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A COMPARISON OF INSULAR SEAWEED FLORAS FROM PENOBSCOT BAY, MAINE, AND OTHER NORTHWEST ATLANTIC ISLANDS

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ABSTRACT. Ninety-seven taxa of seaweeds were collected from nine islands within the Penobscot Bay area of central Maine, including 25 Chlorophyceae, 34 Phaeophyceae, and 38 Rhodophyceae. The patterns of species richness and longevity (#annuals/#perennials) per island are highly variable, with species richness ranging from only 4 taxa on Allen I. to 65 on Wooden Ball I. (mean = 30.8 ± 23.0 taxa) and longevity ratios varying from 0.33–1.0 (0.64 ± 28.1). A total of 48 annuals and 49 perennials is recorded throughout the Bay, giving a longevity ratio of 0.98. This value is lower than that found at many open coastal habitats within the Gulf of Maine. An examination of historical collections by J. Hooper and F. S. Collins from the 1800s revealed three unusual coastal records (*Stilophora rhizoides, Gracilaria tikvahiae,* and *Cladophora ruchingeri*) and sixteen additional seaweeds that were not encountered in our study. Based upon these historical and present collections, as well as extensive sampling from more than 70 nearshore sites, a total of 139 seaweed taxa is known from the Penobscot Bay area, including 40 Chlorophyceae, 47 Phaeophyceae and 52 Rhodophyceae. In a comparison of seaweed floras from fourteen individual islands, from South Wolf I., New Brunswick, to Penikese I., Massachusetts (including a "composite" of Penobscot Bay Islands), 216 seaweed taxa are documented, including 52 Chlorophyceae, 63 Phaeophyceae, and 101 Rhodophyceae. The highest numbers of taxa occur at Smuttynose I., Maine (136), and Penikese I., Massachusetts (131), and the lowest on Wooden Ball I., Maine (65), Monhegan I., Maine (64), and Kent I., New Brunswick (63). Floristic affinities of individual islands tend to mimic patterns of species richness, with Smuttynose having the highest number of shared taxa (mean = 92.4 ± 20.2) and Kent and Wooden Ball Islands the lowest numbers (mean = 50.8 ± 5.2 and 53.9 ± 6.2, respectively). The seaweed diversity of Penikese Island and nearby environs (187 taxa) is comparable to the entire Gulf of Maine.

Key Words: seaweeds, coastal islands, Penobscot Bay, Maine, New Brunswick, New Hampshire, Massachusetts, Gulf of Maine

As noted by Hill (1923), and Pike and Hodgdon (1963), comparative floristic investigations of islands have been grossly neglected within North America, even though there have been many fine studies of individual islands. Although their statement applies

Table 1. Dates and locations of insular collections within the Penobscot Bay area of mid-coastal Maine. Symbols: X = intertidal; X* = subtidal; X** = intertidal and subtidal.

Islands	1985				
	6/2	6/6	6/9	6/11	6/12
Allen I.					
Hurricane I.				X	X
Long I.					
Marshall I.		X			
McGlathery I.			X**		
Monhegan I.					
Pond I.					
Two Bush I.				X	
Wooden Ball I.	X				

to terrestrial vegetation, it is equally true for marine floras (Bowers 1942; Collins 1900; Doty 1948; Koetzner and Wood 1972; Lewis 1924; Scagel 1970; Sears and Wilce 1975). For example, along Maine's extensive and indented coastline there are some two thousand islands (Platt 1996; Simpson 1987), but little attention has been paid to their marine algal floras. Johnson and Skutch (1928a, b) conducted an early ecological study of intertidal algal associations on Mount Desert Island in Bar Harbor, Maine, including a synopsis of species composition, zonation, and ecology. It is still one of the most significant studies of its kind for any Maine island. The only floristic synopsis of multiple insular sites within the Gulf of Maine was conducted at the Isles of Shoals in southern Maine and New Hampshire (Mathieson and Penniman 1986b). We are aware of only one other comparative study of insular marine floras in North America, namely the Channel Islands in Southern California (Murray and Littler 1981; Murray et al. 1980).

In the present study, we evaluate the floristic composition and affinities of seaweed populations from nine islands within the Penobscot Bay area of mid-coastal Maine, including contiguous nearshore Jericho Bay and offshore habitats (Table 1; Appendix). We compare these records with previous documentations of species composition from thirteen other islands, from the Bay of Fundy to southern Massachusetts (Figures 1–3; Table 2, 3). Data from 20 of these 22 islands represent our collections (Hehre et al. 1970; Mathieson and Penniman 1986b; Stone et al. 1970),

Table 1. Extended.

1986										1994			
5/29	5/30	6/1	6/2	6/5	6/6	6/7	6/8	6/9	6/12	7/15	7/16	7/17	7/18
		X											
X	X	X*							X				
			X		X	X							
										X**	X**	X**	X**
			X	X	X								
			X				X**	X					

made in accordance with a uniform protocol for collecting and identifying seaweeds, including the establishment of extensive voucher collections (Druehl 1981). Information for the other two islands (Kent Island, New Brunswick, and Penikese Island, Massachusetts) is based upon the work of others (Bowers 1942; Doty 1948; Koetzner and Wood 1972; Lewis 1924). In summary, the objectives of our study were four-fold as follows: (1) to assess the numbers and types of species from nine islands within the Penobscot Bay area of mid-coastal Maine (Appendix); (2) to evaluate the longevity pattern of seaweed populations from the Penobscot Bay area; (3) to compare the patterns of species richness among 22 individual islands, including nine from Penobscot Bay and thirteen other sites, from the Bay of Fundy, Canada, to Buzzards Bay, Massachusetts; and (4) to compare a "composite" of Penobscot Bay taxa from nine islands with thirteen other Northwest Atlantic islands.

MATERIALS AND METHODS

Collections of intertidal and shallow subtidal seaweeds were made at nine islands within the Penobscot Bay area (Figure 2, 3a, b). The selection of islands was based upon a variety of factors, including accessibility by boat, variation in size, degree of wave exposure, and proximity to other insular and nearshore environments. Four of the nine islands are located within Penobscot Bay proper (Hurricane, McGlathery, Two Bush, and Wooden

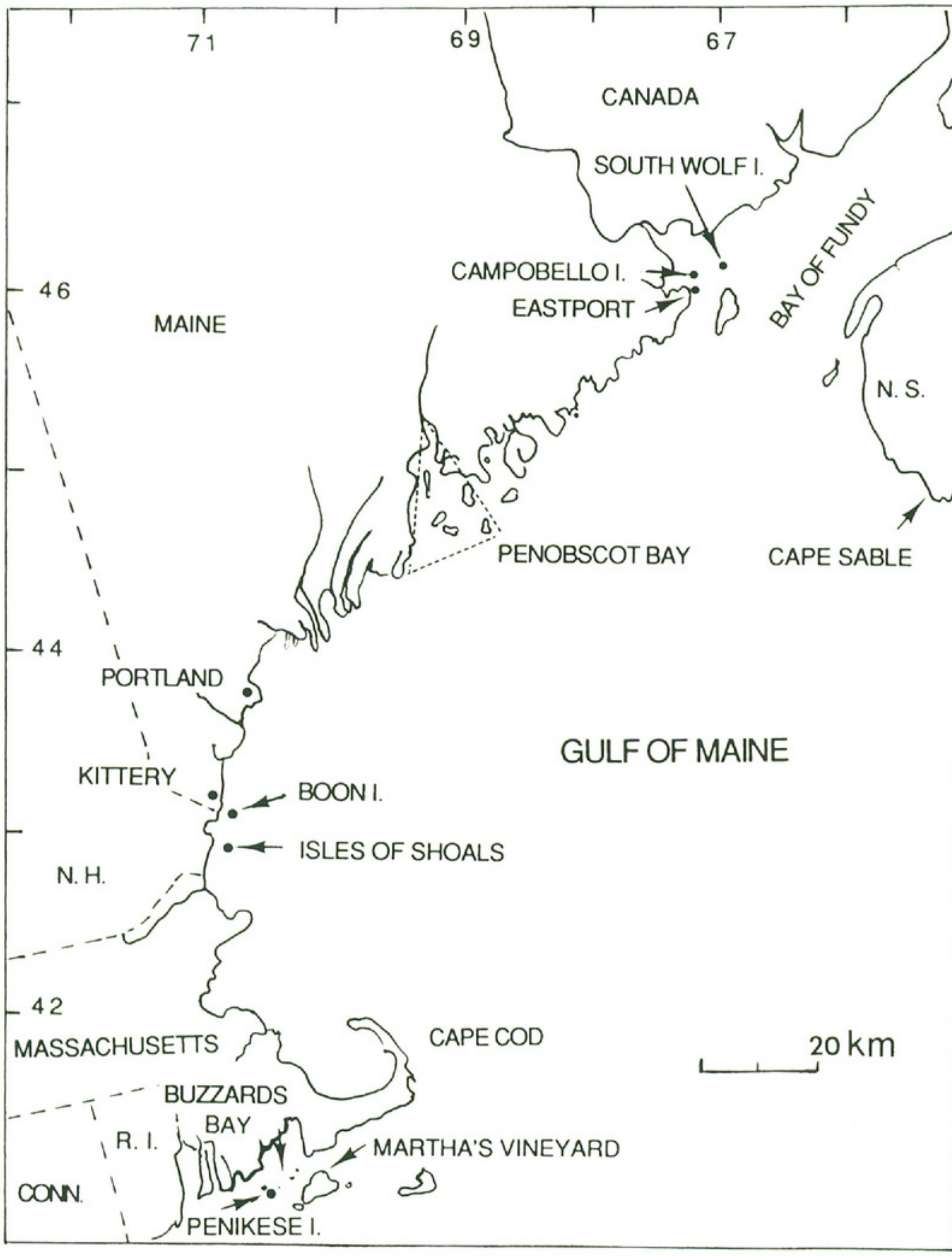

Figure 1. The northeastern coast of North America, from South Wolf Island, New Brunswick, Canada, to Buzzards Bay, Massachusetts, including the mid-coastal Penobscot Bay area of Maine.

Ball); three others (Long, Marshall, and Pond) occur within the contiguous Jericho Bay to the east (Figure 3b), and two (Allen and Monhegan) lie just W of Penobscot Bay proper (Figure 2, 3a). As noted by Conkling (1996), the seaward boundary for Penobscot Bay is somewhat vague but it is approximated by the 50

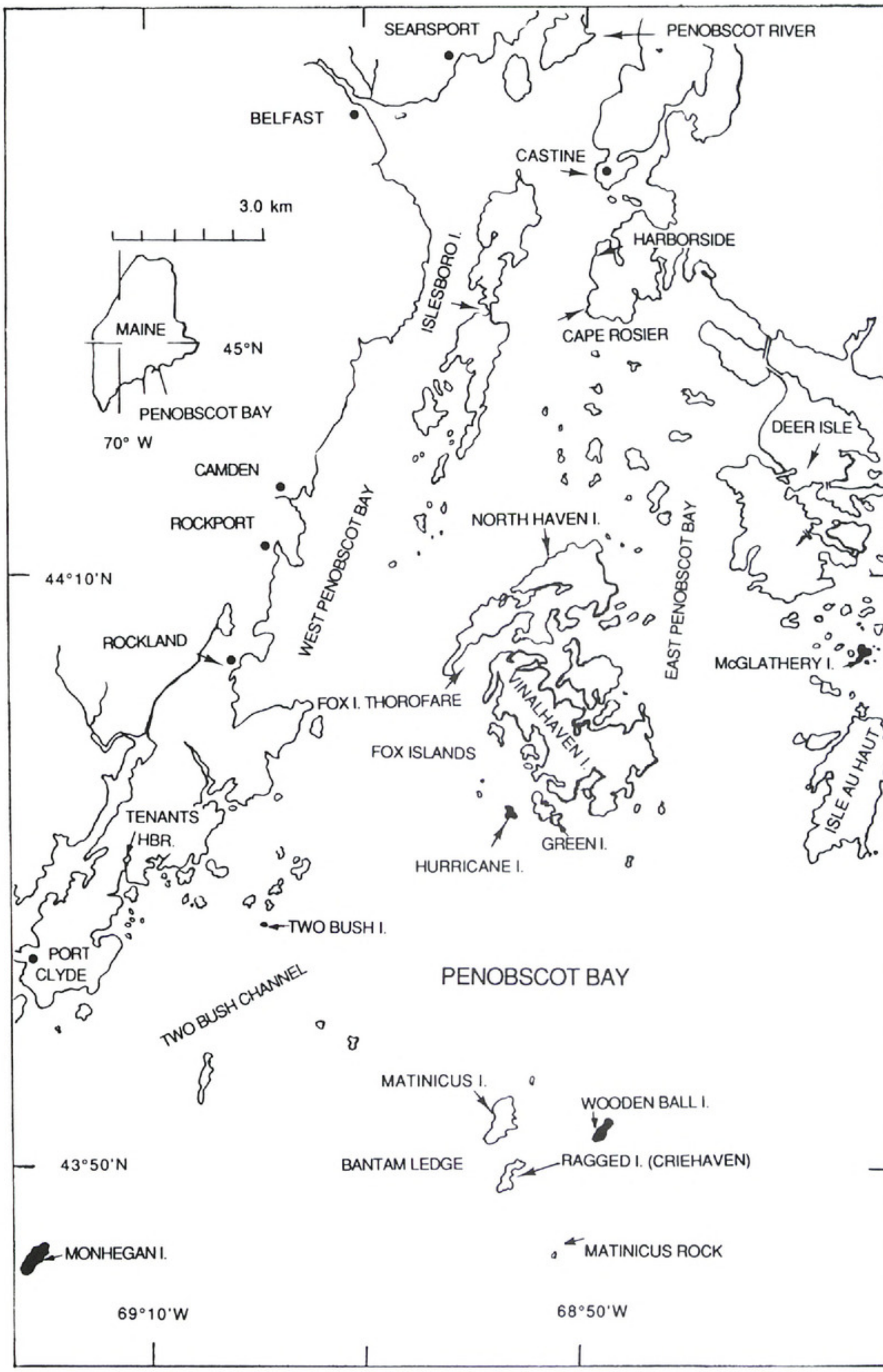

Figure 2. The mid-coastal Penobscot Bay area of Maine, showing the location of Monhegan, Hurricane, Two Bush, and Wooden Ball Islands.

