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Chapter 7: Estuarine Primary Producers
by F.T. Short and A.C. Mathieson

The major contributors to estuarine primary production are the hundreds of plant species that grow in and around the Great Bay Estuary. All of these primary producers use sunlight to produce oxygen and organic matter through the process of photosynthesis. The rate of primary production for each plant species is determined by the characteristics of that species, local environmental conditions and the amount of available light reaching the plant. Primary production is the major source of organic matter to the estuary. Produced material accumulates as living biomass and upon death enters the detrital cycle within the system or is devoured directly by numerous species of estuarine consumers (see Chapter 8).

Phytoplankton

Phytoplankton are a major component of primary production within estuaries. Little data is available concerning phytoplankton species composition, abundances, or production within the Great Bay Estuary. The best data available for the Estuary was collected during 1970 to 1978 as part of a baseline study for the Newington Electric Power Generating Station; measurements of phytoplankton populations (Table 7.1) were made in Great Bay and on the Piscataqua River (NAI 1971-1980). The phytoplankton community was dominated by diatoms, primarily *Chaetoceros* spp. and *Skeletonema costatum*, with seasonal occurrence of *Rhizosolenia* spp. and *Asterionella glacialis*, and the dinoflagellates *Ceratium longipes*, *C. tripos* and *Peridinium depressum* (NAI 1979a). Phytoplankton cell densities generally ranged from 20 to 5000 cells per liter.

Some of the phytoplankton in Great Bay are pennate diatoms (e.g. *Navicula* spp. and *Fragilaria* spp.) that have been suspended in the water column by the currents that also resuspend benthic sediments (Donovan 1974). *Denotula confervacea* was a major component of the winter-spring Bay phytoplankton and dominated over *Thalassiosira* spp. in areas of lower salinity (Donovan 1974). *D. confervacea* was infrequent at the coastal stations in the Estuary (Donovan 1974).

Phytoplankton primary production in the Estuary is generally greatest during April to July, declining through August and September with a slight increase in October (NAI 1978a, b). The average annual phytoplankton production for the Estuary during 1977-78 was greater in Great Bay (14 mg C/m^3/h on ebb tide) than at more coastal stations. Chlorophyll *a* values were similarly distributed, with 6 mg/m^3 occurring in the surface ebb tide sample for Great Bay (NAI 1978a, b). Within the middle and upper estuary during 1973-1981, chlorophyll *a* concentrations varied from 1 to 14 mg/m^3, with an average of 5 mg/m^3 (Loder et al. 1983a).

Comparison of 1976-78 chlorophyll *a* and phaeophyton data (Loder et al. 1983a) with recent values (Langan et al. 1990) shows an absence of a "typical" April-May phytoplankton bloom (Fig. 7.1). Historic reports state that this spring

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Table 7.1. Phytoplankton species collected during 1977 by net and whole water sampling within the Great Bay Estuary (modified from NAI 1978).

Class: BACILLARIOPHYCEAE

Order: CENTRALES
Actinoptychus undulatus
Biddulphia alternans
Biddulphia aurita
Ceratulina bergoni
Chaetoceros affinis
Chaetoceros atlanticus
Chaetoceros brevis
Chaetoceros compressus
Chaetoceros concavicornis
Chaetoceros danicus
Chaetoceros debilis
Chaetoceros decipiens
Chaetoceros diadema
Chaetoceros furcellatus
Chaetoceros laciniosus
Chaetoceros lauderi
Chaetoceros lorenzianus
Chaetoceros lorenzianus f. *forceps*
Chaetoceros similis
Chaetoceros socialis
Chaetoceros teres
Chaetoceros spp.
Corethron hysterix
Coscinodiscus spp.
Ditylum brightwellii
Detonula confervacea
Detonula sp.
Eucampia zoodiacus
Guinardia flaccida
Leptocylindrus danicus
Lithodesmium undulatum
Melosira moniliformis
Melosira nummuloides
Paralia sulcata
Porosira glacialis
Rhizosolenia alata
Rhizosolenia delicatula
Skeletonema costatum
Thalassiosira nordenskioldii
Thalassiosira rotula
Thalassiosira spp.

Order: PENNALES
Amphora spp.
Asterionella formosa
Asterionella glacialis
Bacillaria paxillifer
Campylodiscus echeneis
Climacosphenia moniligera
Cocconeis scutellum
Cylindrotheca closterium
Fragilaria oceanica
Fragilaria spp.
Grammatophora marina
Gyrosigma balticum
Gyrosigma fasciola
Gyrosigma/Pleurosigma spp.
Isthmia nervosa
Licomophora abbreviata
Licomophora flabellata
Navicula crucigera
Navicula spp.
Nitzschia delicatissima
Nitzschia longissima
Nitzschia paradoxa
Nitzschia seriata
Rhabdonema arcuatum
Rhabdonema adriaticum
Surirella spp.
Thalassionema nitzschioides
unspecified Pennales

Class: CHRYSOPHYCEAE

Order: OCHROMONADALES
Dinobryon spp.
Olisthodiscus luteus

Order: DICTYOCHALES
Dictyocha fibula
Distephanus speculum
Ebria tripartita

Class: DINOPHYCEAE

Order: GYMNODINIALES
Amphidinium crassum
Gymnodinium spp.

Order: PROROCENTRALES
Prorocentrum micans
Prorocentrum triestinum

Order: PERIDINIALES
Ceratium furca
Ceratium fusus
Ceratium horridum
Ceratium longipes
Ceratium minutum
Ceratium spp.
Ceratium tripos
Peridinium conicum
Peridinium depressum
Peridinium trochoideum
Peridinium spp.

Order: DINOPHYSIALES
Dinophysis norvegica

Class: HAPTOPHYCEAE

Order: PRYMNESIALES
Phaeocystis pouchetti

Class: CRYPTOPHYTA

Order: CRYPTOMONADALES
Chroomonas spp.

Class: CHLOROPHYCEAE

Order: ZYGNEMATALES
Staurastrum paradoxa

Class: CYANOPHYCEAE

Order: CHROOCOCCALES
Agmenellum sp.

Order: OSCILLATORIALES
Arthrospira subsalsa

Class: EUGLENOPHYCEAE

Order: EUGLENALES
Eutreptia spp.
Eutreptiella spp.

