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ALGAL VEGETATION OF THE YORK RIVER ESTUARY AND THE ADJACENT OPEN COAST OF SOUTHERN MAINE[1]

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ABSTRACT

A total of 72 seaweed taxa were recorded from the York River Estuary, Maine, including 29 Rhodophyceae, 19 Phaeophyceae and 24 Chlorophyceae. A synopsis of several distributional patterns is given, as well as floristic comparisons of the York River with two nearby open coastal sites in Maine (Cape Neddick and Sea Point) and 12 estuarine locations within New Hampshire and northern Massachusetts. In contrast to the Great Bay Estuarine System (New Hampshire/Maine) where coastal species occur upstream to approximately 8.5 miles, a relatively rapid attrition of species occurs within the York River after 2–3 miles, presumably due to hydrographic variability, the dominance of saltmarsh habitats and reduced availability of rocky substrata. Overall, species composition within the York River compares favorably with several mid-estuarine environments within the Great Bay Estuary as well as saltmarsh habitats of the Hampton-Seabrook Estuary System (New Hampshire). Relatively few of the "southerly" taxa common to the Great Bay Estuary are present within the York River and Hampton-Seabrook Estuary, presumably because of a lack of suitable habitat. Three floristic records of particular interest include the presence of *Fucus vesiculosus* megecad *limicola* from the York River Estuary, and the occurrence of *Porphyra amplissima* and *Codium fragile* ssp. *tomentosoides* from southern Maine.

Key Words: seaweeds, estuarine, coastal, York River, Maine, New Hampshire, Massachusetts

INTRODUCTION

In contrast to the southeastern United States, where saltmarsh (*Spartina* spp.) and eelgrass communities (*Zostera marina*) are dominant primary producers of organic carbon within estuarine habitats, seaweeds play a major role within north temperate estuaries of the Gulf of Maine (Josselyn and Mathieson, 1980). Estuarine seaweeds within the latter geography provide valuable habitats for a myriad of organisms, generate significant amounts of organic carbon via primary productivity, and contribute to detrital cycles and an "outwelling" of biological productivity to

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nearshore coastal waters (Josselyn and Mathieson, 1978, 1980; Mann, 1972, 1982). Although these fundamental roles are becoming better known, very few detailed assessments of estuarine seaweed resources within the Gulf of Maine exist, except from New Hampshire (Mathieson and Fralick, 1972; Mathieson and Hehre, 1982, 1983, 1986; Mathieson and Penniman, 1986b, 1991; Mathieson et al., 1981) and Massachusetts (Mathieson and Fralick, 1973; Webber and Wilce, 1971). Thus, the only comprehensive seasonal collections of estuarine seaweeds in Maine have been made within the Piscataqua and Salmon Falls Rivers of the Great Bay Estuary System (cf. Mathieson and Hehre, 1986; Mathieson and Penniman, 1991), while only selected collections have been made at other northernmost sites (Bell and MacFarlane, 1933; Eaton, 1873; Stone et al., 1970).

The present study was initiated to enhance our knowledge of Maine estuarine seaweed populations. Specifically, we have summarized distributional and floristic patterns of seaweed populations within the York River Estuary (Maine), comparing them with previous synopses of the Hampton-Seabrook (New Hampshire), Merrimack River (Massachusetts) and Great Bay Estuarine Systems (New Hampshire and Maine), including the various subsets of the latter ecosystem (Figures 1 and 2). The proximity of the four estuarine systems within the southern Gulf of Maine (Figure 1), plus their varying sizes, habitats, industrial development and eutrophication, provides several meaningful comparisons.

METHODS AND MATERIALS

Seasonal collections and observations were made at twenty sites within the York River Estuary, ranging from just outside York Harbor to a point about 1.5 miles below the river's tidal headwater (Figure 2, Table 1). A detailed description of each study site, including its location, habitat(s) and substrata is given in Appendix 1. Collections were made during 1978, 1985 and periodically thereafter. Overall, methods of collection and identification were similar to those outlined in Mathieson and Penniman (1991). Representative samples of all conspicuous seaweeds at each site were collected from the littoral (on foot) and sublittoral zones (by SCUBA). The nomenclature of South and Tittley (1986) was applied for most taxa. The author(s) of each binomial and many

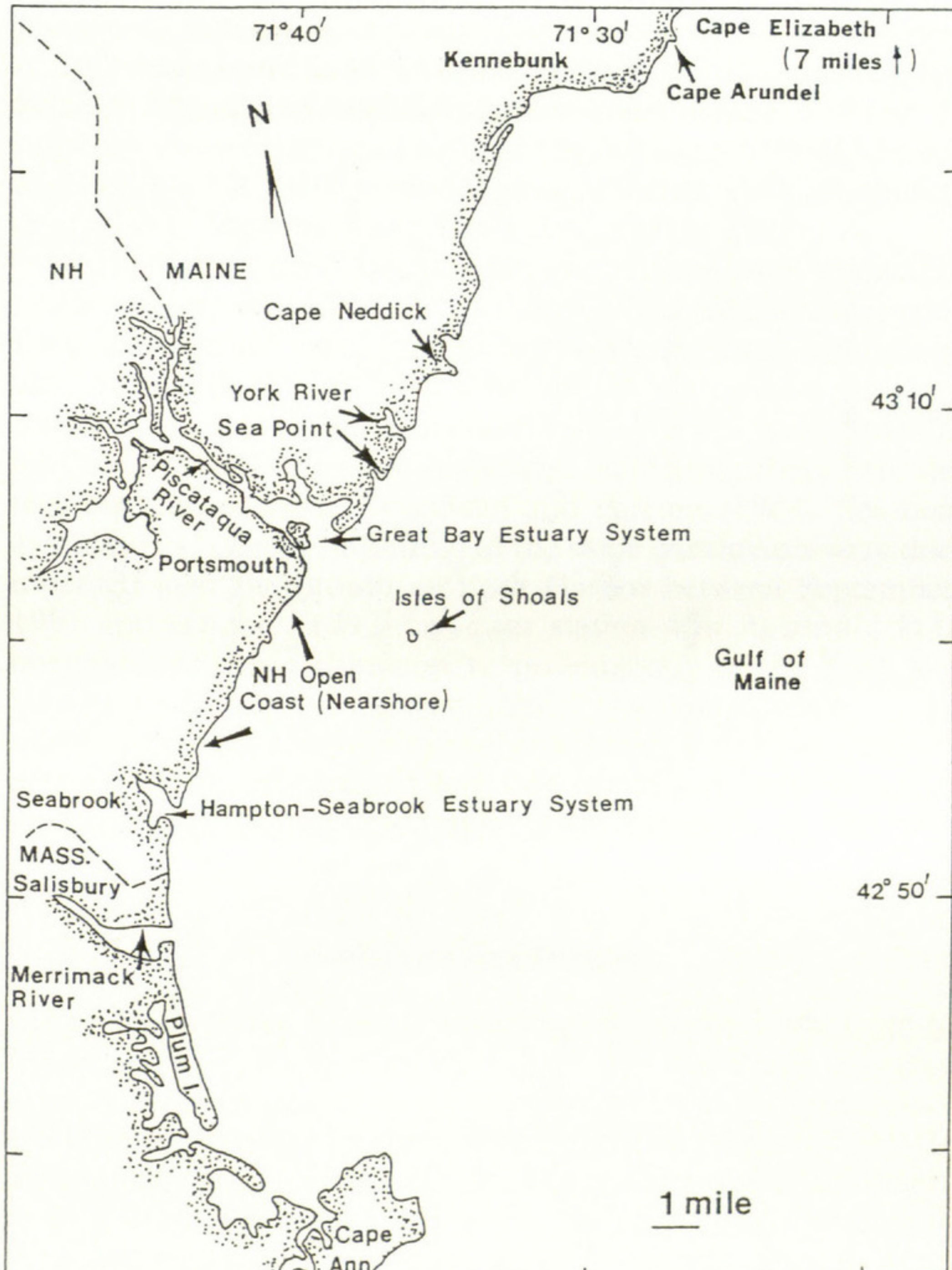
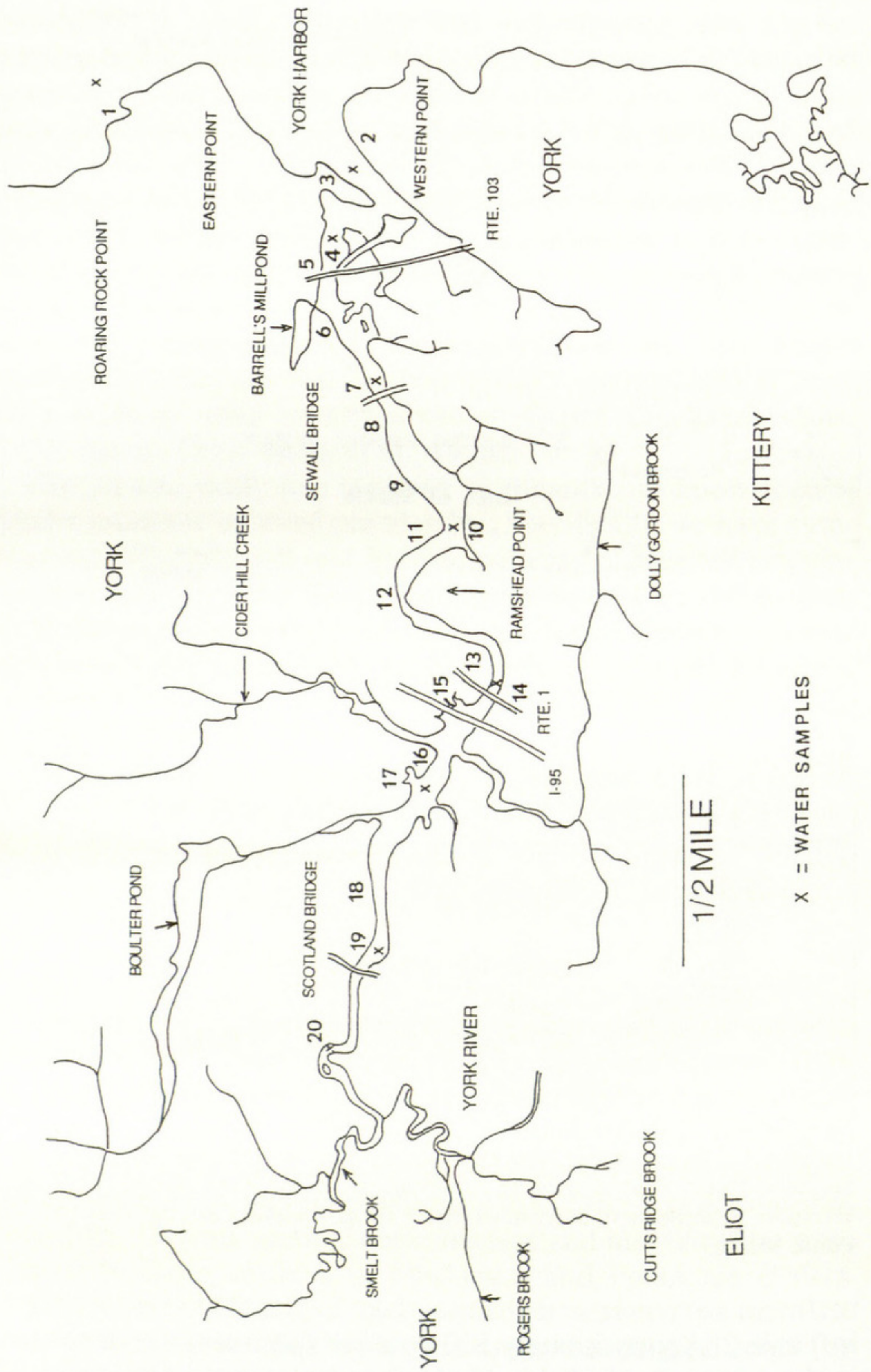