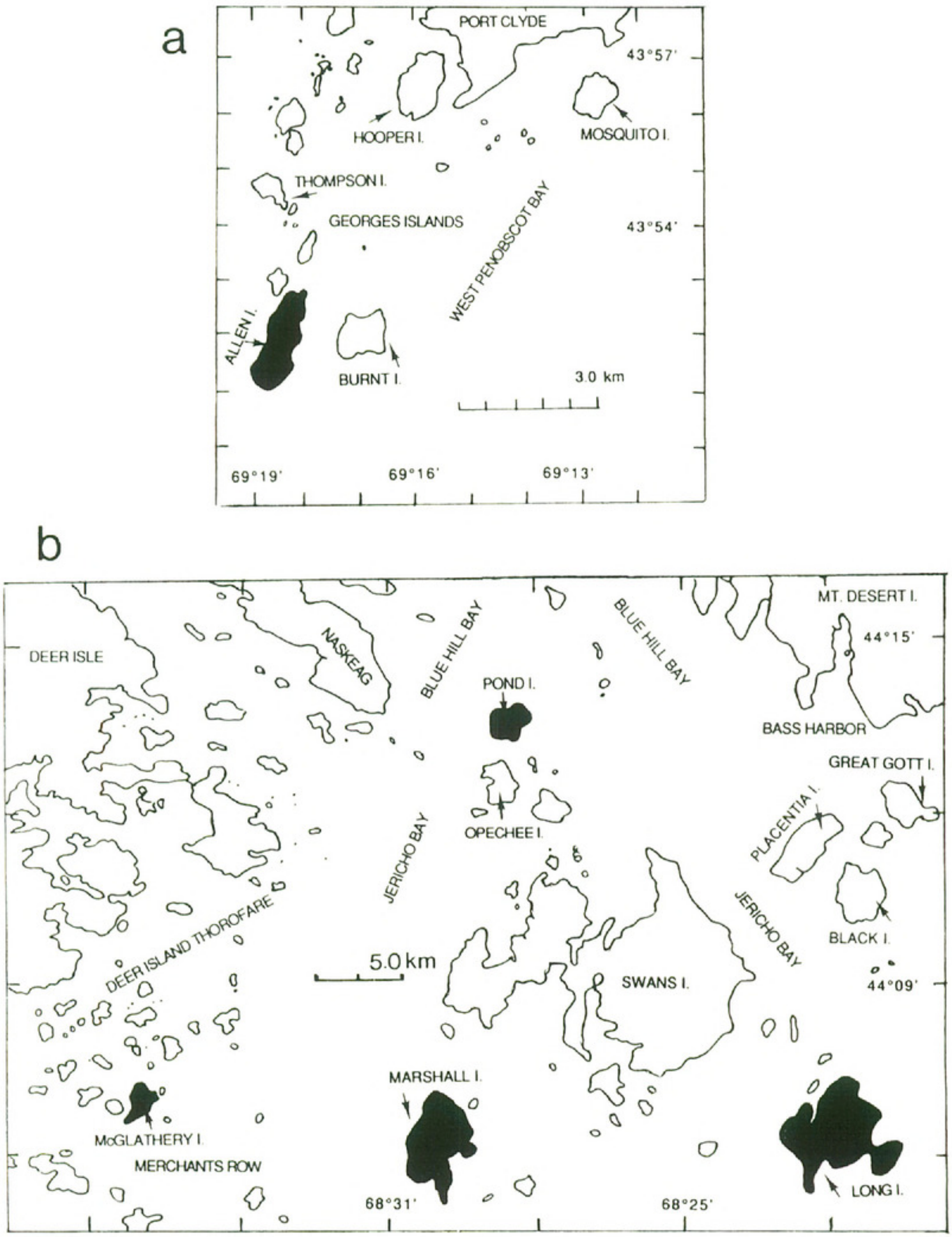

Figure 3. Penobscot Bay and contiguous Jericho Bay, Maine. a) West Penobscot Bay, showing Allen Island that is located south of Port Clyde; b) Eastern-most Penobscot Bay area, showing the locations of McGlathery Island near Deer Island Thorofare and three islands within contiguous Jericho Bay (Pond, Long, and Marshall).

fathom line near Matinicus Rock. As Monhegan lies just W of Matinicus Rock, we have chosen to include it within our study. Similarly, the other three islands (Long, Marshall, and Pond) are east of Penobscot Bay proper (Figure 3a, b).

Most of our Penobscot insular collections were made during the summers of 1985 and 1986, when one of us (JH) was working on Hurricane Island (Table 1). The notable exceptions are the collections made on Monhegan Island during the summer of 1994. Intertidal samples were collected on foot during low tides; subtidal collections were made by SCUBA diving to approximately 10–12m below mean low water (M.L.W.). Although an attempt was made to sample all conspicuous seaweeds on each island, limitations of boat time and diving personnel did not allow detailed subtidal sampling of all nine islands. Therefore, floristic documentations for individual islands should be considered preliminary; the "composite" for the Penobscot Bay area probably is more representative of the geography as a whole. The most detailed collections were made on Hurricane Island with six sampling dates (Table 1; Appendix), followed by Wooden Ball (4), Monhegan (4), Long (3), and Pond Islands (3); single collections were made on Allen, Marshall, McGlathery, and Two Bush Islands.

Seaweed samples either were pressed immediately or preserved in 2% formalin in seawater and stored in the dark. Several references were utilized for these identifications (Adey and Adey 1973; Bird and McLachlan 1992; Blair 1983; Bliding 1963, 1968; Burrows 1991; Dixon and Irvine 1977; Düwel and Wegeberg 1996; Farlow 1881; Fletcher 1987; Hoek 1963, 1982; Irvine 1983; Irvine and Chamberlain 1994; Kingsbury 1969; Maggs and Hommersand 1993; Schneider and Searles 1991; Taylor 1957; Villalard-Bohnsack 1995; Webber and Wilce 1971; Woelkerling 1973; Wynne and Heine 1992). Nomenclature primarily follows South and Tittley (1986), except for several recent changes noted above and in Villalard-Bohnsack (1995). Approximately 600 voucher specimens are deposited in the Albion R. Hodgdon Herbarium at the University of New Hampshire (NHA) documenting Penobscot Bay's insular flora.

In addition to our insular Penobscot Bay collections, we have made extensive collections at over 70 nearshore sites (Mathieson and Hehre, unpubl. data). The latter collections, which were made during 1993 to 1996, are utilized to characterize Penobscot Bay's total flora, in concert with several historical collections by F. S. Collins, W. G. Farlow, and J. Hooper during the last century. Many of Collins' and Farlow's specimens are deposited either at the New York Botanical Garden (NY) or the Farlow Herbarium

Table 2. Seaweed taxa from fourteen individual islands from the Bay of Fundy, Canada, to Buzzards Bay, Massachusetts, plus a "composite" of nine islands from the Penobscot Bay area of mid-coastal Maine. Key to symbols: X = a taxon's presence; % = percent occurrence at 13 individual islands and the "composite" value for nine Penobscot Bay islands — i.e., excluding Wooden Ball I. as an individual. The values in ( ) indicate the 14 individual islands — i.e., including Wooden Ball I. and excluding Penobscot Bay's "composite" value; " " = stage in the life history of another seaweed but recognizable as a distinct entity. Key to abbreviations: SW = South Wolf I., New Brunswick; CA = Campobello I., New Brunswick; KI = Kent I., New Brunswick; PB = a "composite" of nine islands from the Penobscot Bay area of Maine — i.e., Allen, Hurricane, Long, Marshall, McGlathery, Monhegan, Pond, Two Bush, and Wooden Ball Islands; WB = Wooden Ball I., Penobscot Bay, ME; BO = Boon I., ME; AP = Appledore I., ME (Isles of Shoals); CE = Cedar I., ME (Isles of Shoals); DU = Duck I., ME (Isles of Shoals); LU = Lunging I., NH (Isles of Shoals); MA = Malaga I., ME (Isles of Shoals); SM = Smuttynose I., ME (Isles of Shoals); ST = Star I., NH (Isles of Shoals); WH = White I., NH (Isles of Shoals); PI = Penikese I., Buzzards Bay, Mass.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Chlorophyta																
Acrochaete viridis (Reinke) R. Nielsen				X						X				X		21.4 (14.3)
Acrochaete wittrockii (Wille) R. Nielsen															X	7.1
Blidingia minima (Nägeli ex Kützing) Kylin	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Bryopsis plumosa (Hudson) C. Agardh							X	X		X					X	28.6
Capsosiphon fulvescens (C. Agardh) Setchell et Gardner		X		X	X											14.3
Capsosiphon groenlandicum (J. Agardh) Vinogradova	X	X														14.3
Chaetomorpha aerea (Dillwyn) Kützing		X		X	X		X	X	X	X	X	X	X	X	X	78.6
Chaetomorpha brachygona Harvey									X					X		14.3
Chaetomorpha linum (O. F. Müller) Kützing				X			X	X	X	X	X	X	X	X	X	71.4 (64.3)
Chaetomorpha melagonium (Weber et Mohr) Kützing	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Chaetomorpha minima Collins et Hervey												X				7.1

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Chaetomorpha picquotiana Montagne ex Kützing				X	X			X	X	X	X	X	X	X		57.1
Chlorochytrium cohnii Wright				X	X											7.1
Cladophora albida (Nees) Kützing						X	X	X		X		X	X		X	50.0
Cladophora ruchingeri (J. Agardh) Kützing															X	7.1
Cladophora rupestris (L.) Kützing			X			X	X		X	X		X	X	X		57.1
Cladophora sericea (Hudson) Kützing		X	X	X	X	X	X	X	X	X	X	X	X	X	X	92.9
"*Codiolum gregarium* A. Braun"	X	X				X		X	X	X		X	X	X	X	71.4
"*Codiolum petrocelidis* Kuckuck"	X	X		X		X	X	X	X	X		X	X	X		78.6 (71.4)
"*Codiolum pusillum* (Lyngbye) Kjellman"	X	X				X		X	X	X		X	X	X		64.3
Codium fragile (Suringar) Har. ssp. *tomentosoides* (Goor) P. C. Silva							X		X	X	X	X			X	42.9
Derbesia marina (Lyngbye) Solier									X	X	X	X		X		35.7
Enteromorpha clathrata (Roth) Greville			X				X	X	X	X	X	X	X		X	64.3
Enteromorpha compressa (L.) Nees			X			X	X	X	X	X	X	X	X		X	71.4
Enteromorpha flexuosa (Wulfen ex Roth) J. Agardh ssp. *paradoxa* (Dillwyn) Bliding		X		X			X			X		X	X			42.9 (35.7)
Enteromorpha intestinalis (L.) Nees	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Enteromorpha linza (L.) J. Agardh	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Enteromorpha prolifera (O. F. Müller) J. Agardh		X	X	X	X	X	X	X	X	X	X	X	X		X	85.7
Epicladia flustrae Reinke	X	X								X						21.4
"*Gomontia polyrhiza* (Lagerheim) Bornet et Flahault"									X						X	14.3
Kornmannia leptoderma (Kjellman) Bliding	X	X														14.3

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Monostroma grevillei (Thuret) Wittrock	X	X		X	X		X	X	X	X	X	X	X	X		78.6
Monostroma oxyspermum Kützing												X				7.1
Ochlochaete hystrix Thwaites ex Harvey															X	7.1
Percursaria percursa (C. Agardh) Bory		X					X		X				X			28.6
Prasiola stipitata Suhr in Jessen	X	X	X			X	X		X	X	X	X	X		X	78.6
Pringsheimiella scutata (Reinke) Hoehnel ex Marchewianka							X									7.1
Protomonostroma undulatum (Wittrock) Vinogr. f. *pulchrum* (Farlow) M. Wynne	X	X		X	X	X	X	X	X	X	X	X	X	X		85.7
Pseudendoclonium submarinum Wille	X	X		X	X				X						X	35.7
Rhizoclonium riparium (Roth) Kützing ex Harvey	X	X		X	X	X	X	X	X	X	X	X	X	X	X	92.9
Rhizoclonium tortuosum (Dillwyn) Kützing	X	X	X	X	X	X	X	X	X	X	X	X	X	X		92.9
Spongomorpha aeruginosa (L.) Hoek															X	7.1
Spongomorpha arcta (Dillwyn) Kützing	X	X	X	X	X		X	X	X	X	X	X	X	X	X	92.9
Spongomorpha spinescens Kützing	X	X	X	X	X	X	X	X	X	X	X	X	X	X		92.9
Stichococcus marinus (Wille) Hazen												X		X		14.3
Tellamia contorta Batters															X	7.1
Ulothrix flacca (Dillwyn) Thuret in Le Jolis		X	X	X	X		X	X	X	X	X	X	X	X	X	85.7
Ulothrix speciosa (Carmichael ex Harvey in Hooker) Kützing	X	X							X		X			X		35.7
Ulva lactuca L.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Ulvaria obscura (Kützing) Gayral	X	X	X	X	X	X	X	X	X	X	X	X		X		85.7
Urospora penicilliformis (Roth) Areschoug	X	X		X	X	X	X	X	X	X	X	X	X	X	X	92.9
Urospora wormskjoldii (Mertens in Hornemann) Rosenvinge	X	X					X	X		X		X	X	X		57.1
Total Chlorophyta taxa = 52	23	30	17	25	21	20	30	27	33	34	25	34	29	28	27	

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Phaeophyta																
Acrothrix gracilis Kylin															X	7.1
Agarum clathratum Dumort.	X	X	X	X		X	X	X	X	X	X	X	X	X		92.9 (85.7)
Alaria esculenta (L.) Greville	X	X	X	X	X	X	X	X	X			X	X	X		78.6
Ascocyclus distromaticus W. R. Taylor							X		X			X			X	28.6
Ascophyllum nodosum (L.) Le Jolis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Ascophyllum nodosum ecad *scorpioides* (Reinke) Hauck			X													7.1
Asperococcus fistulosus (Reinke) Hauck	X		X				X	X		X		X	X	X	X	64.3
Chorda filum (L.) Stackhouse		X					X					X			X	28.6
Chorda tomentosa Lyngbye	X	X		X		X	X					X	X			50.0 (42.9)
Chordaria flagelliformis (O. F. Müller) C. Agardh	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Cladostephus spongiosus (Hudson) C. Agardh													X			7.1
Cladosiphon zosterae (J. Agardh) Kylin						X									X	14.3
Delamarea attenuata (Kjellman) Rosenvinge															X	7.1
Desmarestia aculeata (L.) Lamouroux	X	X	X			X	X	X		X	X	X		X	X	78.6
Desmarestia viridis (O. F. Müller) Lamouroux		X	X			X	X	X	X	X	X	X	X	X	X	85.7
Dictyosiphon foeniculaceus (Hudson) Greville	X	X	X	X	X	X	X	X	X	X	X	X	X		X	92.9
Dictyosiphon macounii Farlow		X														7.1
Ectocarpus fasciculatus Harvey		X		X	X							X	X		X	35.7
Ectocarpus siliculosus (Dillwyn) Lyngbye	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Elachista fucicola (Velley) Areschoug	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Eudesme virescens (Carmichael ex Harvey in Hooker) J. Agardh						X									X	14.3
Fucus distichus L. emend. Powell ssp. *anceps* (Harvey et Ward ex Carruther) Powell							X	X	X	X		X	X	X		50.0
Fucus distichus L. emend. Powell ssp. *distichus* Powell	X	X	X	X	X	X	X	X		X		X	X	X		78.6
Fucus distichus L. ssp. *edentatus* (Bach. Pyl.) Powell	X	X	X	X	X	X	X	X	X	X	X	X	X	X		92.9
Fucus distichus L. ssp. *evanescens* (C. Agardh) Powell	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Fucus spiralis L.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Fucus vesiculosus L.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Hincksia granulosa (J. E. Smith) P. C. Silva in P. C. Silva			X			X	X									21.4
Hincksia ovata (Kjellman) P. C. Silva															X	7.1
Isthmoplea sphaerophora (Carmichael ex Harvey in Hooker) Kjellman	X	X		X	X		X	X								35.7
Laminaria digitata (Hudson) Lamouroux	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Laminaria longicruris Bach. Pyl.	X	X	X				X		X				X		X	50.0
Laminaria saccharina (L.) Lamouroux	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Laminariocolax tomentosoides (Farlow) Kylin												X				7.1
Leathesia difformis (L.) Areschoug	X	X		X		X	X	X	X	X	X	X	X	X	X	92.9 (85.7)
Melanosiphon intestinalis (Saunders) M. Wynne				X		X						X		X		28.6 (21.4)
Microspongium globosum Reinke															X	7.1
Mikrosyphar porphyrae Kuckuck							X		X			X	X			28.6
Myrionema balticum (Reinke) Foslie															X	7.1