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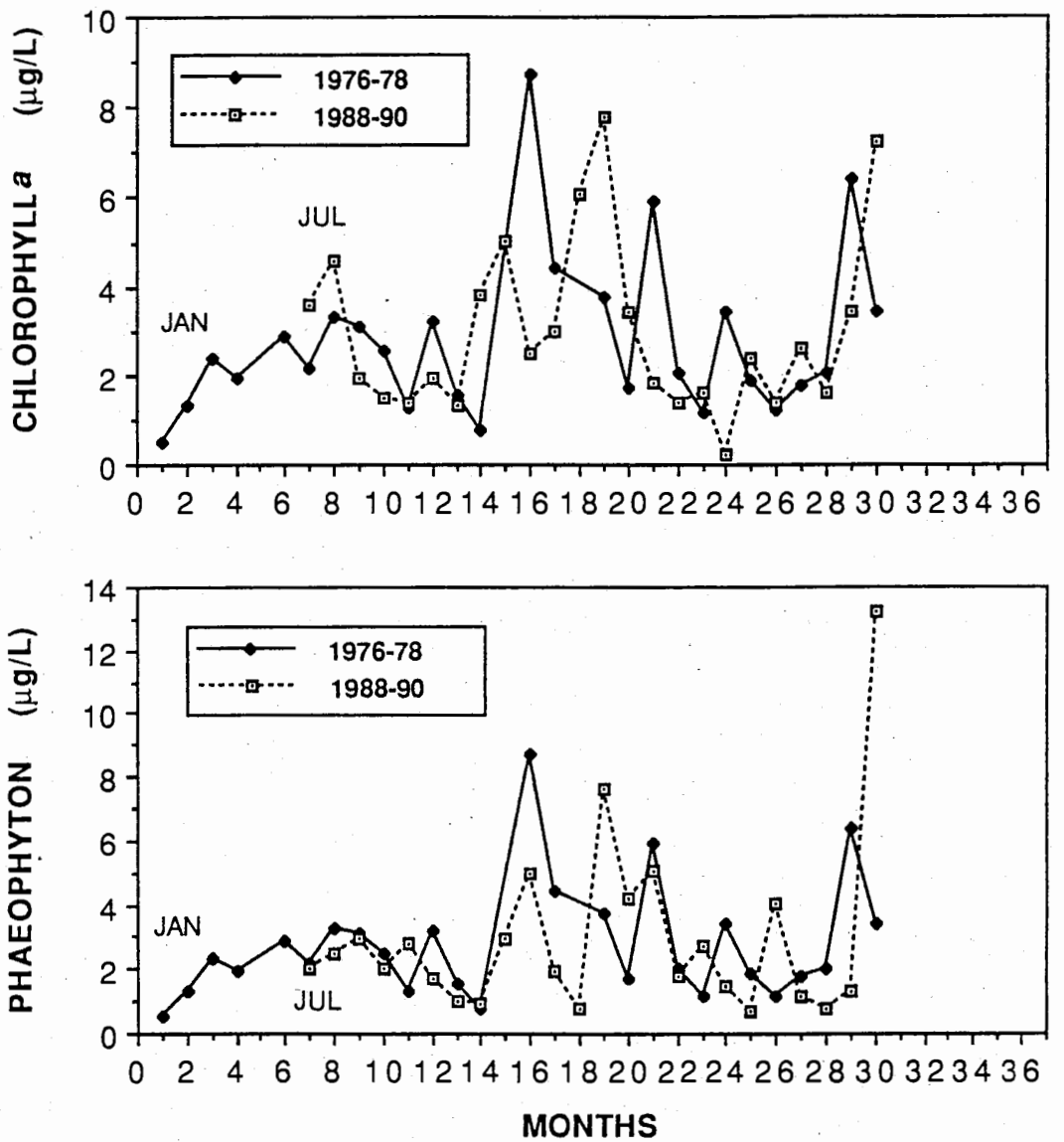

Fig. 7.1 Comparison of chlorophyll and phaeophyton concentrations for 1976-78 and 1988-90 during low tide off Adams Point at the mouth of Great Bay, New Hampshire (Data from Loder et al. 1983b and Langan et al. 1990; see also Table 5.1).

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bloom is frequent, but a large degree of variability is apparent in the data. The peak chlorophyll *a* values observed in data from recent years occurred much later, in June or July. Currently, a project is underway at JEL that will examine the timing and magnitude of the spring bloom in greater detail.

Eelgrass

Eelgrass, *Zostera marina*, is a submerged marine flowering plant that is rooted within the sediments of coastal and estuarine waters, contributing significantly. to the health and productivity of these areas. Eelgrass is known and appreciated by shellfish enthusiasts, fishermen, and duck hunters because of its important role in the life cycle of scallops, crabs, finfish, geese, and ducks. Eelgrass and the ecosystem it fosters are an important component of the Great Bay Estuary, covering 10 km^2 (3.9 mi^2 or 2500 acres), almost half the area of bottom in Great Bay alone.

Eelgrass communities are valuable sediment traps and help stabilize bottom sediments (Thayer et al. 1975). Their leaves form a three-dimensional baffle in the water, thus acting as dampers and reducing water motion. Eelgrass meadows act as a filter of estuarine waters, removing both suspended sediments and dissolved nutrients (Jackson 1944, Short and Short 1984). Suspended materials carried by currents move into eelgrass beds and are rapidly settled to the bottom. Polluting levels of nutrients entering the Estuary from coastal development are taken up by eelgrass leaves for their growth (see review by Short 1987). However, in the Great Bay Estuary and elsewhere, too many nutrients from wastewater effluent and fertilizers can produce algal blooms that shade and destroy eelgrass ecosystems. For these reasons, eelgrass health is both a factor in and an indicator of the overall health of bays and estuaries.

The three-dimensional structure of an eelgrass bed provides breeding and nursery areas for young finfish and shellfish, such as flounder, scallops, and crabs (Thayer et al. 1984). The dense underwater meadows provide a vertical substratum, or place of attachment, in the water column as well as a haven from predators. In addition, birds such as Canada geese, brant geese, and ducks consume the leaves and seeds of eelgrass as a principal food source.

In the normal life cycle of eelgrass, many of the leaves break away from the base of the shoots, especially in the fall. Some float away, carried by the currents; others fall to the bottom where they decompose (Phillips 1984). Detritivores begin to break down the leaves into smaller particles, which are consumed by bacteria and fungi. In this detrital process many invertebrates also consume the decaying eelgrass. The adult and larval forms of these invertebrates become food for larger life forms such as fish and crabs.

A catastrophic decline of eelgrass in the early 1930s (Rasmussen 1977), subsequently known as the wasting disease, killed over 90% of the North Atlantic eelgrass population (Milne and Milne 1951). As a result, scallops, clams, crabs, and many fish species suffered from the loss of protective habitat and from the sedimentation and erosion that occurred because eelgrass no longer anchored the bottom sediments. The effects of eelgrass loss in Great Bay, the increased suspended sediments, and the changes in the Bay habitats after the 1930s decline were described by Jackson (1944) and were the basis of the review by Milne and Milne (1951).

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In most areas along the North Atlantic coast including the Great Bay Estuary, eelgrass recovered from the wasting disease by the 1960s, although in some locations the eelgrass never grew back (Thayer et al. 1984). Now a new outbreak of the disease, discovered first in the Great Bay Estuary and now found on both sides of the Atlantic, is threatening eelgrass populations again (Short et al. 1986). The symptoms of the current disease are similar to those in the 1930s. First, pinhead-sized black dots appear on the leaves (Short et al. 1988). The dots spread, forming large black stripes and patches. Eventually the whole leaf blackens, dies, and sinks or breaks off and floats away. The causal agent of the wasting disease has recently been identified as a marine slime mold, *Labyrinthula zosterae* (see Chapter 10). The recurrence of the disease was first noticed in 1984 in the Great Bay Estuary (Short et al. 1986) and has continued during recent years (Fig. 10.2). Now diseased plants have been found from Nova Scotia to North Carolina, on the west coast of the United States, on the coast of Europe (Short et al. 1988), and Japan (Short et al. in press).

