>	0.1±0.1	0.1	15	0.1±0.1	0.1	15
<i>Lycopus uniflorus</i>	0.0	0.0	0	0.1±0.1	0.1	5
<i>Mitchella repens</i>	0.3±0.3	0.2	5	0.0	0.0	0
<i>Myrica pensylvanica</i>	37.1±5.3	27.4	95	37.2±4.3	35.4	100
<i>Plantago lanceolata</i>	0.0	0.0	0	0.0	0.0	0
<i>Platanthera clavellata</i>	0.0	0.0	0	0.0	0.0	0
<i>Platanthera lacera</i>	0.0	0.0	0	0.0	0.0	0
<i>Platanthera viridis</i>	0.0	0.0	0	0.0	0.0	0
<i>Poa pratensis</i>	0.0	0.0	0	0.0	0.0	0
<i>Potentilla tridentata</i>	0.0	0.0	0	0.0	0.0	0
<i>Prenanthes trifoliolata</i>	0.0	0.0	0	0.0	0.0	0
<i>Rhinanthus crista-galli</i>	0.0	0.0	0	0.1±0.1	<0.1	15
<i>Rosa virginiana</i>	1.0±0.5	0.7	30	2.7±1.0	2.6	50
<i>Rubus hispida</i>	0.0	0.0	0	1.1±0.8	1.0	15
<i>Rumex acetosella</i>	0.1±0.1	0.1	10	1.0±0.5	1.0	45
<i>Sisyrinchium angustifolium</i>	0.0	0.0	0	0.0	0.0	0
<i>Smilacina stellata</i>	0.1±0.1	0.1	10	0.3±0.3	0.3	5
<i>Solidago sempervirens</i>	0.1±0.1	0.1	10	0.3±0.2	0.3	15
<i>Spartina pectinata</i>	0.0	0.0	0	0.0	0.0	0
<i>Spiranthes romanzoffiana</i>	0.0	0.0	0	0.0	0.0	0
<i>Thalictrum polygamum</i>	0.0	0.0	0	0.0	0.0	0
<i>Trientalis borealis</i>	0.2±0.1	0.1	20	0.2±0.1	0.2	15
<i>Trifolium repens</i>	0.0	0.0	0	0.0	0.0	0
<i>Vaccinium angustifolium</i>	21.8±5.6	16.2	90	33.8±6.2	32.3	85
<i>Vaccinium macrocarpon</i>	0.0	0.0	0	<0.1	<0.1	5
<i>Viburnum cassinoides</i>	0.0	0.0	0	0.0	0.0	0
<i>Viola lanceolata</i>	0.0	0.0	0	0.4±0.2	0.4	30
<i>Viola septentrionalis</i>	0.0	0.0	0	0.0	0.0	0
unidentified	0.0	0.0	0	0.0	0.0	0

Table XI Summary of the vegetation of the Cranberry Heath communities.¹

Species	Site CH-1			Site CH-2		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	0.1±0.1	<0.1	10	0.0	0.0	0
<i>Agalinus neoscotica</i>	1.0±1.0	0.4	5	0.0	0.0	0
<i>Agrostis scabra</i>	0.5±0.4	0.2	15	0.6±0.2	0.3	30
<i>Agrostis stolonifera</i>	0.0	0.0	0	0.8±0.8	0.4	5
<i>Ammophila breviligulata</i>	0.3±0.1	0.1	20	0.4±0.3	0.2	15
<i>Anaphalis margaritacea</i>	0.0	0.0	0	0.0	0.0	0
<i>Anthoxanthum odoratum</i>	0.0	0.0	0	0.2±0.1	0.1	15
<i>Arenaria lateriflora</i>	0.1±0.1	<0.1	5	0.1±0.1	<0.1	5
<i>Aronia prunifolia</i>	0.0	0.0	0	0.2±0.2	0.1	5
<i>Aster novi-belgii</i>	7.1±1.7	3.1	80	2.1±1.1	1.0	25
<i>Bartonia paniculata</i>	0.0	0.0	0	P	P	P
<i>Calopogon pulchellus</i>	1.3±0.4	0.6	45	0.9±0.2	0.4	60
<i>Calluna vulgaris</i>	0.0	0.0	0	5.9±3.9	2.7	20
<i>Carex echinata</i>	0.0	0.0	0	0.0±0.0	0.0	0
<i>Carex silicea</i>	0.0	0.0	0	0.2±0.1	0.1	10
<i>Centaurium umbellatum</i>	P	P	P	0.0	0.0	0
<i>Drosera intermedia</i>	0.0	0.0	0	0.0	0.0	0
<i>Drosera rotundifolia</i>	0.0	0.0	0	0.0	0.0	0
<i>Empetrum nigrum</i>	0.0	0.0	0	0.3±0.3	0.1	5
<i>Festuca rubra</i>	2.7±0.5	1.2	70	0.2±0.1	0.1	10
<i>Fragaria virginiana</i>	0.6±0.4	0.3	15	0.1±0.1	0.1	5
<i>Hypericum boreale</i>	0.0	0.0	0	0.0	0.0	0
<i>Hypericum virginicum</i>	0.8±0.8	0.4	5	1.1±0.5	0.5	30
<i>Iris versicolor</i>	0.0	0.0	0	0.1±0.1	<0.1	5
<i>Juncus balticus</i>	10.6±1.1	4.7	100	19.3±2.8	8.9	100
<i>Juncus canadensis</i>	0.2±0.2	0.1	5	0.6±0.3	0.3	20
<i>Juniperus horizontalis</i>	0.0	0.0	0	0.0	0.0	0
<i>Luzula campestris</i>	0.1±0.1	<0.1	5	0.0	0.0	0
<i>Lycopodium inundatum</i>	0.0	0.0	0	0.0	0.0	0
<i>Lycopus uniflorus</i>	2.5±1.2	1.1	30	9.8±2.8	4.5	60
<i>Lysimachia terrestris</i>	0.0	0.0	0	0.4±0.2	0.2	15
<i>Myrica pensylvanica</i>	28.9±4.8	12.8	90	22.8±6.9	10.5	55
<i>Platanthera clavellata</i>	P	P	P	0.0	0.0	0
<i>Poa pratensis</i>	0.6±0.3	0.3	30	0.1±0.1	<0.1	5
<i>Potentilla tridentata</i>	0.0	0.0	0	0.9±0.5	0.4	15
<i>Rhinanthus crista-galli</i>	1.4±0.6	0.6	25	0.0	0.0	0
<i>Rosa virginiana</i>	3.5±1.1	1.6	45	0.9±0.6	0.4	10
<i>Rumex acetosella</i>	0.2±0.2	0.1	5	0.1±0.1	<0.1	5
<i>Scirpus americanus</i>	0.0	0.0	0	0.0	0.0	0
<i>Sisyrinchium angustifolium</i>	0.0	0.0	0	0.2±0.2	0.1	10
<i>Smilacina stellata</i>	0.2±0.2	0.1	5	0.0	0.0	0
<i>Solidago sempervirens</i>	0.0	0.0	0	0.0	0.0	0
<i>Spiranthes romanzoffiana</i>	0.4±0.3	0.2	10	P	P	P
<i>Trientalis borealis</i>	0.2±0.1	0.1	10	0.0	0.0	0
<i>Trifolium repens</i>	6.2±2.7	2.7	35	0.1±0.1	<0.1	5
<i>Vaccinium angustifolium</i>	0.0	0.0	0	0.0	0.0	0
<i>Vaccinium macrocarpon</i>	154.0±12.2	68.2	100	148.5±10.1	68.3	100
<i>Viola lanceolata</i>	2.5±0.8	1.1	45	0.6±0.3	0.3	25
unidentified	<0.1	<0.1	5	0.0	0.0	0

¹P = present; data are based on twenty random 50 cm x 50 cm quadrats per site.

In water up to 1.5 m deep, the most frequently encountered aquatics are *Potamogeton epihydrus*, *P. oblongus*, and *Polygonum hydropiperoides* var. *psilostachyum*. These floating-leaved species are associated with peaty substrates to some degree. Where the substrate is largely coarse sand, dense beds of *Myriophyllum tenellum* occur, sometimes with *Scirpus americanus*. The bryophyte *Fontinalis sulli-*

Species	Site CH-3			Site CH-4		
	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)	Cover (%, $\bar{x} \pm S.E.$)	Rel. Cover (%)	Frequency (%)
<i>Achillea lanulosa</i>	0.1±0.1	<0.1	5	0.0	0.0	0
<i>Agalinus neoscotica</i>	P ¹	P	P	P	P	P
<i>Agrostis scabra</i>	2.2±1.1	1.0	50	0.6±0.2	0.3	35
<i>Agrostis stolonifera</i>	0.0	0.0	0	0.0	0.0	0
<i>Ammophila breviligulata</i>	0.1±0.1	<0.1	5	0.1±0.1	0.1	5
<i>Anaphalis margaritacea</i>	0.2±0.2	<0.1	5	P	P	P
<i>Anthoxanthum odoratum</i>	0.1±0.1	<0.1	10	0.0	0.0	0
<i>Arenaria lateriflora</i>	0.0	0.0	0	P	P	P
<i>Aronia prunifolia</i>	0.0	0.0	0	0.0	0.0	0
<i>Aster novi-belgii</i>	0.6±0.6	0.3	5	2.1±1.4	1.1	15
<i>Bartonia paniculata</i>	0.0	0.0	0	0.0	0.0	0
<i>Calopogon pulchellus</i>	2.6±0.6	1.2	70	1.2±0.3	0.6	65
<i>Calluna vulgaris</i>	0.0	0.0	0	0.0	0.0	0
<i>Carex echinata</i>	0.1±0.1	0.1	10	0.0	0.0	0
<i>Carex silicea</i>	<0.1	<0.1	5	0.0	0.0	0
<i>Centaurium umbellatum</i>	0.0	0.0	0	0.0	0.0	0
<i>Drosera intermedia</i>	0.1±0.1	<0.1	5	0.5±0.3	0.3	20
<i>Drosera rotundifolia</i>	0.0	0.0	0	0.3±0.1	0.2	25
<i>Empetrum nigrum</i>	0.0	0.0	0	1.5±1.5	0.8	5
<i>Festuca rubra</i>	0.1±0.1	0.1	10	0.2±0.2	0.1	10
<i>Fragaria virginiana</i>	0.1±0.1	<0.1	5	0.0	0.0	0
<i>Hypericum boreale</i>	<0.1	<0.1	5	0.0	0.0	0
<i>Hypericum virginicum</i>	3.5±1.7	1.6	25	3.5±1.4	1.8	65
<i>Iris versicolor</i>	0.2±0.2	0.1	5	0.5±0.5	0.3	5
<i>Juncus balticus</i>	12.4±1.6	5.8	100	8.6±1.1	4.4	95
<i>Juncus canadensis</i>	0.6±0.4	0.3	15	2.1±0.7	1.1	50
<i>Juniperus horizontalis</i>	0.0	0.0	0	P	P	P
<i>Luzula campestris</i>	0.0	0.0	0	0.0	0.0	0
<i>Lycopodium inundatum</i>	0.0	0.0	0	1.4±1.2	0.6	15
<i>Lycopus uniflorus</i>	3.9±1.9	1.8	40	2.2±0.8	1.1	30
<i>Lysimachia terrestris</i>	0.0	0.0	0	1.2±0.7	0.6	25
<i>Myrica pensylvanica</i>	4.6±1.7	2.1	50	4.8±1.9	2.4	45
<i>Platanthera clavellata</i>	0.1±0.1	0.1	5	0.2±0.2	0.1	5
<i>Poa pratensis</i>	0.0	0.0	0	0.0	0.0	0
<i>Potentilla tridentata</i>	0.0	0.0	0	0.0	0.0	0
<i>Rhinanthus crista-galli</i>	0.0	0.0	0	0.0	0.0	0
<i>Rosa virginiana</i>	0.1±0.1	0.1	10	0.1±0.1	<0.1	5
<i>Rumex acetosella</i>	0.0	0.0	0	0.0	0.0	0
<i>Scirpus americanus</i>	0.0	0.0	0	1.2±0.8	0.6	25
<i>Sisyrinchium angustifolium</i>	0.1±0.1	<0.1	5	P	P	P
<i>Smilacina stellata</i>	0.0	0.0	0	0.0	0.0	0
<i>Solidago sempervirens</i>	0.1±0.1	<0.1	5	0.0	0.0	0
<i>Spiranthes romanzoffiana</i>	0.0	0.0	0	0.0	0.0	0
<i>Trientalis borealis</i>	0.4±0.3	0.2	10	0.0	0.0	0
<i>Trifolium repens</i>	0.0	0.0	0	0.0	0.0	0
<i>Vaccinium angustifolium</i>	0.0	0.0	0	0.2±0.2	0.1	5
<i>Vaccinium macrocarpon</i>	182.5±18.6	84.3	100	163.3±9.8	82.6	100
<i>Viola lanceolata</i>	1.9±0.6	0.9	50	1.6±0.6	0.8	45
unidentified	0.0	0.0	0	0.0	0.0	0

¹P = present; data are based on twenty random 50 cm x 50 cm quadrats per site.

vantii is sometimes codominant with *Myriophyllum tenellum*, and both of these species frequently have an epiphytic freshwater sponge (*Heteromeyenia macounii*). Although characteristic of certain fresh pools in various parts of the island, *Sparganium angustifolium* and *Nuphar variegatum* are not abundant. *Potamogeton perfoliatus* var. *bupleuroides* and *Hippuris vulgaris* are apparently confined, on the

island, to the pool complex at West Light, which is characterized by higher (neutral) pH and higher conductivity (see numbers 5 & 6, Table II). In some of these embayments a species of *Nitella* is particularly abundant. Rather than forming associations, any one of these aquatics can be a dominant in a pool or portion of a pool system.

Where slopes are gradual, there is a band of wetland vegetation surrounding the pools. At higher levels the band is replaced by the previously described Cranberry Heath vegetation. It is likely that both Cranberry Heath and wetland borders of pools are periodically inundated, but the border vegetation, being lower, would be inundated for longer periods.

Species characteristic of pool borders (in approximate order of frequency) include: *Scirpus americanus*, *Eleocharis palustris*, *Juncus balticus*, *Viola lanceolata*, *Ranunculus flammula* var. *filiformis*, *Hypericum boreale*, *Agrostis stolonifera*, *Lycopus uniflorus*, *Triadenum fraseri*, *Juncus bulbosus*, *Juncus pelocarpus* var. *sabulnensis*, and *Lysimachia terrestris*. In predominantly sandy areas *Eriocaulon septangulare* may be common. Certain bryophytes may be important components of pond-edge vegetation; notably *Drepanocladus exannulatus*, *Aulocomium palustre*, *Cladopodiella fluitans*, and various *Sphagnum* spp. Somewhat less frequent vascular plants include *Scirpus validus*, *Carex echinata*, *C. canescens* ssp. *disjuncta*, *C. viridula*, *Juncus articulatus*, *Potentilla palustris* var. *parviflora*, *Bidens frondosa*, *Bidens connata* var. *petiolata*, and *Lathyrus palustris* var. *macrantha*.

Where the slopes surrounding pools are relatively steep, Cranberry Heath vegetation (often with *Sphagnum* moss) will extend to the water's edge. No floating *Sphagnum* mats were observed.

Certain isolated pools are much frequented by horses and by gulls and terns. There are without any aquatic vegetation and they have borders ranging from bare mud to a more or less continuous turf comprised of various low growing and decumbent species, including *Tillaea aquatica*, *Sagina procumbens*, *Ranunculus flammula* var. *filiformis*, *Juncus bufonius*, *J. nodosus*, *Agrostis stolonifera*, *Centunculus minimus*, *Hypericum boreale*, and *Viola lanceolata*.