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Myrionema corunnae Sauvageau				X		X	X	X	X	X	X			X		57.1 (50.0)
Myrionema strangulans Greville	X	X		X		X	X			X		X			X	57.1 (50.0)
Myriotrichia clavaeformis Harvey															X	7.1
Petalonia fascia (O. F. Müller) Kuntze	X	X		X	X	X	X	X	X	X	X	X	X	X	X	92.9
Petalonia zosterifolia (Reinke) Kuntze												X	X			14.3
Petroderma maculiforme (Wollny) Kuckuck				X	X											7.1
Pilayella littoralis (L.) Kjellman	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Protectocarpus speciosus (Børgesen) Kuckuck		X					X			X	X	X	X	X		50.0
Pseudolithoderma extensum (P. Crouan et H. Crouan) S. Lund				X	X			X	X	X						28.6
Punctaria latifolia Greville		X	X	X	X										X	21.4
Punctaria plantaginea (Roth) Greville				X		X	X	X		X		X			X	50.0 (42.9)
Punctaria tenuissima (C. Agardh) Greville								X						X	X	21.4
"*Ralfsia bornetii* Kuckuck"		X							X		X	X	X	X		42.9
"*Ralfsia clavata* (Carmichael) Crouan *sensu* Farlow"		X		X					X		X	X	X	X		50.0 (42.9)
Ralfsia fungiformis (Gunnerus) Setchell et Gardner	X	X	X													21.4
Ralfsia verrucosa (Areschoug) J. Agardh		X		X		X	X	X	X	X	X	X	X		X	78.6 (71.4)
Saccorhiza dermatodea (Bach. Pyl.) J. Agardh		X		X		X	X	X				X				42.9 (35.7)
Sargassum filipendula C. Agardh															X	7.1
Scytosiphon simplicissimus (Clemente) Cremades	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Sphacelaria cirrosa (Roth) C. Agardh	X	X		X	X		X	X	X	X	X	X	X	X	X	85.7
Sphacelaria fusca (Hudson) S. F. Gray												X				7.1

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Sphaerotrichia divaricata (C. Agardh) Kylin			X	X	X											21.4 (14.3)
Spongonema tomentosum (Hudson) Kützing		X				X	X		X	X				X	X	50.0
Ulonema rhizophorum Foslie				X			X	X		X	X	X	X	X		57.1 (50.0)
Total Phaeophyta taxa = 63	26	37	25	34	23	31	38	31	29	30	25	40	33	30	37	
Rhodophyta																
Agardhiella subulata (J. Agardh) Kraft et M. Wynne															X	7.1
Aglaothamnion westbrookiae Rueness et L'Hardy-Halos							X								X	14.3
Ahnfeltia plicata (Hudson) Fries	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Antithamnion cruciatum (C. Agardh) Nägeli															X	7.1
Antithamnionella floccosa (O. F. Müller) Whittick	X	X		X			X	X	X	X	X	X	X	X		78.6 (71.4)
Audouinella alariae (Jónsson) Woelkerling	X			X		X		X		X		X	X			50.0 (42.9)
Audouinella dasyae (Collins) Woelkerling															X	7.1
Audouinella daviesii (Dillwyn) Woelkerling			X?												X	14.3
Audouinella membranacea (Magnus) Papenfuss	X	X							X							21.4
Audouinella microscopica (Nägeli in Kützing) Woelkerling															X	7.1
Audouinella purpurea (Lightfoot) Woelkerling	X	X		X	X	X	X	X	X	X	X	X	X	X		85.7
Audouinella saviana (Meneghini) Woelkerling															X	7.1

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Audouinella secundata (Lyngbye) P. Dixon in M. Parke et P. Dixon	X	X	X	X	X		X					X		X	X	57.1
Bangia atropurpurea (Roth) C. Agardh	X	X		X	X			X			X	X	X	X	X	64.3
Bonnemaisonia hamifera Hariot						X	X	X	X	X	X	X		X	X	64.3
Callithamnion corymbosum (J. E. Smith) Lyngbye															X	7.1
Callithamnion tetragonum (Withering) S. F. Gray				X		X	X	X	X	X	X	X	X	X	X	78.6 (71.4)
Callocolax neglectus Schmitz ex Batters							X	X		X		X	X	X		42.9
Callophyllis cristata (C. Agardh) Kützing	X	X	X			X	X	X	X	X	X	X	X	X		85.7
Ceramium cimbricum H. E. Petersen in Rosenvinge															X	7.1
Ceramium deslongchampii Chauvin ex Duby	X	X		X	X	X	X	X	X	X	X	X	X	X	X	92.7
Ceramium diaphanum (Lightfoot) Roth															X	7.1
Ceramium nodulosum (Lightf.) Ducluzeau	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Ceramium strictum Harvey															X	7.1
Ceratocolax hartzii Rosenvinge							X	X		X		X				28.6
Champia parvula (C. Agardh) Harvey															X	7.1
Chondria baileyana (Mont.) Harvey															X	7.1
Chondria capillaris (Hudson) M. Wynne															X	7.1
Chondria sedifolia Harvey															X	7.1
Chondrus crispus Stackhouse	X	X		X	X	X	X	X	X	X	X	X	X	X	X	92.9
Choreocolax polysiphoniae Reinsch	X	X		X		X		X	X	X		X	X		X	71.4 (64.3)
Clathromorphum circumscriptum (Strömfelt) Foslie	X	X		X	X	X	X	X	X	X	X	X	X	X		85.7
Coccotylus truncatus (Pallas) M. Wynne et Heine			X			X	X	X	X	X	X	X	X	X	X	78.6

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Corallina officinalis L.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Cystoclonium purpureum (Hudson) Batters	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Dasya baillouviana (S. Gmelin) Montagne															X	7.1
Devaleraea ramentacea (L.) Guiry	X	X	X	X	X	X	X	X		X	X	X	X	X		85.7
Dumontia contorta (S. Gmelin) Ruprecht		X	X	X		X	X	X	X	X	X	X	X	X	X	92.9 (85.7)
Erythrodermis traillii (Holmes ex Batters) Guiry et Garbary						X	X		X	X		X		X		42.9
Erythrotrichia carnea (Dillwyn) J. Agardh							X	X		X	X	X			X	42.9
Erythrotrichopeltis ciliaris (Carmichael ex Harvey in Hooker) Kornmann							X	X	X	X	X		X	X		50.0
Fimbrifolium dichotomum (Lepechkin) Hansen							X					X				14.3
Gloiosiphonia capillaris (Hudson) Carmichael ex Berkeley				X		X	X		X			X				35.7 (28.6)
Griffithsia globulifera Harvey ex Kütz.															X	7.1
Grinnellia americana (C. Agardh) Harvey															X	7.1
Gymnogongrus crenulatus (Turner) J. Agardh							X	X	X	X	X	X	X	X		57.1
Halosacciocolax kjellmanii Lund												X				7.1
Harveyella mirabilis (Reinsch) F. Schmitz et Reinke							X			X			X			21.4
Hildenbrandia rubra (Sommerfelt) Meneghini	X	X	X	X	X			X	X	X	X	X	X		X	78.6
Lithothamnion glaciale Kjellman	X	X		X	X	X	X	X	X	X	X	X	X	X	X	92.9
Lomentaria baileyana (Harvey) Farlow															X	7.1
Lomentaria clavellosa (Turner) Gaillon						X										7.1
Lomentaria orcadensis (Harvey) Collins ex W. R. Taylor								X		X		X				21.4

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Mastocarpus stellatus (Stackhouse in Withering) Guiry in Guiry et al.	X	X	X	X	X		X	X	X	X	X	X	X	X		85.7
Membranoptera alata (Hudson) Stackhouse	X	X				X	X	X	X	X		X	X	X		71.4
Nemalion helminthoides (Velley in Withering) Batters						X	X					X	X		X	35.7
Palmaria palmata (L.) Kuntze	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Pantoneura baerii (Postels et Ruprecht) Kylin							X									7.1
"*Petrocelis cruenta* J. Agardh"	X	X		X		X	X	X	X	X	X	X	X	X		85.7 (78.6)
Peyssonnelia rosenvingii Schmitz in Rosenvinge	X	X									X	X				28.6
Phycodrys rubens (L.) Batters	X	X	X	X		X	X	X	X	X	X	X	X	X	X	100 (92.9)
Phyllophora pseudoceranoides (Gmelin) Newroth et A. Taylor				X		X	X	X	X	X		X	X	X	X	71.4 (64.3)
Phymatolithon foecundum (Kjellman) Düwel et Wegeberg						X		X	X	X		X	X	X		50.0
Phymatolithon laevigatum (Foslie) Foslie						X		X	X	X	X	X				42.9
Phymatolithon lenormandii (Areschoug in J. Agardh) Adey	X			X		X	X	X	X	X	X	X	X	X	X	85.7 (78.6)
Phymatolithon polymorphum (L.) Foslie															X?	7.1
Phymatolithon rugulosum Adey											X	X				14.3
Phymatolithon tenue (Rosenvinge) Düwel et Wegeberg						X	X	X	X	X	X	X		X		57.1
Pleonosporium borreri (J. E. Smith) Nägeli ex Hauck															X	7.1
Plumaria plumosa (Hudson) Kuntze	X	X		X	X	X	X	X	X	X	X	X	X	X	X	92.9
Pneophyllum fragile Kützing							X	X	X	X		X	X	X	X	57.1

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Polyides rotundus (Hudson) Greville	X	X						X	X	X	X	X	X	X	X	71.4
Polysiphonia denudata (Dillwyn) Greville ex Harvey in Hooker															X	7.1
Polysiphonia elongata (Hudson) Sprengel															X	7.1
Polysiphonia fibrillosa (Dillwyn) Sprengel															X	7.1
Polysiphonia flexicaulis (Harvey) Collins		X		X		X	X	X	X		X	X	X	X	X	78.6 (71.4)
Polysiphonia fucoides (Hudson) Greville		X	X			X	X	X	X	X	X	X	X	X	X	85.7
Polysiphonia harveyi J. Bailey			X	X		X	X	X	X	X	X	X	X	X	X	85.7 (78.6)
Polysiphonia lanosa (L.) Tandy	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Polysiphonia nigra (Hudson) Batters													X		X	14.3
Polysiphonia stricta (Dillwyn) Greville	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Polysiphonia subtilissima Montagne															X	7.1
Porphyra amplissima (Kjellman) Setchell et Hus	X	X		X		X	X					X				42.9 (35.7)
Porphyra leucosticta Thuret in Le Jolis	X						X	X	X	X	X	X	X	X		64.3
Porphyra linearis Greville	X											X	X			21.4
Porphyra miniata (C. Agardh) C. Agardh		X		X		X	X		X			X	X	X		57.1 (50.0)
Porphyra umbilicalis (L.) J. Agardh	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Pterothamnion plumula (Ellis) Nägeli								X				X			X	21.4
Ptilota serrata Kützing	X	X	X			X	X	X	X	X	X	X	X	X	X	92.9
Rhodomela confervoides (Hudson) Silva	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	100
Rhodophysema elegans (P. Crouan et H. Crouan ex J. Agardh) P. Dixon				X	X					X	X		X			28.6
Rhodophysema georgii Batters		X													X	14.3
Scagelia pylaisaei (Mont.) M. Wynne	X	X		X		X	X	X	X			X	X	X	X	78.6 (71.4)
Scinaia forcellata Bivona															X	7.1
Seirospora interrupta (J. E. Smith) F. Schmitz															X	7.1

Table 2. Continued.

	SW	CA	KI	PB	WB	BO	AP	CE	DU	LU	MA	SM	ST	WH	PI	%
Spermothamnion repens (Dillwyn) Rosenvinge		X					X								X	23.1
Spyridia filamentosa (Wulfen) Harvey in Hooker															X	7.1
Stylonema alsidii (Zanardini) Drew								X		X	X					21.4
Titanoderma corallinae (P. Crouan et H. Crouan) Woelkerling, Chamberlain et Silva		X		X			X	X	X	X				X		50.0 (42.9)
Titanoderma pustulatum (Lamouroux) Woelkerling, Chamberlain et Silva		X				X	X	X	X	X	X	X	X	X	X	78.6
"*Trailliella intricata* Batters"				X			X	X				X	X	X	X	50.0 (42.9)
Total Rhodophyta taxa = 101	36	40	21	38	21	43	55	54	48	52	44	62	51	48	67	
Grand total seaweed taxa = 216	85	107	63	97	65	94	123	112	110	116	94	136	113	106	131	

Table 3. Summary of seaweed taxa from nine islands within the Penobscot Bay area of mid-coastal Maine. Key to symbols: X = a taxon's presence; % = percent occurrence based upon all nine islands. Key to abbreviations: Islands: A I = Allen I.; H I = Hurricane I.; L I = Long I.; M I = Marshall I.; Mc I = McGlathery I.; MO I = Monhegan I.; P I = Pond I.; TB I = Two Bush I.; WB I = Wooden Ball I. Longevity: Ann. = seasonal annual; AAnn = aseasonal annual; Per. = perennial; PPer. = pseudoperennial.

	A I	H I	L I	M I	Mc I
Chlorophyta					
Acrochaete viridis					
Blidingia minima					
Capsosiphon fulvescens					
Chaetomorpha aerea					
Chaetomorpha linum					
Chaetomorpha melagonium		X	X	X	
Chaetomorpha picquotiana					
Chlorochytrium cohnii					
Cladophora sericea				X	
"*Codiolum petrocelidis*"					
Enteromorpha flexuosa ssp. *paradoxa*					
Enteromorpha intestinalis					
Enteromorpha linza		X			
Enteromorpha prolifera		X			
Monostroma grevillei					
Protomonostroma undulatum f. *pulchrum*		X	X	X	
Pseudendoclonium submarinum					
Rhizoclonium riparium					
Rhizoclonium tortuosum		X	X		X
Spongomorpha arcta		X			
Spongomorpha spinescens		X	X		X
Ulothrix flacca			X		
Ulva lactuca		X	X	X	X
Ulvaria obscura		X	X	X	
Urospora penicilliformis			X		
Total Chlorophyta taxa = 25	0	9	8	5	3
Phaeophyta					
Agarum clathratum		X	X	X	
Alaria esculenta		X	X		
Ascophyllum nodosum	X	X	X	X	
Chorda tomentosa		X	X		X
Chordaria flagelliformis					X
Dictyosiphon foeniculaceus		X	X		
Ectocarpus fasciculatus					
Ectocarpus siliculosus		X			

Table 3. Extended.