Besides the wasting disease, another major factor that limits the production and survival of eelgrass in coastal areas is pollution resulting in decreased water clarity. Decreased water clarity reduces the amount of light reaching eelgrass and therefore reduces eelgrass growth (Dennison 1987). Of the two main factors contributing to water clarity reduction, suspended sediments shade or smother the plants directly while nutrient loading shades the plants by promoting planktonic and macroalgal growth.

The causes for the many recently reported declines of eelgrass along the East Coast are varied and include: the wasting disease (Short et al. 1987, Short 1988, Short et al. 1988), reduced water quality from coastal eutrophication (Orth and Moore 1983 and 1988, Kemp et al. 1983, Twilley et al. 1985), and intensive phytoplankton blooms (Dennison et al. 1989).

Eelgrass abundance in the Great Bay has been monitored seasonally in a number of studies through the 1970s and 1980s. Monthly samples of eelgrass abundance were monitored in 1972 by Riggs and Fralick (1975), in 1980-81 by Nelson (1981, 1982), and in 1986-90 by Short, Jones and Burdick (1991). The results of all these studies (Fig. 7.2) show the same seasonal pattern of abundance with low biomass occurring during the winter and rapid biomass increase during the spring and early summer. Maximum biomass, 250 g dry wt/m^2, occurs in late July or August. Such a pattern of abundance appears typical for eelgrass at this latitude (Short et al. 1989). Detailed analyses of seagrass populations in the Great Bay Estuary are presented in a recent summary report for the National Estuarine Research Reserve Program (Short et al. 1992) and in an ongoing investigation of the Portsmouth Naval Shipyard (Munns et al. 1992).

Seaweed

The Great Bay Estuary is typical of northern New England estuaries in having a wide diversity of seaweed species. The dominant species within the Estuary are the substantial intertidal populations of the fucoid macroalgae, *Ascophyllum nodosum* and *Fucus vesiculosus*, covering an area of 0.011 km^2 (0.010 mi^2 or 7 acres) within Great Bay alone, growing on the shingle cobble and granitic outcrops.

A total of 219 seaweed species are known in New Hampshire marine and estuarine waters, including the Isles of Shoals (Mathieson and Hehre 1986,

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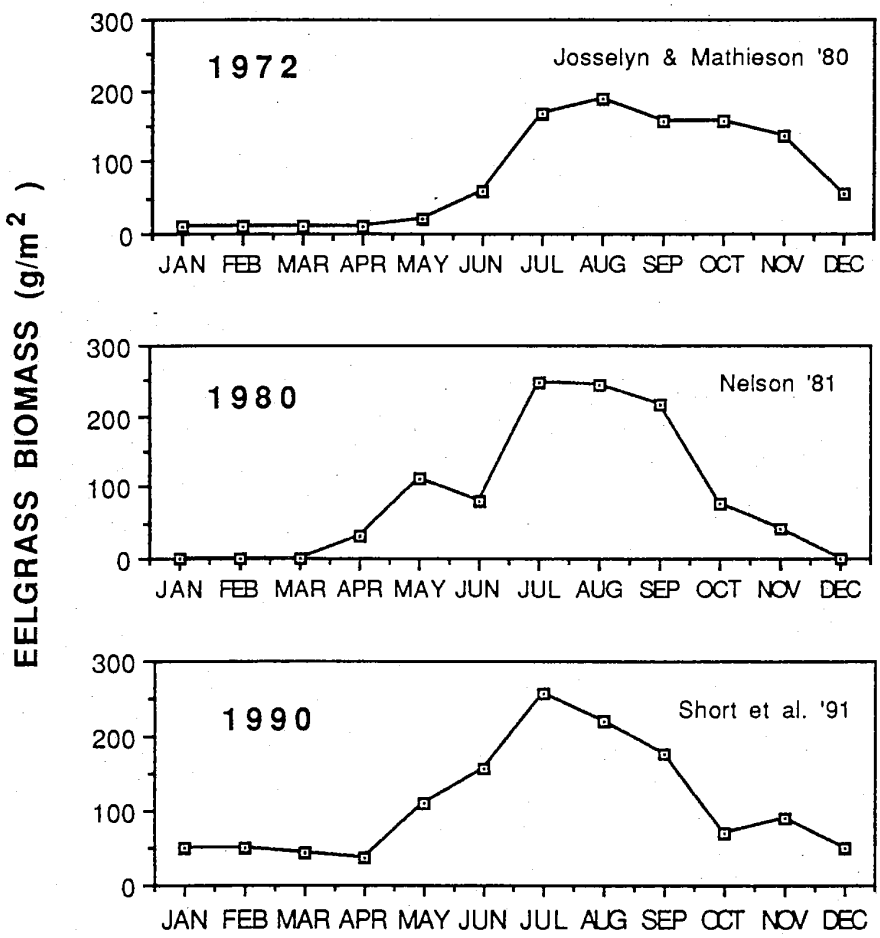

Fig. 7.2 Comparison of eelgrass biomass in Great Bay for 1972, 1980 and 1990. Data source for each year is indicated on the respective graph.

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Mathieson and Penniman 1991). Of this total, 169 taxa (77.2% of total) are recorded within the Great Bay Estuary, including 45 Chlorophyceae, 46 Phaeophyceae and 78 Rhodophyceae (Table 7.2). A "typical" estuarine reduction pattern occurs from the Piscataqua River (144 taxa, 85.2% total estuarine) to Little Bay (132 taxa, 89.1% total estuarine) and Great Bay proper (90 taxa, 53.3% total estuarine). Each of the seven tidal rivers entering the Great Bay Estuary has a relatively reduced flora, ranging from only 4 taxa within the Winnicut River to 49 taxa in the Oyster River.

Within the Great Bay Estuary, two basic distributional patterns have been identified (Mathieson and Penniman 1991):

- Cosmopolitan - present in both estuarine and open coastal environments
- Estuarine - restricted to estuarine environments

Most species (i.e. 85% or 144 taxa) exhibit cosmopolitan distributional patterns of varying degrees - i.e. 66 Rhodophyceae, 41 Phaeophyceae and 39 Chlorophyceae. Twenty-five taxa (15%) are restricted to estuarine habitats - i.e. 13 Rhodophyceae, 6 Phaeophyceae and 6 Chlorophyceae. Six of the latter only occur within riverine habitats near the headwaters of tidal tributaries - i.e. *Mougeotia, Oedogonium, Spirogyra* and *Stigeoclonium* species, plus *Audouinella violacea* and *Sacheria fucina.*

Of the 169 total taxa within the Great Bay Estuary, 83 species are interpreted as annuals (49.1%), 2 (1.2%) as aseasonal annuals or pseudoperennials, and 84 (49.7%) as perennials (Table 7.2). Overall, the green algae exhibit the highest number of annuals (38 taxa, 84.4%), while the browns are intermediate (23 taxa, 50%) and the reds the lowest (25 taxa, 32.1%).