Figure 1. The northern New England coastline between southern Maine and northern Massachusetts showing the locations of the York River, Great Bay, Hampton-Seabrook and Merrimack River Estuaries, plus Cape Neddick and Sea Point, Maine.

pertinent nomenclatural changes since Taylor (1957) are included in Table 2. Approximately 500 voucher specimens are deposited in the Albion R. Hodgdon Herbarium (NHA) at the University of New Hampshire in order to document the river's flora. A com-


ROARING ROCK POINT
EASTERN POINT
YORK HARBOR
WESTERN POINT
RTE. 103
YORK
BARRELL'S MILLPOND
SEWALL BRIDGE
CIDER HILL CREEK
YORK
RAMSHEAD POINT
DOLLY GORDON BROOK
KITTERY
RTE. 1
I-95
BOULTER POND
SCOTLAND BRIDGE
YORK RIVER
SMELT BROOK
ROGERS BROOK
CUTTS RIDGE BROOK
ELIOT
YORK
1/2 MILE
X = WATER SAMPLES
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parison of two nearshore open coastal sites in southern Maine (Cape Neddick and Sea Point) plus twelve other estuarine habitats between Maine and Massachusetts is given (Figure 1, Table 1), utilizing several published records (Mathieson, 1979; Mathieson and Fralick, 1972, 1973; Mathieson and Hehre, 1986; Mathieson et al., 1981; Mathieson and Penniman, 1986b, 1991).

Surface water temperature, salinity, pH and total suspended solids were recorded (winter/spring, 1978) at eight sites, ranging from the mouth to the tidal headwaters. Temperature and salinity were recorded (*in situ*) with a hand-held thermometer and refractometer (.1°C & .5‰ accuracy), while pH was measured with an Orian pH meter. Total suspended solids (mg/liter) were determined according to Strickland and Parsons (1968). Seasonal assessments (approx. monthly) of the same parameters were documented near the mouth of York Harbor between September, 1991 and January, 1992 (i.e., near station 4 in Appendix 1) in conjunction with a comparative investigation of the York and Piscataqua Rivers (R. Langan, unpubl. data). Records of *in situ* temperature and salinity were recorded with a YSI conductivity meter (model CST), while ionic concentrations were measured with a Fisher Alumet pH meter. Total suspended solids were determined as outlined above.

HABITAT DESCRIPTION

The York River Estuary, located in southern York County, Maine, between Cape Neddick (York) and Sea Point (Kittery), extends approximately 7 miles inland from its mouth near Western Point to its tidal headwaters in East Eliot (Figures 1 and 2). Most of the estuary is within York, except for a small tidal marsh in East Eliot. The source of the river is York Pond, which is in the northeast corner of Eliot township. Three major brooks drain into the river near its headwaters (Smelt Brook in York and Cutts Ridge and Rogers Brooks in Eliot), while three large tributaries (Boulter Pond Brook, Cider Hill Creek and Dolly Gordon Brook) are within .5 mile of the Maine Turnpike (I-95). Boulter and

←

Figure 2. Twenty study sites within the York River Estuary (Maine) and the adjacent open coast, including the location of water sampling sites.

Table 1. Synopsis of collecting sites between southern Maine and northern Massachusetts, including the York River Estuary.

Geographical Areas	Individual Sites	Distance from Open Coast (miles)	References
Nearshore open coastline of southern Maine: Cape Neddick (York) and Sea Point (Kittery)	2	= nearshore open coast	Mathieson (1979) Mathieson & Hehre (1986)
York River Estuary, Maine (York and Eliot)	20	0–7	present study
Great Bay Estuary System New Hampshire–Maine	147	0–22.7	Doty and Newhouse (1954) Hehre and Mathieson (1970) Mathieson and Hehre (1986) Mathieson et al. (1981, 1983) Mathieson and Penniman (1986b, 1991) Norall et al. (1982) Reynolds and Mathieson (1975)
Piscataqua River, N.H./Maine	59	0–12.1	Mathieson and Hehre (1986) Mathieson et al. (1977)
Little Bay, New Hampshire	21	8.6–12.4	Reynolds and Mathieson (1975)
Great Bay, New Hampshire	16	12.9–15.7	Mathieson and Hehre (1986) Mathieson et al. (1982)
Bellamy River, New Hampshire	10	10.4–14.3	Mathieson and Hehre (1986)
Cocheco River, New Hampshire	17	12.6–15.8	Mathieson and Hehre (1986)
Lamprey River, New Hampshire	9	15.8–17.5	Mathieson and Hehre (1986)
Oyster River, New Hampshire	14	11.5–14.2	Mathieson and Hehre (1986)
Salmon Falls River, Hew Hampshire/Maine	16	12.5–16.5	Mathieson and Hehre (1986)
Sqamscott River, New Hampshire	16	16.2–22.7	Mathieson and Hehre (1986)
Winnicut River, New Hampshire	4	15.8–17.3	Mathieson and Hehre (1986)
Hampton–Sea-	49	0–5.2	Hehre and Mathieson (1970)

Table 1. Continued.

Geographical Areas	Individual Sites	Distance from Open Coast (miles)	References
brook Estuary, New Hampshire			Mathieson and Fralick (1972) Mathieson and Hehre (1986)
Merrimack River Estuary, Massachusetts			Mathieson and Fralick (1973)

Middle Ponds, which lie to the north, are sources of the first two tributaries, while Dolly Gordon Brook originates from a saltmarsh to the southeast.

As outlined in Appendix 1, the substratum available for seaweed growth is both limited and scattered. Boulders, cobbles, pebbles and rock outcrops primarily occur in high energy areas (i.e., due to waves) near the mouth of the river, while York Harbor is mostly sandy (cf. Figure 2). Several artificial structures (bridge abutments, pilings and boat moorings) are located immediately upstream from York Harbor, while saltmarshes dominate most shorelines between Route 1A (Sewall Bridge) and tidal headwaters (Figure 2). The main channel of the river is relatively straight, with only one large meander at Ramshead Point, as opposed to its tributaries that have sharply developed meanders indicative of youthful streams. About one mile upstream from Scotland Bridge the river branches into two major channels associated with the confluence of Smelt Brook and the York River (Figure 2). A major oxbow occurs downstream from this confluence, while several smaller ones are found upstream. Each inner channel has a steep-sided shoreline that cuts across broad expanses of saltmarsh with peat and clay soils. The saltmarshes are dominated by *Spartina alterniflora, S. patens* and *Juncus gerardii,* along with several other vascular plants. In some instances (e.g., near house construction), the marshes are very narrow and only contain *S. alterniflora.* Overall, the most expansive mudflat habitats are found near York Harbor where saltmarshes are either reduced or absent.

Figure 3 illustrates "typical" winter/spring hydrographic conditions within the estuary. Surface water temperatures ranged from approximately 3.0°C (0 miles) to 0°C (4.4 miles), while salinities were approximately 31‰ on the open coast and varied from 0–16‰ at station 8 (4.4 miles inland). Thus, surface water temperatures during late winter and spring are relatively low and

Table 2. Systematic list of algal species found within the York River Estuary and the adjacent open coast of Maine, with synonyms in parentheses referring to names in Taylor (1957).

CHLOROPHYCEAE

MICROSPORALES

Microsporaceae

Microspora pachyderma (Wille) Lagerheim

ULOTRICHALES

Ulotrichaceae

Ulothrix flacca (Dillwyn) Thuret in Le Jolis
Ulothrix speciosa (Carmichael ex Harvey in Hooker) Kützing

ULVALES

Percursariaceae

Percursaria percursa (C. Agardh) Bory

Ulvaceae

Capsosiphon fulvescens (C. Agardh) Setchell et Gardner
Enteromorpha clathrata (Roth) Greville
Enteromorpha flexuosa (Wulfen ex Roth) J. Agardh ssp. *paradoxa* (Dillwyn) Bliding
Enteromorpha intestinalis (Linnaeus) Link
Enteromorpha linza (Linnaeus) J. Agardh
Enteromorpha prolifera (O. F. Müller) J. Agardh
Ulva lactuca Linnaeus
Ulvaria obscura (Kützing) Gayral [= *Monostroma fuscum* (Postels et Ruprecht) Wittrock]
Ulvaria oxysperma (Kützing) Bliding [= *Monostroma oxyspermum* Kützing]

Monostromataceae

Blidingia minima (Nägeli ex Kützing) Kylin [includes *Enteromorpha minima, E. micrococca, E. marginata*]
Monostroma grevillei (Thuret) Wittrock
Monostroma pulchrum Farlow

PRASIOLALES

Prasiolaceae

Prasiola stipitata Suhr in Jessen

ACROSIPHONIALES

Acrosiphoniaceae

"*Codiolum pusillum*" (Lyngbye) Kjellman [= sporophytic stage in the life history of *Urospora wormskioldii* and probably conspecific with *Codiolum gregarium*]
Urospora penicilliformis (Roth) Areschoug
Urospora wormskioldii (Mertens in Hornemann) Rosenvinge [includes *U. collabens* (C. Agardh) Holmes et Batters]
Spongomorpha arcta (Dillwyn) Kützing
Spongomorpha spinescens Kützing

Table 2. Continued.

CLADOPHORALES

Cladophoraceae

Chaetomorpha brachygona Harvey [including *C. cannabina* (Areschoug) Kjellman]

Chaetomorpha linum (O. F. Müller) Kützing

Chaetomorpha melagonium (Weber et Mohr) Kützing

Chaetomorpha picquotiana Montagne ex Kützing [= *C. atrovirens* Taylor]

Cladophora sericea (Hudson) Kützing [includes *C. glaucescens, C. rudolphiana, C. flexuosa* and *C. gracilis*]

Rhizoclonium riparium (Roth) Kützing ex Harvey

Rhizoclonium tortuosum (Dillwyn) Kützing

BRYOPSIDALES

Bryopsidaceae

Bryopsis plumosa (Hudson) C. Agardh

Codiaceae

Codium fragile (Suringar) Hariot ssp. *tomentosoides* (van Goor) Silva

PHAEOPHYCEAE

ECTOCARPALES

Ectocarpaceae

Ectocarpus fasciculatus Harvey

Ectocarpus siliculosus (Dillwyn) Lyngbye [includes *E. dasycarpus, E. confervoides* and *E. penicillatus*]

Giffordia granulosa (J. E. Smith) Hamel

Laminariocolax tomentosoides (Farlow) Kylin [= *Ectocarpus tomentosoides* Farlow]

Mikrosyphar porphyrae Kuckuck

Pilayella littoralis (Linnaeus) Kjellman

Spongonema tomentosum (Hudson) Kützing [= *Ectocarpus tomentosus* (Hudson) Lyngbye]

Ralfsiaceae

Petroderma maculiforme (Wollny) Kuckuck

Pseudolithoderma extensum (P. Crouan et H. Crouan) S. Lund [= *Lithoderma extensum* (Crouan) Hamel]

Ralfsia verrucosa (Areschoug) J. Agardh

Sorapion kjellmanii (Wille) Rosenvinge

Myrionemataceae

Ascocyclus distromaticus Taylor

Elachistaceae

Elachista fucicola (Velley) Areschoug [includes *Elachista lubrica* Ruprecht]

CHORDARIALES

Leathesiaceae (= Corynophlaeaceae)

Leathesia difformis (Linnaeus) Areschoug

Table 2. Continued.