MO I	P I	TB I	WB I	Longevity	%
X				AAnn.	11.1
X			X	AAnn.	22.2
			X	Ann.	11.1
			X	Per.	11.1
X				Per.	11.1
X			X	Per.	55.6
X			X	Per.	22.2
			X	Ann.	11.1
X			X	PPer.	33.3
X				Ann.?	11.1
X				Ann.	11.1
X			X	AAnn.	22.2
			X	AAnn.	22.2
			X	AAnn.	22.2
			X	Ann.	11.1
			X	Ann.	44.4
			X	AAnn.	11.1
			X	AAnn.	11.1
X	X	X	X	AAnn.?	77.8
X			X	Ann.	33.3
X			X	Ann.	55.5
			X	Ann.	22.2
X			X	PPer.	66.7
X			X	Ann.	55.6
			X	Ann.	22.2
14	1	1	21		
				Per.	33.3
X			X	Per.	44.4
X	X		X	Per.	77.8
				Ann.	33.3
X			X	Ann.	33.3
X			X	Ann.	44.4
			X	Ann.	11.1
X			X	Ann.	33.3

Table 3. Continued.

	A I	H I	L I	M I	Mc I
Phaeophyta					
Elachista fucicola	X	X	X	X	X
Fucus distichus ssp. *distichus*					
Fucus distichus ssp. *edentatus*		X	X		
Fucus distichus ssp. *evanescens*		X	X		
Fucus spiralis					
Fucus vesiculosus		X	X	X	X
Isthmoplea sphaerophora					
Laminaria digitata		X	X	X	
Laminaria saccharina		X		X	
Leathesia difformis					
Melanosiphon intestinalis				X	
Myrionema corunnae					
Myrionema strangulans					
Petalonia fascia		X	X		
Petroderma maculiforme					
Pilayella littoralis	X	X	X	X	X
Pseudolithoderma extensum					
Punctaria latifolia					
Punctaria plantaginea		X			
"*Ralfsia clavata*"					
Ralfsia verrucosa					
Saccorhiza dermatodea		X			
Scytosiphon simplicissimus		X	X		
Sphacelaria cirrosa					
Sphaerotrichia divaricata		X	X		
Ulonema rhizophorum					
Total Phaeophyta taxa = 34	3	18	14	8	5
Rhodophyta					
Ahnfeltia plicata				X	
Antithamnionella floccosa			X		
Audouinella alariae					
Audouinella purpurea					
Audouinella secundata					
Bangia atropurpurea			X		
Callithamnion tetragonum		X			
Ceramium deslongchampii					
Ceramium nodulosum		X	X	X	X
Chondrus crispus		X	X	X	X
Choreocolax polysiphoniae		X		X	
Clathromorphum circumscriptum					X
Corallina officinalis		X	X	X	X
Cystoclonium purpureum		X		X	
Devaleraea ramentacea		X	X		

Table 3. Extended, Continued.

MO I	P I	TB I	WB I	Longevity	%
X	X	X	X	Per.	100
			X	Per.	11.1
X			X	Per.	44.4
X			X	Per.	44.4
X			X	Per.	22.2
X	X	X	X	Per.	88.9
X			X	Ann.	22.2
X			X	Per.	55.6
X			X	Per.	44.4
X				Ann.	11.1
				Ann.	11.1
X				Ann.	11.1
X				Ann.	11.1
X		X	X	Ann.	55.6
			X	Per.	11.1
X	X	X	X	Ann.	100
			X	Per.	11.1
			X	Ann.	11.1
				Ann.	11.1
X				Per.?	11.1
	X			Per.	11.1
				Ann.	11.1
X	X		X	Ann.	55.6
			X	Per.	11.1
			X	Ann.	33.3
X	X			Ann.	22.2
21	7	4	23		
X			X	Per.	33.3
X				AAnn.	22.2
X				Ann.	11.1
			X	Per.	11.1
X			X	AAnn.	22.2
			X	Ann.	22.2
	X			Per.	22.2
X			X	Per.?	22.2
X			X	Per.	66.7
X	X	X	X	Per.	88.9
X				Per.	33.3
X			X	Per.	33.3
X			X	Per.	66.7
X			X	Per.	44.4
X			X	Per.	44.4

Table 3. Continued.

	A I	H I	L I	M I	Mc I
Rhodophyta					
Dumontia contorta		X	X	X	X
Gloiosiphonia capillaris		X			
Hildenbrandia rubra					
Lithothamnion glaciale					
Mastocarpus stellatus		X	X		X
Palmaria palmata		X	X		X
"*Petrocelis cruenta*"					
Phycodrys rubens					
Phyllophora pseudoceranoides					
Phymatolithon lenormandii					
Plumaria plumosa					
Polysiphonia flexicaulis		X			
Polysiphonia harveyi					
Polysiphonia lanosa	X	X	X	X	
Polysiphonia stricta		X	X		
Porphyra amplissima		X			
Porphyra miniata				X	X
Porphyra umbilicalis		X	X	X	
Rhodomela confervoides		X	X		
Rhodophysema elegans					
Scagelia pylaisei		X	X		
Titanoderma corallinae				X	
"*Trailliella intricata*"					
Total Rhodophyta taxa = 38	1	18	14	11	8
Grand total seaweed taxa = 97	4	45	36	24	16
Total no. annual taxa	1	21	17	7	3
Total no. perennial taxa	3	24	19	17	16
Longevity ratio (annual/perennial taxa)	0.33	0.88	0.90	0.41	0.19
% Annual taxa	25.0	47.0	47.2	29.2	18.8
% Perennial taxa	75.0	53.0	52.8	70.8	81.2

of Harvard University (FH). Most of Hooper's collections are in the Herbarium at the Brooklyn Botanic Garden (BKL), with a few occurring at the University of New Hampshire (NHA). An examination of all Penobscot Bay specimens from each of these historical collections was made and pertinent details are discussed in a later section.

Specific information regarding the locations and shoreline di-

Table 3. Extended, Continued.

MO I	P I	TB I	WB I	Longevity	%
X	X	X		Ann.	77.8
				Ann.	11.1
	X		X	Per.	22.2
X			X	Per.	22.2
X		X	X	Per.	66.7
X		X	X	Per.	66.7
X				Per.	11.1
X				Per.	11.1
X				Per.	11.1
X				Per.	11.1
X			X	Per.	22.2
X				Per.	22.2
X				Ann.	11.1
X	X		X	Per.	77.8
X			X	Per.	44.4
		X		Ann.	22.2
				Ann.	22.2
X			X	Ann.	55.6
X			X	Per.	44.4
			X	Per.	11.1
				AAnn.	22.2
X				Per.	22.2
X				Per.	11.1
29	5	5	21		
64	13	10	65		
26	5	5	29	(Mean = 12.7 ± 10.7)	
38	8	5	36	(Mean = 18.4 ± 12.5)	
0.68	0.63	1.0	0.81	(Mean = 0.65 ± 0.28)	
40.6	38.5	50.0	44.6	(Mean = 37.9 ± 11.0)	
59.4	61.5	50.0	55.4	(Mean = 62.1 ± 11.0)	

mensions (at high tide) of the nine Penobscot Bay islands (Allen, Hurricane, Long, Marshall, McGlathery, Monhegan, Pond, Two Bush, and Wooden Ball) is given in the Appendix. The latter values were enumerated by tracing each island's outline with a piece of thread on a National Oceanic Survey chart and converting it via the map's scalar (Mathieson and Penniman 1986b). As noted previously, thirteen other islands from the Bay of Fundy to southern Massachusetts also were compared (Table 2). Detailed characterizations of nine of these islands (Appledore, Cedar, Duck, Lunging, Malaga, Smuttynose, Star, and White within the Isles of Shoals, plus Boon) are given by Mathieson and Penniman (1986b). Hehre et al. (1970) and Stone et al. (1970) describe South Wolf and Campobello Islands, New Brunswick; Doty (1948) and Lewis (1924) characterize Penikese Island (Buzzards Bay, Massachusetts); Koetzner and Wood (1972) describe Kent Island, New Brunswick, at the mouth of the Bay of Fundy.

Two comparisons of the Penobscot Bay floras and the thirteen other Northwest Atlantic sites are given here (Tables 2–4). A "composite" of the nine islands from the Penobscot area is used in one comparison, due to limited seasonal and subtidal collections of individual islands (Table 1); a comparison with Wooden Ball Island, which shows the most diverse flora within Penobscot Bay, also is given. The number and percentage of taxa in common to these different sites are presented (Table 4), with the percent similarity (C) determined using Czekanowski's coefficient (Bray and Curtis 1957):

$$C = \frac{2w}{a + b}$$

where "w" = the number of taxa in common to both sites, "a" = the number of taxa at one site, and "b" = the number of taxa at the second site.

Longevity characteristics of all seaweed taxa from the Penobscot Bay area are enumerated according to the scheme outlined by Knight and Parke (1931). The different taxa are designated as annuals (aseasonal or seasonal), perennials, or pseudoperennials, depending upon their life span, growth, and reproductive characteristics (Mathieson 1989). Longevity delineations are based on a number of field studies throughout New England (Coleman and Mathieson 1975; Hehre and Mathieson 1970; Hehre et al. 1970; Mathieson and Hehre 1982, 1983, 1986; Mathieson et al. 1993; Mathieson, Hehre, and Reynolds 1981; Mathieson and Penniman 1991; Mathieson, Reynolds, and Hehre 1981; Reynolds and Mathieson 1975; Sears and Wilce 1975; Stone et al. 1970).

Habitat description. Penobscot Bay (Figure 1) is the second largest embayment on the Atlantic Coast of the United States (Platt et al. 1996) and the largest within Maine (Apollonio 1979;

Conkling 1996; Doyle et al. 1970; Platt 1996; Porter 1966; Rich 1975). The Bay is located approximately 43 km northeast of Portland. It extends northward nearly 38 km from the edge of the Gulf of Maine to the mouth of the Penobscot River (near Searsport), encompassing hundreds of insular habitats (Figure 2, 3). In plan view, Penobscot Bay is triangular in shape, with its apex being near the mouth of the Penobscot River at Searsport and its base stretching about 19 km east-west between Port Clyde and Isle Au Haut (offshore of these sites). As noted by Conkling (1996), the precise delineation as to where the Bay ends and the Gulf of Maine begins is somewhat arbitrary, but a physical oceanographic boundary of sorts is the 50 fathom line that is just seaward of Matinicus Rock. Overall, the Bay embraces about 186 km^2 and has an irregular perimeter of 93 km (Doyle et al. 1970). Approximately twenty percent of the total river water entering the Gulf of Maine passes through the Penobscot watershed, which originates some 200 miles inland from the mouth of the Penobscot River (Platt et al. 1996).

Historically, the Penobscot Bay occupied the lower channel of a preglacial river (the Penobscot River), which flowed out onto the continental shelf at a time when sea levels were considerably lower than today. A rise in sea level since the retreat of the Wisconsin ice sheet (approximately 10,000 years ago) drowned the ancestral valley to form the Penobscot Bay and estuary (Kelly 1992). Because submergence affected the land surface which was modified by glacial activity, the Bay should be classified as a fjord-type habitat. The coastline displays a narrow, glacially scoured channel, a relatively uniform nearshore bottom, and a seaward shelf.

As noted by Collins (1899), the Penobscot Bay area is seldom exposed to the open sea. It is guarded by a thick fringe of both large and small islands, which provides a variety of sheltered habitats; only the outer islands are exposed to heavy seas. Overall, there are hundreds of islands and seven major harbors (Belfast, Camden, Castine, Deer Isle Harbor, Rockland, Rockport, and Searsport) within the Bay (Figure 2, 3). The two largest islands are Vinalhaven and Deer Isle, which are in the central and northeastern portions, respectively. The Fox Islands (Green, Hurricane, North Haven, and Vinalhaven, plus many smaller ones) cover an area of 6.2–7.4 km^2. The islands were so named by an explorer in 1603 who was intrigued by the number of silver-gray foxes

Table 4. Floristic affinities of fourteen individual islands from the Bay of Fundy, Canada, to Buzzards Bay, Masssachusetts, plus a "composite" of nine islands from the Penobscot Bay area of mid-coastal Maine, expressed as the number and % of shared taxa/location. Key to abbreviations: see Table 2.

	SW	CA	KI	PB
South Wolf	85			
	100%			
Campobello	80	107		
	83%	100%		
Kent	42	52	63	
	57%	61%	100%	
Penobscot Bay	64	78	47	97
"composite"	70%	76%	59%	100%
Wooden Ball	52	59	42	65
	69%	69%	66%	80%
Boon	62	73	47	68
	69%	73%	60%	71%
Appledore	66	85	57	80
	63%	74%	61%	73%
Cedar	70	78	53	78
	71%	71%	61%	75%
Duck	67	80	52	73
	69%	74%	60%	71%
Lunging	69	77	53	76
	69%	71%	59%	71%
Malaga	61	73	50	68
	68%	73%	64%	84%
Smuttynose	76	89	55	85
	69%	73%	55%	73%
Star	71	83	51	78
	72%	76%	58%	74%
White	67	78	49	75
	70%	73%	58%	74%
Penikese	51	65	49	59
	47%	55%	51%	52%
Mean (#)	65.5	77.1	50.8	72.7
	±10.8	±12.4	±5.2	±11.3
Similarity	69.7	73.5	62.0	73.5
(all islands) (%)	±11.0	±9.4	±10.7	±10.2
Mean (#)	66.6	78.0	50.9	73.7
	±10.4	±12.3	±5.4	±11.1
Similarity	71.4	74.8	62.8	75.1
(except Penikese) (%)	±9.5	±8.3	±10.7	±8.7

Table 4. Extended.