A variety of seaweed species occur within Great Bay that are absent on the open Atlantic coast north of Cape Cod. These species, which have a disjunct distributional pattern, may represent relict populations that were more widely distributed during a previous time when coastal water temperatures were warmer (Bousfield and Thomas 1975). Alternatively, they may be introduced from the south. These seaweeds (e.g. *Gracilaria tikvahiae, Bryopsis plumosa, Dasya baillouviana, Chondria tenuissima, Lomentaria clavellosa, Lomentaria orcadensis* and *Polysiphonia subtilissima*) grow and reproduce during the warm summer and are able to tolerate colder winter temperatures (Fralick and Mathieson 1975, Mathieson and Hehre 1986). Several of these seaweed taxa exhibiting this same pattern also occur in the Great Salt Bay at the head of the Damariscotta River in Maine, an area somewhat similar to Great Bay. The disjunct distributional pattern described for the seaweeds is also found for several marine/estuarine invertebrates (Bousfield and Thomas 1975, Turgeon 1976).

Ascophyllum nodosum, rockweed, reaches maximum development in Great Bay because it is intolerant of extreme wave exposure and prefers the sheltered shoreline. Throughout the Estuary, the percent cover of *Ascophyllum* varies from 0 to 97.8% within the mid-intertidal zone (Nelson 1981a). The standing crop of fucoids throughout the Estuary has a range of 0-5,474 g dry wt/m^2 (average 2,073 g dry wt/m^2) (Nelson 1982). Maximum seasonal growth of *Ascophyllum* occurs during spring and fall in the Great Bay Estuary (Mathieson et al. 1976). *Ascophyllum* plants may be quite long-lived in some areas, persisting for 15 years (Baardseth 1970). Within Great Bay *Ascophyllum* can be heavily pruned annually by ice, losing up to one-half its standing crop (Mathieson et al. 1982). The

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TABLE 7.2. Summary of seaweed species composition from ten Great Bay Estuarine areas (modified from Mathieson and Penniman 1991).

CHLOROPHYTA	Piscataqua R.	Little Bay	Great Bay	Bellamy R.	Cocheco R.	Lamprey R.	Oyster R.	Salmon Falls	Squamscott R.	Winnicut R.	Longevity*
Acrochaete repens	x**										A
Blidingia minima	x	x	x	x	x	x	x	x	x	x	AA
Bryopsis plumosa	x	x	x	x	x						A
Capsosiphon fulvescens	x	x	x				x	x			A
Chaetomorpha aerea	x										P
Chaetomorpha brachygona	x	x	x								A
Chaetomorpha linum	x	x	x			x			x		P
Chaetomorpha melagonium	x	x									P
Chaetomorpha picquotiana	x	x	x								P
Cladophora albida		x	x								AA
Cladophora pygmaea	x	x	x								P
Cladophora sericea	x	x	x	x	x	x	x	x	x	x	AA/PP
Codiolum gregarium	x	x**									A
Codiolum pusillum		x**									A
Enteromorpha clathrata	x	x	x	x	x	x	x		x		A
Enteromorpha compressa	x	x	x				x	x			AA
Enteromorpha flexuosa ssp. *flexuosa*							x				A
Enteromorpha flexuosa ssp. *paradoxa*	x	x	x	x	x		x	x	x		A
Enteromorpha intestinalis	x	x	x	x	x	x	x	x	x		AA
Enteromorpha linza	x	x	x	x	x		x				AA
Enteromorpha prolifera	x	x	x	x	x	x	x	x	x	x	AA
Enteromorpha torta	x	x									A
Entocladia viridis		x	x								AA
Kornmannia leptoderma	x	x									A
Microspora pachyderma		x**	x				x		x		A
Monostroma grevillei	x	x	x								A
Monostroma pulchrum	x	x									A
Mougeotia sp.							x				A
Oedogonium sp.							x				A
Percursaria percursa	x	x									AA
Prasiola stipitata	x										AA
Pseudendoclonium submarium	x										AA
Rhizoclonium riparium	x	x	x	x	x	x	x	x	x	x	AA
Rhizoclonium tortuosum	x	x	x	x			x				AA
Spirogyra sp.							x				A
Spongomorpha arcta	x	x									A
Spongomorpha spinescens	x	x									A
Stigeoclonium sp.						x			x		A
Ulothrix flacca	x	x	x	x	x	x	x	x	x		A
Ulothrix speciosa	x	x									A
Ulva lactuca	x	x	x	x	x	x	x	x	x		A/PP
Ulvaria obscura	x	x	x	x			x		x		A
Ulvaria oxysperma	x	x	x	x	x	x	x	x	x		A
Urospora penicilliformis	x	x	x								A
Urospora wormskioldii	x	x									A
Total Chlorophyta Taxa	35	37	25	14	12	11	20	11	14	4	

* = Longevity designations (A = annual, AA = aseasonal annual, P = perennial, PP = pseudoperennial)
** = Only found in culture

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Table 7.2 (continued)

PHAEOPHYTA	Piscataqua R.	Little Bay	Great Bay	Bellamy R.	Cocheco R.	Lamprey R.	Oyster R.	Salmon Falls	Squamscott R.	Winnicut R.	Longevity*
Agarum cribrosum	x										P
Ascophyllum nodosum	x	x	x	x	x	x	x	x	x		P
Ascophyllum nodosum ecad *scorpioides*	x	x	x	x			x				P
Chorda filum	x	x									A
Chorda tomentosa	x	x									A
Chordaria flagelliformis	x	x									A
Delamarea attenuata	x										A
Desmarestia aculeata	x										P
Desmarestia viridis	x										A
Desmotrichum undulatum	x										A
Dictyosiphon foeniculaceus	x										A
Ectocarpus fasciculatus	x										A
Ectocarpus siliculosus	x	x	x	x	x		x				A
Elachista fucicola	x	x		x							P
Fucus distichus ssp. *distichus*	x										P
Fucus distichus ssp. *edentatus*		x									P
Fucus distichus ssp. *evanescens*	x	x	x				x				P
Fucus spiralis	x	x	x								P
Fucus vesiculosus	x										P
Fucus vesiculosus var. *spiralis*	x	x	x	x	x	x	x	x	x		P
Giffordia granulosa	x	x									A
Giffordia sandriana	x	x									A
Isthmoplea sphaerophora	x	x**									A
Laminaria digitata	x	x									P
Laminaria longicruris	x	x									P
Laminaria saccharina	x	x	x								P
Myrionema corunnae		x									A
Myrionema strangulans		x	x	x							A
Petalonia fascia	x	x	x	x			x				A
Petalonia zosterifolia		x									A
Petroderma maculiforme	x	x	x								P
Pilayella littoralis	x	x	x	x	x	x	x				A
Pseudolithoderma extensum	x	x	x								P
Punctaria latifolia	x	x									A
Ralfsia bornetii	x	x	x								P(?)
Ralfsia clavata	x	x	x								P(?)
Ralfsia fungiformis	x										P
Ralfsia verrucosa	x	x	x								P
Scytosiphon lomentaria var. *complanatus*		x									A
Scytosiphon lomentaria var. *lomentaria*	x	x	x				x				A
Sorocarpus micromorus		x									A
Sphacelaria cirrosa	x	x	x								P
Spongonema tomentosum		x									P(?)
Stictyosiphon griffithsianus	x	x									A
Ulonema rhizophorum	x	x									A
Total Phaeophyta Taxa	38	35	18	7	4	3	8	2	2	0	