Chordariaceae
Chordaria flagelliformis (O. F. Müller) C. Agardh
Eudesme virescens (Carmichael ex Harvey *in* Hooker) J. Agardh

SPHACELARIALES

Sphacelariaceae
Sphacelaria arctica Harvey [= *Sphacelaria racemosa* Greville var. *arctica* (Harvey) Reinke]
Sphacelaria cirrosa (Roth) C. Agardh

DESMARESTIALES

Desmarestiaceae
Desmarestia aculeata (Linnaeus) Lamouroux
Desmarestia viridis (O. F. Müller) Lamouroux

DICTYOSIPHONALES

Punctariaceae
Punctaria plantaginea (Roth) Greville

Dictyosiphonaceae
Dictyosiphon foeniculaceus (Hudson) Greville

Scytosiphonaceae
Petalonia fascia (O. F. Müller) Kuntze
"*Ralfsia bornetii*" Kuckuck [sporophytic stage in the life history of *Petalonia fascia*]
Scytosiphon lomentaria (Lyngbye) Link var. *lomentaria*

LAMINARIALES

Chordaceae
Chorda filum (Linnaeus) Stackhouse
Chorda tomentosa Lyngbye

Laminariaceae
Agarum cribrosum (Mertens) Bory
Laminaria digitata (Hudson) Lamouroux
Laminaria saccharina (Linnaeus) Lamouroux
Saccorhiza dermatodea (de la Pylaie) J. Agardh

Alariaceae
Alaria esculenta (Linnaeus) Greville

FUCALES

Fucaceae
Ascophyllum nodosum (Linnaeus) Le Jolis
Ascophyllum nodosum ecad *scorpioides* (Reinke) Hauck [= *Ascophyllum mackaii* (Turner) Holmes et Batters]
Fucus distichus Linnaeus emend. Powell ssp. *distichus* Powell [= *Fucus filiformis* Gmelin]
Fucus distichus Linnaeus emend. Powell ssp. *edentatus* (de al Pylaie) Powell [= *Fucus edentatus* de la Pylaie]

Table 2. Continued.

Fucus distichus Linnaeus emend. Powell ssp. *evanescens* (C. Agardh) Powell [= *Fucus evanescens* C. Agardh]
Fucus spiralis Linnaeus
Fucus vesiculosus Linnaeus

RHODOPHYCEAE: BANGIOPHYCIDAE

PORPHYRIDIALES

Goniotrichaceae

Stylonema alsidii (Zanardini) Drew [= *Goniotrichum alsidii* (Zanardini) Howe]

BANGIALES

Erythropeltidaceae

Erythrotrichia carnea (Dillwyn) C. Agardh

Bangiaceae

Bangia atropurpurea (Roth) C. Agardh
Porphyra amplissima (Kjellman) Setchell et Hus *in* Hus
Porphyra linearis Greville
Porphyra miniata (C. Agardh) C. Agardh
Porphyra umbilicalis (Linnaeus) J. Agardh

RHODOPHYCEAE: FLORIDEOPHYCIDAE

NEMALIALES

Acrochaetiaceae

Audouinella alariae (H. Jónsson) Woelkerling [= *Kylinia alariae* (H. Jónsson) Kylin]
Audouinella purpurea (Lightfoot) Woelkerling [= *Rhodochorton purpureum* (Lightfoot) Rosenvinge]
Audouinella secundata (Lyngbye) Dixon [includes *Kylinia secundata* and *K. virgatula*]

Bonnemaisoniaceae

Bonnemaisonia hamifera Hariot [= *Asparagopsis hamifera* (Hariot) Okamura]

PALMARIALES

Palmariaceae

Devaleraea ramentacea (Linnaeus) Guiry [= *Halosaccion ramentaceum* (Linnaeus) J. Agardh]
Palmaria palmata (Linnaeus) Kuntze [= *Rhodymenia palmata* (Linnaeus) Greville]

CRYPTONEMIALES

Dumontiaceae

Dumontia contorta (Gmelin) Ruprecht [= *D. incrassata* (O. F. Müller) Lamouroux]

Choreocolacaceae

Harveyella mirabilis (Reinsch) Schmitz et Reinke

Table 2. Continued.

Kallymeniaceae
- *Callocolax neglectus* Schmitz ex Batters
- *Callophyllis cristata* (C. Agardh) Kützing [= *Euthora cristata* (Linnaeus ex Turner) J. Agardh]

Gloiosiphoniaceae
- *Gloiosiphonia capillaris* (Hudson) Carmichael ex Berkeley

HILDENBRANDIALES

Hildenbrandiaceae
- *Hildenbrandia rubra* (Sommerfelt) Meneghini [= *H. prototypus* Nardo]

CORALLINALES

Corallinaceae
- *Clathromorphum circumscriptum* (Strömfelt) Foslie [= *Phymatolithon evanescens* (Foslie) Foslie]
- *Corallina officinalis* Linnaeus
- *Dermatolithon pustulatum* (Lamouroux) Foslie [= *Lithophyllum pustulatum* (Lamouroux) Foslie]
- *Leptophytum laeve* (Strömfelt) Adey [= *Lithothamnium laeve* (Strömfelt) Foslie]
- *Lithophyllum corallinae* (Crouan frat.) Heydrich
- *Lithothamnion glaciale* Kjellman
- *Phymatolithon laevigatum* (Foslie) Foslie
- *Phymatolithon lenormandii* (Areschoug in J. Agardh) Adey [= *Lithothamnion lenormandii* (Areschoug) Foslie]
- *Pneophyllum fragile* Kützing [= *Fosliella lejolisii* (Rosanoff) Howe]

GIGARTINALES

Phyllophoraceae
- *Ahnfeltia plicata* (Hudson) Fries
- *Ceratocolax hartzii* Rosenvinge
- *Gymnogongrus crenulatus* (Turner) J. Agardh [= *G. norvegicus* (Gunnerus) J. Agardh]
- *Phyllophora pseudoceranoides* (Gmelin) Newroth et A. Taylor [= *P. membranifolia* (Goodenough et Woodward) J. Agardh]
- *Phyllophora truncata* (Pallas) Zinova [includes *P. brodiaei* and *P. interrupta*]

Petrocelidaceae
- *Mastrocarpus stellatus* (Stackhouse in Withering) Guiry [= *Gigartina stellata* (Stackhouse) Batters]

Gigartinaceae
- *Chondrus crispus* Stackhouse

Polyideaceae
- *Polyides rotundus* (Hudson) Greville [= *P. caprinus* (Gunnerus) Papenfuss]

Table 2. Continued.

Cystocloniaceae
Cystoclonium purpureum (Hudson) Batters
Fimbrifolium dichotomum (Lepeschkin) Hansen [= *Rhodophyllis dichotoma* (Lepeschkin) Gobi]

RHODYMENIALES

Champiaceae
Lomentaria baileyana (Harvey) Farlow
Lomentaria clavellosa (Turner) Gaillon
Lomentaria orcadensis (Harvey) Collins ex Taylor

CERAMIALES

Ceramiaceae
Antithamnionella floccosa (O. F. Müller) Whittick [= *Antithamnion floccosum* (O. F. Müller) Kleen]
Callithamnion byssoides Arnott ex Harvey in Hooker
Callithamnion tetragonum (Withering) S. F. Gray [= *C. baileyi* Harvey]
Ceramium rubrum (Hudson) C. Agardh
Ceramium strictum Harvey
Plumaria plumosa (Hudson) Kuntze [= *P. elegans* (Bonnemaison) Schmitz]
Ptilota serrata Kützing
Scagelia pylaisei (Montagne) Wynne [= *Antithamnion pylaisaei* (Montagne) Kjellman]

Delesseriaceae
Membranoptera alata (Hudson) Stackhouse [includes *M. denticulata* (Montagne) Kylin]
Phycodrys rubens (Linnaeus) Batters

Dasyaceae
Dasya baillouviana (Gmelin) Montagne [= *D. pedicellata* (C. Agardh) C. Agardh]

Rhodomelaceae
Polysiphonia denudata (Dillwyn) Greville ex Harvey
Polysiphonia flexicaulis (Harvey) Collins
Polysiphonia harveyi Bailey
Polysiphonia lanosa (Linnaeus) Tandy
Polysiphonia nigra (Hudson) Batters
Polysiphonia nigrescens (Hudson) Greville
Polysiphonia subtilissima Montagne
Polysiphonia urceolata (Lightfoot ex Dillwyn) Greville
Rhodomela confervoides (Hudson) Silva

uniform, while a conspicuous reduction in salinities occurs within inner estuarine habitats (3.3–4.4 miles), particularly during spring runoff (late March–April). The pattern of total suspended solids showed peak values near the open coast (approx. 177 mg/liter) and a general decrease upstream (47–25 m/liter), except for a slight peak near the I-95 bridge (57 mg/liter); pH varied from approximately 8.2–8.0 between 0–2.4 miles, with lower values occurring upstream (7.7–7.4).

Seasonal variability of hydrographic conditions near York Harbor are illustrated in Figure 4. Surface water temperatures ranged from approximately 16.0°C (September, 1991) to 2.0°C (February), while salinities varied from approximately 32.0‰ (September, 1991) to 21.0‰ (April), pH from 8.4 (November, 1991) to 7.6 (December, 1992), and total suspended solids from 22.9 (February) to 5.6 mg/liter (December, 1992). Each parameter shows a relatively broad range throughout the year, with spring runoff occurring in late March–April. Greater hydrographic amplitudes were no doubt evident within inner estuarine stations (cf. Figure 3), although they weren't documented. Monthly values for total suspended solids during 1991–1992 were never as high as those recorded after a major "northeaster" during February of 1978 (approx. 177 mg/liter; Figure 3).

Overall, water quality within the York River appears to be very good, as the region is sparsely populated (particularly upriver of Route 1) and totally devoid of industry. The only signs of pollution are evident near Rice's Bridge (i.e., stations 13 and 14) where two discharge pipes occur. A localized enhancement of siltation and turbidity was evident during repair work on the I-95 Bridge (Figure 3).

SPECIES COMPOSITION AND DISTRIBUTIONAL PATTERNS

A total of 131 taxa were recorded from the York River Estuary and two nearby open coastal sites in southern Maine (Cape Neddick and Sea Point), including 61 Rhodophyceae, 39 Phaeophyceae and 31 Chlorophyceae (Figure 5, Table 3). Seventy-two taxa were found in the York River (29 Rhodophyceae, 19 Phaeophyceae and 24 Chlorophyceae), while 59 were restricted to the open coast. The seaweeds within this open coastal-estuarine gradient exhibited three major distributional patterns (Figure 5, Table 3):

(1) Coastal—restricted to the nearshore open coast (59 taxa or 45%).