WB	BO	AP	CE	DU	LU	MA
65						
100%						
46	94					
58%	100%					
53	85	123				
56%	78%	100%				
56	81	97	112			
63%	79%	83%	100%			
53	80	93	91	110		
61%	78%	80%	82%	100%		
54	82	100	102	94	116	
60%	78%	84%	89%	83%	100%	
53	68	82	85	85	88	94
67%	72%	76%	83%	83%	87%	100%
57	89	110	104	97	104	88
57%	77%	85%	84%	79%	83%	77%
56	77	95	94	91	95	81
54%	74%	81%	84%	82%	83%	78%
52	76	93	92	91	92	81
61%	76%	81%	84%	84%	83%	81%
45	67	73	72	68	66	60
46%	60%	57%	59%	56%	53%	53%
53.9	73.0	86.1	84.3	81.7	84.5	74.5
±6.2	±13.3	±18.2	±16.4	±15.9	±18.0	±13.3
64.5	73.5	75.5	77.9	76.1	76.7	76.2
±12.2	±9.8	±11.6	±10.8	±10.9	±12.2	±10.6
47.6	73.4	87.1	85.2	82.6	85.9	75.5
±18.4	±13.7	±18.5	±16.7	±16.0	±17.8	±13.2
65.8	74.5	76.8	79.2	77.6	78.4	77.9
±11.5	±9.4	±10.8	±9.9	±9.9	±10.8	±8.9

Table 4. Extended, continued.

	SM	ST	WH	PI	Grand Mean
South Wolf					
Campobello					
Kent					
Penobscot Bay "composite"					
Wooden Ball					
Boon					
Appledore					
Cedar					
Duck					
Lunging					
Malaga					
Smuttynose	136 100%				
Star	106 85%	113 100%			
White	98 81%	90 82%	106 100%		
Penikese	77 58%	69 57%	63 53%	131 100%	
Mean (#)	92.4 ±20.2	83.3 ±16.5	80.2 ±16.2	67.7 ±19.1	75.2 ±11.4
Similarity (all islands) (%)	75.7 ±11.8	76.0 ±11.7	76.1 ±12.1	57.1 ±12.5	72.3 ±6.0
Mean (#)	92.4 ±20.2	84.3 ±16.7	81.4 ±16.1		76.8 ±12.7
Similarity (except Penikese) (%)	77.0 ±11.2	77.4 ±10.9	77.7 ±10.1		74.7 ±4.7

that lived freely in their woods and roamed the shores to catch fish (Simpson 1987). The Thorofare, a passage between North Haven and Vinalhaven (Figure 2), was a prehistoric deep valley between mountains. Ragged (Criehaven), Wooden Ball, and Matinicus Islands, plus Matinicus Rock, represent the most exposed habitats seaward of the Fox Islands. Matinicus Rock (commonly called The Rock), with its lighthouse, is the outermost marker for Penobscot Bay and the coast of Maine. It consists of about 13 hectares of precipitous granitic ledges arising from the continental shelf 3.1 km seaward of Matinicus Island. The Rock serves as a rookery for Atlantic Puffin, and it is one of only a few islands in the western Atlantic where these birds nest (Porter 1966; Simpson 1987).

The Fox Islands (Figure 2) divide Penobscot Bay into western and eastern basins (Doyle et al. 1970). On the northern portion of West Penobscot Bay, two deep channels (over 52 m) extend along both sides of Islesboro Island and then coalesce further seaward (to the south). Deep water habitats, therefore, are in close proximity to the land in West Penobscot Bay. Seaward of Islesboro, several channels breach the sill between the two Bays, allowing east-west access via Two Bush Island Channel and between Matinicus and Wooden Ball Islands near Bantam Ledge. The Bay's western shore has numerous coastal irregularities that mark the harbor towns of Searsport, Belfast, Camden, Rockport, and Rockland. The upper half of the eastern shore is very irregular, with Castine, Harborside, and Cape Rosier forming major harbors; the mid-eastern shore is characterized by numerous islands, the most prominent being Deer Isle and Isle Au Haut. Together, they form the boundary of East Penobscot Bay, i.e., offshore to the 50 fathom line (Conkling 1996).

Penobscot Bay is underlain primarily by rocks originating from the lower Paleozoic (Doyle et al. 1970). These former sedimentary rocks are highly metamorphosed into complex schists and gneisses. Granitic outcrops are most common on the north and east sides. The mean tidal range varies spatially from about 1.2–3.6 m (Anonymous 1985). Tidal currents average 2.5 knots, except within upper Bay channels (between islands) where they can range from 4 to 7 knots. Because of these strong currents, water masses below 9.0 m are remarkably homogeneous, with salinities varying from 29.9–31.8 ‰. As noted previously, the Penobscot River is the major source of fresh water to the Bay; it is also the second largest drainage basin within New England (Anonymous 1989), draining Hancock, Penobscot, and Waldo Counties. Its tidal limits extend inland about 22.0 km to a tidal dam in Bangor. A series of minor rivers and streams drains into the area, including the Passagassawakeag River at Belfast, the Union and Megunticook Rivers from Camden Hills, and the Bagaduce River from the Castine and Cape Rosier basins on the east side of the estuary.

In characterizing environmental quality within Penobscot Bay, Larsen (1992) states that nickel and zinc concentrations within some sediments are moderately high (29 and 88 ppm dry weight, respectively). The concentrations of other contaminants (chromium, copper, lead, polychlorinated biphenyls, and polycyclic aromatic hydrocarbons) are elevated locally and well above preindustrial levels (Larsen et al. 1984a, b). For example, sediment polycyclic aromatic hydrocarbons in Penobscot Bay averaged 2,600 ppb (Johnson et al. 1985) versus 4,300 ppb for Casco Bay (Larsen et al. 1983). Surprisingly, such values are comparable to some of the most industrialized regions of the world (Larsen 1992). Typically, industrial contamination is highest near the head of the Bay, indicating that river flow is the major pathway into this marine environment. The occurrence of uniform sediment chromatographs also suggests that the major source of contamination is via runoff of compounds deposited within the Penobscot Bay watershed.

RESULTS

Species composition, distribution, and longevity patterns. Ninety-seven seaweed taxa, which include 25 Chlorophyceae, 34 Phaeophyceae, and 38 Rhodophyceae, were collected from the nine islands within the Penobscot Bay area (Table 3). Species richness per island is highly variable (Figure 4) and appears to be a function of collecting frequency (Table 1). The highest numbers of taxa and percentages of the total flora were recorded from Wooden Ball (65 taxa, 67%), Monhegan (64 taxa, 66%), and Hurricane Islands (45 taxa, 46%) where 4 or 5 collections per site were made; the lowest numbers were recorded from Allen (4 taxa, 4%) and Two Bush Islands (10 taxa, 10%), where single collections were made. Green, brown, and red algae are most diverse on Wooden Ball (21, 23, and 21 taxa, respectively) and

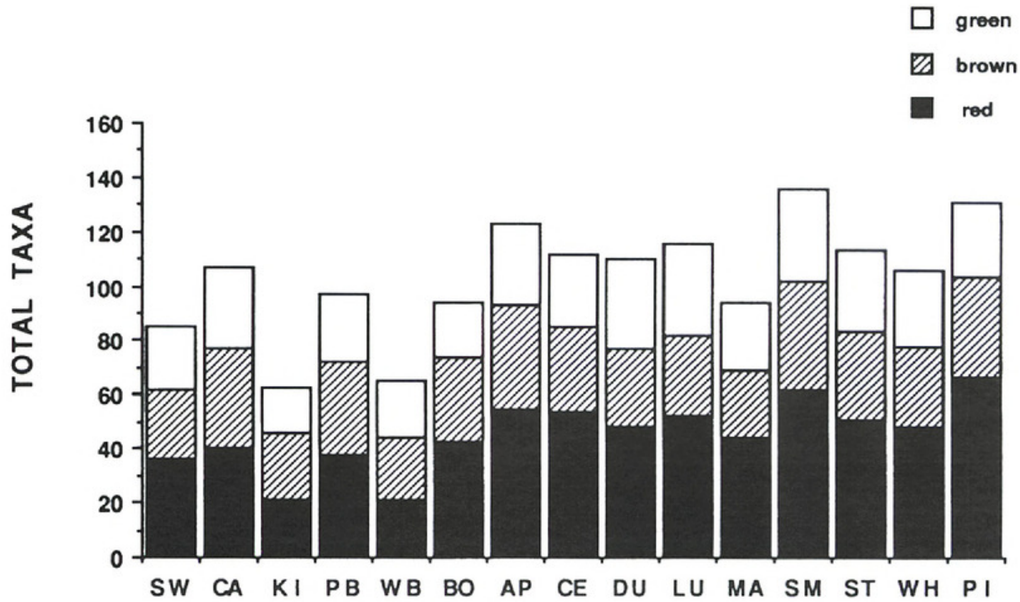

Figure 4. The number of seaweed taxa (green, brown and red) at fourteen individual islands from the Bay of Fundy, Canada, to Buzzards Bay, Massachusetts, plus a "composite" of nine islands from the Penobscot Bay area of Maine. Abbreviations: SW = South Wolf I., New Brunswick; CA = Campobello I., New Brunswick; KI = Kent I., New Brunswick; PB = a "composite" of nine islands from the Penobscot Bay area of Maine (ME)—i.e. Allen, Hurricane, Long, Marshall, McGlathery, Monhegan, Pond, Two Bush, and Wooden Ball Islands; WB = Wooden Ball I., Penobscot Bay, ME; BO = Boon I., ME; AP = Appledore I., ME; CE = Cedar I., ME; DU = Duck I., ME; LU = Lunging I., NH; MA = Malaga I., ME; SM = Smuttynose I., ME; ST = Star I., NH; WH = White I., NH; PI = Penikese I., MA.

Monhegan (14, 21, and 29 taxa), intermediate on Hurricane (9, 18, and 18 taxa) and Long Islands (8, 14, and 14 taxa), and lowest on Allen (0, 3, and 1 taxa). Overall, the mean number of taxa per island is very low, being 30.8 ± 23.0 SD; the green algae contribute 6.9 ± 7.0, the brown algae 11.4 ± 7.7, and the red algae 12.4 ± 9.0.

As outlined in Figure 5 and Table 3, 34 of the 97 total taxa from the Penobscot Bay area (10 green, 14 brown, and 10 red algae) are restricted to a single island (11.1% occurrence), while 23 taxa (7 green, 3 brown, and 13 red algae) occur on two islands (22.2% occurrence). Thirty seaweeds occur on 4–9 islands (44.4–100% occurrence); this includes 6 greens, 12 browns, and 12 reds. The most ubiquitous taxa are *Elachista fucicola* and *Pilayella littoralis* (100% occurrence); *Fucus vesiculosus* and *Chondrus crispus* occur at 88.9% of the sites, while *Rhizoclonium tortuo-*

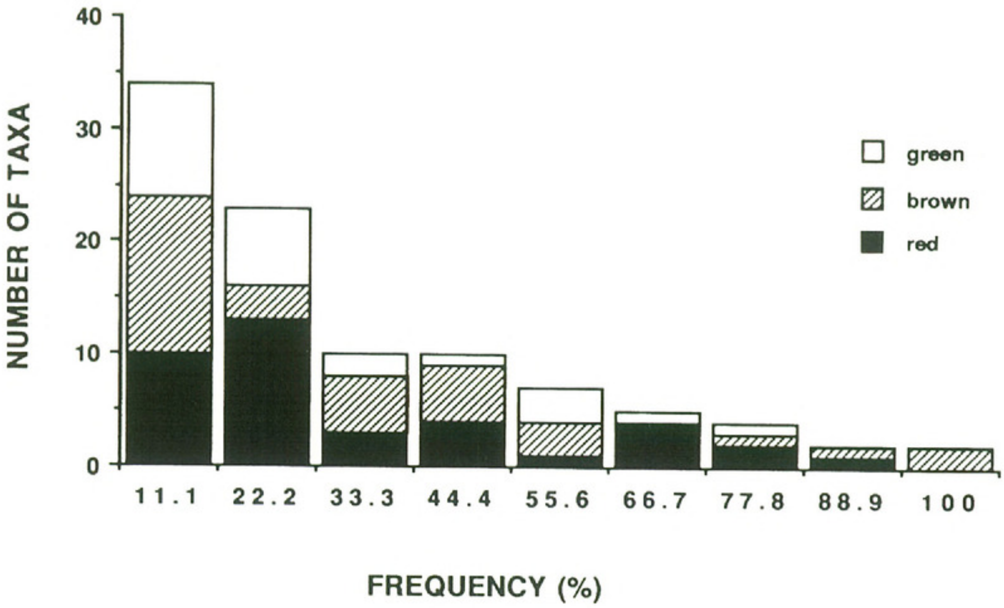

Figure 5. Frequency distribution patterns of 97 seaweed taxa recorded from nine islands within the Penobscot Bay area. Taxa found on only one of the nine islands (11.1% occurrence) are represented by the left-most bar of the graph; those found on only two islands (22.2%) are represented by the next bar, etc.

sum, Ascophyllum nodosum, and *Dumontia contorta* occur at 77.8% (Table 3).

The longevity patterns of seaweeds at each of the nine Penobscot Bay islands are summarized in Table 3. The numbers of annuals range from 29 taxa on Wooden Ball to only 1 on Allen Island (mean = 12.7 ± 10.7 taxa); perennials vary from 38 taxa on Monhegan to 3 on Allen Island (mean = 18.4 ± 12.5 taxa). The longevity ratios (annuals/perennials) at the various sites range from a maximum of 1 on Two Bush Island to 0.19 on McGlathery Island (mean = 0.65 ± 0.28). As shown in Figure 6, the "composite" flora consists of 48 annuals and 49 perennials, giving an overall longevity ratio of 0.98. With respect to individual groups, the green algae are predominantly annuals (19/25 or 76%), the brown algae are intermediate (18/34 or 53%), and the red algae exhibit the lowest percentage of annuals (11/38 or 29%).

Floristic comparisons. A total of 216 seaweed taxa (52 Chlorophyceae, 63 Phaeophyceae, and 101 Rhodophyceae) is recorded from fourteen individual islands, ranging from the Bay of Fundy (South Wolf Island, New Brunswick) to Buzzards Bay

(Penikese Island), Massachusetts, including a "composite" of Penobscot Bay's insular flora (Table 2; Figure 4). The "composite" data are presented due to limited seasonal and subtidal collections from individual islands within the Penobscot Bay area; collections from Wooden Ball provide the most realistic representation of an individual island within this embayment. Overall, the highest numbers of species are recorded from Smuttynose (136 taxa) and Penikese Islands (131 taxa), with Kent, Monhegan, and Wooden Ball Islands having the lowest numbers (63–65 taxa). Penobscot Bay's "composite" insular flora (97 taxa) exceeds the last three sites, as well as those of South Wolf (85 taxa), Boon, and Malaga Islands (94 taxa each). The last-named site is the smallest island within the Shoals archipelago. The two islands having the most diverse floras within the Penobscot Bay area (Table 3), Wooden Ball (65 taxa) and Monhegan (64 taxa), have approximately the same number of taxa as Kent Island (63 taxa), while the other thirteen individual islands (Table 2) have more diverse floras. Based upon the data in Table 2, the following values for species richness (mean $\pm$ SD) are calculated for the fourteen individual islands, plus the "composite" data for the Penobscot Bay area: (1) 103.9 $\pm$ 21.9 taxa for fourteen individual islands, excluding Penobscot Bay's "composite" value; (2) 106.2 $\pm$ 19.0 taxa for thirteen individual islands and Penobscot Bay's "composite," excluding Wooden Ball Island as an individual; (3) 106.9 $\pm$ 19.5 taxa for thirteen individual islands, excluding Penobscot Bay's "composite" value and Wooden Ball Island; (4) 101.8 $\pm$ 21.3 taxa for thirteen individual islands, excluding Penobscot Bay's "composite" and Penikese Island; (5) 104.3 $\pm$ 18.3 taxa for twelve individual islands and Penobscot Bay "composite," excluding Wooden Ball and Penikese Islands; (6) 104.9 $\pm$ 19.0 taxa for twelve individual islands, excluding Penobscot Bay "composite," Wooden Ball and Penikese Islands. Thus, the values are very uniform.