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Table 7.2 (continued)

RHODOPHYTA	Piscataqua R.	Little Bay	Great Bay	Bellamy R.	Cocheco R.	Lamprey R.	Oyster R.	Salmon Falls	Squamscott R.	Winnicut R.	Longevity*
Ahnfeltia plicata	x	x	x								P
Antithamnion cruciatum	x	x	x				x				A
Antithamnionella floccosa	x	x	x								AA
Audouinella membranacea	x	x	x								P(?)
Audouinella purpurea	x	x									P
Audouinella secundata	x	x	x				x				AA
Audouinella violacea			x			x	x				A
Bangia atropurpurea	x	x					x				A
Bonnemaisonia hamifera	x	x	x								P
Callithamnion byssoides		x	x								A
Callithamnion hookeri	x	x									A
Callithamnion tetragonum	x	x	x	x	x	x	x		x		P
Callocolax neglectus	x										P(?)
Callophyllis cristata	x										P
Ceramium deslongchampii var. *hooperi*	x		x								P(?)
Ceramium elegans			x								A
Ceramium rubrum	x	x	x	x	x	x	x		x		P
Ceramium strictum	x	x	x	x	x	x	x	x	x		A
Chondria baileyana	x	x	x	x		x	x				A
Chondrus crispus	x	x	x	x	x		x		x		P
Choreocolax polysiphoniae	x										P
Clathromorphum circumscriptum	x	x	x								P
Corallina officinalis	x										P
Cruoriopsis ensis	x										P(?)
Cystoclonium purpureum var. *cirrhosum*	x	x	x								P
Cystoclonium purpureum forma *stellatum*	x										P
Dasya baillouviana	x	x	x	x	x	x	x	x	x		A
Dermatolithon pustulatum	x	x	x								P
Dumontia contorta	x	x	x								A
Erythrotrichia carnea	x	x	x					x			A
Fimbrifolium dichotomum	x										P
Fosliella lejolisii	x	x	x								P
Gloiosiphonia capillaris		x									A
Goniotrichum alsidii	x	x	x								A
Gracilaria tikvahiae	x	x	x	x		x	x		x		P
Gymnogongrus crenulatus	x	x	x						x		P
Hildenbrandia rubra	x	x	x			x	x				P
Leptophytum laeve	x										P
Lithophyllum corallinae	x										P
Lithothamniom glaciale	x										P
Lomentaria baileyana	x		x	x		x					A
Lomentaria clavellosa	x	x	x								P(?)
Lomentaria orcadensis	x	x									P
Mastocarpus stellatus	x	x									P
Membranoptera alata	x										P
Palmaria palmata	x	x	x	x							P
Petrocelis cruenta	x	x									P
Peyssonnelia rosenvingii	x	x	x								P
Phycodrys rubens	x	x									P

DOVER 001714

Table 7.2 (continued)

	Piscataqua R.	Little Bay	Great Bay	Bellamy R.	Cocheco R.	Lamprey R.	Oyster R.	Salmon Falls	Squamscott R.	Winnicut R.	Longevity*
Phyllophora pseudoceranoides	x	x	x								P
Phyllophora truncata	x	x	x								P
Phymatolithon laevigatum	x	x									P
Phymatolithon lenormandii	x	x									P
Polyides rotundus	x	x	x								P
Polysiphonia denudata	x	x	x	x	x	x	x		x		A
Polysiphonia elongata	x	x	x	x	x	x	x		x		P
Polysiphonia flexicaulis	x	x		x							P
Polysiphonia harveyi	x	x	x	x	x	x	x		x		A
Polysiphonia lanosa	x	x									P
Polysiphonia nigra	x	x	x	x	x		x				P(?)
Polysiphonia nigrescens	x	x	x	x		x					P
Polysiphonia novae-angliae		x									P(?)
Polysiphonia subtilissima	x	x	x		x	x	x	x	x		P
Polysiphonia urceolata	x	x									P
Porphyra leucosticta	x	x									A
Porphyra linearis		x									A
Porphyra miniata	x	x	x								A
Porphyra umbilicalis	x	x	x	x			x		x		A
Porphyra umbilicalis forma *epiphytica*	x	x	x								A
Porphyrodiscus simulans	x										P(?)
Pterothamnion plumula	x	x	x								AA
Ptilota serrata	x										P
Rhodomela confervoides	x	x									P
Rhodophysema elegans	x	x	x								P
Rhodophysema georgii	x	x									P(?)
Sacheria fucina			x	x		x	x		x		P
Scagelia corallina	x		x								AA
Trailliella intricata	x										P
Total Rhodophyta Taxa	71	60	47	17	10	15	21	3	14	0	
Grand Total Seaweed Taxa	144	132	90	38	26	29	49	16	30	4	

DOVER 001715

distal tips of fronds freeze into ice cover and are then torn free when ice-out occurs (Mathieson et al. 1982). Fragments of *Ascophyllum* torn loose by ice-pruning may enter the detrital cycle or they may lodge amongst *Spartina alterniflora* culms and grow, forming the unattached ecad *scorpioides* of *Ascophyllum nodosum* (Chock and Mathieson 1983). In certain areas of Great Bay, the biomass of the ecad *scorpioides* within the upper intertidal can reach 896 g dry wt/m^2 (Chock and Mathieson 1983).

Ascophyllum produces an abundance of reproductive cells over an annual cycle (Baardseth 1970). Lateral shoots, termed receptacles, bear the gametes that are released during March-May within the Great Bay Estuary (Mathieson et al. 1976) and may equal the standing biomass of vegetative plant material (Josselyn 1978, Josselyn and Mathieson 1978, 1980). Intertidal seaweeds such as *Ascophyllum* and *Fucus*, release large quantities of dissolved organic matter into the Estuary.