(h) *Brackish Ponds*. Brackish ponds (Figs. 17 & 18) comprise some 51.8 ha, or 1.5% of the island's area (Table IV, Fig. 6). Brackish ponds receive seawater overwash during violent storms, and this affects both their size and the chemical composition of their waters (spot measurements of the concentrations of major ions and other parameters for two brackish ponds are in Table II).

In water 0.5 to 1.5 m deep these brackish pools have dense growths of *Ruppia maritima* mixed with *Potamogeton pectinatus* (the latter comprising up to 15% of the total cover). Shallower water and edges are either bare or have swards of *Eleocharis parvula*. In some places along sandy margins various other halophytes occur, including *Plantago maritima*, *Limosella subulata*, *Rumex maritimus*, *Atriplex patula* var. *hastata*, *Spergularia marina* var. *leiosperma*, *Juncus bufonius* var. *halophilus*, *Tillaea aquatica*, *Centunculus minimus*, and *Puccinellia* sp. At higher levels around these pools *Agrostis stolonifera*, *Agropyron repens*, *Sagina procumbens*, *Juncus balticus*, *Potentilla pacifica*, *Carex hormathodes*, *Sonchus* ssp., *Solidago sempervirens*, and *Achillea lanulosa* are prevalent, with *Spartina pectinata*, *Ammophila breviligulata*, and *Ligusticum scoticum* on relatively well-drained knolls.

Wallace Lake and East Wallace Lake receive seawater inflow more frequently and are consequently very brackish. *Zostera marina* is the only submersed vascular aquatic here. No vascular plants presently occur around the shore in contrast to the situation described by St. John (1921) in 1913, when seawater inflows and sand deposition into the lake basin may have been less.



Fig 14. Freshwater pond near West Light. The dominant emergent macrophyte is *Hippuris vulgaris*. The floating-leaved plant is *Potamogeton oblongus*, and emergent *Scirpus americanus* is in the foreground.

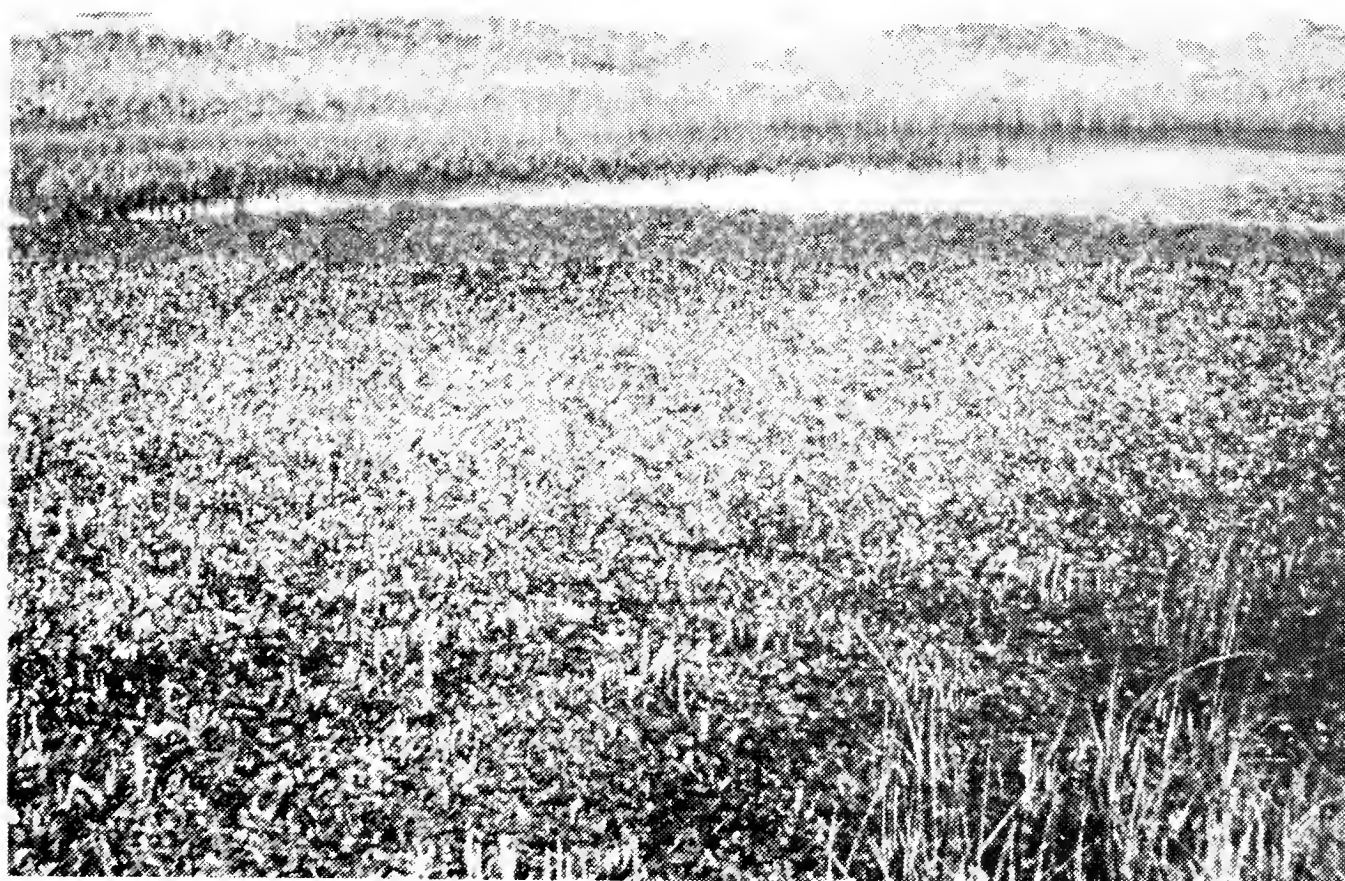


Fig 15. Freshwater pond near West Light, with dense stand of *Potamogeton oblongus*.

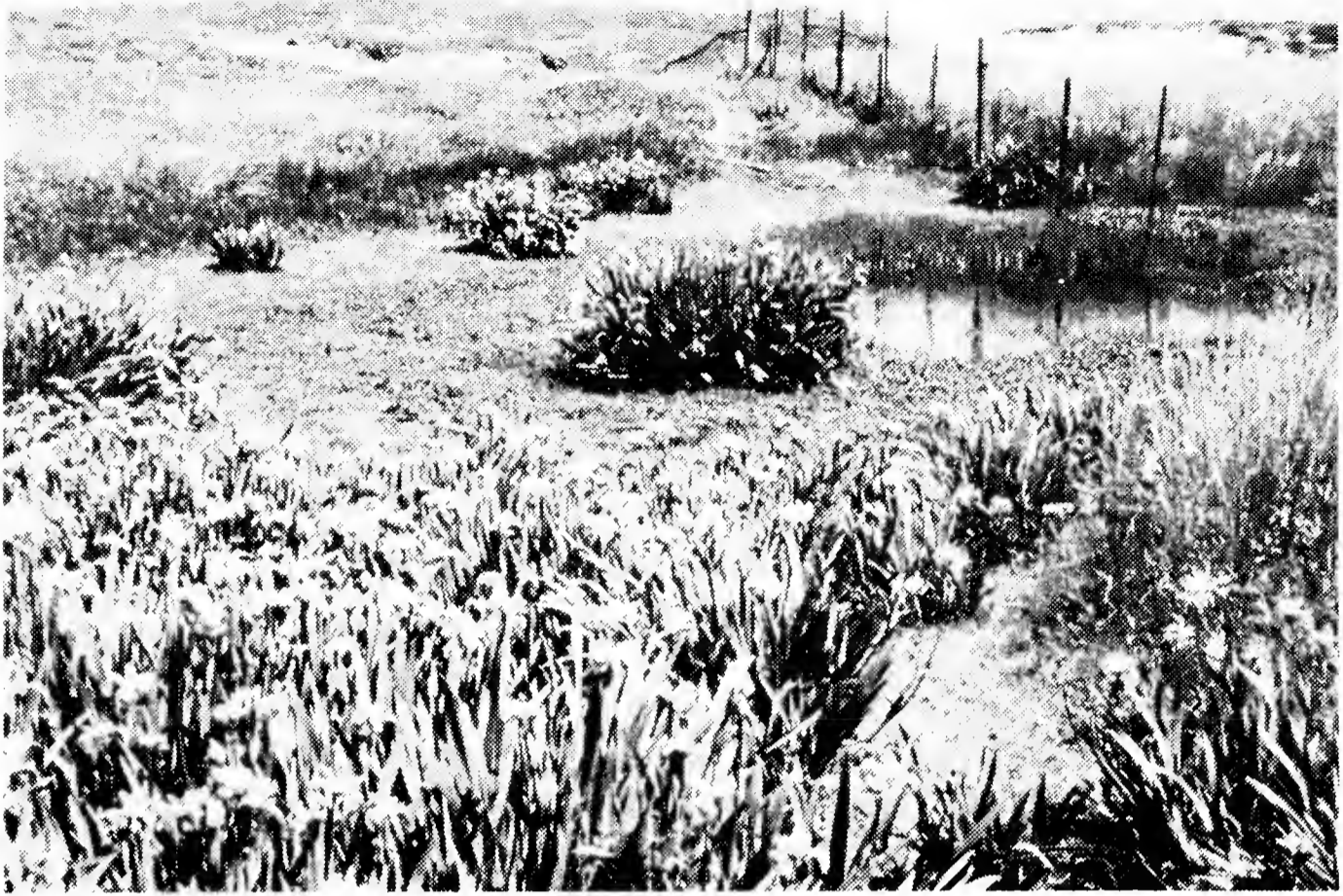


Fig 16. Freshwater pond near Main Station, with *Iris versicolor* and *Potamogeton oblongus*.



Fig 17. Sward of *Eleocharis parvula* around the edges of a brackish pond near No. 3 Life Saving Station.

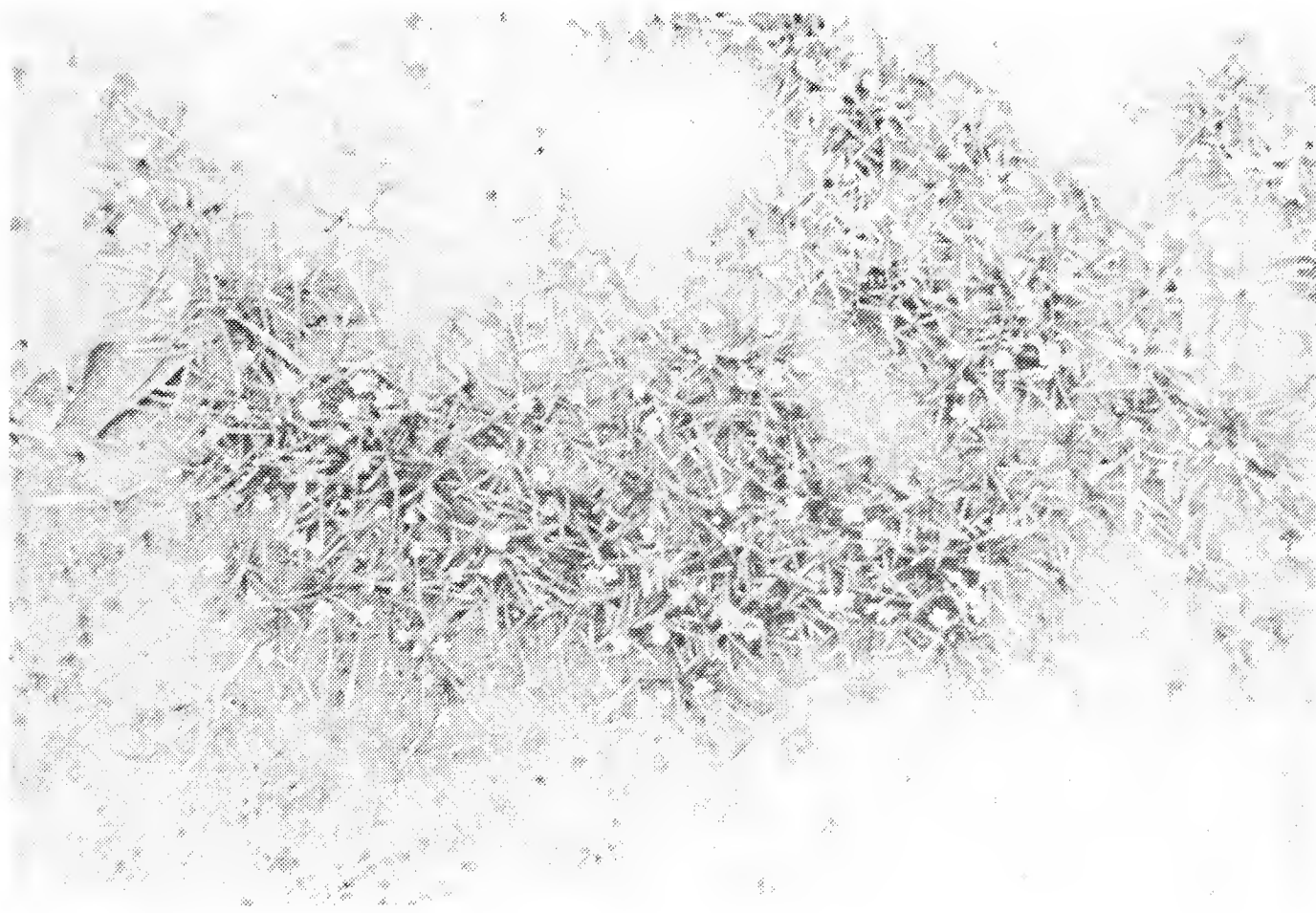


Fig 18. *Limosella subulata*, less than 2 cm high, on moist sand beside brackish pool near No. 3 Life Saving Station.

4. SUCCESSIONAL TRENDS

Conclusions regarding succession are based entirely on circumstantial evidence, but this has frequently been the basis for interpretations of succession in ecological studies. Such interpretations may be modified and improved as new information accumulates.

Since Marram-Forb vegetation occurs only along the oceanic shores, it appears that it is maintained by active wind deposition of sand. The Marram communities also are characterized by windblown sand but they are frequently inland and often receive only eroded sand from older shifting dunes and blowouts. With decreasing sand deposition, Marram communities appear to be replaced by Marram-Fescue vegetation, which, with a longer period of stability is apparently replaced by Shrub Heath vegetation. This latter community is confined to stable and protected inland sites. With increased sand deposition Shrub Heath and Marram-Fescue vegetation may be replaced by a more Marram-dominated community. Only the sand-loving Marram (*Ammophila breviligulata*; Greek *Amos* = sand, *philein* = love) is adapted to establish on and grow up through rapidly accumulating sand. Extensive smothering of vegetation by windblown sand has been documented (see section 2(e) and St. John 1921).