Figure 7 summarizes the distributional patterns of the 216 total seaweed taxa in Table 2 and is expressed as percent occurrence on fourteen individual islands, excluding the Penobscot Bay "composite." A bimodal pattern is evident, with peak numbers occurring at one and all fourteen islands. Fifty-one seaweeds are restricted to a single island (7.1% occurrence), while 25 occur on all fourteen. The most ubiquitous taxa (100% occurrence) consist of 5 green algae (*Blidingia minima, Chaetomorpha melagonium,*

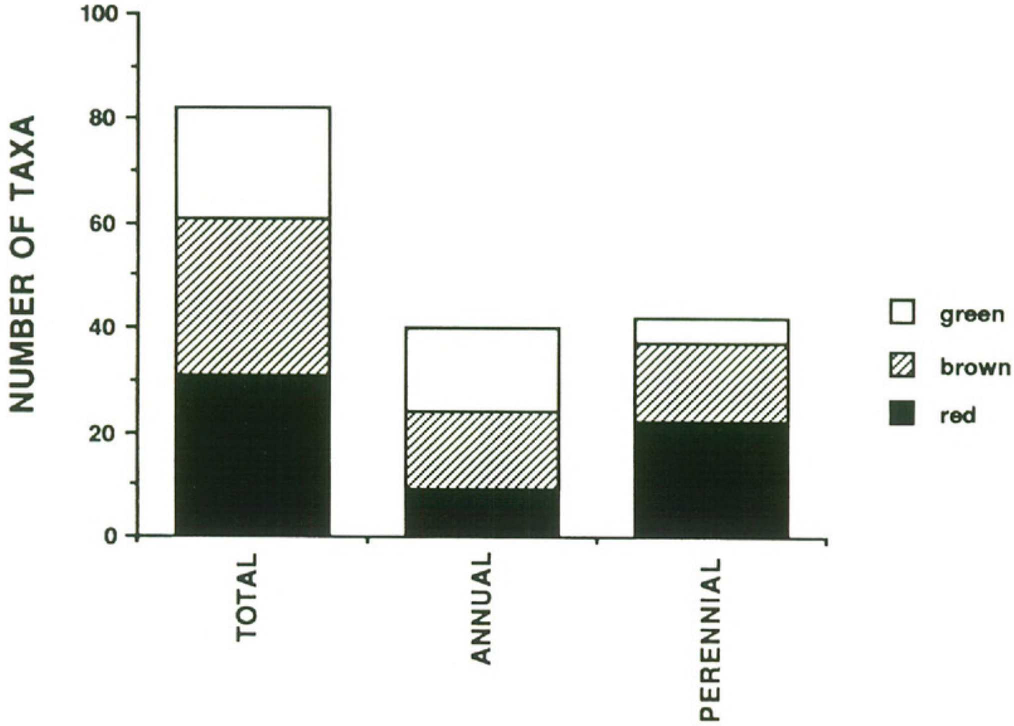

Figure 6. Longevity patterns of 97 seaweed taxa within Penobscot Bay area of Maine, expressed as the number of annuals, perennials, and total seaweed taxa.

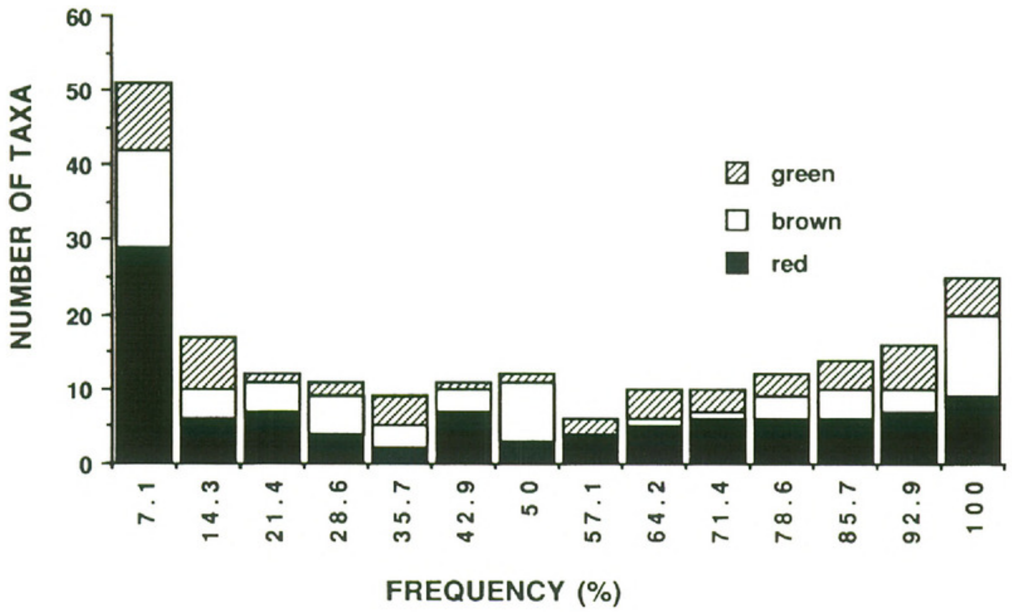

Figure 7. Frequency distribution patterns of 216 seaweed taxa recorded from fourteen individual islands from South Wolf Island, New Brunswick, to Penikese Island, Massachusetts. Taxa found on only one of the fourteen islands (7.1% occurrence) are represented by the left-most bar of the graph; those found on only two islands (14.3%) are represented by the next bar, etc.

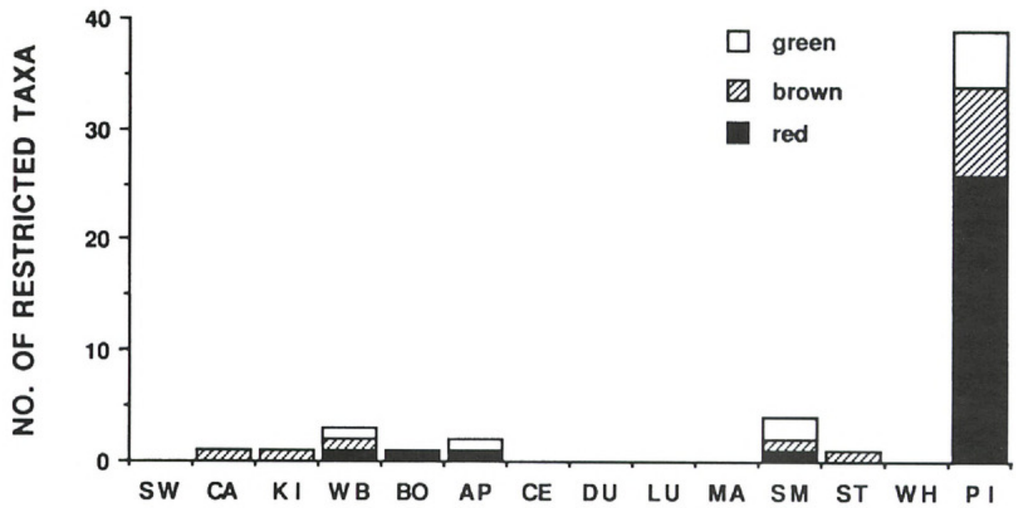

Figure 8. Spatial occurrence of restricted taxa on fourteen individual islands.

Enteromorpha intestinalis, E. linza, and *Ulva lactuca*), 11 brown algae (*Ascophyllum nodosum, Chordaria flagelliformis, Ectocarpus siliculosus, Elachista fucicola, Fucus distichus* ssp. *evanescens, F. spiralis, F. vesiculosus, Laminaria digitata, L. saccharina, Pilayella littoralis,* and *Scytosiphon simplicissimus*), and 9 red algae (*Ahnfeltia plicata, Ceramium nodulosum, Corallina officinalis, Cystoclonium purpureum, Palmaria palmata, Polysiphonia lanosa, P. stricta, Porphyra umbilicalis,* and *Rhodomela confervoides*).

Figure 8 outlines the spatial occurrence of 51 "localized" taxa or those restricted to only one of the fourteen individual islands from the Bay of Fundy to Buzzards Bay (Table 2). Penikese has the largest number of these taxa (38), consisting of 5 green, 7 brown, and 26 red algae. The other 13 localized taxa occur on the following islands: Appledore (*Pringsheimiella scutata* and *Pantoneura baeri*), Boon (*Lomentaria clavellosa*), Campobello (*Dictyosiphon macounii*), Kent (*Ascophyllum nodosum* ecad *scorpioides*), Smuttynose (*Chaetomorpha minima, Ulvaria oxysperma, Laminariocolax tomentosoides, Sphacelaria fusca,* and *Halosacciocolax kjellmanii*), Star (*Cladostephus spongiosus* forma *verticillatus*), and Wooden Ball (*Chlorochytrium cohnii* and *Petroderma maculiforme*).

Table 4 summarizes floristic affinities of fourteen individual islands plus a "composite" for the Penobscot Bay area, with values expressed as the mean number and percentage of shared taxa

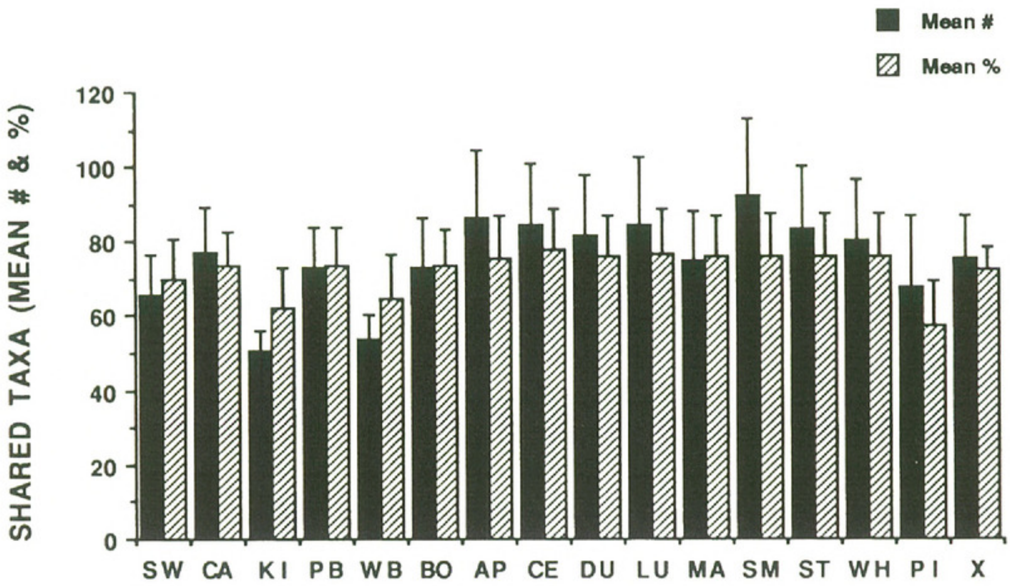

Figure 9. Mean number and percentage (±SD) of shared taxa/site at fourteen individual islands from the Bay of Fundy, Canada, to Buzzards Bay, Massachusetts, plus a "composite" of nine islands from the Penobscot Bay area of Maine. See Figure 4 for abbreviations. X = overall mean value.

per island and per total sites. The combined mean values for all fifteen sites are relatively high (75.2 ± 11.4 taxa and 72.3 ± 6.0%). Of the fifteen sites, Smuttynose has the most diverse flora (136 taxa), the highest mean number of shared taxa (92.4 ± 20.2), and an intermediate percent similarity pattern (75.7 ± 11.8%). By contrast, Kent Island, with a flora represented by only 63 taxa, exhibits the lowest mean number of shared taxa (50.8 ± 5.2) and a percent similarity of 62.0 ± 10.7%. Penikese Island, with 131 total and 38 "localized" taxa, has only 67.7 ± 19.1 shared taxa and the lowest percent similarity value recorded (57.1 ± 12.5%). An analogous comparison of fourteen sites (excluding Penikese Island) shows slightly higher mean values of 76.8 ± 12.7 taxa and 74.7 ± 4.7% (Table 4). Smuttynose, with its diverse flora, has the highest number of shared taxa (92.4 ± 20.2) and intermediate percent similarity (77.0 ± 11.2%), while Kent and Wooden Ball Islands show the lowest numbers (50.9 ± 5.4 and 47.6 ± 18.4) and percent similarity values (62.8 ± 10.7% and 65.8 ± 11.5%). A graphical summary of the average number of shared taxa and percent similarity patterns for the fifteen insular sites is given in Figure 9.

The floristic affinities of Penobscot Bay's "composite" insular flora are illustrated in Figure 10, with the number and percent

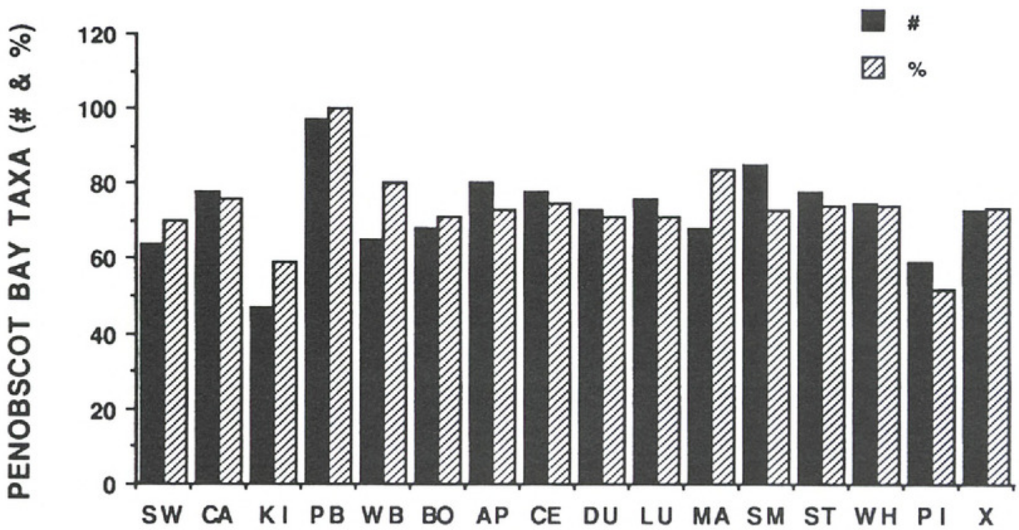

Figure 10. Number and percentage of Penobscot Bay taxa ("composite") at fourteen individual islands from the Bay of Fundy, Canada, to Buzzards Bay, Massachusetts, including overall mean values. See Figure 4 for abbreviations.

similarity values for the other fourteen islands given in Table 4. As noted above, floristic affinities of individual islands tend to "mimic" patterns of species richness. The highest numbers of shared taxa occur on Smuttynose (85 taxa) and Appledore Islands (80 taxa), while Kent and Penikese Islands show the lowest numbers (47 and 59 taxa, respectively). By contrast, the percent similarity values are highest on Malaga (84%) and lowest on Penikese (52%) and Kent Islands (59%). The mean number and percent similarity of Penobscot Bay taxa on all fourteen islands are 72.7 ± 11.3 taxa and 73.5 ± 10.2%, respectively. An analogous calculation for thirteen islands (minus Penikese) gives slightly higher mean values of 73.7 ± 11.1 taxa and 75.1 ± 8.7%.