(2) Cosmopolitan—present in both estuarine and open coastal environments (45 taxa or 34%).

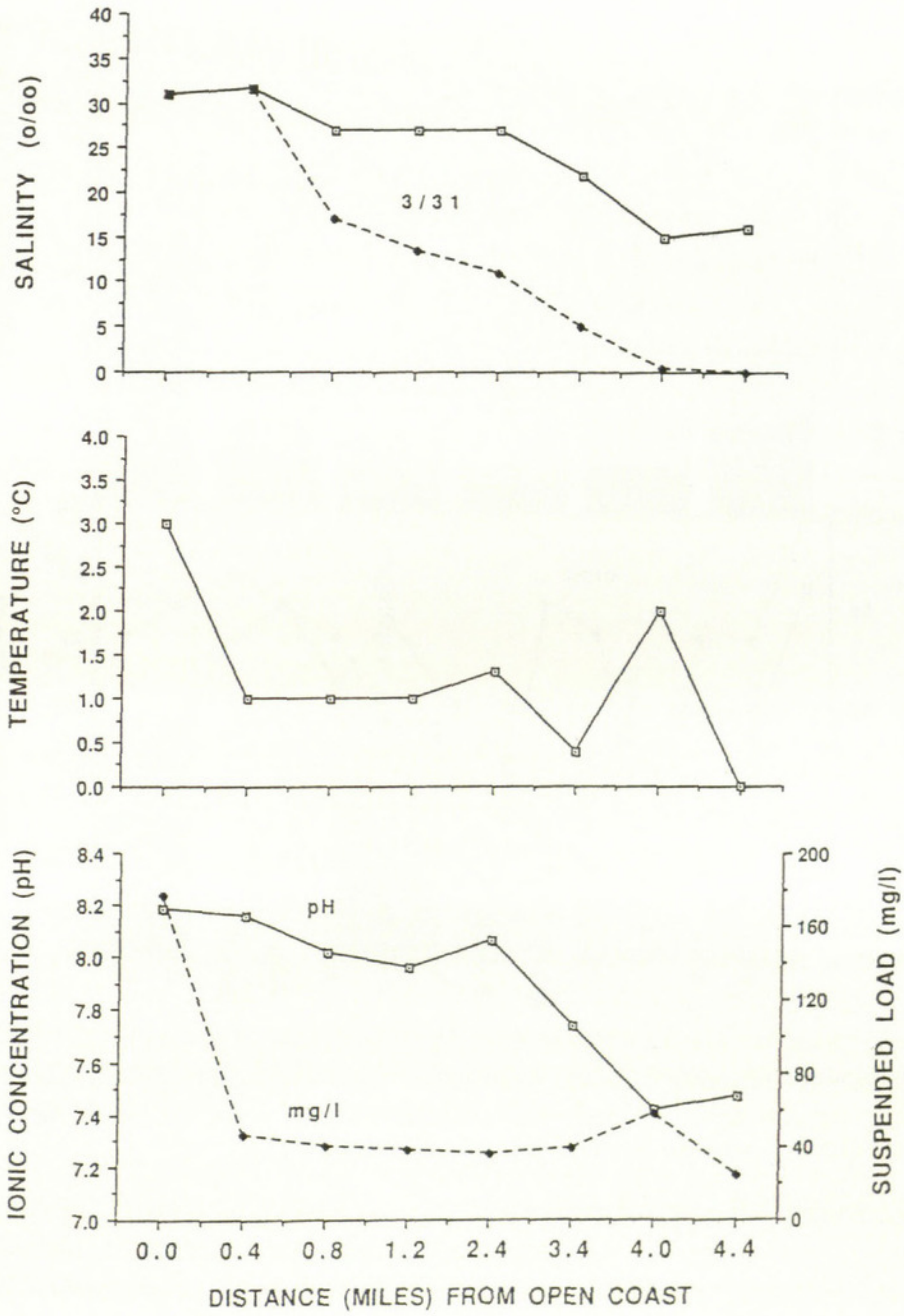

Figure 3. Surface water hydrographic conditions (i.e., temperature, salinity, pH and total suspended loads) within the York River Estuary during February and March (salinity only) of 1978.

(3) Estuarine—restricted to the York River Estuary (27 taxa or 21%).

As outlined in Table 3 approximately 47% of the coastal taxa occurred at both Cape Neddick and Sea Point, while the remain-

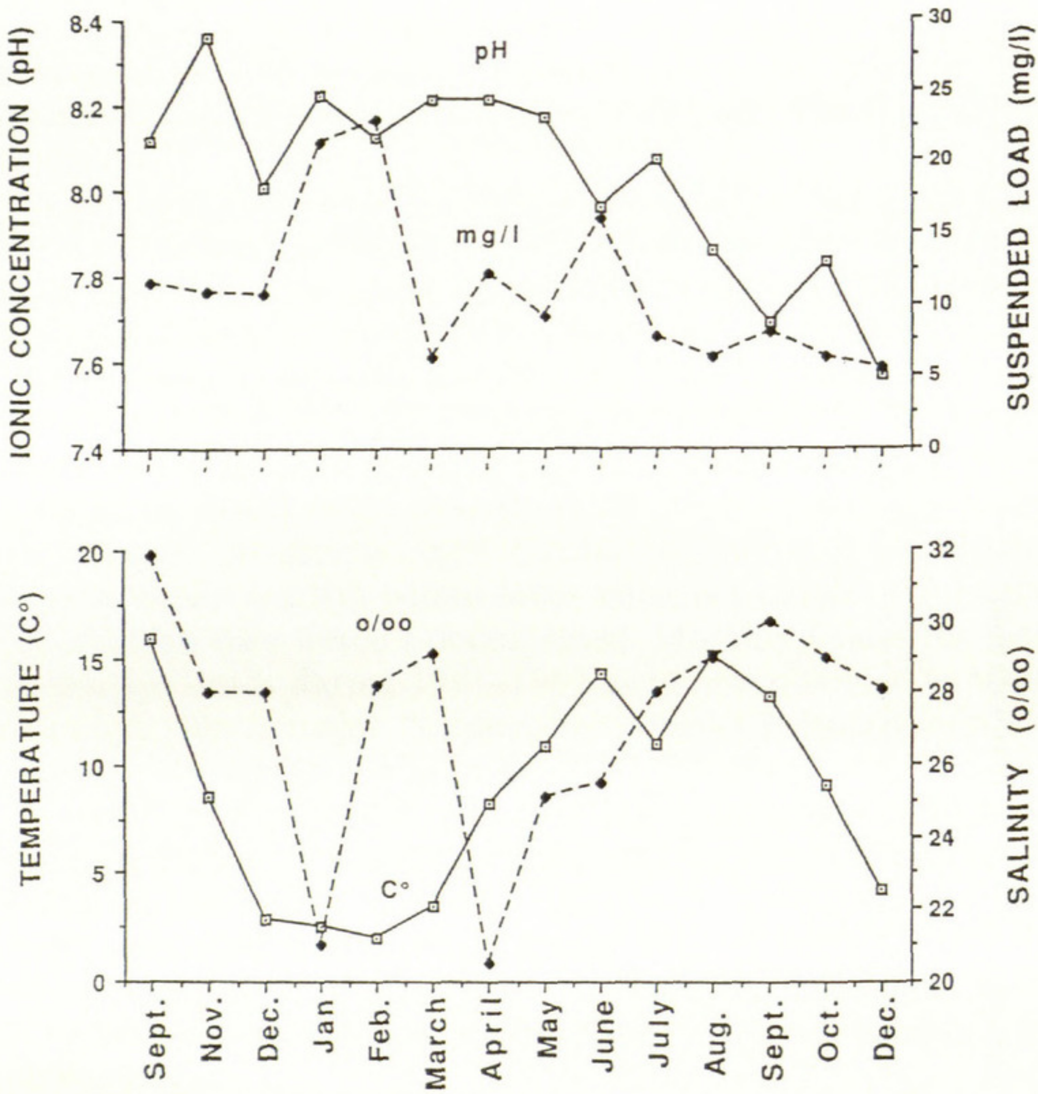

Figure 4. Monthly variability of surface water hydrographic conditions (i.e., temperature, salinity, pH and total suspended solids) at the mouth of the York River Estuary between September, 1991–December, 1992.

der (53%) were restricted to a single station (i.e., *Codiolum pusillum, Codium fragile* ssp. *tomentosoides, Enteromorpha linza, Prasiola stipitata, Ascocyclus distromaticus, Chorda filum, C. tomentosa, Dictyosiphon foeniculaceus, Eudesme virescens, Laminariocolax tomentosoides, Leathesia difformis, Mikrosyphar porphyrae, Punctaria plantaginea, Saccorhiza dermatodea, Sphacelaria arctica, S. cirrosa, Spongonema tomentosum, Antithamnionella floccosa, Audouinella alariae, A. purpurea, Callithamnion tetragonum, Devaleraea ramentacea, Gloiosiphonia capillaris, Gymnogongrus crenulatus, Harveyella mirabilis, Lomentaria or-*

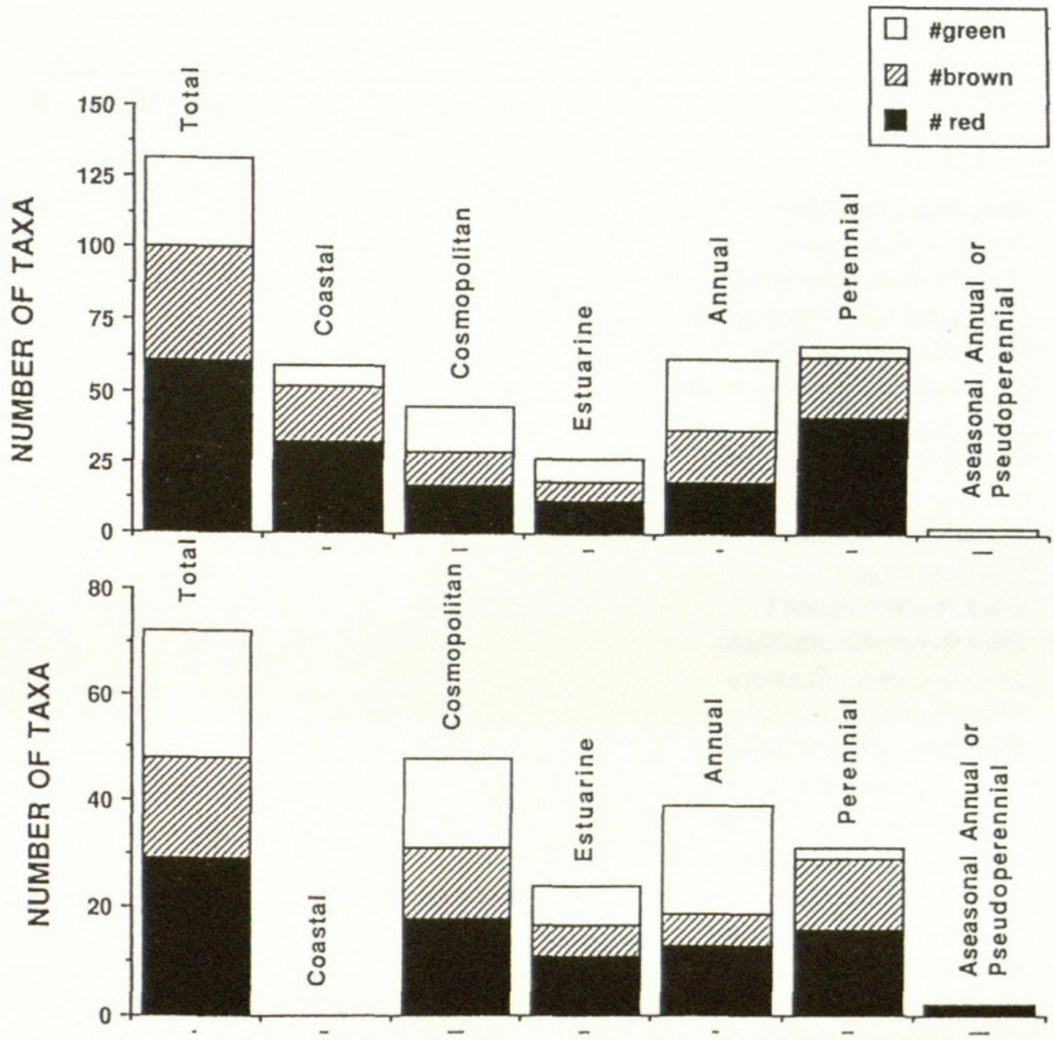

Figure 5. Patterns of species richness, local distribution and longevity of seaweed taxa within the York River Estuary and at two nearshore open coastal sites in southern Maine (Cape Neddick and Sea Point).