There is also evidence for a succession in pond and pond-edge vegetation. One of the pools at West Light appears to have infilled and separated from periodic seawater inflow quite recently, judging by the lack of organic material on the sandy bottom. It was likely somewhat brackish in the recent past but, although the pH is still relatively high, the salt level and conductivity are relatively low (Table X, no. 6). *Potamogeton perfoliatus* var. *bupleuroides* is dominant in water 0.5 to 1.0 m deep in this pool, and patches of *Scirpus maritimus* and *Sparganium angustifolium* occur

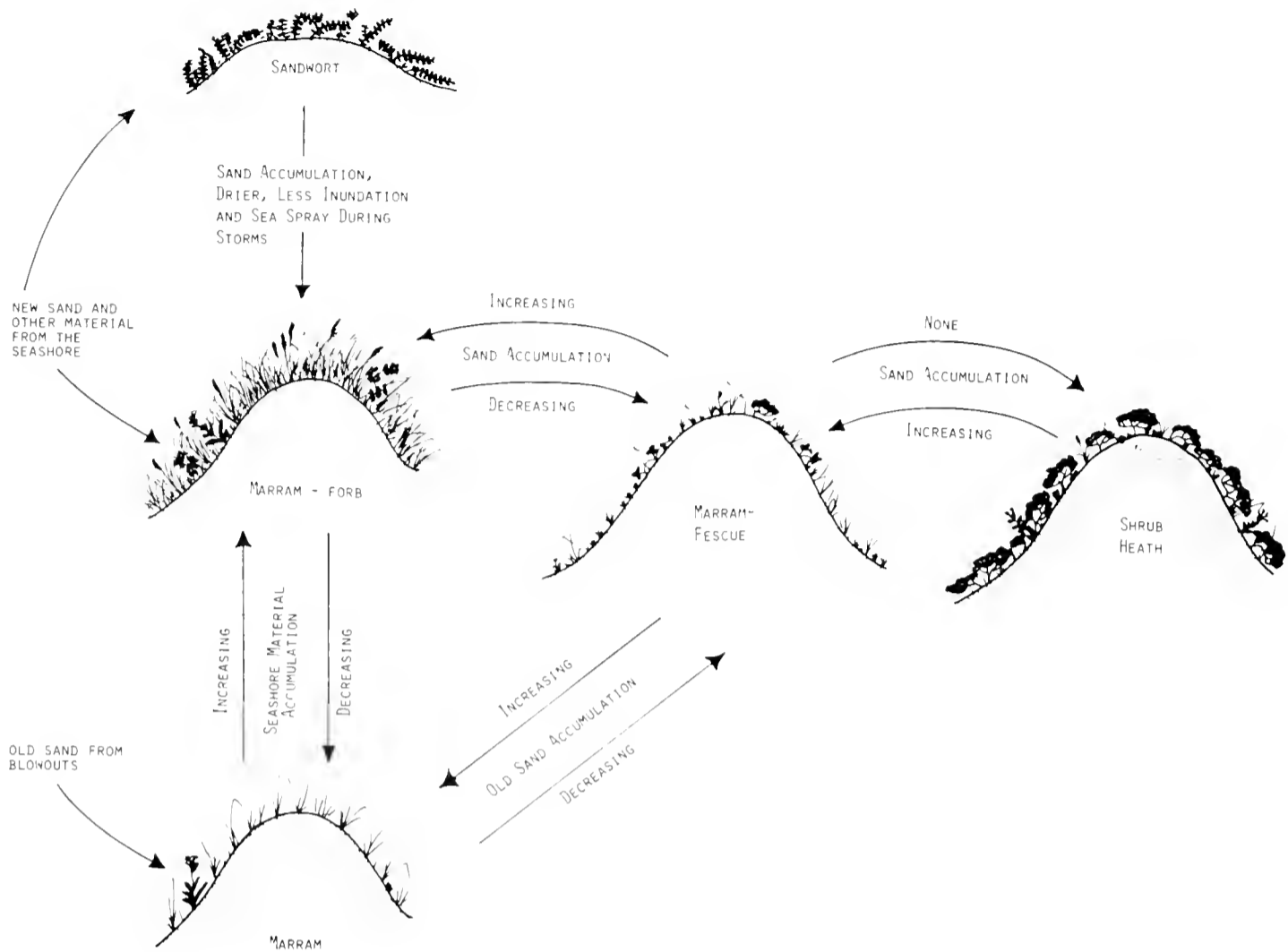


Fig 19. Summary of probable vascular plant succession on dry sites.

in water up to 0.5 m deep. *Spergularia marina* var. *leiosperma*, *Limosella subulata*, and *Juncus bufonius* occur on the moist shores. The higher pH, the predominantly sandy bottom and shores, and the halophytic species composition of the West Light pool suggests a succession of vegetation in newly formed pools, beginning with species adapted to higher salt levels when the pools are first formed and isolated from the sea. This may be followed by a decrease in salt content and conductivity accompanied by replacement by species that are not adapted to (and do not require) high salt levels. Gradually pH and perhaps nutrient availability decline, organic matter increases, and pools become increasingly acidic, with a group of softwater aquatic species (see 3(g)) becoming prevalent. Of course new seawater inflows can occur, with a return to salty or at least brackish conditions. Other evidence for a succession from brackish to fresh water vegetation, and the periodic inflow of seawater restoring brackish vegetation is discussed under section 3(e) and summarized in Fig. 20.

With continuous sand deposition in pools accompanied by increasing time of isolation from the sea, a brackish pool or a fresh pool may be replaced by Cranberry Heath. Exposure of old peat layers beneath pure sand along the coast suggests that dense and sparse Marram vegetation on dunes has replaced wetlands or heaths in some areas.

5. FLORISTIC COMPOSITION AND PHYTOGEOGRAPHY

The total recorded flora of Sable Island is comprised of 154 native species and 79 introduced species (see note on the distinction in section 6). Introduced species have taken over some islands to the exclusion of native and endemic taxa (Melville 1979). This has not been the case on Sable Island. Almost all of the native species

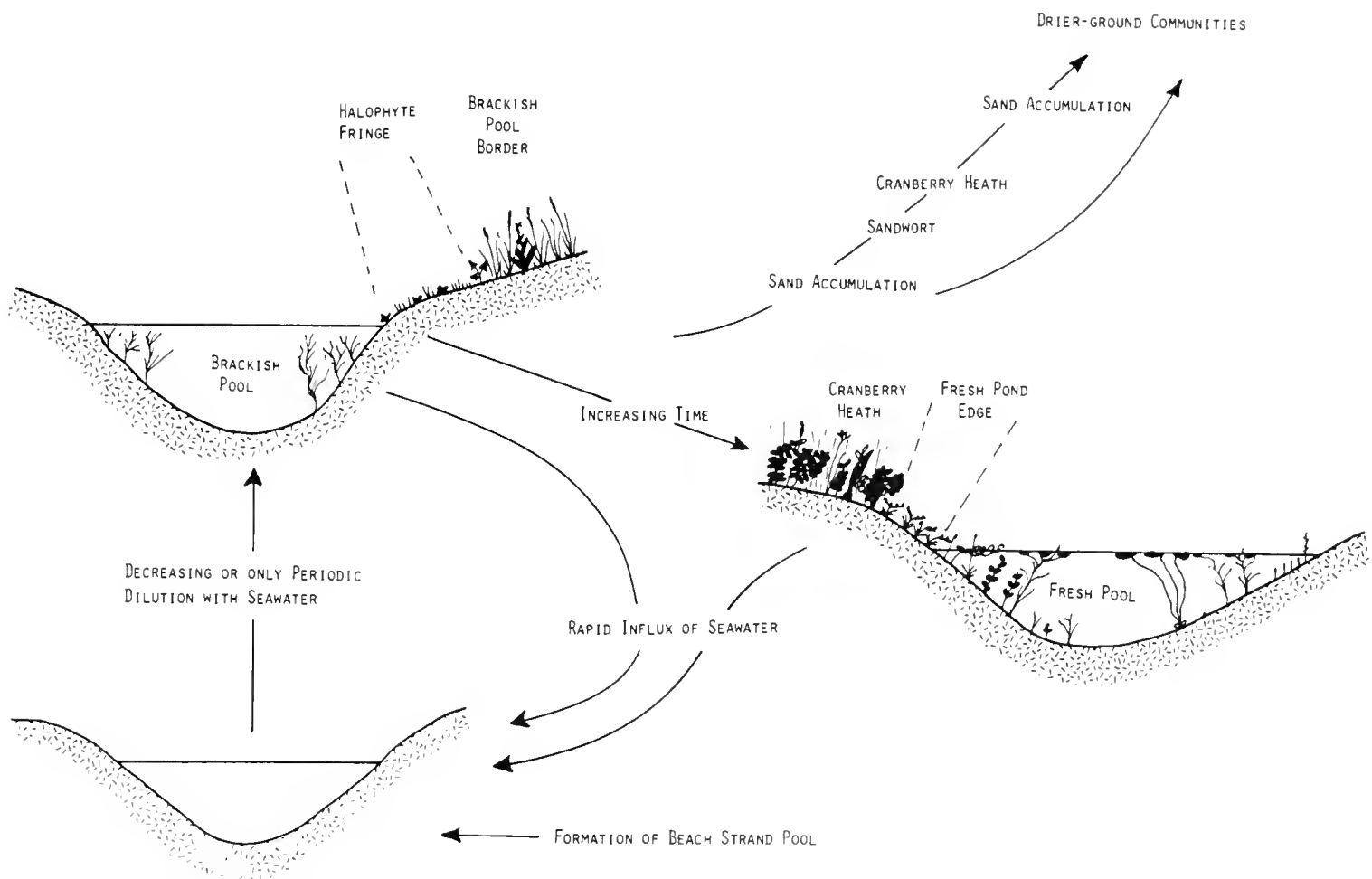


Fig 20. Summary of probable vascular plant succession in pools and pool borders.

found by the early botanists are still present (although some are rare) and the major plant communities are characterized by native species. Despite the intensive introduction of woody plants (section 2(d) and section 6 preamble) and disturbance due to cultivation, livestock, and feral horses, an introduced weedy flora has not become well established and introductions are generally confined to disturbed areas near buildings. In fact, many of the introduced species found by earlier botanists are now extinct, since they were not recorded during our survey (see section 6).

(a) *Phytogeography*

St. John (1921) classified the native flora of Sable Island into three major groups on the basis of the geographical distributions of the constituent species. His separations are somewhat arbitrary and here we take a more general view emphasizing distributional limits.

Most of the native flora is typical of mainland Nova Scotia and northeastern North America (e.g. *Eriocaulon septangulare*, *Lysimachia terrestris*, *Juncus articulatus*, *Myriophyllum tenellum*, and *Viburnum cassinoides*). Many generally widespread species occur (including *Convolvulus sepium*, *Cornus canadensis*, *Drosera rotundifolia*, *Smilacina stellata*, and *Scirpus vallisus*). In addition there are many species that are widespread along the north Atlantic Coast (including *Ammophila breviligulata*, *Eleocharis parvula*, *Lathyrus maritimus*, *Rumex maritimus*, and *Zostera marina*). The portion of the flora that is characteristic of the general region comprises about 95 taxa representing 62.5% of the native flora (Table XII). The remaining 70 are characteristic of areas to the north, to the south, across the Atlantic, or are generally restricted to a small geographical area.

Boreal. Twenty-four native taxa on Sable Island representing 15.8% of the native flora (Table XIII), are characteristic of areas to the north. The distribution of *Em-*

Table XII Phytogeographic affinities of the Sable Island flora.

	No. of Taxa	%
Characteristic of the general region (northeastern, generally widespread, widespread along the Atlantic coast)	95	62.5
Boreal	24	15.8
Southern	8	5.3
Amphi-Atlantic	2-4	1.3-2.6
Restricted	13	8.6
Unknown (phytogeography not readily ascertained)	8	5.3

Table XIII List of plant taxa with northern affinity occurring on Sable Island.

<i>Anaphalis margaritacea</i> (L.) Benth. & Hook. var. <i>subalpina</i> Gray
<i>Angelica lucida</i> L.
<i>Carex deflexa</i> Hornem.
<i>Empetrum nigrum</i> L.
<i>Euphrasia bottnica</i> Kihlm.
<i>Fragaria virginiana</i> Duch. var. <i>terrae-novae</i> (Rydb.) Fern. & Wieg.
<i>Galium trifidum</i> L. var. <i>trifidum</i>
<i>Hippuris vulgaris</i> L.
<i>Juniperus communis</i> L. var. <i>megistocarpa</i> Fern. & St. John
<i>Juniperus horizontalis</i> Moench.
<i>Lonicera villosa</i> (Michx.) R. & S. var. <i>pubescens</i>
<i>Lycopodium inundatum</i> L.
<i>Potentilla pacifica</i> Howell
<i>Potentilla palustris</i> (L.) Scop. var. <i>parviflora</i> (Raf.) Fern.
<i>Potentilla tridentata</i> Ait.
<i>Prenanthes nana</i> (Bigel.) Torr.
<i>Ranunculus flammula</i> L. var. <i>filiformis</i> DC.
<i>Rhinanthus crista-galli</i> L.
<i>Sparganium angustifolium</i> Michx.
<i>Spiranthes romanzoffiana</i> Cham.
<i>Senecio pseudo-arnica</i> Less.
<i>Thalictrum pubescens</i> Pursh. var. <i>hebecarpum</i> (Fern.) Boivin
<i>Torreyochloa pallida</i> (Torrey Church var. <i>fernaldii</i> (A.S. Hitchc.) Dore ex Koyama & Kawano
<i>Triglochin palustris</i> L.

Table XIV List of plant taxa with southern affinity occurring on Sable Island.

<i>Carex emmonsii</i> Dewey
<i>Myrica pensylvanica</i> Loisel
<i>Rhus radicans</i> L. ssp. <i>radicans</i>
<i>Teucrium canadense</i> L.
<i>Gnaphalium obtusifolium</i> L.
<i>Viola lanceolata</i> L.
<i>Sisyrinchium angustifolium</i> Mill.
<i>Viola primulifolia</i> L.

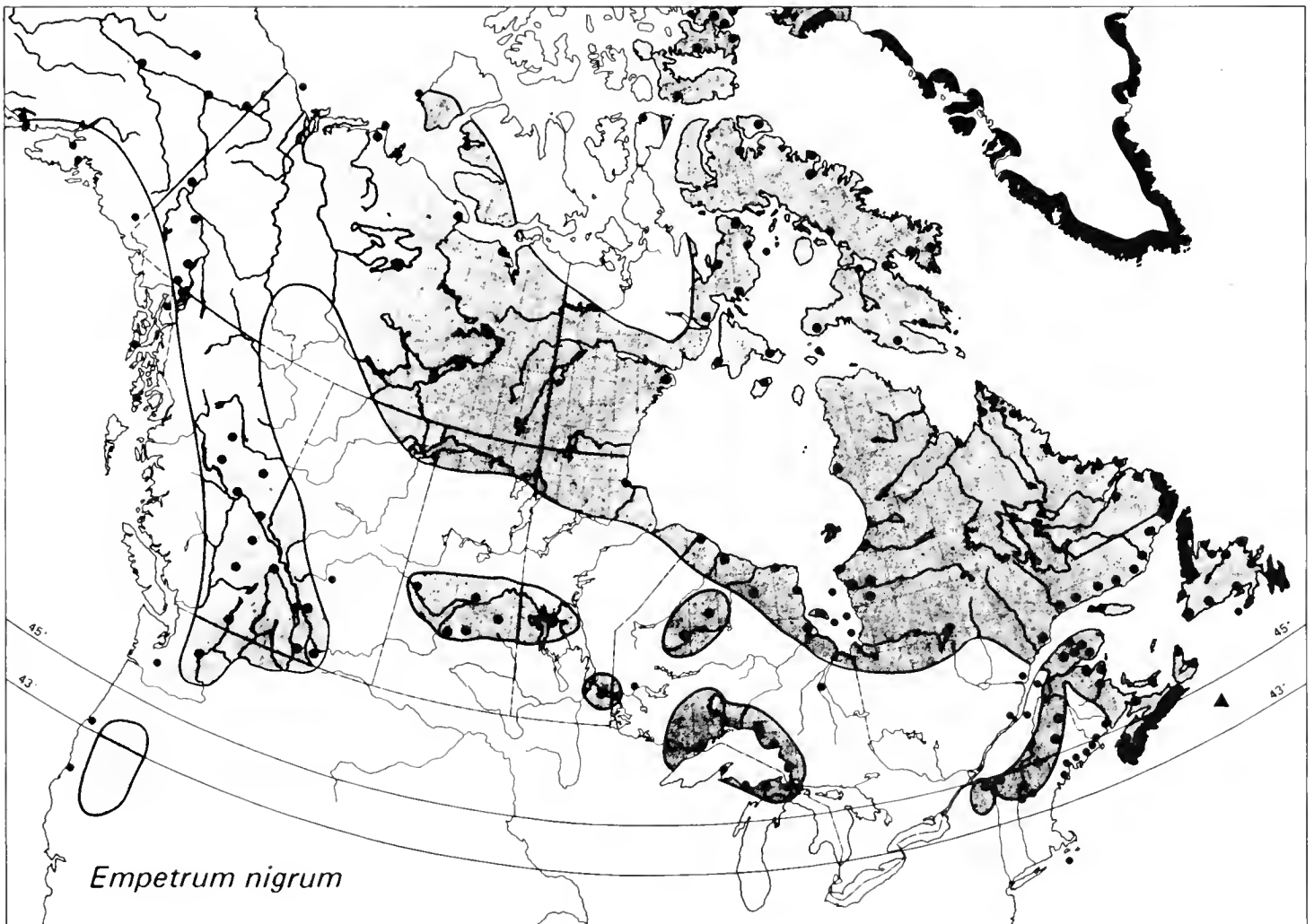


Fig 21. North American distribution of *Empetrum nigrum* based on Fernald (1925), Hultén (1970) and specimens at CAN and DAO. Sable Island is shown with a solid triangle.

petrum nigrum (Fig. 21) provides a good example. With few exceptions its area of geographical distribution is north of 45°N and it is on the southern edge of its range on Sable Island. The examples of boreal species extend beyond vascular plants, and include the lichen *Coelocaulon aculeatum* (I. Brodo, pers. comm.). With regard to the fauna, the Least Sandpiper is near the southern limit of its breeding range on Sable Island (McLaren 1981).