DISCUSSION

Although Penobscot Bay is the largest embayment on Maine's irregular coastline (Apollonio 1979; Doyle et al. 1970; Platt 1996; Porter 1966), its algal flora has been documented previously by only a few published records of individual taxa. For example, Taylor (1957) gives no specific records for the Bay, simply citing Maine. However, in a discussion of historical data (p. 22), he mentions the early Maine collections of Franklin W. Hooper that are deposited in BKL. A recent examination of these collections revealed that they were, in fact, collected by John Hooper during September 1851 and bequeathed to the Long Island Historical Society upon his death in 1869. Most of John Hooper's Penobscot Bay collections are from inshore sites near Camden, Maine, while the precise locations of others are not given. The collections at BKL also include several isotypes. The fact that F. W. Hooper was born just seven months prior to the Camden collections in 1851 confirms this misinterpretation. Perhaps F. W. Hooper's affiliation with Harvard University and W. G. Farlow, and his subsequent directorship (1889) at the Brooklyn Institute contributed to this confusion (Anonymous 1887, 1906).

Eaton (1873) mentions *Ceramium hooperi* from Penobscot Bay, noting that it was collected by Hooper and named by W. H. Harvey for its discoverer. The name now is considered conspecific with *C. deslongchampii* (South and Tittley 1986; Taylor 1957). Seven additional taxa documented by Hooper (in NHA and BKL) have not been observed by us: *Cladophora rupestris, Enteromorpha clathrata, Stilophora rhizoides, Myriotrichia clavaeformis, Gymnogongrus crenulatus, Polyides rotundus,* and *Gracilaria tikvahiae* (Tables 2 and 3). With the exception of *S. rhizoides* and *G. tikvahiae,* which are warm-water disjuncts in the northwest Atlantic (South and Tittley 1986; Taylor 1957), the other five taxa are likely to occur on nearshore islands within Penobscot Bay (Appendix). The coastal occurrence of *G. tikvahiae* and *S. rhizoides* in Maine is particularly noteworthy (Bourque 1996). We have collected *Gracilaria* only from shallow estuarine habitats in northern New England: the Great Bay Estuary System of Maine/New Hampshire (Mathieson and Hehre 1986), the Salt Bay area near Newcastle, Maine, and within the upper reaches of the New Meadow River near Bath, Maine. *Stilophora rhizoides* has been found only within the same Salt Bay area in Newcastle. The NHA specimen of *G. tikvahiae* from Penobscot Bay was initially identified by J. Hooper as *Gymnogongrus norvegicus*; there are, however, correctly identified specimens of both taxa within Hooper's collections (BKL).

Collins (1891, 1896a, b, 1899, 1901) collected at several inshore (Camden and Cape Rosier) and insular habitats within the Penobscot Bay area (Eagle, Great Duck, Spectacle, and York Islands). We have found most of the taxa documented by Collins, with the following exceptions: *Cladophora albida, C. ruchingeri, Gononema aecidioides, "Hecatonema maculans," Leptonematel-*

la fasciculata, Ralfsia fungiformis, Streblonema fasciculatum, Ceramium strictum, and *Erythrodermis traillii.* As noted by Hoek (1982), *Cladophora ruchingeri* was identified initially by Collins (1899) as *Cladophora gracilis* forma *elongata,* based upon collections from Spectacle Island. An isotype of this taxon is deposited in the Farlow Herbarium (*Phycotheca Boreali-Americana* #725). Although there are several other records of *C. ruchingeri* from Maine's open coast (Hoek 1982, p. 20), our New England records are restricted to a single estuarine tidal rapids site at Dover Point, New Hampshire.

Aside from the 97 insular (Table 3) and 16 historical records noted above, we have recently documented 26 additional taxa from more than 70 inshore Penobscot Bay habitats (Mathieson and Hehre, unpubl. data). These include 11 green algae (*Bryopsis plumosa, Capsosiphon groenlandicum, Codiolum pusillum, Enteromorpha compressa, E. torta, Epicladia flustrae, Microspora pachyderma, Percursaria percursa, Prasiola stipitata, Ulothrix speciosa,* and *Ulvaria oxysperma*), 6 brown algae (*Ascophyllum nodosum* ecad *scorpioides, Chorda filum, Desmarestia viridis, Fucus vesiculosus* ecad *limicola, Hincksia granulosa,* and "*Ralfsia bornetii*"), and 9 red algae (*Audouinella dasyae, A. membranacea, Erythrotrichia carnea, Erythrotrichopeltis ciliaris, Peyssonnelia rosenvingii, Porphyra leucosticta, Ptilota serrata, Saccheria fucina,* and *Stylonema alsidii*). Thus, a total of 139 seaweed taxa is recorded from the Penobscot Bay area, which is slightly greater than floristically diverse islands like Smuttynose (136) and Penikese Islands (131 taxa) but less than that of nearby Casco and Passamaquoddy Bays within southern Maine and New Brunswick, respectively (Collins 1911; Tittley et al. 1987).

The reduced mean number of taxa per island within Penobscot Bay (30.8 $\pm$ 23.0) versus the Isles of Shoals (114.0 $\pm$ 11.4) should be noted (Mathieson and Penniman 1986b). While riverine contamination within Penobscot Bay (Larsen 1992; Larsen et al. 1984a, b) might be a contributing factor to this low species diversity, several islands are considerably offshore (Appendix), diminishing the effects of nearshore pollution. More likely, the low diversity is associated with the very sheltered nature of Penobscot Bay (Collins 1899), which would allow a dominance of selected taxa (Mathieson et al. 1991; Tittley et al. 1987; Vadas et al. 1976). Further, the occurrence of limited seasonal and subtidal collections is no doubt a contributing factor (Mathieson 1979; Mathieson and Penniman 1986a), as well as the fact that only 9 of several hundred islands were studied (Hill 1923). For the above reasons, it is premature to make any detailed statistical inferences of insular species richness within Penobscot Bay as a function of area, shoreline length or exposure to wave action (Mathieson and Penniman 1986b). For example, the lowest number of taxa is found on Allen Island (4 taxa) having a shoreline of approximately 7620 m, while the highest number of taxa (65) is found on Wooden Ball with a smaller shoreline of about 5560 m (Table 3; Appendix).

As noted previously, we are aware of only two comparative studies of insular marine floras in North America, those involving the Channel Islands in Southern California (Murray and Littler 1981; Murray et al. 1980) and the Isles of Shoals in southern Maine/New Hampshire (Mathieson and Penniman 1986b). Although both archipelagos contain eight islands, this is where the analogies end. The maximum distance between islands at the Shoals is very small (4.8 km) and individual islands exhibit a wide range of wave exposure and relatively uniform hydrography and substrata (Sze 1982). By contrast, the distances between the individual Channel Islands are much greater and they collectively extend over a much broader geographical range. They occur just offshore and south of Point Conception and their oceanographic and meteorological conditions are complex and spatially variable due to the proximity of the cold California Current and the warm Southern California Countercurrent (Lüning 1990). Not suprisingly, the floristic similarities of the Channel Islands are relatively low (mean = 45.4%) and the different islands contain a mixture of both northern and southern elements. Even so, the islands have their greatest affinities with the mainland south of Point Conception, while individual islands exhibit a pattern of variable affinities to the central California flora. In contrast to such low floristic affinities and spatially variable and complex oceanographic parameters within the Southern California Bight, oceanographic conditions within the Gulf of Maine are more stable spatially (Mathieson and Penniman 1986b; Mathieson et al. 1991). Such uniformity may contribute to the relatively high floristic affinities of Gulf of Maine islands as a whole (mean = 72.3 ± 6.0%; Table 4). Surprisingly, an analogous comparison of the percent similarity of Gulf of Maine sites, minus the southernmost Penikese Island, shows only a slightly higher mean value of 74.7 ± 4.7%.

Thus, floristic similarities within these Northwest Atlantic islands are much higher than those of the Channel Islands, which show maximum and minimum interisland values of 64.2 and 32.6%, respectively. In contrast to the latter situation, Scagel (1963) emphasizes that the northeast Pacific flora is relatively uniform and exhibits a gradual transition in species composition from northern California to Sitka, Alaska. Such patterns are more comparable to those of the Gulf of Maine and Bay of Fundy (Figure 9).

A comparison of the floras north and south of Cape Cod (the Gulf of Maine and Bay of Fundy versus Buzzards Bay) reveals differences in species richness and numbers of warm-temperate taxa (Lüning 1990). For example, of the different insular sites discussed above (Figure 7; Table 2), only Smuttynose has more taxa (136) than Penikese (131). Amazingly, the Penikese records are based almost entirely upon summer collections from the intertidal and shallow subtidal zones (Doty 1948; Jordan 1874; Lewis 1924), while those from Smuttynose are based upon detailed seasonal collections of both intertidal and subtidal seaweeds (to the lower limits of vegetation). No doubt, enhanced seasonal and subtidal collections on Penikese would increase the number of known taxa. In a detailed seasonal study of subtidal seaweeds (from 1.2 to 41.0 m) within nearby Martha's Vineyard, Waquoit Bay, and Buzzards Bay, Sears and Wilce (1975) record 132 taxa, consisting of 13 Chlorophyceae, 52 Phaeophyceae, and 67 Rhodophyceae. Thus, a total of 187 taxa is recorded from Penikese and adjacent subtidal sites, which is comparable to the entire Gulf of Maine (Mathieson and Hehre 1986; Mathieson and Penniman 1986b; South and Tittley 1986). Seventy-six of these taxa are common throughout the region (6 Chlorophyta, 24 Phaeophyta, 46 Rhodophyta), while 55 are restricted to Penikese (19 Chlorophyta, 14 Phaeophyta, 22 Rhodophyta) and 56 are recorded only by Sears and Wilce (7 Chlorophyta, 28 Phaeophyta, 21 Rhodophyta). Overall, the intertidal flora at Penikese has a greater number of green algae, while crustose browns are more common at the adjacent subtidal sites.

In a comparison of multiple nearshore sites north and south of Cape Cod, Massachusetts, Coleman and Mathieson (1975) found an enhancement of annuals to the south, while perennials were more abundant to the north. They state that greater numbers of annuals occur where large temperature amplitudes are evident south of Cape Cod, while the opposite pattern exists with reduced temperature variations north of the Cape. Similarly, Littler and Littler (1981) state that annuals or opportunistic forms dominate in seasonally disturbed environments due to catastrophic environmental fluctuations, while long-lived perennials are more conspicuous in environmentally constant habitats.

Mathieson and Penniman (1986b) summarize longevity ratios (#annual/#perennial taxa) for 11 island floras and 4 nearshore habitats, from South Wolf Island, New Brunswick, to Woods Hole, Massachusetts; the values vary from 1.29 (Woods Hole) to 0.66 (Scituate), with an overall mean of 0.85 (greater # of perennials than annuals). The latter value (0.85) is intermediate between Penobscot Bay's "composite" flora (0.97) and the mean for the nine individual islands (0.65 ± 0.28). Mathieson and Penniman (1986b) also note that similar values may result from different combinations of perennials and annuals. They find a ratio of 0.95 for Smuttynose Island, an exposed offshore habitat within the Isles of Shoals, and at Dover Point, a mid-estuarine site, with the two calculations based upon values of 61 annuals/64 perennials and 45 annuals/47 perennials, respectively. Comprehensive seasonal and spatial collections (intertidal and subtidal) are obviously necessary before any meaningful comparisons of such ratios can be made. The wide range of values in Table 3 confirms the preliminary nature of the individual insular collections within Penobscot Bay.

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LITERATURE CITED

ADEY, W. H. AND P. J. ADEY. 1973. Studies of the biosystematics and ecology of the epilithic crustose Corallinaceae of the British Isles. Brit. Phycol. J. 8: 343–407.

ANONYMOUS. 1887. Appleton's Cyclopedia of American Biography, Vol. III. D. Appleton and Co., New York. p. 252.
———. 1906. The National Cyclopedia of American Biography, Vol. XIII. James T. White and Co., New York. p. 46.
———. 1985. Tide Tables 1985, High and Low Water Predictions, East Coast of North and South America, Including Greenland. United States Department of Commerce, NOAA, Washington, DC.
———. 1988. National Status and Trends Program for Marine Environmental Quality: Progress Report—A summary of selected data on chemical contaminants in sediments collected during 1984, 1985, 1986, and 1987. NOAA Techn. Mem. NOS OMA 44.
APOLLONIO, S. 1979. The Gulf of Maine. Courier-Gazette, Inc., Rockland, ME.
BIRD, C. J. AND J. L. MCLACHLAN. 1992. Seaweed Flora of the Maritimes 1. Rhodophyta—the Red Algae. Biopress Ltd., Bristol, England.
BLAIR, S. M. 1983. Taxonomic treatment of the *Chaetomorpha* and *Rhizoclonium* species (Cladophorales; Chlorophyta) in New England. Rhodora 85: 175–211.
BLIDING, C. 1963. A critical survey of European taxa in Ulvales, Part I. *Capsosiphon, Percursaria, Blidingia, Enteromorpha.* Opera Bot. 8: 1–60.
———. 1968. A critical survey of European taxa in Ulvales, Part II. *Ulva, Ulvaria, Monostroma, Kornmannia.* Bot. Not. 121: 535–629.
BOURQUE, B. J. 1996. Prehistoric cultural responses to changes in the Gulf of Maine. Abstracts, Gulf of Maine Ecosystem Dynamics, St. Andrews, NB, Canada.
BOWERS, C. H. 1942. Algae of Kent Island. Bowdoin Sci. St. Bull. 8: 36–37.
BRAY, J. R. AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325–349.
BURROWS, E. M. 1991. Seaweeds of the British Isles. Vol. 2, Chlorophyta. Natural History Museum, London.
COLEMAN, D. C. AND A. C. MATHIESON. 1975. Investigations of New England marine algae VII: seasonal occurrence and reproduction of marine algae near Cape Cod, Massachusetts. Rhodora 77: 76–104.
COLLINS, F. S. 1891. Notes on New England marine algae. V. Bull. Torrey Bot. Club 18: 335–341.
———. 1896a. Notes on New England marine algae. VI. Bull. Torrey Bot. Club 23: 1–6.
———. 1896b. Notes on New England marine algae. VII. Bull. Torrey Bot. Club 23: 458–462.
———. 1899. A seaweed colony. Rhodora 1: 69–71.
———. 1900. The marine flora of Great Duck Island, Maine. Rhodora 2: 209–211.
———. 1901. Notes on algae, IV. Rhodora 3: 289–293.
———. 1911. The marine algae of Casco Bay. Proc. Portland Soc. Nat. Hist. 2: 257–282.
CONKLING, P. W. 1996. Marine Ecology of Penobscot Bay, pp. 33–44. *In:* D. D. Platt, ed., Penobscot: The Forest, River and Bay. Island Institute, Rockland, ME.
DIXON, P. S. AND L. M. IRVINE. 1977. Seaweeds of the British Isles. Vol. 1,

Rhodophyta. Part 1, Introduction, Nemaliales, Gigartinales. British Museum (Natural History), London.