cadensis, Plumaria plumosa, Pneophyllum fragile, Porphyra amplissima, P. linearis and *Scagelia pylaisei*).

Cosmopolitan taxa exhibited varying estuarine distributional patterns (cf. Table 3). The fucoid brown algae *Ascophyllum nodosum* and *Fucus vesiculosus* plus the red alga *Dumontia contorta* occurred at 86–96% of coastal and estuarine stations, while twelve others occurred at >60% of these sites (e.g., *Blidingia minima, Enteromorpha intestinalis, Monostroma grevillei, Urospora penicilliformis, Ascophyllum nodosum* ecad *scorpioides, Petalonia fascia, Pilayella littoralis, Scytosiphon lomentaria* var. *lomentaria, Chondrus crispus, Hildenbrandia rubra, Polysiphonia harveyi* and *Porphyra umbilicalis*). Some taxa exhibited restricted (<20%) and

Table 3. Summary of seaweed taxa at twenty study sites within the York River Estuary, plus the adjacent open coast at Cape Neddick and Sea Point Maine.

	NL	SP	1	2	3	4	5	6	7
Chlorophyta									
Blidingia minima	x	x	x			x			x
Bryopsis plumosa									
Capsosiphon fulvescens									
Chaetomorpha brachygona		x							
Chaetomorpha linum	x	x		x	x				x
Chaetomorpha melagonium	x	x							
Chaetomorpha picquotiana		x			x		x	x	x
Cladophora sericea	x	x							
"*Codiolum pusillum*"		x							
Codium fragile ssp. *tomentosoides*	x								
Enteromorpha clathrata									
Enteromorpha flexuosa ssp. *paradoxa*	x								
Enteromorpha intestinalis	x	x				x	x	x	
Enteromorpha linza	x								
Enteromorpha prolifera	x	x				x			
Microspora pachyderma									
Monostroma grevillei	x	x	x	x			x	x	x
Monostroma pulchrum	x	x							
Percursaria percursa									
Prasiola stipitata	x								
Rhizoclonium riparium	x								x
Rhizoclonium tortuosum	x	x		x	x				
Spongomorpha arcta	x	x							
Spongomorpha spinescens	x	x							
Ulothrix flacca		x	x				x	x	x
Ulothrix speciosa							x	x	x
Ulva lactuca	x	x				x			x
Ulvaria obscura	x	x					x	x	x
Ulvaria oxysperma									
Urospora penicilliformis	x	x	x			x	x	x	x
Urospora wormskioldii	x	x					x		x
Total Chlorophyta taxa	20	19	4	3	3	5	8	7	11
Mean (±SD) Chlorophyta taxa	(7.9 ± 2.8)								
Phaeophyta									
Agarum cribrosum	x	x							
Alaria esculenta	x	x							
Ascocyclus distromaticus	x								
Ascophyllum nodosum	x	x	x	x	x		x		x

Table 3. Extended.

8	9	10	11	12	13	14	15	16	17	18	19	20	Longevity	%*
x		x		x	x	x		x	x	x	x	x	Ann.	68.2 (65)
						x							Ann.	4.5 (5)
											x		Ann.	4.5 (5)
					x								Ann.?	9.1 (5)
					x								Per.	27.3 (20)
													Per.	9.1 (0)
							x						Per.	27.3 (25)
								x					AAnn or PPer.	13.6 (5)
													Ann.	4.5 (0)
													Per.	4.5 (0)
x													Ann.	4.5 (5)
						x							Ann.	9.1 (5)
	x	x			x	x	x	x	x		x	x	AAnn.	63.6 (60)
													AAnn.	4.5 (0)
	x	x			x				x	x	x	x	AAnn.	45.5 (40)
								x	x		x		Ann.	13.6 (15)
x	x		x	x	x	x	x	x	x		x		Ann.	77.3 (75)
													Ann.	9.1 (0)
						x							AAnn.	4.5 (5)
													AAnn.	4.5 (0)
	x		x	x		x	x	x	x		x	x	AAnn.	50.0 (50)
													AAnn.	18.2 (10)
x	x	x											Ann.	22.7 (15)
													Ann.	9.1 (0)
		x	x	x	x		x	x			x	x	Ann.	59.1 (55)
x	x	x	x	x	x		x	x	x				Ann.	54.5 (60)
x	x						x	x	x	x		x	AAnn. or PPer.	50.0 (45)
x						x	x	x					Ann.	41.0 (35)
				x	x	x	x		x	x	x	x	Ann.	36.4 (40)
x	x	x	x	x	x	x	x	x	x		x	x	Ann.	86.4 (85)
x	x		x	x		x	x	x	x			x	Ann.	59.1 (55)
8	10	7	6	8	10	11	11	12	11	4	10	9		
													Per.	9.1 (0)
													Per.	9.1 (0)
													Ann.	4.5 (0)
x	x	x	x	x	x	x	x	x	x	x	x	x	Per.	91.0 (90)

Table 3. Continued.

	NL	SP	1	2	3	4	5	6	7
Ascophyllum nodosum									
ecad scorpioides						x	x	x	
Chorda filum	x								
Chorda tomentosa	x								
Chordaria flagelliformis	x	x							
Desmarestia aculeata	x	x							
Desmarestia viridis	x	x							
Dictyosiphon foeniculaeus	x								
Ectocarpus fasciculatus			x			x			
Ectocarpus siliculosus	x		x			x			
Elachista fucicola	x	x	x		x	x	x		x
Eudesme virescens	x								
Fucus distichus ssp. *distichus*	x	x							
Fucus distichus ssp. *edentatus*	x	x			x				
Fucus distichus									
ssp. *evanescens*	x	x	x						
Fucus spiralis	x	x		x					
Fucus vesiculosus	x	x	x	x		x	x	x	x
Giffordia granulosa									
Laminaria digitata	x	x							
Laminaria saccharina	x	x						x	
Laminariocolax tomentosoides	x								
Leathesia difformis	x								
Mikrosyphar porphyrae	x								
Petalonia fascia	x	x	x		x	x	x	x	x
Petroderma maculiforme						x			
Pilayella littoralis	x	x	x		x	x	x		x
Pseudolithoderma extensum									
Punctaria plantaginea	x								
"*Ralfsia bornetii*"									x
Ralfsia verrucosa	x	x		x	x	x		x	
Sacchorhiza dermatodea	x								
Scytosiphon lomentaria									
var. *lomentaria*	x	x	x	x	x	x	x	x	x
Sorapion kjellmanii						x			
Sphacelaria arctica	x								
Sphacelaria cirrosa	x								
Spongonema tomentosum	x								
Total Phaeophyta taxa	32	18	10	5	7	11	7	6	7
Mean (±SD) Phaeophyta taxa	(7.0 ± 1.8)								
Rhodophyta									
Ahnfeltia plicata	x	x							
Antithamnionella floccosa	x								
Audouinella alariae	x								

Table 3. Extended, continued.

8	9	10	11	12	13	14	15	16	17	18	19	20	Longevity	%*
	x	x	x	x	x	x	x	x	x	x	x	x	Per.	68.2 (75)
													Ann.	4.5 (0)
													Ann.	4.5 (0)
													Ann.	9.1 (0)
													Per.	9.1 (0)
													Ann.	9.1 (0)
													Ann.	4.5 (0)
													Ann.	9.1 (0)
													Ann.	13.6 (10)
x		x	x			x		x					Per.	54.5 (50)
													Ann.	4.5 (0)
													Per.	9.1 (0)
	x												Per.	18.2 (0)
	x												Per.	18.2 (10)
		x											Per.	18.2 (10)
x	x	x	x	x	x	x	x	x	x	x	x	x	Per.	95.5 (95)
											x		Ann.	4.5 (5)
													Per.	9.1 (0)
													Per.	13.6 (5)
													Ann.	4.5 (0)
													Ann.	4.5 (0)
													Ann.	4.5 (0)
x	x	x	x	x	x		x	x	x	x			Ann.	81.8 (80)
		x								x			Per.	13.6 (15)
x	x	x	x	x	x	x	x		x	x			Ann.	77.3 (75)
				x		x		x					Per.	13.6 (15)
													Ann.	4.5 (0)
										x	x		Per.?	13.6 (15)
x				x				x	x	x			Per.	50.0 (45)
													Ann.	4.5 (0)
x	x	x	x	x			x				x		Ann.	72.7 (70)
										x			Per.	9.1 (0)
													Per.	4.5 (0)
													Per.	4.5 (0)
													Per.?	4.5 (0)
7	8	9	7	8	5	6	6	7	6	9	6	3		
													Per.	9.1 (0)
													AAnn.	4.5 (0)
													Ann.	4.5 (0)

Table 3. Continued.

	NL	SP	1	2	3	4	5	6	7
Audouinella purpurea	x								
Audouinella secundata	x							x	
Bangia atropurpurea	x	x	x					x	x
Bonnemaisonia hamifera	x	x							
Callithamnion byssoides									x
Callithamnion tetragonum		x							
Callocolax neglectus	x	x							
Callophyllis cristata	x	x							
Ceramium rubrum	x	x		x					x
Ceramium strictum									
Ceratocolax hartzii	x	x							
Chondrus crispus	x	x	x	x	x	x	x	x	x
Clathromorphum circumscriptum	x	x			x	x			
Corallina officinalis	x	x	x	x	x				
Cystoclonium purpureum	x	x							
Dasya baillouviana									
Dermatolithon pustulatum	x	x							
Devaleraea ramentacea	x								
Dumontia contorta	x	x	x	x	x	x	x	x	x
Erythrotrichia carnea								x	
Fimbrifolium dichotomum		x							
Gloisiphonia capillaris	x								
Gymnogongrus crenulatus	x								
Harveyella mirabilis	x								
Hildenbrandia rubra	x	x	x	x	x	x	x	x	x
Leptophytum laeve									x
Lithophyllum corallinae		x	x						
Lithothamnion glaciale	x	x			x	x			
Lomentaria baileyana									
Lomentaria clavellosa									x
Lomentaria orcadensis	x								
Mastocarpus stellatus	x	x		x	x		x		
Membranoptera alata	x	x							
Palmaria palmata	x	x							
Phycodrys rubens	x	x							
Phyllophora pseudoceranoides	x	x							
Phyllophora truncata	x	x							
Phymatolithon laevigatum	x	x							
Phymatolithon lenormandii			x		x				
Plumaria plumosa	x								
Pneophyllum fragile		x							
Polyides rotundus	x	x							
Polysiphonia denudata									
Polysiphonia flexicaulis	x	x							
Polysiphonia harveyi	x	x		x	x	x		x	x

Table 3. Extended, continued.