Southern. At least 8 taxa on Sable Island, representing 5.3% of the native flora are characteristic of regions to the south (Table XIV) and these species are at or very near to their northern geographical limits. A good example is provided by *Rhus radicans* var. *radicans* (Fig. 22). Sable Island represents the absolute northeastern limit of this species. Among the bryophytes, *Fontinalis sullivantii* and *Dicranum condensatum* are both rare in the Maritimes and are at their northern limits on Sable Island (R. Ireland, pers. comm.). A southern affinity is also present in the fauna, an example being the northernmost breeding colony of the Roseate Tern (McLaren 1981).

Amphi-Atlantic. Two of the native plants belonging to this category have a very restricted North American distribution but are widespread in Europe. The distribution of *Potamogeton oblongus* (Fig. 23) provides a good example, and corresponds generally to the distribution of *Juncus bulbosus* (Hultén 1958). *Polygonum raii* also belongs to this category but like *Centaureium umbellatum*, its status as a native plant on Sable Island has been questioned. *Lobelia dortmanna* has an amphi-Atlantic distribution but is much more widespread in North America than the preceding species. Two or four native species represent 1.3 or 2.6 of the native flora respectively.

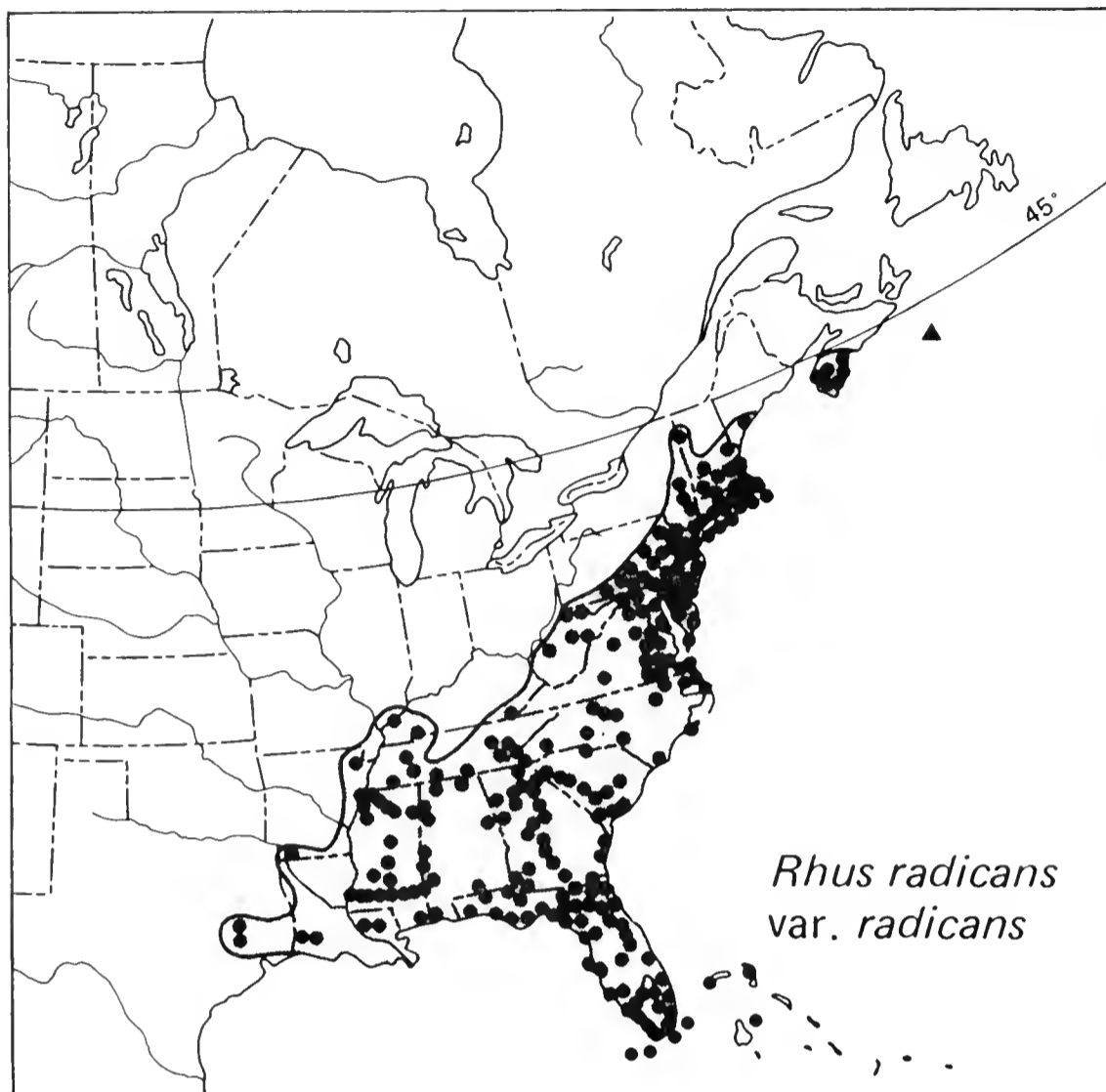


Fig 22. Distribution of *Rhus radicans* var. *radicans* based on Gillis (1971) and specimens at CAN and DAO. Sable Island is indicated with a solid triangle.

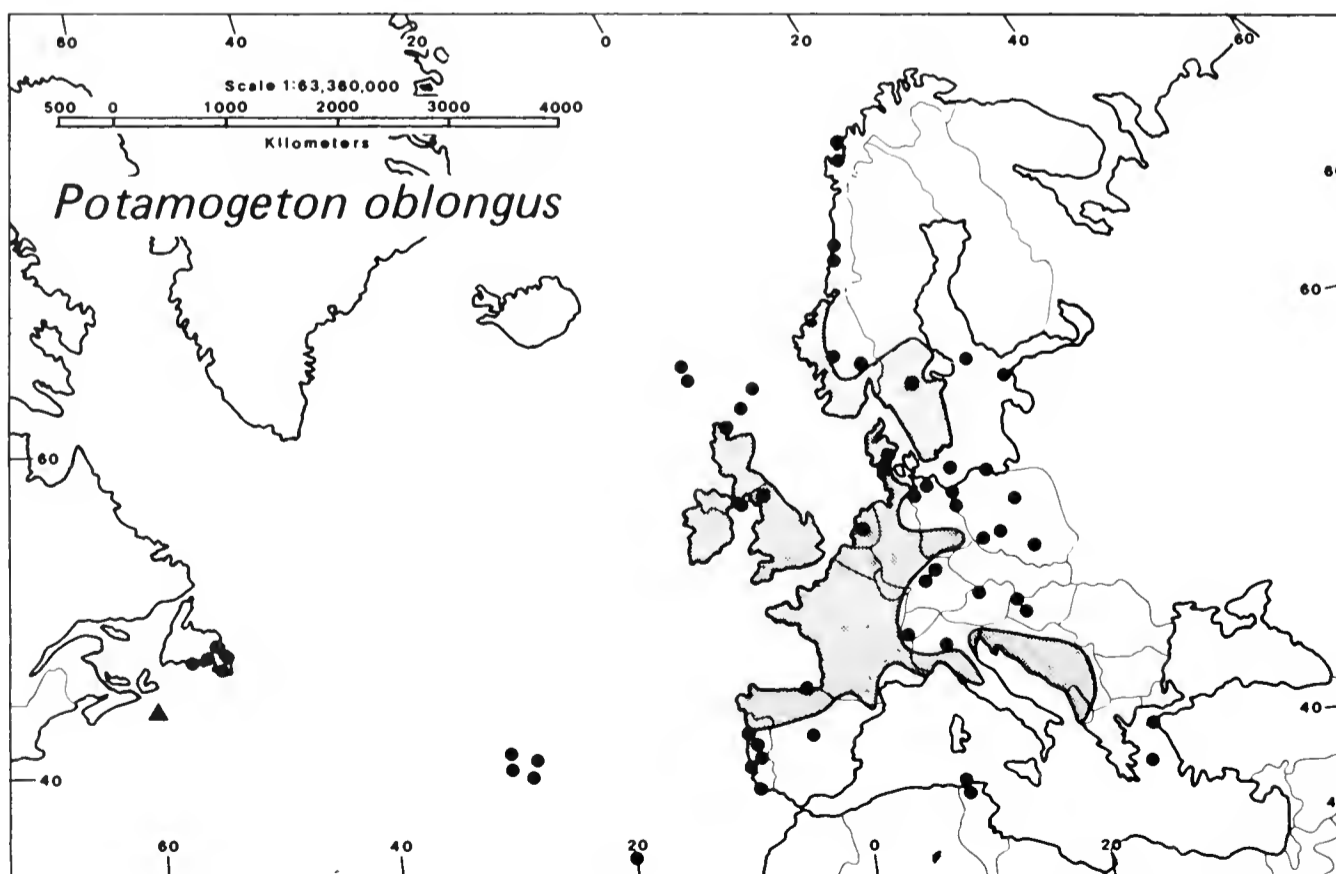


Fig 23. Distribution of *Potamogeton oblongus* based on Hultèn (1958) and specimens at CAN and DAO. Sable Island is indicated with a solid triangle.

Table XV List of restricted plant taxa occurring on Sable Island (+ = type locality, ** = endemic, * = largely endemic.)

	<i>Juniperus communis</i> L. var. <i>megistocarpa</i> Fernald & St. John
†*	<i>Juncus pelocarpus</i> Mey. var. <i>sabulonensis</i> St. John
	<i>Platanthera lacera</i> (Michx.) Don var. <i>terrae-novae</i> (Fern.) Luer
†*	<i>Calopogon tuberosus</i> (L.) BSP var. <i>latifolius</i> (St. John) Boivin
†	<i>Polygonum hydropiperoides</i> Michx. var. <i>psilostachyum</i> St. John
	<i>Rubus X arcuans</i> Fernald & St. John
†*	<i>Lathyrus palustris</i> L. var. <i>retusus</i> Fernald & St. John
†**	<i>Epilobium nesophilum</i> Fern. var. <i>sabulonense</i> (Fern.) Fern.
†**	<i>Oenothera cruciata</i> Nutt. var. <i>sabulonensis</i> Fernald
†*	<i>Bartonia paniculata</i> (Michx.) Muhl. var. <i>sabulonensis</i> Fernald
†	<i>Lycopus uniflorus</i> Michx. var. <i>ovatus</i> Fernald
	<i>Agalinus neoscotica</i> (Greene) Fernald
†**	<i>Hieracium scabrum</i> Michx. var. <i>leucocaula</i> Fernald & St. John

Restricted. Thirteen taxa have been reported from Sable Island that have a very restricted total distribution (Table XV). This represents 8.6% of the native flora (Table XII). Some of these were described by St. John (1921) as "endemic" taxa. An endemic plant is one that occurs in a very limited geographical area. Such plants are especially vulnerable to interference by man and domestic animals and by competition from introduced weeds and crop plants (Melville 1979). The distinctive features of the restricted taxa of Sable Island (Table XV) have not been considered sufficiently discrete for recognition at the species level and all have been accorded the rank of form or variety by the authors recognizing them. These taxa are recognized by some authors, notably St. John (*loc. cit.*) and Fernald (1950), but are disregarded completely by others, presumably because they are considered to be indistinct variations on the common theme of a more widespread taxon. A careful study of variation in the taxa, and in their close relatives, and a consideration of the effects of environment may help to resolve some of these differences of opinion. It is not our purpose here to make taxonomic judgments other than to say that we are presently unaware of any comprehensive study that indicates that the restricted taxa should not be recognized. Interestingly, our preliminary studies of *Calopogon tuberosus* (L.) BSP var. *latifolius* (St. John) Boivin suggest that it is worthy of taxonomic recognition, despite its rejection by many recent authors (Catling and Lucas, in prep.).

Of the thirteen restricted taxa, three are endemic to Sable Island and four are also known from a limited area in the Gulf of St. Lawrence (Magdalen Islands, St. Pierre and Miquelon, or southwestern Newfoundland). Sable Island is the type locality for 9 of the restricted taxa (Table XV).

In the following paragraphs we have listed each of the restricted taxa (in alphabetical order of their genus names), with their places of publication, the most up-to-date information on total distribution and reference to their distinguishing features. Details regarding their occurrence on the island may be found in section 6.

Restricted Taxa

Agalinus neoscotica (Greene) Fernald (*Agalinus paupercula* (Gray) Britton var. *neoscotica* Pennell and St. John, Boston Society of Natural History Proceedings, 36(1):93. 1921). This species, although rather restricted, is common where it occurs (*i.e.* Sable Island and western Nova Scotia). It was described from Middleton, Nova Scotia (type probably at ND-G). *Agalinus neoscotica* is distinguished by its calyx lobes, which exceed the calyx tube and the relatively short corolla with scarcely spreading lobes.