DOTY, M. S. 1948. The flora of Penikese, seventy-four years after. I. Penikese Island marine algae. Rhodora 50: 253–269.

DOYLE, R. G., W. A. ANDERSON, AND FRANK M. BLACKETT, JR. 1970. Penobscot Bay physical resources report (preliminary). Maine Dept. Economic Development, Augusta, ME.

DRUEHL, L. D. 1981. Geographical distribution, pp. 306–325. *In:* C. S. Lobban and M. J. Wynne, eds., The Biology of Seaweeds. Botanical Monographs, Vol. 17. Blackwell Scientific Publications, London.

DÜWEL, L. AND S. WEGEBERG. 1996. The typification and status of *Leptophytum* (Corallinaceae, Rhodophyta). Phycologia 35: 470–483.

EATON, D. C. 1873. List of marine algae collected near Eastport, Maine in August and September, 1872, in connection with the work of the U.S. Fish Comm. under Prof. S. F. Baird. Trans. Connecticut Acad. Arts 2: 343–350.

FARLOW, W. G. 1881. Marine algae of New England. Rep. U.S. Comm. Fish and Fisheries for 1879, Appendix A-1: 1–210.

FLETCHER, R. L. 1987. Seaweeds of the British Isles. Vol. 3, Fucophyceae (Phaeophyceae), Part 1. British Museum (Natural History), London.

HEHRE, E. J., J. R. CONWAY, AND R. A. STONE. 1970. Flora of the Wolf Islands Part III: The marine algae. Rhodora 72: 115–118.

——— AND A. C. MATHIESON. 1970. Investigations of New England marine algae II. Composition, seasonal occurrence and reproductive periodicity of the marine Rhodophyceae in New Hampshire. Rhodora 72: 194–239.

HILL, A. F. 1923. The vegetation of the Penobscot Bay region, Maine. Proc. Portland Soc. Nat. Hist. 3: 305–438.

HOEK, C. VAN DEN. 1963. Revision of the European species of *Cladophora.* E. J. Brill, Leiden, Netherlands.

———. 1982. A taxonomic revision of the American species of *Cladophora* (Chlorophyceae) in the North Atlantic Ocean and their geographic distribution. North-Holland Publ. Co., Amsterdam.

IRVINE, L. M. 1983. Seaweeds of the British Isles. Vol. 1, Rhodophyta. Part 2A, Cryptonemiales (*sensu stricto*), Palmariales, Rhodymeniales. British Museum (Natural History), London.

——— AND Y. M. CHAMBERLAIN. 1994. Seaweeds of the British Isles. Vol. 1, Rhodophyta. Part 2B, Corallinales, Hildenbrandiales. Natural History Museum, London.

JOHNSON, A. C., P. F. LARSEN, D. F. GADBOIS, AND A. W. HUMASON. 1985. The distribution of polycyclic aromatic hydrocarbons in the surficial sediments of Penobscot Bay (Maine, U.S.A.) in relation to possible sources and to other sites worldwide. Mar. Environ. Res. 15: 1–16.

JOHNSON, D. S. AND A. F. SKUTCH. 1928a. Littoral vegetation on a headland of Mt. Desert Island, Maine. Submersible or strictly littoral vegetation. Ecology 9: 188–215.

——— AND ———. 1928b. Littoral vegetation on a headland of Mt. Desert Island, Maine. II. Tidepools and the environment and classification of submersible plant communities. Ecology 9: 307–338.

Jordan, D. S. 1874. The flora of Penikese Island. Amer. Naturalist 8: 193–197.

Kelly, J. T. 1992. Sea-level change and coastal erosion in the western Gulf of Maine, pp. 27–44. *In:* D. D. Townsend and P. F. Larsen, eds., The Gulf of Maine. NOAA Coastal Ocean Program, Regional Synthesis Series No. 1, Washington, D.C.

Kingsbury, J. M. 1969. The Seaweeds of Cape Cod and the Islands. Chatham Press Inc., Chatham, MA.

Knight, M. and M. W. Parke. 1931. Manx algae: an algal survey of the south end of the Isle of Man. L. M. B. C. Memoirs 30: 1–155.

Koetzner, K. L. and R. D. Wood. 1972. On the marine algae of Kent Island, Bay of Fundy. Rhodora 74: 264–271.

Larsen, P. F. 1992. An overview of the environmental quality of the Gulf of Maine, pp. 71–95. *In:* D. D. Townsend and P. F. Larsen, eds., The Gulf of Maine. NOAA Coastal Ocean Program, Regional Synthesis Series No. 1, Washington, D.C.

———, D. F. Gadbois, and A. C. Johnson. 1984a. Trace metal distributions in the surficial sediments of Penobscot Bay, Maine. Bull. Environ. Contam. Toxicol. 31: 566–573.

———, ———, and ———. 1984b. Sediment PCB distribution in the Penobscot Bay region of the Gulf of Maine. Mar. Poll. Bull. 15: 34–35.

———, ———, ———, and L. F. Doggett. 1983. Distribution of polycyclic aromatic hydrocarbons in the surficial sediments of Casco Bay, Maine. Bull. Environ. Contam. Toxicol. 30: 530–535.

Lewis, I. F. 1924. The flora of Penikese, fifty years after. Rhodora 26: 181–195.

Littler, M. M. and D. S. Littler. 1981. Intertidal macrophyte communities from Pacific Baja California and the upper Gulf of California: Relatively constant versus environmentally fluctuating systems. Mar. Ecol. Prog. Ser. 4: 145–158.

Lüning, K. 1990. Seaweeds: Their Environment, Biogeography and Ecophysiology. Wiley-Interscience Publ., New York.

Maggs, C. A. and M. H. Hommersand. 1993. Seaweeds of the British Isles. Vol. 1, Rhodophyta. Part 3A, Ceramiales. Natural History Museum, London.

Mathieson, A. C. 1979. Vertical distribution and longevity of subtidal seaweeds in northern New England, U.S.A. Bot. Mar. 22: 511–520.

———. 1989. Phenological patterns of northern New England seaweeds. Bot. Mar. 32: 419–438.

——— and E. J. Hehre. 1982. The composition, seasonal occurrence and reproductive periodicity of the marine Phaeophyceae in New Hampshire. Rhodora 84: 411–437.

——— and ———. 1983. The composition and seasonal periodicity of the marine Chlorophyceae in New Hampshire. Rhodora 85: 275–299.

——— and ———. 1986. A synopsis of New Hampshire seaweeds. Rhodora 88: 1–139.

———, ———, and M. Costa. 1993. Algal vegetation of the York River Estuary and the adjacent open coast of southern Maine. Rhodora 95: 285–324.

———, ———, AND N. B. REYNOLDS. 1981. Investigations of New England marine algae I: A floristic and descriptive ecological study of the marine algae at Jaffrey Point, New Hampshire. Bot. Mar. 24: 521–532.

——— AND C. A. PENNIMAN. 1986a. Species composition and seasonality of New England seaweeds along an open coastal-estuarine gradient. Bot. Mar. 29: 161–176.

——— AND ———. 1986b. A phytogeographic interpretation of the marine flora from the Isles of Shoals, U.S.A. Bot. Mar. 29: 413–434.

——— AND ———. 1991. Floristic patterns and numerical classification of New England estuarine and open coastal seaweed populations. Nova Hedwigia 52: 453–485.

———, ———, AND L. G. HARRIS. 1991. Northwest Atlantic rocky shore ecology, pp. 109–191. *In:* A. C. Mathieson and P. H. Nienhuis, eds., Intertidal and Littoral Ecosystems. Elsevier, Amsterdam.

———, N. B. REYNOLDS, AND E. J. HEHRE. 1981. Investigations of New England marine algae II: The species composition, distribution and zonation of seaweeds in the Great Bay Estuary System and the adjacent open coast of New Hampshire. Bot. Mar. 24: 521–532.

MURRAY, S. N. AND M. M. LITTLER. 1981. Biogeographical analysis of intertidal macrophyte floras of southern California. J. Biogeogr. 8: 339–351.

———, ———, AND I. A. ABBOTT. 1980. Biogeography of the California marine algae with emphasis on the Southern California Islands, pp. 325–339. *In:* D. M. Powers, ed., The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

PIKE, R. B. AND A. R. HODGDON. 1963. The flora of the Wolf Islands, New Brunswick Part 1. Rhodora 65: 82–96.

PLATT, D. D., ed. 1996. Penobscot: The Forest, River and Bay. Island Institute, Rockland, ME.

———, P. W. CONKLING, A. NAEGEL, S. DICKERSON, T. AMES, AND C. OLDHAM. 1996. Introduction, pp. 8–9. *In:* D. D. Platt, ed., Penobscot: The Forest, River and Bay. Island Institute, Rockland, ME.

PORTER, E. 1966. Summer Island: Penobscot County. Sierra Club, Ballantine Books, San Francisco, CA.

REYNOLDS, N. B. AND A. C. MATHIESON. 1975. Seasonal occurrence and ecology of marine algae in a New Hampshire tidal rapid. Rhodora 77: 512–533.

RICH, L. D. 1975. The Coast of Maine: An Informal History and Guide. Down East Books, Camden, ME.

SCAGEL, R. F. 1963. Distribution of attached marine algae in relation to oceanographic conditions in the northeast Pacific, pp. 37–50. *In:* M. J. Dunbar, ed., Marine Distributions. Roy. Soc. Canada Spec. Publ. No. 5, University of Toronto Press, Toronto.

———. 1970. Benthic algae of Bowie Seamount. Syesis 3: 15–16.

SCHNEIDER, C. W. AND R. B. SEARLES. 1991. Seaweeds of the Southeastern United States. Duke Univ. Press, Durham, NC.

SEARS, J. R. AND R. T. WILCE. 1975. Sublittoral benthic marine algae of southern Cape Cod and adjacent islands: seasonal periodicity, associations, diversity, and floristic composition. Ecol. Monogr. 45: 337–365.

SIMPSON, D. 1987. The Maine Islands. Blackberry Books, Nobleboro, ME.

SOUTH, G. R. AND I. TITTLEY. 1986. A Checklist and Distributional Index of the Benthic Marine Algae of the North Atlantic Ocean. Huntsman Mar. Lab. and British Museum (Natural Hist.), St. Andrews, New Brunswick and London.

STONE, R. A., E. J. HEHRE, J. M. CONWAY, AND A. C. MATHIESON. 1970. A preliminary checklist of the marine algae of Campobello Island, New Brunswick, Canada. Rhodora 72: 313–338.

SZE, P. 1982. Distribution of macroalgae in tidepools on the New England coast. Bot. Mar. 25: 269–276.

TAYLOR, W. R. 1957. The Marine Algae of the Northeastern Coast of North America. Univ. Michigan Press, Ann Arbor, MI.

TITTLEY, I., W. F. FARNHAM, G. R. SOUTH, AND D. KEATS. 1987. Seaweed communities of the Passamaquoddy region, southern Bay of Fundy, Canada. Brit. Phycol. J. 22: 313.

VADAS, R. L., M. KESER, AND P. C. RUSANOWSKI. 1976. Influence of thermal loading on the ecology of intertidal algae, pp. 202–212. *In:* G. W. Esch and R. W. MacFarlane, eds., Thermal Ecology II. ERDA Symposium Series, Augusta, GA.

VILLALARD-BOHNSACK, M. 1995. Illustrated Key to the Seaweeds of New England. Rhode Island Natural History Survey, Kingston, RI.

WEBBER, E. E. AND R. T. WILCE. 1971. Benthic salt marsh algae at Ipswich, Massachusetts. Rhodora 73: 262–291.

WOELKERLING, W. J. 1973. The morphology and systematics of the *Audouinella* complex (Acrochaetiaceae, Rhodophyceae) in northeastern United States. Rhodora 75: 529–621.

WYNNE, M. J. AND J. N. HEINE. 1992. Collections of marine red algae from St. Matthew and St. Lawrence Islands, the Bering Sea. Nova Hedwigia 55: 55–97.

APPENDIX: STUDY SITES WITHIN THE PENOBSCOT BAY (MAINE) AREA

1. Allen Island: one of the Georges Islands at the mouth of the St. George River on the southwesterly portion of Penobscot Bay, due north of Monhegan Island and south of Port Clyde (43°52′N, 69°19.8′W); ~7620m of shoreline.
2. Hurricane Island: located in the mid-central part of Penobscot Bay (44°02′N, 68°54.6′W), offshore from the southwesterly side of Vinalhaven Island and near Green Island; ~2930m of shoreline.
3. Long Island: located within Jericho Bay (44°07′N, 68°21.5′W), offshore (SE) from Swans Island and northeast from Isle Au Haut; ~16770m of shoreline. Collections were made on the NW side near Frenchboro.
4. Marshall Island: located within Jericho Bay (44°06.5′N, 68°30.5′W), offshore (S) from Swans Island and northeast from Isle Au Haut; ~11940m of shoreline. Collections were made in Baxam Cove.

5. McGlathery Island: located within Merchants Row of Penobscot Bay (44°08.5′N, 68°37′W), due north of Isle au Haut and south of Deer Isle; ~4020m of shoreline.
6. Monhegan Island: located seaward of Penobscot Bay (43°46′N, 69°19′W); due south of Allen Island and almost equidistant from New Harbor to the northwest and Port Clyde to the north; ~8567m of shoreline.
7. Pond Island: located within Jericho Bay (44°13.3′N, 68°28.6′W) due north of Swans Island; ~4318m of shoreline. Collections were made on the sheltered SE and NE sides.
8. Two Bush Island: located within the western part of Penobscot Bay, due east (and somewhat south) of Tenants Harbor, as well as SW of Hurricane Island (43°58.2′N, 69°04.3′W); ~1700m of shoreline.
9. Wooden Ball Island: located within the south central (exposed) part of the Penobscot Bay (43°51.3′N, 68°49.05′W), offshore (S) from Vinalhaven Island and Isle Au Haut (SW), and near Matinicus and Ragged Islands; ~5560m of shoreline. Collections were made on the sheltered NW and exposed eastern sides.