On stable rocky substrata, within the low intertidal to upper subtidal zone, Irish moss, *Chondrus crispus*, forms significant communities. Even so, the most abundant subtidal macroalga within Great Bay is *Gracilaria tikvahiae* (Penniman et al. 1986). The primary occurrence of *G. tikvahiae* in Great Bay (e.g. Footman Islands, Thomas Point, and Nannie Island) is limited by a lack of stable subtidal substrata in the euphotic zone. *G. tikvahiae*, as well as other subtidal seaweeds, grow attached to oyster shells, small rocks, discarded bottles and sunken logs.

The growth of *G. tikvahiae* may reach 10%/day during the summer; overall its growth is primarily limited by water temperature and light, while dissolved nutrients (i.e. nitrogen and phosphorus) do not appear to limit production (Penniman 1983, Penniman and Mathieson 1987). In contrast to the detailed studies of intertidal macrophytes at Cedar Point, Little Bay (Chock and Mathieson 1983), no quantitative studies have been conducted to determine standing crops of subtidal seaweeds throughout Great Bay.

In recent years, other subtidal seaweeds have appeared to dominate seaweed populations in part of the Great Bay Estuary. *Ulva lactua* and *Enteromorpha* spp. are found in large abundance often intermixed with or attached to eelgrass or overgrowing oyster beds. The proliferation of these nuisance seaweeds is often an indicator of coastal eutrophication (Lewis 1964, Harlin and Thorne-Miller 1981, and Short et al. 1991).

Salt Marsh

Salt marshes are an important component of the Great Bay Estuary, forming continuous meadows and fringing areas around the shoreline. Approximately 4.1 km^2 (1.6 mi^2 or 1000 acres) of salt marsh surround Great Bay. Within Great Bay, extensive salt marshes are found along the Squamscott 1.6 km^2 (0.6 mi^2 or 400 acres) and Winnicut Rivers, and Lubberland and Crommett Creeks.

Salt marshes in the Great Bay Estuary are dominated by *Spartina alterniflora* (cord grass) and *Spartina patens* (salt hay). Both species are perennial grasses, annually producing large amounts of organic matter that are exported from the marshes into the detrital food web or deposited within the marshes, contributing to the underlying marsh peat (Nixon 1982, Teal and Teal 1962). The "New England salt marsh", typical of salt marshes in the Estuary, is dominated by monospecific stands of *S. alterniflora* in the low marsh and monospecific stands of *S. patens* in the high marsh. The ecology of these two species in the Great Bay Estuary has had only limited study in the past.

DOVER 001716

The other primary high salt marsh species in the Great Bay Estuary include *Juncus gerardii*, and *Distichlis spicata*. A variety of other plant species also occur in the Great Bay Estuary salt marshes (Table 7.3) appearing as a mosaic of plant zones. Furthermore, several species found within the Estuary salt marshes are classified as rare or endangered by the state of New Hampshire (e.g. *Iva frutescens*).

In the mid '70s, the seasonality of leaf production in *S. alterniflora* was monitored at Cedar Point in Little Bay (Chock 1975). The data show the seasonal maximum biomass, 630 g dry wt/m^2, occurring in August (Fig. 7.3). Flower production of *S. alterniflora* begins in July and continues into October, after which the main vegetative stalks begin to die, the entire above ground plant biomass dies off, and enters the detrital cycle, either being exported from the Bay or decomposing within the estuarine system. Much research has dealt with efforts to restore *S. alterniflora* in areas where it has been destroyed or introduce it into new areas as part of mitigation efforts (see Chapter 10).

The annual production of *S. patens* was assessed during the mid 1980s. Stem density and standing biomass was measured in the Squamscott River north of Chapman's Landing at the time of seasonal maximum standing crop (Fig. 7.4). The biomass measured at this site was extremely high compared to other sites in northern Massachusetts, on the New Hampshire coast, and at the Wells Estuarine Research Reserve in southern Maine (Short 1988). This biomass of 820 g dry wt/m^2 was almost 20% higher than any other sites measured. On the same samples, the measurement of stem density was 6600 stems/m^2 similar to other sites measured in New Hampshire and slightly less than those measured in the Parker River Marsh in Massachusetts (Fig. 7.5).

The marshes surrounding the Great Bay Estuary are subject to extreme environmental variation. The large tidal amplitude in the region enhances the export of marsh grass from the marshes to the Estuary. Annual ice scouring of the intertidal marsh surface removes most the remaining marsh grass during the high spring tides in late winter. Ice cover and freezing activity in intertidal salt marsh dislodge portions of the surface peat. Whole sections of marsh with intact intertidal communities are rafted into lower intertidal or subtidal areas that are often too deep for them to survive (Hardwick-Witman 1985). Ice-rafted marsh segments that are deposited within the intertidal zone are a potential means of salt marsh propagation within the Great Bay (Hardwick-Witman 1985, 1986).

Breeding et al. (1974) described the numerous soil types of coastal New Hampshire salt marshes. Marshes bordering streams on the Squamscott River and Crommett and Lubberland Creeks in Great Bay, as well as the other rivers in the Estuary, are generally sulfihemist. Fringing marshes, which are common around the Estuary, also have sulfihemist soils of varying thicknesses; these overlay a variety of substrata (i.e. mud, sand or bedrock). The sulfihemist soil type has slow internal drainage, a very high water table, and contains large amounts of organic matter and sulfidic minerals. Studies of gas flux from the Squamscott River marsh demonstrates that sulfur gas is a major emission from this marsh system (Chapter 9).

Clearly, the salt marshes of the Great Bay Estuary are a productive part of the estuarine environment. A project to map the salt marsh of the Great Bay Estuary is currently underway through funding from NH Coastal Zone Management Program (Ward per. com.). Other studies within the Great Bay Estuary have shown the

DOVER 001717

Table 7.3. Major plant species occurring within New Hampshire salt marshes (modified from Breeding et al. 1974).

Acnida cannabina	Water hemp
Aster subulatus	Annual salt marsh aster
Aster tenuifolius	Perennial salt marsh aster
Atriplex glabriuscula	Orach
Atriplex patula	Orach
Bassia hirsuta	Hairy smotherweed
Carex scoparia	Sedge
Carex hormathodes	Marsh straw sedge
Cladium mariscoides	Twig rush
Distichlis spicata	Spike grass
Eleocharis halophila	Salt marsh spike-rush
Eleocharis parvula	Dwarf spike-rush
Eleocharis smallii	Small's spike-rush
Elymus virginicus	Virginia rye grass
Euphorbia polygonifolia	Seaside spurge
Gerardia maritima	Seaside gerardia
Glaux maritima	Sea milkwort
Hordeum jubatum	Squirrel-tail grass
Iva frutescens	Marsh elder
Juncus balticus	Baltic rush
Juncus canadensis	Canadian rush
Juncus gerardii	Black grass
Lathyrus japonicus	Beach pea
Limonium nashii	Sea lavender
Lythrum salicaria	Purple loosestrife
Myrica pensylvanica	Northern bayberry
Panicum virgatum	Switchgrass
Phragmites australis	Common reed
Plantago maritima	Seaside plantain
Polygonum aviculare	Knotweed
Polygonum ramosissimum	Bushy knotweed
Potamogeton pectinatus	Sago pondweed
Prunus maritima	Beach plum
Puccinellia maritima	Seashore alkali grass
Puccinellia paupercula	Alkali grass
Quercus alba	White oak
Quercus bicolor	Swamp white oak
Ranunculus cymbalaria	Seaside crowfoot
Rosa rugosa	Rugosa rose
Rosa virginiana	Low rose
Ruppia maritima	Widgeon grass
Sanguisorba canadensis	Canadian burnet