- Bartonia paniculata* (Michx.) Muhl. var. *sabulonensis* Fernald. (*B. iodandra* Robinson var. *sabulonensis* Fernald, Boston Society of Natural History Proceedings, 36(1):89. 1921). This variety was described from Sable Island (type at GH), and was subsequently reported from St. Pierre and Miquelon (Fernald 1950, p. 1165). It is distinguished by the dichotomously branching inflorescence, more clavate peduncles, basally connate calyx with oblong lobes, and corolla 3-5 mm long.
- Calopogon tuberosus* (L.) BSP var. *latifolius* (St. John) Boivin, (= *Calopogon pulchellus* (SW) R.Br. f. *latifolius* St. John, Boston Society of Natural History Proceedings, 36(1):67. 1921). This small, wide-leaved variety was described from Sable Island (type at GH) and subsequently reported from the Magdalen Islands (Fernald 1950, p. 476). It is distinguished by its broadly lanceolate leaves, which approximately equal the height of the very short scape.
- Epilobium nesophilum* (Fernald.) var. *sabulonense* (Fernald.) Fernald. (*Epilobium molle* Torr. var. *sabulonense* Fernald; *Rhodora* 20:31. 1918). Described from Sable Island (type at GH), where it was found around fresh pools at No. 3 Life Saving Station. This variety has apparently not been found elsewhere (Fernald 1950, p. 1059). It is distinguished by its oblong-lanceolate leaves with a blunt or merely acutish (instead of attenuate) tip, and longest fruiting pedicels 1.0 - 1.5 cm long.
- Hieracium scabrum* Michx. var. *leucocaula* Fernald and St. John, *Rhodora*, 16:182. 1914. This variety was described from Sable Island (type at GH) and has never been reported from anywhere else. The variety *leucocaula* is distinguished from other varieties by its possession of both glands and dense white tomentum to 0.7 mm long on the lower internodes, more than 15 crowded leaves, and both leaf surfaces glandular pilose (Fernald 1950, p. 1566).
- Juncus pelocarpus* Mey. var. *sabulonensis* St. John, Boston Society of Natural History Proceedings, 36(1):67. 1921. This variety was described from Sable Island (type at GH), but was subsequently reported also from southwestern Newfoundland (Fernald 1950, p. 416). It differs from the typical variety in being a smaller, prostrate plant with curving culms.
- Juniperus communis* L. var. *megistocarpa* Fernald and St. John, Boston Society of Natural History Proceedings, 36(1):58. 1921. The type (GH) of this large-fruited, trailing variety is from the Magdalen Islands but Sable Island collections are cited in the original description. This is the only variety of *J. communis* that occurs on Sable Island. It occurs along coasts from Nova Scotia to Newfoundland, Labrador, Ungava, and Hudson Bay.
- Lathyrus palustris* L. var. *restusus* Fernald and St. John, Boston Society of Natural History Proceedings, 36(1):81. 1921. Described from Sable Island (type at GH), the range of this variety was subsequently extended to the islands of St. Pierre and Miquelon (Fernald 1950, p. 935). The leaves are notched at the rounded leaf apex.
- Lycopus uniflorus* Michx. var. *ovatus* Fernald and St. John, Boston Society of Natural History Proceedings, 36(1): 92. 1921. Described from Sable Island (type at GH), but reports from Canso, N.S. and the state of Oregon accompanied the type description. This was the only variety reported from the island by St. John, but interestingly was not included by Fernald (1950, p. 1246). This variety is distinguished by its more or less sessile, ovate-lanceolate leaves, which are coarsely serrate with forwardly directed teeth.
- Oenothera cruciata* Nutt. var. *sabulonensis* Fernald, *Rhodora*, 51:67. 1949. Described from Sable Island (type at GH), this variety has apparently not been reported elsewhere. Obovate-oblong petals, canescent-strigose stems, and crowded leaves are characteristic.

Platanthera lacera (Michx.) Don var. *terraenovae* (Fernald) Luer. (*Habenaria lacera* (Michx.) R. Brown var. *terrae-novae* Fern., *Rhodora*, 28:21. 1926). This variety with less deeply lacerate lip divisions and creamy flowers was described from Newfoundland (type at GH) and is known only from Newfoundland and Sable Island, Nova Scotia (Luer 1975).

Polygonum hydropiperoides Michx. var. *Psilostachyum* St. John, *Boston Society of Natural History Proceedings*, 36(1):71. 1921. This glabrous variety was described from Sable Island (type at GH) but locations in the state of Washington were given along with the type description, and it was subsequently reported from Shelburne Co., Nova Scotia.

Rubus X arcuans Fernald & St. John, (*Rubus arcuans* Fernald & St. John, *Boston Society of Natural History Proceedings*, 36(1):78. 1921). This variety was described from Prince Edward Island (type at GH) but specimens from Sable Island, elsewhere in Nova Scotia, and Massachusetts were cited with the original description and its range has apparently not been extended beyond that point (Fernald 1950, p. 843). Distinctive features include abundant strong prickles, thickened at the base, and relatively large dark coriaceous leaves.

(b) Provincially Rare Taxa

Eight taxa occur on Sable Island that have been listed as rare in Nova Scotia (Maher *et al.* 1978, Table XVI). Two of these have not been recently observed. All are listed in section 6 with general comments on habitat and status. Other plants on the island may be rare in the province but judgments on this await additional taxonomic and distributional evidence.

Table XVI Plant taxa reported from Sable Island that are listed as "rare" in Nova Scotia (Maher *et al.* 1978). (° = not recently observed.)

Centunculus minimus L.

Coeloglossum viride (L.) Hartm. var. *virescens* (Muhl.) Luer

° *Epilobium nesophilum* Fern. var. *sabulonense* Fern.

Juncus bulbosus L.

Juncus pelocarpus Mey. var. *sabulonensis* St. John

Potamogeton oblongus Viviana

° *Senecio pseudo-arnica* Less.

Tillaea aquatica L.

(c) Summary of occurrence of significant taxa

Most (*i.e.* 17 of 19) of the significant (restricted, rare, endemic) species occur in vegetation types that together account for less than 5.8% of the present island surface (Table XVIII). These vegetation types, the heathlands, fresh ponds and pond borders, are the most threatened on the island. They are the most easily destroyed by accumulating sand, and they take the longest time to develop.

6. ANNOTATED LIST OF VASCULAR PLANTS

This section includes information on habitat, status and distribution on the island of 154 native and 79 introduced taxa. The list is arranged in phylogenetic sequence. Introduced taxa are marked with an asterisk (*). In some cases there has been dispute over origin. For example, some botanists have considered *Anthoxanthum odoratum* native on Sable Island (Macoun 1899, p. 218A), while others have treated it as an introduction (Erskine 1953). Similarly, St. John (1921) has suggested the possibility that *Centaureum umbellatum* is native to Sable Island, contrary to the suggestion of numerous other authors. In general, however, the distinction between native and introduced taxa is not contentious.

Table XVIII Community affiliation of various significant taxa and the areal extent of these community types on the island.

Taxon	Habitat				Significance		
	Brackish Pool borders	Fresh Pools and borders	Marran-Fescue and Marram	Cranberry Heath	Shrub Heath	Restricted	Rare in N.S.
<i>Agalinus neoscotica</i>		x		x		x	
<i>Bartonia paniculata</i> var. <i>sabulonense</i>				x		x	
<i>Calopogon tuberosus</i> var. <i>latifolius</i>				x			
<i>Centunculus minimus</i>		x					x
<i>Coeloglossum viride</i> var. <i>virescens</i>	x				x		x
<i>Epilobium nesophilum</i> var. <i>sabulonense</i>		x			x		x
<i>Hieracium scabrum</i> var. <i>leucocaula</i>					x		
<i>Juncus bulbosus</i>		x					x
<i>Juncus pelocarpus</i> var. <i>sabulonense</i>		x				x	x
<i>Juniperus communis</i> var. <i>megistocarpa</i>					x		
<i>Lathyrus palustris</i> var. <i>retusus</i>		x				x	
<i>Lycopus uniflorus</i> var. <i>ovatus</i>		x					
<i>Oenothera cruciata</i> var. <i>sabulonensis</i>			x			x	
<i>Platanthera lacera</i> var. <i>terrae-novae</i>					x		
<i>Polygonum hydropiperoides</i> var. <i>psilostoachyum</i>		x				x	
<i>Potamogeton oblongus</i>		x					x
<i>Rubus arcuans</i>					x		
<i>Senecio pseudo-arnica</i>							x
<i>Tillaea aquatica</i>	x						x
Total No. Taxa	2	10	2	3	5	13	8
Total Area (ha)	12.1	49.9	1071.5		147.0		
% Island surface	0.4	1.5	31.2		4.3		

Status is based on frequency distribution: rare taxa were recorded from 1-2 locations; occasional taxa were recorded from 3-6; locations and common taxa were recorded from more than seven localities. Plant localities were counted as separate if they lie at least 0.5 km apart.

In brackets following each entry an indication is given of the taxa found during the earlier surveys of J. Macoun (JM) in 1899, H.T. Gussow (HG) in 1911, H. St. John (SJ) in 1913 (St. John 1921), and J.S. Erskine (JE) in 1952 and others reported simultaneously (Erskine 1953), and by us (CFL) during our 1981 survey with a few additional records of P.A. Keddy and A. Wilson. Additional information on previous surveys (specimen documentation, etc.) is provided in the introduction. Specimen vouchers for the 1981 survey were deposited at DAO and MICH, with some additional specimens collected by P. Keddy at CAN.

The names in the following list have been brought up-to-date through reference to recent taxonomic work. Certain older generic and species names are listed in brackets. Varieties reported for the island, but not recently accepted, are also listed in brackets following the species name.

DELETIONS

Sisyrinchium atlanticum Bickn.

Using the key in Gleason and Cronquist (1963) and Gleason (1952), the Sable Island plants key to *S. atlanticum*, (since *S. angustifolium* appears in a couplet with sessile or short-peduncled spathes). However, having examined a large amount of herbarium material at CAN and DAO, the identification of *S. atlanticum* and *S. angustifolium* has become more clear.

Many keys (e.g. Roland & Smith 1969) indicate that plants with stems over 2 mm wide, inner bract of spathe over 15 mm long, and capsule over 4 mm in diameter are referable to *S. angustifolium*. These relatively robust plants differ from the more delicate plants (referred to *S. atlanticum*) in a number of other ways as well. In a recent study, Voss (1972) suggested that the robust plant dries a darker green colour, and has the stems minutely denticulate in the margins. Our observations of plants from all over the northeast confirm these differences. The delicate plants referred to *S. atlanticum* often have a few small bumps on the edges of the stem below the peduncles (under high magnification), but never the distinctly curved teeth seen on the robust plants referable to *S. angustifolium*. The delicate plants have very narrow peduncles which are often bent at a joint at the base of the spathe. The Sable Island plants are clearly *S. angustifolium*, taking these differences into account. They are, however, somewhat narrower than most *S. angustifolium* at the top of the scape, being 2.0-2.5 mm wide.

Our previous report of *S. atlanticum* from Sable Island (Freedman, Catling & Lucas 1982) should be deleted.

Polygonum aviculare L.

The only specimens we have seen were collected in 1913 (weed at Main Station, 19 Aug. 1913, H. St. John 1211 (CAN); weed at No. 3 Life Saving Station, 8 Sept. 1913, H. St. John 1212 (CAN)). These are neither *P. monspeliense* (*P. aviculare* s.1.) nor *P. arenastrum*, and their correct assignment is dependent upon additional taxonomic work (J. McNeill, pers. comm.).

Euphrasia nemorosa (Pers.) Wallr. (*E. americana* Wettst.)

This species was reported by Gussow (St. John 1921, p. 93). The specimen at DAO (H.T.G., Sept. 1911) has been revised to *E. randii* B.L. Robinson var. *randii*.

Hieracium pilosella L.

Vegetative material resembling this species was collected in two Shrub Heath communities (Freedman, Catling & Lucas 1982) and reported in the table summarizing Shrub Heath vegetation. The only vouchers collected were later determined as *H. scabrum*, so *H. pilosella* is to be deleted.

There are no other records to be deleted from previous lists. We have checked all voucher specimens that represent species reported only once or twice, and all were correctly identified. There were earlier, erroneous reports for the island, but these were all corrected by St. John (1921). Most of these earlier errors were never published, being in personal communications and names on herbarium specimen labels.

Comparison with previous surveys

The numbers of native and introduced taxa reported in previous botanical surveys are shown in Table XVII. In general the number of native species has not changed much over the past 81 years. Macoun was the only one to find *Carex deflexa*, *Polypodium virginianum*, and *Utricularia cornuta*. Gussow was the only one to find *Viola incognita* var. *forbesii*. St. John was the only one to find *Lathyrus palustris* var. *retusus*, *Galium trifidum* var. *tinctorium*, and *Prenanthes nana*. Erskine was the only one to find *Cornus canadensis*. We were the only ones to find *Onoclea sensibilis*, *Carex emmonsii*, *Juncus pelocarpus* var. *pelocarpus*, *Drosera intermedia* x *rotundifolia*, *Puccinellia pumila*, *Scutellaria galericulata*, *Spiranthes lacera* var. *lacera*, *Rhus radicans* var. *rydbergii* and *Viola septentrionalis*. All of these unique finds are supported by vouchers in institutional herbaria.

Table XVII Numbers of native and introduced taxa reported in botanical surveys of Sable Island.

	Native	Introduced
J. Macoun (1899)	124	30
H.T. Gussow (1911)	75	8
H. St. John (1913)	132	56
J.S. Erskine (1952)	109	27
B. Freedman, P.M. Catling, Z. Lucas (1981)	135	42

With introduced species the situation is quite different. The major discrepancies in the numbers of introduced taxa (Table XVII) suggest that introduced species and human disturbance on the island reached a peak around 1913. This was shortly after the great afforestation attempt of 1901 (see section 2(d)) when many weedy species were probably introduced accidentally. In addition there still were at this time livestock, farming, and extensive settlement associated with the five life saving stations along the length of the island. The decline of introductions is discussed more extensively below under "Aspects of Status".

Comparisons of the 1981 survey frequency values with past statements of frequency are not likely to be reliable since previously the terms were not quantified and were often used rather loosely.

Aspects of Status

Approximately 67.7% of the recorded flora is native and 32.3% is introduced. Of the 178 species found on Sable Island during our 1981 survey, only 65 (38%) are common plants characteristic of major vegetation types. Of the introduced flora, 46.8% is extirpated and only 6.3% (i.e. five species) is presently common. This contrasts with 5.8% of the total recorded native flora extirpated and 39.2%

Table XIX Status of the total recorded native and introduced taxa on Sable Island.

	Native		Introduced	
	No. Taxa	%	No. Taxa	%
extirpated	9	5.8	37	46.8
rare	52	34.0	27	34.2
occasional	31	20.3	10	12.7
common	61	39.2	5	6.3
Total	153	<100	79	<100

(i.e. 60 species) common (Table XIX). The decline of the 1901 plantings was particularly dramatic (see annotations). Thus, most plants introduced to the island have not been able to maintain themselves, probably due to specific climatic or other environmental conditions. At present, most introduced taxa occur only around habitations or on ground recently disturbed by man. Habitations may provide some protection from the wind. Overall, a quite different situation occurs on many other islands (especially tropical and subtropical) where introduced plants often outcompete and replace some of the native species (Melville, 1979).



Fig 24. Dense stand of *Potamogeton oblongus* in a pool near West Light.



Fig 25. *Juncus bulbosus*, an amphi-atlantic species with a very restricted North American distribution, on damp sand near West Light.

Annotated List

Lycopodiaceae—Club-moss Family

Lycopodium inundatum L.—Bog Club-moss

Occasional, in Cranberry Heath near Main Station and West Light, and less often elsewhere. JM,HG,SJ,CFL.

Osmundaceae—Flowering Fern Family

Osmunda cinnamomea L.—Cinnamon-Fern

Rare, fresh pond edges at West Light and east of Life Saving Station No. 3. JM,HG,SJ,CFL.

Polypodiaceae—Fern Family

Polypodium virginianum L. (*P. vulgare*)—Rock-Polypody

Extirpated, known only from Macoun's 1899 collection "on the old land at Island Pond, very rare". JM.

Onoclea sensibilis L.—Sensitive Fern

Rare. Near West Light. CFL.

Pinaceae—Pine Family

**Pinus mugo* Turra (*Pinus montana*)—Mugo Pine

Extirpated. Of five thousand planted in 1901, six survived to 1913. SJ.

**Pinus sylvestris* L.—Scotch Pine

Rare. A few trees remained from the planting of 10,000 up until 1921 (St. John 1921) but one decumbent plant (Fig. 4) protected among dunes south of Main Station, is a survivor of a recent planting.

**Picea glauca* (Moench) Voss (*P. canadensis*)—White Spruce

Rare. Two trees surviving south of Main Station, about 1/2 m high on slopes in Shrub Heath. 2,500 planted in 1901. SJ,CFL.

Cupressaceae—Juniper Family

Juniperus communis L. var. *megistocarpa* Fern & St. John—Juniper

Common in Shrub Heath. First noted on the island in 1753 (St. John 1921). JM,HG,SJ,JE,CFL.

Juniperus horizontalis Moench.—Creeping Juniper

Common in Shrub Heath. Macoun described a buried specimen with a main stem 15 cm in diameter (St. John 1921, p. 58). JM,SJ,JE,CFL.

Typhaceae—Cat-tail Family

Typha latifolia L.—Common Cat-tail

Apparently extirpated. Previously bordering fresh ponds at the east end of Wallace Lake near Life Saving Station No. 3. JM, SJ.