8	9	10	11	12	13	14	15	16	17	18	19	20	Longevity	%*
													Per.	4.5 (0)
													AAnn.	9.1 (5)
													Ann.	22.7 (15)
													Per.	9.1 (0)
						x		x	x	x			Ann.	22.7 (25)
													Per.	4.5 (0)
													Per.	9.1 (0)
x													Per.	13.6 (5)
											x		Per.	22.7 (15)
						x						x	Ann.	9.1 (10)
													Per.	9.1 (0)
x	x		x	x	x	x	x			x			Per.	77.3 (75)
													Per.	18.2 (10)
													Per.	22.7 (15)
													Per.	9.1 (0)
						x				x			Ann.	9.1 (0)
													Per.	9.1 (0)
													Per.	4.5 (0)
x	x	x	x	x	x	x	x			x	x		Ann.	86.4 (85)
x									x	x			Ann.	18.2 (20)
													Per.	4.5 (0)
													Ann.	4.5 (0)
													Per.	4.5 (0)
													Per.	4.5 (0)
	x	x	x	x	x	x			x	x			Per.	77.3 (75)
													Per.	4.5 (5)
													Per.	9.1 (5)
													Per.	18.2 (10)
						x							Ann.	4.5 (5)
					x								Per.?	9.1 (10)
													Per.	4.5 (0)
													Per.	27.3 (20)
													Per.	9.1 (0)
													Per.	9.1 (0)
													Per.	9.1 (0)
													Per.	9.1 (0)
													Per.	9.1 (0)
													Per.	9.1 (0)
													Per.	9.1 (0)
													Per.	4.5 (0)
													Per.	4.5 (0)
													Per.	9.1 (0)
												x	Ann.	4.5 (5)
													Per.	9.1 (0)
x					x	x	x	x	x	x			Ann.	63.6 (60)

Table 3. Continued.

	NL	SP	1	2	3	4	5	6	7
Polysiphonia lanosa	x	x		x	x				
Polysiphonia nigra									
Polysiphonia nigrescens	x							x	
Polysiphonia subtilissima									
Polysiphonia urceolata	x	x							
Porphya amplissima	x								
Porphyra linearis	x								
Porphyra miniata	x	x							
Porphyra umbilicalis	x	x	x			x	x		x
Ptilota serrata	x	x							
Rhodomela confervoides	x	x							
Scagelia pylaisei	x								
Stylonema alsidii									
Total Rhodophyta taxa	45	35	8	8	10	7	5	8	10
Mean (±SD) Rhodophyta taxa	(6.5 ± 2.3)								
Grand total seaweed taxa	97	72	22	16	20	23	20	21	28
Mean (±SD) total seaweed taxa	(21.4 ± 3.2)								

* The two % values represent calculations based upon a total of 22 combined and 20 estuarine stations, respectively.

patchy estuarine distributions (*Chaetomorpha brachygona, Cladophora sericea, Enteromorpha flexuosa* ssp. *paradoxa, Fucus distichus* ssp. *edentatus, F. distichus* ssp. *evanescens, F. spiralis, Laminaria saccharina, Audouinella secundata, Callophyllis cristata* and *Polysiphonia urceolata*), while others were restricted (<20%) to the outer estuary (e.g., *Rhizoclonium tortuosum, Ectocarpus siliculosus, Clathromorphum circumscriptum, Lithophyllum corallinae* and *Lithothamnion glaciale*).

Estuarine taxa also showed various distributional patterns (cf. Table 3). *Ulvaria oxysperma* and *Ascophyllum nodosum* ecad *scorpioides* occurred at 36% and 68% of the sites, respectively. Most taxa either exhibited a restricted (<20%) inner distribution (i.e., *Capsosiphon fulvescens, Microspora pachyderma, Giffordia granulosa, Polysiphonia denudata* and *P. nigra*) or a patchy/restricted (<20%) distribution (e.g., *Bryopsis plumosa, Enteromorpha clathrata, Percursaria percursa, Ectocarpus fasciculatus, Giffordia granulosa, Petroderma maculiforme, Pseudolithoderma extensum, Ralfsia bornetii, Sorapion kjellmanii, Ceramium strictum, Dasya baillouviana, Erythrotrichia carnea, Leptophytum laevae, Lo-

Table 3. Extended, continued.

8	9	10	11	12	13	14	15	16	17	18	19	20	Longevity	%*
x					x			x	x	x	x	x	Per.	50 (45)
									x	x			Per.?	9.1 (10)
							x	x	x				Per.	22.7 (20)
x												x	Per.	9.1 (10)
x													Per.	13.6 (5)
													Ann.	4.5 (1)
													Ann.	4.5 (1)
													Ann.	9.1 (0)
x		x		x		x	x	x	x		x	x	Ann.	68.2 (65)
													Per.	9.1 (0)
													Per.	9.1 (0)
													AAnn.	4.5 (0)
								x					Ann.	4.5 (5)
9	3	3	3	4	6	10	5	6	8	7	4	5		
24	21	19	16	20	21	27	22	25	25	20	20	17		

mentaria baileyana, L. clavellosa, Phymatolithon lenormandii and *Polysiphonia subtilissima*).

FLORISTIC COMPARISONS

Figure 6 compares species richness patterns in the York River Estuary with two nearshore open coastal sites (Cape Neddick and Sea Point) and twelve other estuarine habitats in southern Maine, New Hampshire and Massachusetts. Ninety-five taxa were recorded at Cape Neddick, while Sea Point and the York River Estuary both had 72 taxa, albeit their species compositions were very different. A comparison of the York, Great Bay, Hampton-Seabrook and Merrimack River Estuaries suggests an intermediate pattern of species richness (Figure 6). A "typical" estuarine reduction pattern (cf. Mathieson and Penniman, 1991) is evident within the ten primary subareas of the Great Bay Estuary System (Table 1), ranging from the Piscataqua River (143 taxa), Little Bay (130 taxa), Great Bay (90 taxa), and inner riverine sites like the Salmon Falls (16 taxa) and Winnicut Rivers (4 taxa). The York River has a more diverse flora than the Hampton-Seabrook Estuary (63 taxa) or the tidal waters of the Merrimack River (25 taxa). Thus, the York River has its greatest affinities to several mid-estuarine habitats within the Hampton-Seabrook and Great Bay Estuaries (Table 1). A comparison of the number and percentage of York River taxa within these same open coastal and estuarine sites confirms many of the above described patterns (cf. Figure 6). The greatest floristic affinities were between the York and Piscataqua Rivers (i.e., 68 taxa and 94%), followed by Little Bay (63 and 88%), Great Bay (52 and 72%) and the Hampton-Seabrook Estuary (41 and 57%). By contrast, the York River showed reduced affinities with the Merrimack River (20 taxa and 28%), as well as a variety of inner estuarine sites (e.g., Winnicut River, 4 taxa and 5.5%). The York River only shares a modest number of taxa with the nearby coastal sites at Cape Neddick (42 and 58%) and Sea Point (41 taxa and 57%).

The numbers of seaweed taxa at each site within the York River Estuary, plus those at Cape Neddick and Sea Point, are illustrated in Figure 7 and Table 3. Overall, patterns of species richness within the estuary were irregular and reduced in numbers. A total of 16–28 taxa per site were recorded within the York River (mean = 21.4 ± 3.2 taxa), while Cape Neddick and Sea Point had 95 and 72 taxa, respectively. A comparison of the mean number of taxa per site within the York River and twelve other estuarine habitats is given in Figure 8. The York River is comparable to the Piscataqua River (mean = 25.3 ± 24.9) and Great Bay (mean = 22.5 ± 18.0), while it is lower than Little Bay (mean = 34.1 ± 29.0). By contrast, the York River has a greater number of taxa per site than several mid- and inner-estuarine areas like the Oyster (mean = 12.6 ± 7.9) and Winnicut Rivers (mean = 1.3 ± 1.6). It is also more diverse than the Hampton-Seabrook (mean = 10.5 ± 5.5) and Merrimack River Estuaries (mean = 3.5 ± 5.2). Thus, the York River is more spatially consistent (mean = 21.4 ± 3.2) than the Piscataqua River, Little Bay and Great Bay, and is analogous to several inner-estuarine sites like the Cocheco (±4.3) and Salmon Falls Rivers (±3.4)—albeit the species richness within the latter rivers is much lower than in the York River (Table 3).

LONGEVITY PATTERNS

Of the 131 taxa recorded from the York River, Cape Neddick and Sea Point, 62 were annuals (47%), 67 (51%) perennials and