DOVER 001718

Table 7.3 (continued)

Salicornia bigelovii	Dwarf glasswort
Salicornia europaea	Common glasswort
Salicornia virginica	Perennial glasswort
Scirpus americanus	Three-square bulrush
Scirpus acutus	Hard-stemmed bulrush
Scirpus atrovirens	Bulrush
Scirpus cyperinus	Wool grass
Scirpus maritimus	Salt marsh bulrush
Scirpus paludosus	Bayonet-grass
Scirpus robustus	Salt marsh bulrush
Scirpus validus	Soft-stemmed bulrush
Smilax rotundifolia	Common greenbrier
Solidago sempervirens	Seaside goldenrod
Spartina alterniflora	Salt water cord grass
Spartina patens	Salt meadow grass
Spartina pectinata	Fresh water cord grass
Spergularia canadensis	Common sand spurrey
Spergularia marina	Salt marsh sand spurrey
Suaeda linearis	Sea blite
Suaeda maritima	Sea blite
Suaeda richii	Sea blite
Toxicodendron radicans	Poison ivy
Triglochin maritima	Seaside arrow grass
Typha angustifolia	Narrow-leaved cattail
Typha latifolia	Broad-leaved cattail
Zannichellia palustris	Horned pondweed
Zostera marina	Eelgrass

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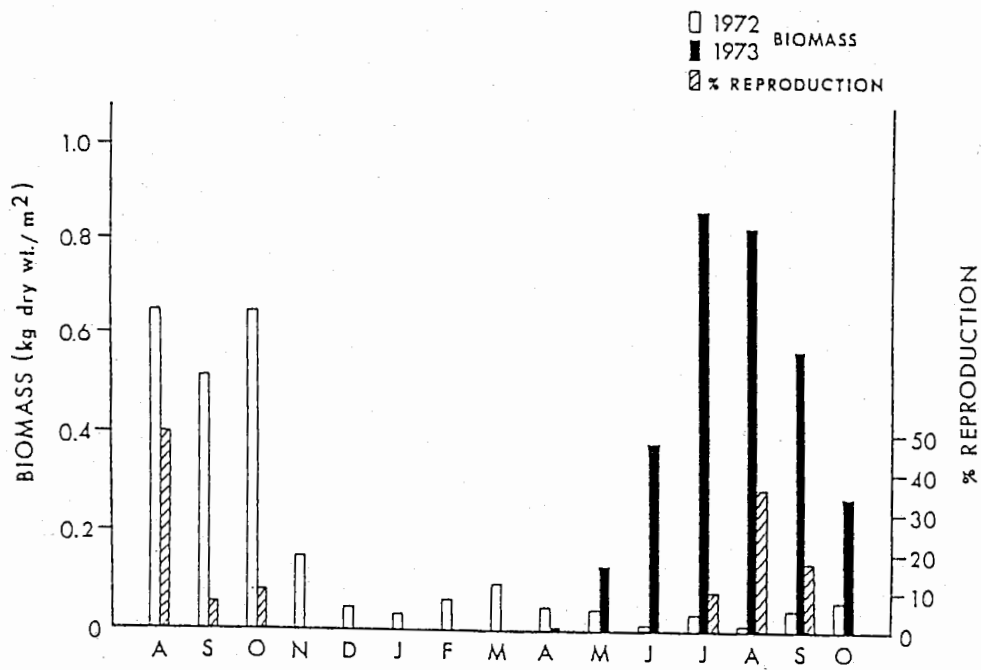

Fig. 7.3. Seasonal comparison of *Spartina alterniflora* biomass and percent reproduction in 1972-73 for Cedar Point, Great Bay Estuary, NH (Chock 1975).

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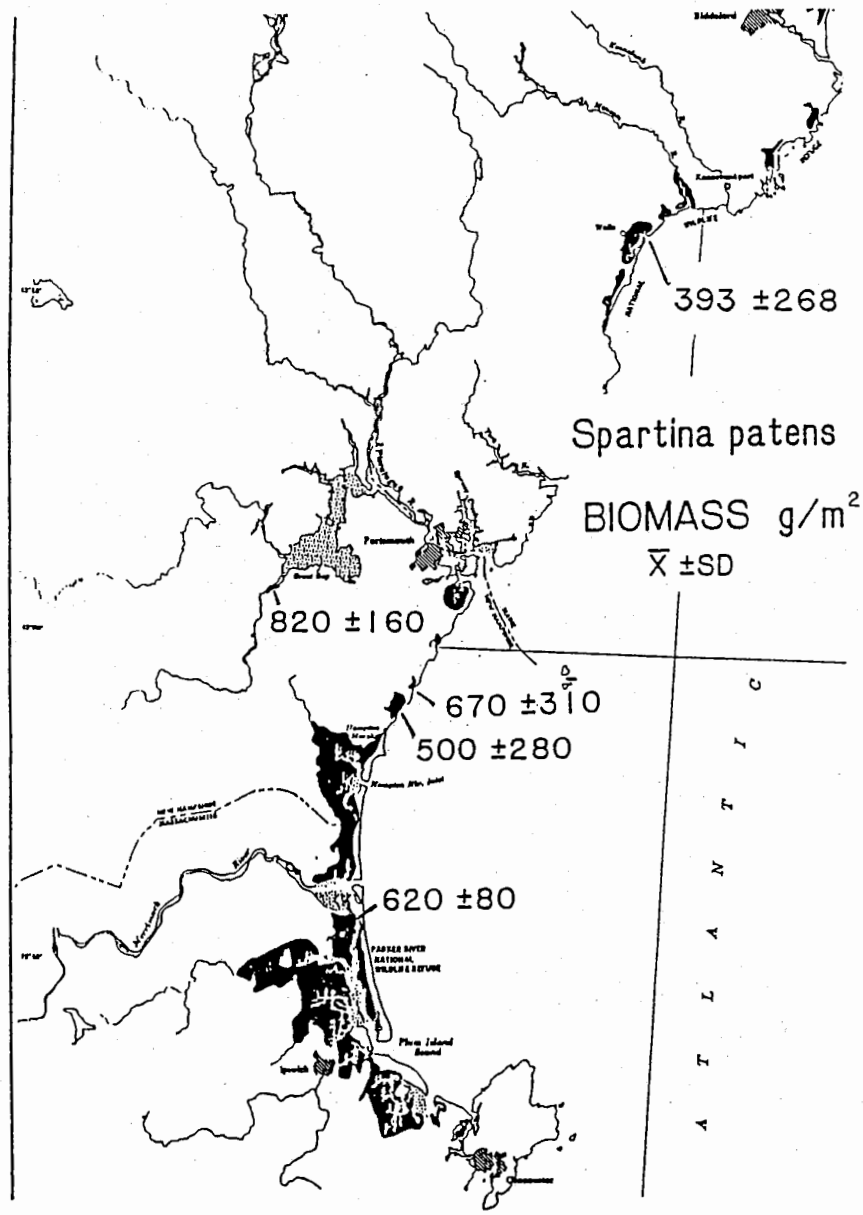

Fig. 7.4. Seasonal maximum biomass (g dry wt/m2) for *Spartina patens* along the northern New England coast (Short 1986).