Sparganiaceae—Bur-reed Family

Sparganium angustifolium Michx.—Narrow-leaved Bur-reed

Occasional in fresh ponds. Locally abundant near West Light. JM,SJ,JE,CFL.

Potamogetonaceae—Pondweed Family

Potamogeton epihydrus Raf.

Common in fresh ponds. JM,SJ,CFL.

Potamogeton oblongus Viviana (*P. polygonifolium*)

Occasional in fresh ponds. JM,SJ,JE,CFL.

Potamogeton pectinatus L.—Sago Pondweed

Rare, only seen in the brackish pond complex near Life Saving Station No. 3, but there locally abundant. JM,SJ,CFL.

Potamogeton perfoliatus L. var. *bupleuroides* (Fern.) Farw.—Red-head Pondweed

Rare, brackish ponds at Life Saving Station No. 3 and West Light. JG,HG, SJ,JE,CFL.

Potamogeton pusillus L. (*P. capitatus*)

Possibly extirpated. Previously in brackish ponds. JM,SJ.

Ruppiaceae—Ditch-grass Family

Ruppia maritima L. var. *longipes* Hagstr.—Ditch-grass

Rare, brackish ponds. Locally abundant at Life Saving Station No. 3. JM,SJ,JE,CFL.

Zosteraceae—Eelgrass Family

Zostera marina L.—Eelgrass

Occasional. Found only in East and West Wallace where it is abundant. JM,HG,SJ,CFL.

Juncaginaceae—Arrow-grass Family

Triglochin palustris L.

Rare. Found on mud flats near brackish pond by P.A. Keddy in 1975 (CAN), but not seen by us. JE,CFL.

Poaceae (Gramineae)

**Bromus inermis* Leyss.—Awnless Brome

Rare. Disturbed ground around buildings at Main Station. CFL.

**Bromus secalinus* L.—Cheat Grass

Extirpated. Macoun found it "in meadow grass" and noted that it was "rare". JM.

Festuca rubra L.—Red Fescue

Common, fresh pond edges and Cranberry Heath particularly. JM,HG,SJ,CFL.

Festuca rubra var. *Juncea* (Hack.) Richter—Red Fescue

Common, Marram and Marram-Fescue vegetation. CFL.

Festuca rubra L. var. *glaucescens* (Hartm.) Holm—Red Fescue

Common, Marram-Fescue vegetation in particular. SJ,JE,CFL.

Puccinellia pumila (Vasey) Hitchc.—Alkali-grass

Rare, brackish pools near West Light, north of East Wallace and near Life Saving Station No. 3. CFL.

Torreyochloa pallida (Torrey) Church var. *fernaldii* (A.S. Hitchc.) Dore ex Koyama & Kawano (*Glyceria fernaldii*)—Pale Manna-grass

Rare. Edge of pond near West Light. Macoun's collection is labelled: "in marshy spots, East End". JM,CFL.

**Poa annua* L.—Annual Bluegrass

Occasional. Around habitations and ruins, and also occasionally fresh pond edges. JM,JE,CFL.

**Poa palustris* L.—Fowl-meadow Grass

Rare. Edges of fresh ponds near Life Saving Station No. 3. JM,CFL.

**Poa pratensis* L.—Kentucky Bluegrass

Common. Found in all major vegetation types on the island. JM,HG,SJ,JE,CFL.

**Dactylis glomerata* L.—Orchard-grass

Rare. Around buildings at Main Station. CFL.

**Agropyron repens* L.—Couch-grass

Occasional. Ruins of Life Saving Stations No. 1 and No. 3 and Main Station, also brackish pond edges at No. 3 Station. JM,SJ,JE,CFL.

Agropyron repens (L.) Beauv. f. *pilosum* (Scribn.) Fern.—Couch-grass

Occasional. Seen only in Marram-Forb vegetation. As noted by St. John, this form is less associated with habitations and probably native. See Fernald, M.L. in *Rhodora* 35:183-185. 1933. SJ,JE,CFL.

Elymus arenarius L. var. *villosus* Mey.—Sea Lyme-grass

Probably extirpated. St. John (1921) noted that it was only on a ridge of dunes on the south side of Wallace Lake that was rapidly washing away and he remarked that the population was "in great danger of being destroyed". We could find no plants on the last remaining vestige of this ridge. SJ,JE.

- **Hordeum jubatum* L.—Squirrel-tail Grass
Rare. Brackish pond edges near West Light and at Life Saving Station No. 3. Previously a weed at Main Station (St. John 1921). JM,SJ,CFL.
- Deschampsia flexuosa* (L.) Trin.—Common Hairgrass
Rare in Shrub Heath on Grassy Plains. P.A. Keddy found it several miles east of Life Saving Station No. 3 (CAN). Our (CFL) specimens are referable to var. *montana* (L.) Ledeb. JM,HG,SJ,CFL.
- **Avena sativa* L.—Oat
Extirpated. Previously a weed at Main Station (St. John 1921, p. 63). SJ,JE.
- **Avena sativa* L. var. *orientalis* (Schreb.) Richter—Oriental Oat
Extirpated. Previously a weed at Main Station (St. John 1921, p. 63). SJ.
- Danthonia spicata* (L.) Beauv.—Poverty-grass
Occasional in Shrub Heath. JM,JE,CFL.
- Ammophila breviligulata* Fern.—Marram
Common, dominant over most of the vegetated portion of the island. JM,HG, SJ,JE,CFL.
- Agrostis hyemalis* (Walt.) BSP. (*A. geminata*)—Hairgrass
Common. Both fresh pond margins and Cranberry Heath. SJ,CFL.
- Agrostis stolonifera* L. var. *major* (Gaud.) Farw. (*A. alba*)—Redtop Bentgrass
Common. Fresh pond margins and less often in Cranberry Heath. JM,HG, SJ,JE,CFL.
- **Phleum pratense* L.—Common Timothy
Rare. Life Saving Station No. 1 ruins and Life Saving Station No. 3 ruins and near West Light. JM,SJ,JE,CFL.
- **Alopecurus geniculatus* L.—Meadow Foxtail
Rare. Higher margins of brackish ponds and near ruins of Life Saving Station No. 3 and near West Light. JM,SJ,JE,CFL.
- **Spartina alterniflora* Loisel—Salt-water Cord-grass
Rare. Introduced near Life Saving Station No. 3 to help bind damp sand. CFL.
- Spartina pectinata* Link (*S. michauxiana*)—Slough-grass
Occasional. In water 1 m deep in fresh pond near West Light, pond edges near Grassy Plains and elsewhere on dune crests. JM,HG,SJ,JE,CFL.
- **Anthoxanthum odoratum* L.—Sweet Vernal Grass
Common. Shrub Heath. Macoun (1899) suggested that it may be native. JM, SJ,CFL.
- Dichanthelium acuminatum* (Swartz) Gould & Clark var. *acuminatum* (*P. languinosum* var. *fasciculatum*, *P. huahucae*)—Panic-grass
Occasional. Fresh pond edges and disturbed areas in Cranberry Heath. JM, SJ,JE,CFL.
- **Echinochloa crusgalli* (L.) BSP.—Barnyard-grass
Extirpated. Previously a garden weed. SJ.
- Cyperaceae**—Sedge Family
- Eleocharis palustris* (L.) R. & S.—Spike-rush
Common on borders of fresh ponds. JM,HG,SJ,CFL.
- Eleocharis halophila* Fern. & Brack. (*E. palustris* var. *glaucescens*)—Spike-rush
Occasional. Brackish pond borders and wet sand. JM,SJ,JE,CFL.
- Eleocharis parvula* (R. & S.) Link. (*Scirpus nanus*)—Spike-rush
Rare, forming a dense sward on damp sand and in shallow brackish water north of East Wallace and near Life Saving Station No. 3. JM,HG,SJ,JE,CFL.
- Scirpus pungens* Vahl (*Scirpus americanus*)—Three-square Bulrush
Common, on pond edges. JM,HG,SJ,JE,CFL.

Scirpus acutus Muhl.—Hard-stem Bulrush

Rare or extirpated. Locations uncertain. See note below under *S. validus*. SJ.

Scirpus validus Vahl—Soft-stem Bulrush

Occasional, fresh and slightly brackish ponds. Erskine (1952) listed *Scirpus validus*, suggesting that *Scirpus actus* was a synonym. St. John (1921) considered all collections from the island to be *S. acutus* and gave reasons, but both Gussow's, Macoun's and our collections are apparently referable to *S. validus*. Our collections have spikelets 2x as long as wide instead of ca. 2.5x or more. The scales are rich orange-brown with a strongly contrasting midrib, instead of pale. The flecks on the back of the scales are more or less limited to the midrib region in the upper scales. St. John's specimens, although having short spikelets, have achenes 2.5 mm long and therefore may be referable to unusual plants of *S. acutus*. JM,HG,SJ,JE,CFL.

**Scirpus maritimus* L. var. *maritimus* (*S. paludosus* A. Nels. in part)—Salt-marsh Bulrush

Probably extirpated. Our recent collections referable to the native var. *fernaldii*. SJ,JE.

Scirpus maritimus L. var. *fernaldii* (Buckn.) Beetle—Salt-marsh Bulrush

Rare. Found by us only in a few slightly brackish ponds near West Light, but recorded by Macoun and St. John (1921) from ponds near Wallace Lake. Our collections as well as that of Macoun have 2 stigmas and flat achenes, but unlike var. *fernaldii* the spikelets are relatively short resembling those of var. *maritimus*. JM,SJ,JE,CFL.

Carex hormathodes Fern.—Sedge

Occasional. Fresh pond edges. JM,SJ,JE,CFL.

Carex silicea Olney—Sedge

Common. Marram-Fescue, Shrub Heath and Cranberry Heath vegetation. JM,SJ,JE,CFL.

Carex echinata Murr. subsp. *echinata*—(incl. var. *cephalantha*)—Sedge

Common. Fresh pond edges and Cranberry Heath. JM,SJ,CFL.

Carex canescens L. ssp. *disjuncta* (Fern.) Toivonen—Sedge

Occasional. Fresh pond edges. JM,SJ,JE,CFL.

Carex deflexa Hornem.—Sedge

Possibly extirpated. Known only from Macoun's 1899 collection: "on old banks. Main Station". JM.

Carex emmonsii Dewey (*C. albicans*)—Sedge

Rare, in Shrub Heath on Grassy Plains and east of West Light. CFL.

Carex viridula Michx. (*C. oederi* var. *pumila*)—Sedge

Occasional. Fresh pond edges and moist sandy dune hollows. JM,SJ,JE,CFL.

Eriocaulaceae—Pipewort Family*Eriocaulon septangulare* With.

Occasional. Fresh pond borders and moist sand, most abundant between West Light and Main Station. JM,SJ,JE,CFL.

Juncaceae—Rush Family*Juncus bufonius*—Toad-rush

Occasional. Fresh pond edges and moist sand. JM,HG,SJ,JE,CFL.

Juncus bufonius L. var. *halophilus* Buchenau & Fern.—Toad-Rush

Occasional. Both fresh and brackish pond edges. SJ,CFL.

Juncus tenuis Willd.—Path-rush

Common, Disturbed Heathland and pond edges, especially along horse trails. JM,HG,SJ,JE,CFL.

Juncus balticus Willd. var. *littoralis* Engelm.—Baltic-rush

Common. An important component of the Cranberry Heath community and also pond edges and moist sand. JM,HG,SJ,JE,CFL.

Juncus canadensis J. Gay—Rush

Common. Cranberry Heath on fresh pond edges. JM,HG,SJ,JE,CFL.

Juncus pelocarpus Mey. var. *pelocarpus*—Rush

Rare. Moist sand west of Main Station near the north side of the island. CFL.

Juncus pelocarpus Mey. var. *sabulonensis* St. John—Rush

Rare. Fresh pond edges and moist sandy hollows near Main Station. JM, SJ,JE,CFL.

Juncus bulbosus L.—Rush

Occasional. Fresh pond edges and moist sand. JM,SJ,JE,CFL.

Juncus articulatus L. var. *obtusatus* Engelm.—Jointed-rush

Common. Fresh pond edges and moist sand. HG,SJ,JE,CFL.

Luzula campestris (L.) DC var. *multiflora* (Ehrh.) Celak.—Woodrush

Common. Shrub Heath. SJ,CFL.

Liliaceae—Lily Family

Smilacina stellata (L.) Desf.—False Solomon's-seal

Common. Shrub Heath and to a lesser extent Marram-Fescue vegetation. JM, HG,SJ,JE,CFL.

Iridaceae—Iris Family

Iris versicolor L.

Common. Fresh pond margins. JM,HG,SJ,JE,CFL.

Sisyrinchium angustifolium Mill.

Common. Fresh pond edges and Cranberry Heath. JM,SJ,JE,CFL.

Orchidaceae—Orchid Family

Coeloglossum viride (L.) Hartm. var. *virescens* (Muhl.) Luer (*Habenaria viride*)
—Bracted Orchid

Occasional. Shrub Heath. JM,JE,CFL.

Platanthera clavellata (Michx.) Luer (*Habenaria clavellata*)—Club-spur Orchid

Occasional. Shrub Heath and Cranberry Heath. JM,HG,SJ,JE,CFL.

Platanthera lacera (Michx.) G. Don var. *terrae-novae* (Fern.) Luer (*Habenaria lacera*)
—Ragged Fringed-orchid

Occasional. Shrub Heath and Cranberry Heath. JM,HG,SJ,JE,CFL.

Calopogon tuberosus (L.) BSP. var. *tuberosus* (*C. pulchellus*)—Grass-pink

Common. Cranberry Heath. JM,HG,SJ,JE,CFL.

Calopogon tuberosus (L.) BSP. var. *latifolius* (St. John) Boivin—Grass-pink

Rare. Moist peaty sand with *Lycopodium inundatum*. Approximately 300 plants in a dune hollow NE of West Light. A few possibly referable to this variety elsewhere in Cranberry Heath. SJ,JE,CFL.

Spiranthes lacera (Raf.) Raf. var. *lacera*—Northern Slender Ladies'-tresses

Rare. Shrub Heath in the Grassy Plains area. CFL.

Spiranthes romanzoffiana Cham.—Hooded Ladies-tresses

Rare. Cranberry Heath in Grassy Plains area. Macoun's 1899 collection was from damp, boggy spots, but has no more precise location. JM,CFL.

Salicaceae—Willow Family

**Salix viminalis* L.—Osier Willow

Extirpated. Previously a planted specimen survived and grew to 6 feet tall, at Life Saving Station No. 3. SJ.

Myricaceae—Wax-myrtle Family

Myrica pensylvanica Loisel (*M. carolinensis*)

Common. An important component of the vegetation in Marram-Fescue, Shrub Heath and Cranberry Heath communities. JM,HG,SJ,JE,CFL.

Betulaceae—Birch Family

**Betula pendula* Roth.—European Birch

Extirpated. One of the 1901 plantings survived until 1913 at Life Station No. 4 but was overtopped by Marram (St. John 1921). SJ.

**Betula alba* L.—European White Birch

Extirpated. Of 2000 trees planted in 1901, a few still survived in 1913 but none were over 2' in height (St. John 1921). SJ.

Polygonaceae—Buckwheat Family

**Rumex acetosella* L.—Red Sorrel

Common. Marram-Fescue and Shrub Heath. JM,HG,SJ,JE,CFL.

**Rumex crispus* L.—Sour Dock

Rare. Brackish pond borders north of East Wallace and near Life Saving Station No. 3. JM,SJ,CFL.

Rumex maritimus L. (*R. fueginus*)—Golden Dock

Rare. Brackish pool borders north of East Wallace and near Life Saving Station No. 3. JM,SJ,JE,CFL.

Rumex orbiculatus Gray (*R. britannica*)—Great Water Dock

Rare. Seen only near Life Saving Station No. 3 on high banks of a brackish pool and reported only from the same area by St. John (1921). JM,SJ,CFL.