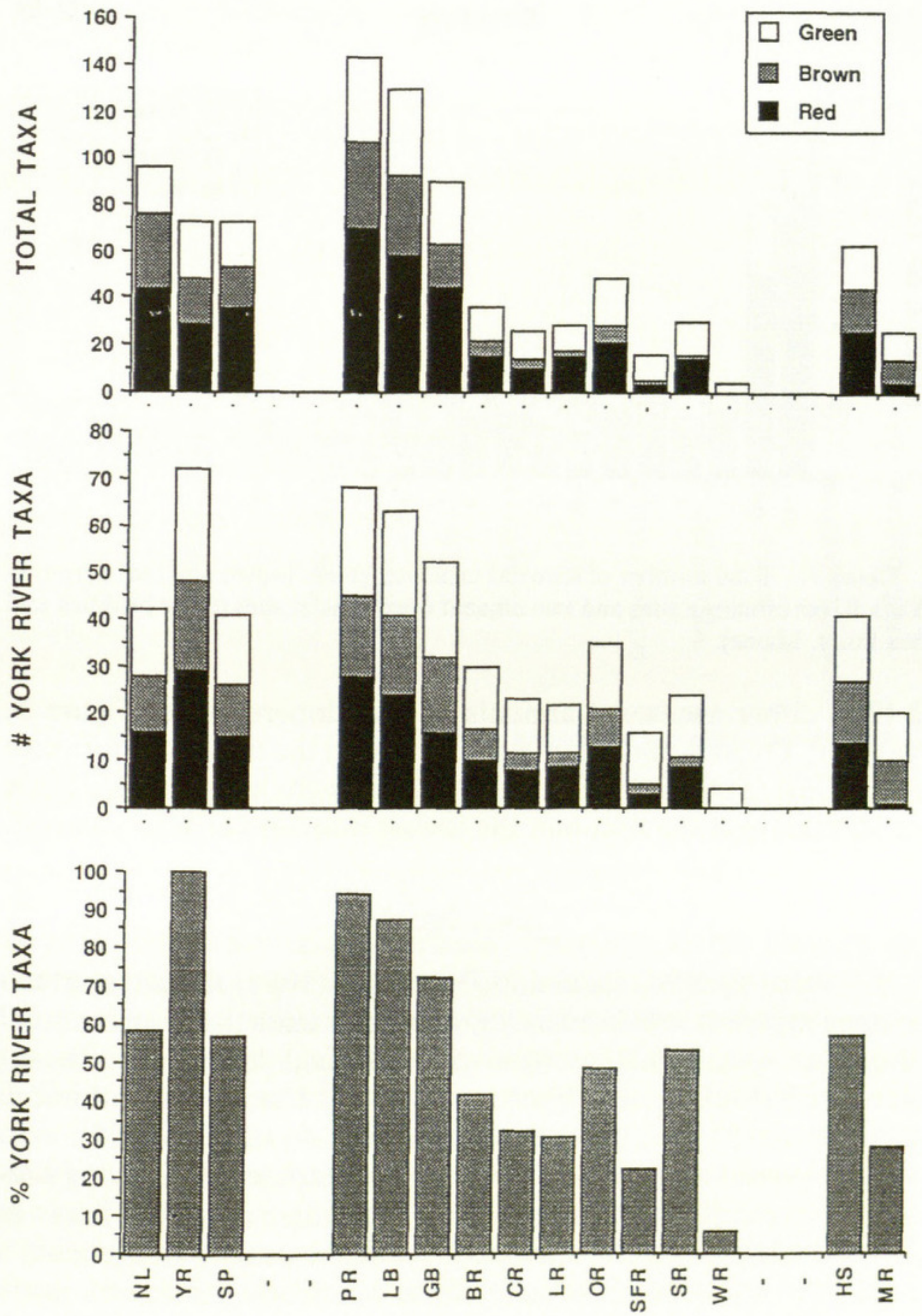

Figure 6. A comparison of the York River estuarine flora with sixteen other coastal and estuarine habitats, expressed as the total number of seaweed taxa/site (green, brown and red), as well as the number and percentage of York River taxa in common. See Table 1 and Appendix I for habitat descriptions. Abbreviations: NL (Nubble Lighthouse or Cape Neddick), YR (York River Estuary), SP (Sea Point), PR (Piscataqua River), LB (Little Bay), GB (Great Bay), BR (Bellamy River), CR (Cocheco River), LR (Lamprey River), OR (Oyster River), SFR (Salmon Falls River), SR (Squamscott River), WR (Winnicut River), HS (Hampton-Seabrook Estuary) and MR (Merrimack River Estuary).

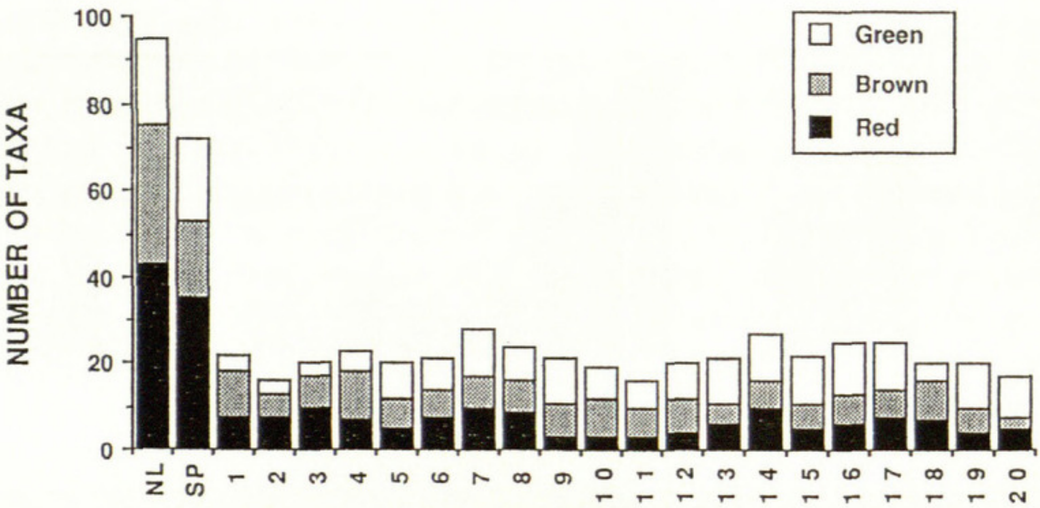

Figure 7. Total number of seaweed taxa/site (green, brown and red) at twenty York River estuarine sites and two adjaent open coastal sites (Cape Neddick and Sea Point, Maine).

2 (2%) either aseasonal annuals or pseudoperennials (Figure 5, Table 3). Overall, the green algae exhibited the highest percentage of annuals (81% or 25 taxa), the browns were intermediate (46% or 18 taxa) and the reds had the lowest number (31% or 19 taxa).

DICUSSION

As noted by Mathieson and Penniman (1991) the physical extremes inherent within estuaries may determine the distributional limits of species where their physiological tolerances are approached (Fralick and Mathieson, 1975; Guo and Mathieson, 1992; Kinne, 1970, 1971; Penniman and Mathieson, 1985). Wilkinson (1980) describes an analogous pattern, citing varying ecological requirements between inner and outer estuarine floras in Great Britain, with the species of the inner estuary comprising a group having wide ecological tolerances, while those with more limited environmental ranges are at an advantage in less harsh conditions of the outer estuary. Such differences in ecological requirements between inner and outer estuarine floras are evident within the York River (Figure 5), Great Bay (Mathieson et al., 1981; Mathieson and Penniman, 1986b) and Hampton-Seabrook Estuaries (Mathieson and Fralick, 1972). The inner estuarine species include seasonally dynamic warm temperate or "mixed floras" (i.e., annuals), while those of the outer estuary are dominated by a separate cold-temperate, perennial-dominated flora (Mathie-

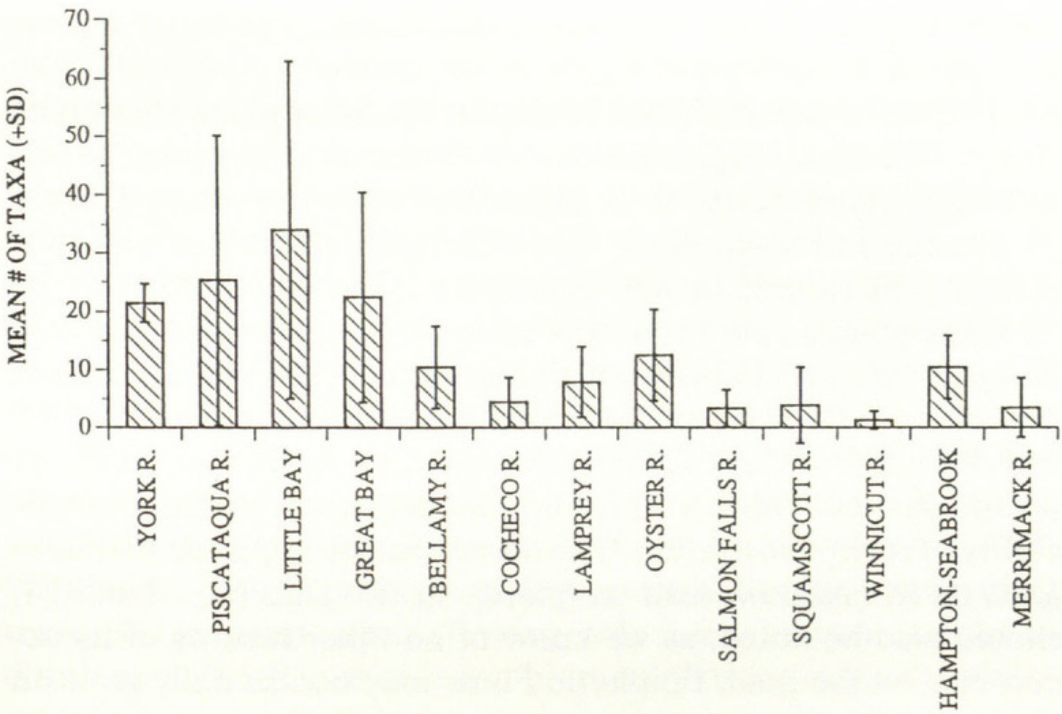

Figure 8. Mean (±SD) number of green, brown and red algal taxa/site within the York River Estuary and fourteen other geographical areas. See Table 1 for a synopsis of number of collection sites/area.

son, 1978; Mathieson and Hehre, 1986). Aside from such hydrographic variability, a conspicuous reduction in the amount of rocky substrata is present upstream within the York River Estuary. A combination of both physical factors probably causes gross fluctuations in numbers of taxa per site, a general reduction in the number of species upstream and the ultimate dominance of riverine habitats by ephemeral Chlorophyceae (Coutinho and Seeliger, 1984; Josselyn and West, 1985; Ketchum, 1983; Mathieson and Penniman, 1986b; Wilkinson, 1980).

Several specific examples of limited rocky substrata can be cited. Foremost, the upper reaches of the York River are composed of steep channels and dissected saltmarshes, which have a limited flora dominated by *Blidingia minima, Enteromorpha* spp., *Ulva lactuca, Urospora* spp., *Ulothrix* spp., *Ulvaria* spp., *Rhizoclonium riparium, Fucus vesiculosus, Ascophyllum nodosum* and *A. nodosum* ecad *scorpioides.* Many of the latter taxa occur as unattached or entangled masses (Norton and Mathieson, 1983). For example, the marsh ecad *scorpioides* of *A. nodosum* grows abundantly at diverse sites (Table 3), forming entangled masses amongst *Spartina alterniflora.* By contrast, only a single detached marsh ecad of *F. vesiculosus* was found at station 16 where it grew as a partially embedded fragment (Appendix 1, Table 3). The morphology and proliferous habitat of the latter plant are similar to *F. vesiculosus* megecad *limicola* (Baker and Bohling, 1916). Although marsh ecads of *F. vesiculosus* are common in Europe (cf. Norton and Mathieson, 1983), they are uncommon and sporadically distributed in New England (Chapman, 1939).

Distributional patterns of several epiphytic algae (e.g., *Elachista fucicola, Pilayella littoralis, Callithamnion byssoides, Ceramium rubrum* and *Polysiphonia lanosa*) paralleled the occurrence of the two dominant canopy fucoids, *Ascophyllum nodosum* and *Fucus vesiculosus* (cf. Table 3), presumably because of reduced availability of rocky substratum. The occurrence of epiphytic *F. vesiculosus* on *A. nodosum* ecad *scorpioides* at two sites (i.e., 7 and 14) should also be noted, as we know of no other records of its occurrence on the ecad. Epiphytic *Fucus* may occasionally grow on attached *A. nodosum,* particularly on isolated rock outcrops within estuarine mudflats such as in Great Bay, New Hampshire (A. Mathieson, unpubl. data). Patchy distributional patterns of several attached taxa on scattered rock outcrops should also be noted, including *Ectocarpus* spp., *Laminaria saccharina, Bangia atropurpurea, Corallina officinallis, Clathromorphum circumscriptum, Leptophytum laeve, Lithophyllum corallinae, Lithothamnion glaciale, Phymatolithon lenormandi and Mastocarpus stellatus* (Table 3). Lastly, the restricted estuarine occurrence of *Callophyllis cristata* on *Littorina littorea* at station 8 (1.6 miles inland) may have been due to its host's migration from the open coast.