**Polygonum* sp. (*aviculare* group)—Prostrate Knotweed

Possibly extirpated. Brackish pond borders, ruins and paths. JM,SJ.

**Polygonum convolvulus* L.—Black Bindweed

Extirpated. Previously a weed at Main Station (St. John 1921). JM,SJ.

**Polygonum cuspidatum* Sieb. and Zucc.—Japanese Knotweed

Beside a shed at Main Station. CFL.

Polygonum hydropiperoides Michx. var. *psilostachyum* St. John—Mild Water-pepper

Common. Fresh ponds. JM,HG,SJ,JE,CFL.

**Polygonum hydropiper* L.—Common Smartweed

Extirpated. Previously around buildings at Main Station (St. John 1921). JM.

**Polygonum lapathifolium*—Smartweed

Rare. Collected by Macoun "in a potato field at East End Post" in 1899, and by us on moist sand near pool at West Light. JM,CFL.

**Polygonum lapathifolium* L. var. *prostratum* Wimmer—Smartweed

Rare. Brackish pond borders near West Light. SJ,JE,CFL.

**Polygonum persicaria* L.—Lady's-thumb

Extirpated. Previously a weed at Main Station (St. John 1921). SJ.

Polygonum raii Bab.—Ray's Knotweed

Rare. In raw sand bordering brackish pools near West Light and at Life Saving Station No. 3. SJ,CFL.

**Polygonum scabrum* Moench—Smartweed

Extirpated. Previously a weed at Main Station. (St. John, 1921). SJ.

Chenopodiaceae—Goosefoot Family

**Chenopodium album* L.—Lamb's-quarters

Rare. Brackish pond borders. Previously a weed at Main Station (St. John 1921). JM,SJ,JE,CFL.

**Chenopodium bushianum* Aellen—Goosefoot

Extirpated. Erskine's location unknown. JE.

Chenopodium rubrum L.—Coast-blite

Rare. Edges of brackish ponds at Life Saving Station No. 3. JM,HG,SJ,JE,CFL.

Atriplex prostrata Buch. (*Atriplex patula* var. *hastata*)—Spearscale

Occasional. Edges of brackish ponds. JM,HG,SJ,JE,CFL.

Portulacaceae—Purslane Family

**Portulaca oleracea* L.—Common Purslane

Extirpated. Previously a weed in the garden at Main Station (St. John 1921). SJ.

Caryophyllaceae—Pink Family

**Spergula arvensis* L.—Corn-spurrey

Extirpated. Previously a weed at Main Station (St. John 1921). JM,SJ.

Spergularia marina (L.) Griseb. var. *leiosperma* (Kindb.) Gurke—Sand-spurrey

Rare. Raw sand around edges of brackish pools at West Light, north of East Wallace and Life Saving Station No. 3. JM,HG,SJ,JE,CFL.

Sagina procombens L.—Birdseye

Occasional. Edges of brackish and fresh ponds. JM,SJ,JE,CFL.

Moehringia lateriflora Fenzl (*Arenaria lateriflora*)—Grove Sandwort

Common. Mostly in Shrub Heath. JM,HG,SJ,JE,CFL.

Honckenya peploides (L.) Ehrh. (*Arenaria peploides*)—Seabeach Sandwort

Common. Dominant over extensive areas at either end of the island and in the East and West Wallace areas. Also in Marram communities but less important there. Often binding windblown sand into mounds. JM,HG,SJ,JE,CFL.

**Stellaria graminea* L.—Common Stitchwort

Occasional. A weed at Main Station and about ruins. JM,SJ,JE,CFL.

**Stellaria media* (L.) Cyrill.—Common Chickweed

Occasional. Ruins of Life Saving Stations and at Main Station. JM,SJ,JE,CFL.

**Cerastium vulgatum* L.—Common Mouse-ear Chickweed

Occasional. Around Life Saving Stations and in Shrub Heath vegetation. JM, SJ,JE,CFL.

**Silene noctiflora* L.—Night-flowering Catchfly

Extirpated. Previously a weed at Life Saving Station No. 3 (St. John 1921). SJ.

Nymphaeaceae—Water-lily Family

Nuphar variegatum Durand in Clinton (*Nymphotozanthus variegatum*)—Yellow pond-lily

Common. Fresh ponds. JM,SJ,JE,CFL.

Ranunculaceae—Crowfoot Family

**Ranunculus acris* L.—Common Buttercup

Rare. Disturbed areas around Main Station and at Life Saving Station No. 3. JM,SJ,JE,CFL.

Ranunculus cymbalaria Pursh—Seaside Crowfoot

Rare. Sandy edges of brackish pond near Life Saving Station No. 3 and north of East Wallace. JM,SJ,JE,CFL.

Ranunculus flammula L. var. *filiiformis* DC. (*R. reptans*)—Spearwort

Common. Edges of fresh ponds. JM,HG,SJ,JE,CFL.

**Ranunculus repens* L.—Creeping Buttercup

Rare. Main Station. Macoun's 1899 specimen label reads: "a rare introduction about barns". JM,CFL.

Thalictrum pubescens Pursh. var. *hebecarpum* (Fern) Boivin (*T. polygamum*)—Tall Meadow-rue

Common. Shrub Heath. JM,HG,SJ,JE,CFL.

Coptis trifolia (L.) Salisb.—Goldthread

Rare. Shrub Heath near Main Station. Although St. John (1921, p. 75) reported it from “grass-covered dunes”, the label on Macoun’s collection reads: “on the old land among *Empetrum*, very rare. JM,SJ,CFL.

Brassicaceae (Cruciferae)—Mustard Family**Brassica arvensis* (L.) Ktze.—Charlock

Extirpated. Previously a weed around the Life Saving Stations (St. John 1921). JM,SJ,JE.

Cakile edentula (Bigel.) Hook.—Sea-rocket

Common. Sandy seashore and sandy barrens in the East and West Wallace areas. JM,HG,SJ,JE,CFL.

**Capsella bursa-pastoris* (L.) Medic.—Shepherd’s-purse

Rare. Disturbed areas at West Light. JM,SJ,CFL.

**Raphanus sativus* L.—Radish

Extirpated. Previously established at Main Station. SJ.

**Raphanus raphanistrum* L.—Jointed Charlock

Probably extirpated. Previous locality unknown. JE.

**Sisymbrium officinale* (L.) Scop.—Hedge-mustard

Extirpated. Previously a weed at Life Saving Station No. 3 (St. John 1921). SJ.

Droseraceae—Sundew Family*Drosera intermedia* Hayne (*D. longifolia*)—Intermediate Sundew

Rare. Moist sand in Cranberry Heath communities. Seen only near Main Station at site SH7 and pond edges. JM,JE,CFL.

Drosera intermedia x *rotundifolia*

Rare. In moist acid sand of Cranberry Heath at site SH7 near Main Station. CFL.

Drosera rotundifolia L.—Round-leaved Sundew

Common. Fresh pond margins and Cranberry Heath. JM,HG,SJ,JE,CFL.

Crassulaceae—Orpine Family*Crassula aquatica* L. (*Tillaea aquatica*—including reports of *T. vaillantii*)
—Pigmyweed

Occasional. Margins of certain fresh and brackish pools especially those much visited by birds and horses. Main Station, Grassy Plains, Life Saving Station No. 3, West Light. JM,SJ,JE,CFL.

Saxifragaceae—Saxifrage Family**Hydrangea paniculata* Sieb. var. *grandiflora* Sieb.

Extirpated. Of 25 planted in 1901, one survived until 1913 at Life Saving Station No. 3 (St. John 1921). SJ.

Rosaceae—Rose Family*Fragaria virginiana* Duch. var. *terrae-novae* (Rydb.) Fern. & Wieg.—Wild Strawberry

Common. An important component of the Merram-Fescue community and persisting in heath communities. JM,HG,SJ,JE,CFL.

Potentilla norvegica L.—Cinquefoil

Occasional. Pond edges and disturbed areas. JM,HG,SJ,JE,CFL.

Potentilla palustris (L.) Scop. var. *palustris*—Marsh Cinquefoil

Possibly extirpated. Previously at the east end of Wallace Lake on edge of fresh pond (St. John 1921). JM,SJ,JE.

Potentilla palustris (L.) Scop. var. *parviflora* (Raf.) Vern.—Marsh Cinquefoil

Rare. Wet area dominated by *Juncus balticus* and aquatic bryophytes in a Cranberry Heath near Main Station. Previously on a fresh pond margin at the east end of Wallace Lake (St. John 1921). SJ,CFL.

Potentilla tridentata Ait.—Three-toothed Cinquefoil

Occasional. Shrub Heath. JM,HG,SJ,JE,CFL.

Potentilla pacifica Howell (*P. oederi*, *P. egedei* var. *groenlandica*)—Cinquefoil

Occasional. Margins of brackish ponds. JM,HG,SJ,JE,CFL.

Rubus hispidus L.—Bristly Dewberry

Rare or extirpated. Known only from a collection by Macoun, which is at GH unlike most of Macoun's specimens which are at CAN. JM.

Rubus x arcuans Fern. & St. John (*recurvicaulis* x *setosus*)—Dewberry

Common. Shrub Heath. JM,HG,SJ,JE,CFL.

**Rosa rugosa* Thunb.—Rose

Rare. A planted clone persists near Life Saving Station No. 1 (Old Main Station). JE,CFL.

Rosa virginiana Mill.—Virginian Rose

Common. Marram-Fescue and Shrub Heath vegetation. JM,HG,SJ,JE,CFL.

Aronia prunifolia (Marsh.) Rehd. (= *Pyrus floribunda*)—Chokeberry

Common. Shrub Heath and less often Marram-Fescue and Cranberry Heath vegetation. JM,SJ,JE,CFL.

Fabaceae (Leguminosae)—Bean Family

**Cytissus scoparius* (L.) Link.—Scotch Broom

Extirpated. Of 1,000 bushes planted in 1901, only one survived in 1913 (St. John 1921). SJ.

**Trifolium agrarium* L.—Hop-clover

Rare. Disturbed ground around buildings at Main Station. CFL.

**Trifolium hybridum* L.—Alsike Clover

Rare. Disturbed ground along road near Main Station. JM,SJ,CFL.

**Trifolium pratense* L.—Red Clover

Occasional. Around buildings, ruins and along paths and pond edges. HG, SJ,JE,CFL.

**Trifolium repens* L.—White Clover

Common. Disturbed areas and pond edges, especially places much frequented by horses, also in Cranberry Heath. JM,SJ,JE,CFL.

**Vicia cracca* L.—Tufted Vetch

Occasional. Around ruins of Life Saving Stations and near West Light and Main Station grassy meadowland. JE,CFL.

Lathyrus maritimus (L.) Bigel. (*L. japonicus*)—Beach-pea

Common. An important component of Marram-dominated communities. Presence of nitrogen-fixing symbionts improves nutrient quality of the substrate. JM,HG,SJ,JE,CFL.

Lathyrus palustris L. var. *macranthus* (T.G.W.) Fern.—Vetchling

Occasional. Fresh pond edges. JM,HG,SJ,JE,CFL.

Lathyrus palustris L. var. *retusus* Fern. & St. John—Vetchling

Probably extirpated. Fresh pond edges, the exact locality unknown. SJ.

Linaceae—Flax Family

**Radiola linoides* Roth (*Millegrana radiola*)—All-seed

Rare. Knoll with closely cropped grass at West Light. CFL.

Empetraceae—Crowberry Family

Empetrum nigrum L.—Black Crowberry

Common. Shrub Heath. JM,HG,SJ,JE,CFL.

Anacardiaceae—Cashew Family

Rhus radicans L. subsp. *radicans*—Poison Ivy

Rare. With *Ammophila*, *Festuca* and *Achillea* on dune between and north of East and West Wallace. CFL.

Aquifoliaceae—Holly Family

Ilex verticillata (L.) Gray—Winterberry

Rare. Sparse Marram dunes between East and West Wallace. SJ,JE,CFL.

Aceraceae—Maple Family

**Acer platanoides* L.—Norway Maple

Rare. Of 500 planted in 1901, one survived in 1913 (St. John 1921), and one in 1981, near Life Saving Station No. 3. SJ,CFL.

Rhamnaceae—Buckthorn Family

**Rhamnus frangula* L.—Alder-buckthorn

Extirpated. One hundred were planted in 1901 and a few lasted until 1913 (St. John 1921). SJ,JE.

Hypericaceae (Guttiferae)—St. John's-wort Family

**Rhamnus frangula* L.—Alder-buckthorn

Extirpated. One hundred were planted in 1901 and a few lasted until 1913 (St. John 1921). SJ,JE.

Hypericaceae (Guttiferae)—St. John's-wort Family

Hypericum mutilum L. ssp. *boreale* (Britton) J.M. Gillett (*Hypericum boreale*)—St. John's-wort

Common. Mostly fresh pond edges but also Cranberry Heath. JM,HG,SJ,JE,CFL.

Triadenum fraseri (Spach) Gl. (previous records of *Hypericum virginicum* belong here)—Marsh St. John's-wort

Common. Fresh pond edges and Cranberry Heath. JM,HG,SJ,JE,CFL.

Violaceae—Violet Family

Viola incognita Brain. var. *forbesii* Brain.—Violet

Occasional. Shrub Heath. HG,CFL.

Viola lanceolata L.—Lance-leaved Violet

Common. Fresh pond edges and Cranberry Heath. JM,HG,SJ,JE, CFL.

Viola pallens (Banks) Brain.—Violet

Rare. Reported from wet dune hollows and borders of fresh ponds (St. John 1921). SJ,JE.

Viola primulifolia L.—Primrose-leaved Violet

Probably rare, but status and locations uncertain. SJ,JE.

Viola septentrionalis Greene—Violet

Rare. Heathy bank at edge of Cranberry Heath on Grassy Plains and fresh pond edge near Main Station. Previously also near Life Saving Station No. 3 (St. John 1931). SJ,CFL.

Onagraceae—Evening-primrose Family

Epilobium nesophilum Fern. var. *sabulonense* Fern. (*E. palustre* in part)—Willow-herb

Extirpated. Previously on the edges of fresh ponds at Life Saving Station No. 3. JM,SJ.

Oenothera cruciata Nutt. var. *cruciata*—Evening Primrose

Probably occasional, but status and localities not precisely determined. Lumped with *O. parviflora* by some recent authors. JM,SJ,CFL.

Oenothera cruciata Nutt. var. *sabulonensis* fern.—Evening Primrose
Common. Marram-Fescue communities and dry disturbed areas. This species is lumped with *O. parviflora* by some recent authors. JM,SJ,JE,CFL.

Oenothera parviflora L. (*O. muricata*)—Small-flowered Evening-primrose
Common. Mostly Marram-Fescue communities. JM,SJ,JE,CFL.

Haloragaceae—Water-milfoil Family

Myriophyllum tenellum Bigel.

Common. Fresh ponds. JM,HG,SJ,JE,CFL.

Hippuridaceae—Mare's-tail Family

Hippuris vulgaris L.

Rare. Found only in fresh ponds near West Light. JM,HG,SJ,JE,CFL.

Apiaceae (Umbelliferae)—Parsley Family

Ligusticum scoticum L.—Scoth Lovage

Rare. Edges of fresh ponds near West Light and edges of brackish ponds near No. 3 Life Saving Station. SJ,CFL.

**Daucus carota* L.—Wild Carrot

Apparently extirpated. Previously a garden weed at Life Saving Station No. 4 (St. John 1921). SJ.

Angelica lucida L. (*Coelopleurum lucidum* (L.) Fern.)—Angelica

Rare. Banks along the road near West Light. JM,HG,SJ,JE,CFL.

**Pastinaca sativa* L.—Parsnip

Extirpated. Previously planted at the East End Lighthouse (St. John 1921). SJ.

Cornaceae—Dogwood Family

Cornus canadensis L.—Bunchberry

Possibly extirpated. Known only from Dwight's collection without locality data (St. John 1921, p.87). JE.

Ericaceae—Heath Family

**Calluna vulgaris* (L.) Hull—Heather

Rare. Locally dominant north of Life Saving Station No. 3 (Site SH3). Gussow reported it from here and 10 miles west in 1911. R.J. Bouteillier, the island superintendent in 1913 suggested that it was introduced during the great forestry planting (i.e. 1901, St. John 1921, p. 87). HG,SJ,CFL.

Vaccinium angustifolium Ait. (*V. pensylvanicum*)—Low Sweet Blueberry

Common. An important component of Shrub Heath communities. JM,HG,SJ,JE,CFL.

Vaccinium macrocarpon Ait.—Large Cranberry

Common. Dominant in Cranberry Heath Communities. Around 1913, 50-200 barrels were picked and exported every year (St. John 1921, p. 88). JM,HG,SJ,JE,CFL.

Primulaceae—Primrose Family

Lysimachia terrestris (L.) BSP.—Yellow Loosestrife

Common. Fresh pond edges and Cranberry Heath. JM,HG,SJ,JE,CFL.

Trientalis borealis Raf.—Star-flower

Common. Shrub Heath. JM,SJ,JE,CFL.

Centunculus minimus L.—Chaffweed

Rare. Borders of brackish pools and fresh pools much used by birds. Found at Life Saving Station No. 3 ponds, in grassy plains area and north of East Wallace. St. John collected it on the "brackish beach of Wallace Lake" (CAN). Macoun's collection is lacking a definite location. JM,SJ,JE,CFL.

Gentianaceae—Gentian Family

Bartonia paniculata (Michx.) Muhl. var. *sabulonensis* Fern. (*B. iodandra*)—Bartonia
Rare. Cranberry Heath on fresh pond border between West Light and Main Station and Cranberry Heath between Life Saving Station No. 3 and Grassy Plains, and between East Wallace and Life Saving Station No. 3. A total of less than 30 plants seen by us. JM,HG,SJ,CFL.

Menyanthes trifoliata L.—Bogbean

Rare. Previously in fresh ponds (since turned brackish) at Life Saving Station No. 3. Not seen by us but reported to be still present (A. Wilson, pers. comm.) near Main Station. JM,JE,CFL.

Centaurium umbellatum Gilib.—Centaury

Common. Margins of fresh ponds and moist disturbed areas. JM,HG,SJ,JE,CFL.

Convolvulaceae—Morning-glory Family

Calystegia sepium (L.) R. Br. (*Convolvulus sepium*)—Morning-glory

Common. Marram-Forb communities and high banks of brackish ponds at Life Saving Station No. 3. JM,SJ,JE,CFL.

Boraginaceae—Borage Family

**Lappula echinata* Gilib.—Stickseed

Extirpated. A single specimen was previously reported from Main Station (St. John 1921). SJ.

Lamiaceae (Labiatae)—Mint Family

Scutellaria galericulata L.—Common Skullcap

Rare. Only on higher banks of brackish ponds at Life Saving Station No. 3. CFL.

**Galeopsis tetrahit* L. var. *bifida* (Boehm.) Leg. & Court—Hemp-nettle

Extirpated. Previously a weed at Main Station (St. John 1921). SJ.

Lycopus uniflorus Michx. var. *ovatus* (Fern.) (St. John)—Bugleweed

Common. Cranberry Heath and fresh pond edges. JM,HG,SJ,JE,CFL.

Teurium canadense L. var. *littorale* (Bickn.) (Fern.)—Wood-sage

Rare. Higher edges of brackish ponds at Life Saving Station No. 3. SJ,CFL.

Mentha arvensis L.—Mint

Rare. High banks of brackish ponds at Life Saving Station No. 3. SJ,CFL.

Solanaceae—Nightshade Family

**Solanum nigrum* L.—Black Nightshade

Occasional. Disturbed places, high banks of brackish pools and ruins, and less often on the beach strand. JM,HG,SJ,JE,CFL.

**Lycium europaeum* L.—Matrimony-vine

Extirpated. Previously planted and persisting near Life Saving Station No. 3 (St. John 1921). SJ.

Scrophulariaceae—Figwort Family

Agalinus neoscotica (Greene) Fern. *Gerardia neoscotica*)—Gerardia

Common. Fresh pond edges, Cranberry Heath and moist sand. JM,SJ,JE,CFL.

Euphrasia randii B.L. Robinson (*E. purpurea*)—Eyebright

Common. Disturbed areas such as paths through Shrub Heath, also fresh pond shores. JM,HG,SJ,JE,CFL.

Rhinanthus minor L. (*Rhinanthus crista-galli*)—Yellow-rattle

Common. Shrub Heath. JM,HG,SJ,JE,CFL.

Limosella subulata Ives—Mudwort

Rare. Raw sand on brackish pool margins, Life Saving Station No. 3, north of East Wallace and West Light. JM,SJ,JE,CFL.

Lentibulariaceae—Bladderwort Family

Utricularia cornuta Michx.—Horned Bladderwort

Extirpated. Known only from Macoun's 1899 collections (3 sheets at CAN with more than 41 flowering plants.). Macoun described it as "common in muddy places". JM.

Plantaginaceae—Plantain Family

**Plantago lanceolata* L.—Ribgrass

Rare. Edges of brackish ponds near Life Saving Station No. 3. CFL.

Plantago major L. (var. *intermedia*)—Common Plantain

Occasional. Brackish pond margins and disturbed areas. JM, HG, SJ, JE, CFL.

Plantago maritima L. (*P. dicipiens*, *P. juncooides*)—Seaside Plantain

Rare. Brackish pond edges near Life Saving Station No. 3. JM, HG, SJ, JE, CFL.

Rubiaceae—Madder Family

Mitchella repens L.—Partridge-berry

Common. Shrub Heath. JM, HG, SJ, JE, CFL.

Galium trifidum L. var. *trifidum*—Bedstraw

Common. Fresh pond edges. JM, HG, SJ, JE, CFL.

Galium trifidum L. var. *tinctorium* (L.) T. & G. (*G. claytonii*)—Bedstraw

Status and locations uncertain. SJ.

Caprifoliaceae—Honeysuckle Family

Lonicera villosa (Michx.) R. & S. var. *calvescens* (Fern. & Wieg.) Fern. (*L. caerulea* var. *calvescens*)—Mountain Fly-honeysuckle

Probably extirpated. Previous localities unknown. JM, JE.

Linnaea borealis L. var. *longiflora* Torr. (*L. americana*)—Twinflower

Occasional. Shrub Heath. JM, HG, SJ, CFL.

Viburnum cassinoides L.—Wild Raisin

Occasional. Shrub Heath. JM, HG, SJ, JE, CFL.

Lobeliaceae—Lobelia Family

Lobelia dortmanna L.—Water-lobelia

Rare, but listed as abundant by St. John. Fresh pool borders near Main Station. JM, SJ, JE, CFL.

Asteraceae (Compositae)—Aster Family

**Rudbeckia hirta* L.—Coneflower

Extirpated. Known only from Macoun's 1899 record, the specimen being without habitat and precise location. JM.

Bidens connata Muhl. var. *petiolata* (Nutt.) Farw. (*B. tripartita* in part)—Bur-marigold

Rare. Borders of fresh ponds, West Light, between East and West Wallace. HG, SJ, CFL.

Bidens frondosa L.—Bur-marigold

Rare. Borders of fresh ponds at West Light. Macoun's label reads: "by the pond at No. 3 (Life Saving Station) very rare". JM, CFL.

**Anthemis cotula* L.—Mayweed

Extirpated. Previously well established at Main Station (St. John 1921). JM, HG, SJ.

Achillea lanulosa Nutt.—Woolly Yarrow

Common. In all major vegetation types on the island but most important in Marram-Forb and Marram-Fescue. JM, HG, SJ, JE, CFL.

- **Leucanthemum vulgare* Lam. (*Chrysanthemum leucanthemum* var. *Pinnatifidum*)—Ox-eye Daisy
Rare. Disturbed ground at Main Station. SJ,JE,CFL.
- **Matricaria matricarioides* (Less.) Port.—Pineapple-weed
Apparently extirpated. Known only from Erskine's collection. JE.
- **Artemesia stelleriana* Besser—Beach Wormwood
Occasional. Several large vigorous clumps along the north side of the island in high Marram dunes in areas of accumulating sand. CFL.
- Senecio pseudo-arnica* Less.—Ragwort
Possibly extirpated. Previously reported from gulches near the sea at the top of the beaches'' by St. John (1921). Macoun's specimen came from ''exposed sands at East Point''. JM,HG,SJ.
- Solidago sempervirens* L.—Seaside Goldenrod
Common. Present in all major vegetation types on the island, but most important in Marram and Marram-Fescue communities. JM,HG,SJ,JE,CFL.
- Aster novi-belgii* L. var. *novi-belgii*—New York Aster
Common. Shrub Heath and Cranberry Heath and to a lesser extent in Marram-Fescue and on fresh pond margins. JM,HG,SJ,JE,CFL.
- Aster novi-belgii* L. var. *litoreus* Gray—New York Aster
Status and locations uncertain. JM,SJ.
- Gnaphalium obtusifolium* L.—Catfoot
Occasional. Shrub Heath. JM,HG,SJ,JE,CFL.
- **Gnaphalium uliginosum* L.—Low Cudweed
Occasional. Edges of fresh ponds much frequented by birds and horses and disturbed ground at Main Station. JM,SJ,CFL.
- Anaphalis margaritacea* (L.) Benth. & Hook. var. *subalpina* Gray—Pearly Everlasting
Common. Marram-Fescue and to a lesser extent in Shrub Heath. JM,SJ,JE,CFL.
- **Cirsium arvense* (L.) Scop.—Canada Thistle
Rare. Although listed as spreading by St. John (1921, p. 96) seen only at Life Saving Station No. 3 and at Main Station by us. JM,HG,SJ,CFL.
- **Centaurea nigra* L.—Knapweed
Rare, on disturbed, grassy, Shrub Heath east of West Light. CFL.
- Prenanthes trifoliata* (Cass.) Fern.—Rattlesnake-root
Common. Shrub Heath. JM,HG,SJ,JE,CFL.
- Prenanthes nana* (Bigel.) Torr.—Rattlesnake-root
Probably extirpated. Known only from St. John's 1913 collection from ''turf covered dunes'' (St. John 1921, p. 97). SJ.
- Hieraceum scabrum* (Michx.) var. *leucocaula* Fern. & St. John—Hawkweed
Common. Shrub Heath. JM,HG,SJ,JE,CFL.
- **Taraxacum officinale* Weber—Dandelion
Rare. Disturbed ground around ruins of buildings at Life Saving Station No. 3. JM,SJ,JE,CFL.
- **Sonchus asper* (L.) Hill—Spiny-leaved Sow-thistle
Rare. Higher edges of brackish pools and ruins at Life Saving Station No. 3. SJ,JE,CFL.
- **Sonchus uliginosus* Bieb. (*S. arvensis* var. *glabrescens*)—Sow-thistle
Rare. About the ruins of Life Saving Station No. 3 and disturbed areas at Main Station. JE,CFL.
- **Cichorium intybus* L.—Chicory
Extirpated. Previously a weed at Main Station (St. John 1921). SJ.
- **Leontodon autumnalis* L.—Fall-dandelion
Common. Disturbed areas, especially disturbed pond edges, paths and to a lesser extent in Shrub Heath. JM,HG,SJ,JE,CFL.



Fig 26. *Bartonia paniculata* var. *sabulonensis*, a variety endemic to Sable Island, photographed near West Light.



Fig 27. *Calopogon tuberosus* var. *latifolius*, a variety of the Grass Pink Orchid endemic to Sable Island and the Magdalen Islands, photographed near West Light.



Fig 28. A freshwater sponge (*Heteromeyenia macounii*) attached to the submerged stems of *Myriophyllum tenellum* in a freshwater pool near Main Station.



Fig 29. Clumps of *Ilex verticillata* and *Rhus radicans* var. *radicans* near East Wallace.

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**PROCEEDINGS OF MEETINGS
1983-84
HALIFAX CHAPTER**

1st Ordinary Meeting, 19 October, 1983

“Continuous fermentation of potato wastes for the small scale production of alcohol for use in gasohol.” R.G. Woodside and M. Comberback. Technical University of Nova Scotia.

2nd Ordinary Meeting, 7 November, 1983

“The Nova Scotia Children’s Dental Health Scheme.” D.P. Cunningham. Dalhousie University Dental School.

3rd Ordinary Meeting, 5 December, 1983

“The Halifax Explosion as a Seismic Event.” A. Ruffman, Geomarine Associates and D. Simpson, Lamont-Doherty Geological Observatory of Columbia University, N.Y.

4th Ordinary Meeting, 6 February, 1984

“The Evolution of Senescence.” M. Rose, Dalhousie University.

5th Ordinary Meeting, 5 March, 1984

“Controlling the Growth of Fungi.” R. Brown, Dalhousie University.

6th Ordinary Meeting, 2 April, 1984

“Peat for Energy and Chemicals—The National Research Council Program.” N. Tibbits, National Research Council, Halifax.

Annual General Meeting, 30 April, 1984

“A Visit to China.” F. Forsyth.

VALLEY CHAPTER

1st Ordinary Meeting, November, 1983

“Greenhouse Industry in Holland.” B. McPhail.

2nd Ordinary Meeting, February, 1984

“The Facts Behind Aids.” W. Schlech.

THE PRESIDENT'S REPORT

I am pleased to report that the year for which I was President was one of comparative tranquility and consolidation.

There were no major projects such as the publication of Dr. Roland's book on the *Geological Background and Physiography of Nova Scotia* which consumed so much energy and expense in the previous year.

This meant that we were able to give attention to improving our present methods of operating and finance.

As the report from the Treasurer indicated, we have now received financial support on a three-year basis from the National Sciences and Engineering Research Council. This provides us with a more secure basis on which to plan.

We have also improved on our excellent relationship with the Nova Scotia Museum, and hence the Provincial Government, in terms of use of facilities, sales of our publications and direct financial support.

One feature of our activities which is still not entirely satisfactory is the communication between the Valley Chapter and Council but I hope we can improve on this at this meeting.

Although the Nova Scotian Institute of Science is probably best known, at least in the Province, as the sponsor of lectures on topics of scientific interest, the Treasurer's Report shows that the overwhelming preponderance of our expense is associated with publishing the Proceedings.

Since the production of the Proceedings is the responsibility of an Editorial Board and is not directly supervised by Council, it is important that there are effective communications between the Editorial Board and Council and some effort was spent this year to improve communications in the future.

Although the lectures sponsored by the Institute had high quality speakers, in some instances the audience was disturbingly small.

This does not reflect well on the Institute and is an indication that we may be providing something for which there is a reduced demand.

When the Nova Scotian Institute of Science was founded in 1862, there were very few opportunities for scientists and those interested in science to meet and discuss their work.

Nowadays there are abundant opportunities to attend seminars, lectures, colloquia, etc., and the need for the Institute to provide a forum for members to speak to other members is not quite so great.

On the other hand, interest by the public in scientific subjects has never been so great and I strongly feel that the Institute has a valuable and an exciting role to play in providing information and opportunities for discussion on scientific matters of public concern.

This function has always existed to some extent but my personal opinion is that this activity should be greatly expanded and I recommend strongly that my successor discuss with his Council how best the Institute may provide information to the general public on scientific and technological matters which affect us all.

Finally, I should like to thank all of the Council for their work and support during my term of office, particularly John Walters whose job as Treasurer is the most demanding, and I should like to wish the incoming President a successful and enjoyable year.

A.Y. McLean

INSTRUCTIONS TO AUTHORS

The *Proceedings of the Nova Scotian Institute of Science* publishes the proceedings of the Institute and original articles, including notes, pertaining to the natural sciences of the Atlantic Provinces, especially in biology and geology. Manuscripts may be either in English or French, and acceptance for publication is based on recommendations of referees.

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