A comparison of the York, Piscataqua and Merrimack Rivers is instructive as all three are outer estuarine habitats with contrasting floras (cf. Mathieson and Fralick, 1972, 1973; Mathieson and Penniman, 1986b; Mathieson et al., 1981). Open coastal species drop out after approximately 1.0 mile on the Merrimack versus 2–3 miles on the York (cf. Table 3) and approximately 8.5 miles on the Piscataqua River (Reynolds and Mathieson, 1975; Mathieson et al., 1983). The latter site on the Piscataqua River (i.e., Dover Point) has strong tidal currents (approx. 5 knots) and diverse rocky substrata. A comparison of temperature and salinity conditions within the York River (cf. Figures 3 and 4) shows that they are comparable to those found at Dover Point (i.e., -2.0 to 24.1°C and .9 to 30.3‰), while hydrographic variability (particularly salinity and siltation) is maximal on the Merrimack (cf.

Mathieson and Fralick, 1973; Miller et al., 1971). The Merrimack River has the most depauperate flora (only 25 taxa), the York is intermediate (72 taxa) and the Piscataqua the most diverse (144 taxa). Several adverse physical factors (cf. above), as well as domestic and industrial pollution, are probably responsible for the reduced diversity of the Merrimack River. Besides being one of the most polluted rivers in New England (cf. Anonymous, 1984, 1987; Jerome et al., 1965; Lyons et al., 1982; Mathieson and Fralick, 1973; Miller et al., 1971), the Merrimack is also one of the largest sources of freshwater discharge into the Gulf of Maine (Apollonio, 1979). As noted by several investigators (Clokie and Boney, 1980; Daly and Mathieson, 1977; Edwards, 1972; Littler, 1980; North et al., 1964; Patrick, 1963, 1964, 1973; Round, 1981; Wilkinson, 1980), patterns of low species diversity are typical responses to stress, often allowing only a few tolerant species to dominate in both numbers and biomass. For example, the abundance of many ulotrichalean green algae, such as *Ulva lactuca, Enteromorpha* and *Ulvaria* (*Monostroma*) spp., typifies many eutrophied estuarine habitats (Cotton, 1910; Fritsch, 1935; Sawyer, 1965). The latter species are not only tolerant of extremes of pollution but of gross fluctuation in hydrographic conditions. While industrial development and eutrophication are limited on the York River (cf. above), they are intermediate on the Piscataqua and highest on the Merrimack (Mathieson and Penniman, 1991). Aside from these contrasting patterns, the Piscataqua River also has the greatest diversity of habitats (e.g., tidal rapids, saltmarshes, boulders, cobbles, shingle, etc.) and stable substrata.

Josselyn and West (1985) compare species richness within several estuaries, including San Francisco Bay and Great Bay. Beyond the mouth of the former site a relatively low number of taxa occurs upstream (i.e., 21–61 taxa/site). Similar patterns of low species richness are known from several other estuaries with high sedimentation and limited solid substrata, including the York, various subsets of the Great Bay and Hampton-Seabrook Estuaries (Figure 8), the Chesapeake Bay (Mathieson and Fuller, 1969; Orris 1980), several British and Dutch estuaries (Hartog, 1967; Nienhuis, 1975; Wilkinson, 1980), and several Icelandic fjords (Munda, 1969, 1978). Within such turbid habitats there is a relatively small pool of common estuarine species (Munda, 1969, 1972; Orris, 1980; Wilkinson, 1980). For example, Orris (1980) lists 62 taxa from the upper reaches of the Chesapeake Bay in

Maryland, with *Cladophora, Enteromorpha, Ulva, Ceramium* and *Polysiphonia* being most frequent.

A comparison of the species richness within the York River and the Great Bay Estuary System (i.e., all ten subareas in Figure 6) also showed pronounced differences, with 72 and 168 taxa occurring at the two sites, respectively. As noted above, such contrasting patterns are probably due to a variety of factors, including habitat diversity, hydrographic stability, pollution, availability of rocky substrata, etc. (Murray and Littler, 1989; Murray et al., 1980). With the exception of the crustose brown alga *Sorapion kjellmanii,* all of the taxa recorded from the York River are known from the Great Bay Estuary (Mathieson and Hehre, 1986). By contrast, a greater number of freshwater, coastal and estuarine taxa are known from the Great Bay Estuary than the York River. Several of these estuarine taxa represent disjunct "southerly" plants (Bird et al., 1976; Mathieson and Hehre, 1986; Novaczek et al., 1987) that are either absent (e.g., *Chondria baileyana, Gracilaria tikvahiae, Polysiphonia elongata*) or rare within the York River (e.g., *Bryopsis plumosa, Ceramium strictum, Dasya baillouviana, Lomentaria baileyana, Polysiphonia denudata* and *P. subtilissima*). A similar pattern exists within the Hampton-Seabrook Estuary: the absence of many "southerly" taxa and a dominance of saltmarshes (Mathieson and Fralick, 1972). Presumably these warm water plants are either unable to grow and/or compete with other saltmarsh-inhabiting taxa. The vast subtidal mudflats of the Great Bay Estuary may be some of the most suitable habitats for such warm water taxa in northern New England; these habitats are essentially absent from the York and Hampton-Seabrook Estuaries, except near outer estuarine sites where water temperatures are too low for optimal growth and/or survival (Figure 4; see also Fralick and Mathieson, 1975; Guo and Mathieson, 1992; Novaczek et al., 1987).

Although this study has primarily dealt with the algal flora of the York River Estuary, our coastal collections have documented two new records from southern Maine and New Hampshire. Foremost, the "arctic" taxon *Porphyra amplissima,* as recently defined by Bird and McLachlan, 1992, has been recorded from Cape Neddick (Table 3). Previously it was included under *P. miniata* (Taylor, 1957). An evaluation of herbarium specimens at Harvard University (FH) and the University of New Hampshire (NHA) has documented its presence from several open coastal sites in Maine, as well as nearshore and estuarine sites within New Hampshire (Hehre and Mathieson, 1993). Some of these samples date to ca. 1880. The presence of *P. amplissima* near the mouth of the York River suggests it may be found within this habitat as well. Recent expansion of the "alien" species *Codium fragile* ssp. *tomentosoides* (Van Patten, 1992) should also be noted (Mathieson and Hehre, 1986). It was initially found at Cape Neddick in November of 1989 and is now abundant at the Isles of Shoals (particularly on Appledore and Smuttynose Islands, Maine). One attached specimen was recently found on the nearshore open coast of New Hampshire at Jaffrey Point, Newcastle (September, 1992), while drift specimens were collected during the same period at nearby Rye Ledge (Rye, New Hampshire) and within the inner reaches of the Great Bay Estuary (Weeks Point). Further expansion of its distributional range may provide a variety of problems (Van Patten, 1992).

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Appendix 1. York River estuarine and adjacent open coastal study sites (Cape Neddick and Sea Point) in southern Maine.

Station	Miles from coast	Longitude	Latitude	Description
Open Coastal				
NL	0.0	70°35′25″W	43°09′56″N	Nubble Light, Cape Neddick, Maine; an exposed site with substrata primarily consisting of massive rock outcrops
SP	0.0	70°30′32″W	43°05′26″N	Sea Point, Kittery, Maine; semi-exposed site with substrata consisting of boulders (cobbles), rock outcrops and sand
York River				
1	0.0	70°37′36″W	43°08′06″N	Cove between Roaring Rock Point and Cow Beach Point; mostly rocky but some sand and gravel habitats also present
2	0.4	70°38′12″W	43°07′18″N	South bank of river, across from Stage Neck; a rocky habitat with limited mudflats
3	0.4	70°38′25″W	43°07′26°N	North bank of river by Stage Neck Condominiums; a rocky habitat with boulders and rock outcrops
4	0.8	70°38′45″W	43°07′31″N	South bank of river, just north of the new Rte. 103 bridge; a variety of habitats including mudflats, saltmarsh and some rocks
5	0.8	70°38′32″W	43°07′44″N	North bank of river at new Rte. 103 bridge; habitats include mudflats, rocks and saltmarshes traversed by many drainage ditches
6	1.0	70°39′00″W	43°07′49″N	North bank of river between Sewall Bridge and Rte. 103 bridge; substratum varied, including mudflats, sand, cobbles and boulders; fast-flowing water draining into York River from Barrells Millpond
7	1.2	70°39′07″W	43°07′42″N	North bank of river at Sewall Bridge; substrata consisting of mudflats and saltmarsh
8	1.6	70°39′45″W	43°07′56″N	North bank of river at Sewall Bridge, upstream from #7; substrata mainly consisting of sand, gravel, and some limited saltmarsh with scattered small rocks

Appendix 1. Continued.

Station	Miles from coast	Longitude	Latitude	Description
9	2.0	70°40′32″W	43°07′52″N	North bank of river, midway between Sewall Bridge and Ramshead Point; extensive mudflats with rock outcrops and a narrow band of saltmarsh
10	2.4	70°40′25″W	43°07′37″N	South bank of river on River Meadow Lane; just south of Ramshead Point; extensive mudflats
11	2.4	70°40′15″W	43°07′50″N	North bank of river approaching Ramshead Point; substrata consisting of rock outcrops, large boulders, saltmarshes and mudflats
12	2.6	70°40′45″W	43°08′04″N	North bank of river, just opposite Ramshead Point; near a private dock with boulders and cobbles, as well as mudflats and saltmarshes
13	2.8	70°41′10″W	43°07′56″N	North bank of river, just downstream from Rice's Bridge on Rte. 1; some rocky areas but mostly mudflats with some saltmarsh
14	3.4	70°43′30″W	43°07′51″N	South bank of river, at Rice's Bridge on Rte. 1; substrata primarily consists of mudflats and saltmarsh, with some scattered rocks; two outfall pipes present
15	3.4	70°41′25″W	43°08′13″N	North bank of river, at I-95 bridge; extensive mudflats and very limited saltmarsh; rocks and cobbles occur at bridge pilings
16	3.6	70°41′45″W	43°08′18″N	Mouth of Cider Hill Creek (north bank) just above the I-95 bridge; extensive mudflats with scattered rocks and some saltmarsh
17	4.0	70°42′05″W	43°08′32″N	Mouth of Boulter Pond Creek (north bank) between I-95 and Scotland Bridge; substrata primarily consisting of mudflats and saltmarsh
18	4.2	70°42′30″W	43°08′50″N	Just downstream from Scotland Bridge (north bank); a mudflat area with very little saltmarsh
19	4.4	70°43′15″W	43°09′01″N	North bank of river, at Scotland Bridge on Scotland Bridge Road; substrata primarily consisting of

Appendix 1. Continued.

Station	Miles from coast	Longitude	Latitude	Description
				mudflats, saltmarsh and bridge pilings
20	4.7	70°43′30″W	43°09′12″N	North bank of river, near a large farm—upstream from Scotland Bridge on Rte. 91; substrata primarily consisting of mudflats and some saltmarsh