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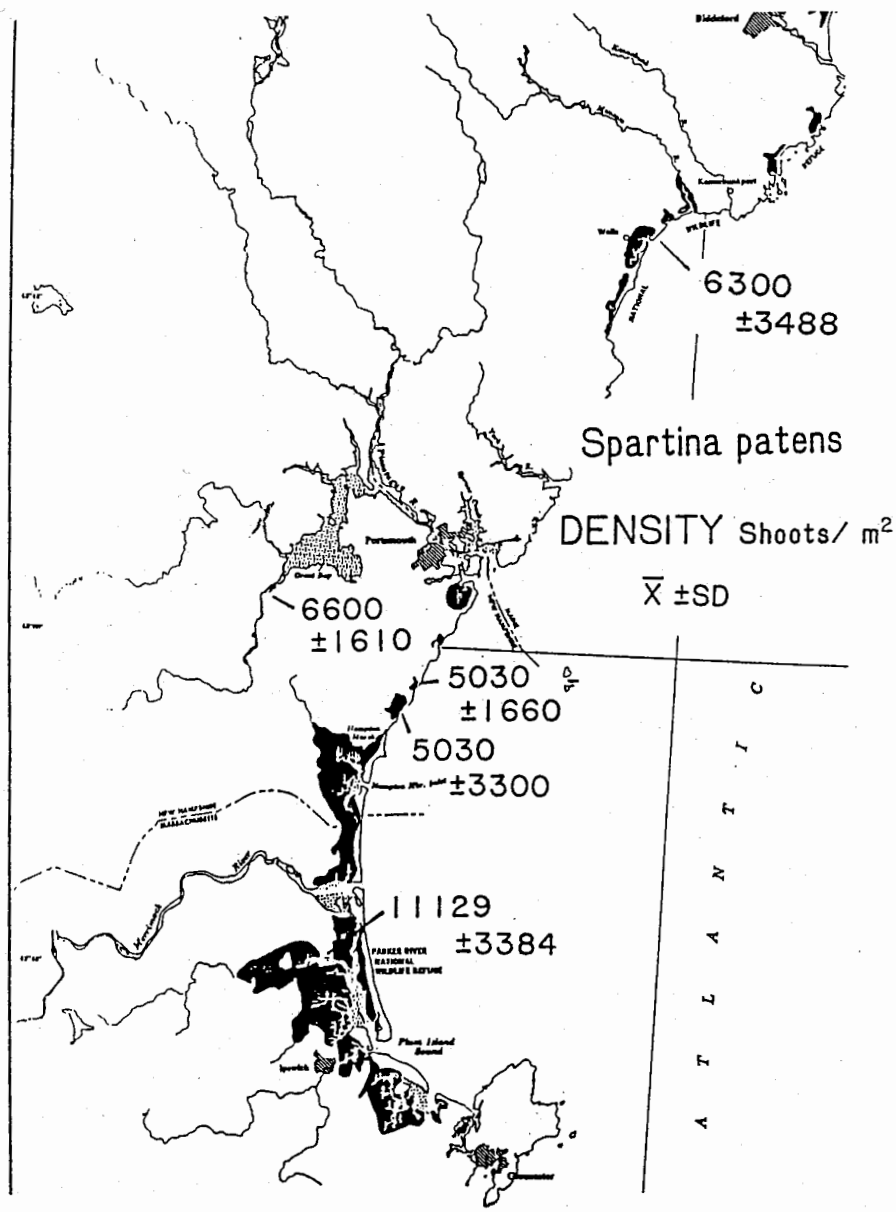

Fig. 7.5. Shoot density (shoots/m2) for *Spartina patens* along the northern New England coast (Short 1986).

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importance of salt marshes in biogeochemical processes (see Chapter 9) and in the uptake and cooperation of methylated tin compounds (see Chapter 6). The importance of salt marsh habitats within the Great Bay Estuary, including the value of these systems as fisheries habitat, is described in Chapter 2.

Benthic Microalgae

Another important microalgal component of the estuarine flora are diatoms and other microscopic algae occurring on mudflats. These microalgae may contribute a substantial portion of total estuarine primary production. Recently, two masters theses have included an assessment of the benthic microalgal biomass in their studies of intertidal sediment stability (Sickley 1989 and Webster 1991). These geologically based studies provide the first quantitative evidence for benthic diatom abundance in Great Bay. Seasonal chlorophyll *a* data from Adams Cove shows a bimodal annual pattern of diatom abundance (Fig. 7.6). A spring diatom bloom occurs in March-April (Webster 1991) and a second bloom begins in late July and lasts through October (Fig. 7.6). The chlorophyll *a* content for the two studies ranged from 8-24 mg/l (Sickley 1989 and Webster 1991).

The diatom layer on the sediment surface was found to be related to a reduction in sediment resuspension (Fig. 7.6) with the benthic algal population binding the sediment surface together (Sickley 1989). Reduction in the binding of sediments was associated with the grazing and disturbing activity of both mud snails and horseshoe crabs on the mudflat (Sickley 1989). No clear relationship was found between benthic diatom abundance and grain size or total organic carbon (Fig. 7.6).

Upland

The uplands surrounding the Great Bay Estuary have both deciduous and coniferous forests. The most common tree species includes white pine, red oak, red pine, hemlock, red maple, gray birch, and quaking aspen. A more complete listing of the common upland vascular plants found within Strafford County, N.H., is presented in Table 7.4.

The plants comprising the upland which surrounds the Great Bay Estuary form a valuable buffer that protects the estuarine ecology in several ways. Research on riverine systems has shown clearly that an intact buffer zone or riparian zone along a river system has a significant role in maintaining the water quality, wildlife value, aesthetic beauty and riverine health (Jones 1986). Similarly, the buffer zone around an estuary provides the same functions.

In particular, for the Great Bay Estuary, these buffer zones are important in trapping nutrients and sediments that would otherwise wash into the Estuary contributing to the reduction in water quality. These zones also provide shelter and habitat for animals and birds that frequent the Estuary and utilize estuarine resources. In addition to these values, the upland also provides large amounts of organic matter to the Estuary, adding fuel to the detrital food chain. These materials include leaf fall and other dead plant material. Overall, the upland buffer is critical to the continued maintenance of a healthy Estuary and is an important consideration in regulating shoreline development.

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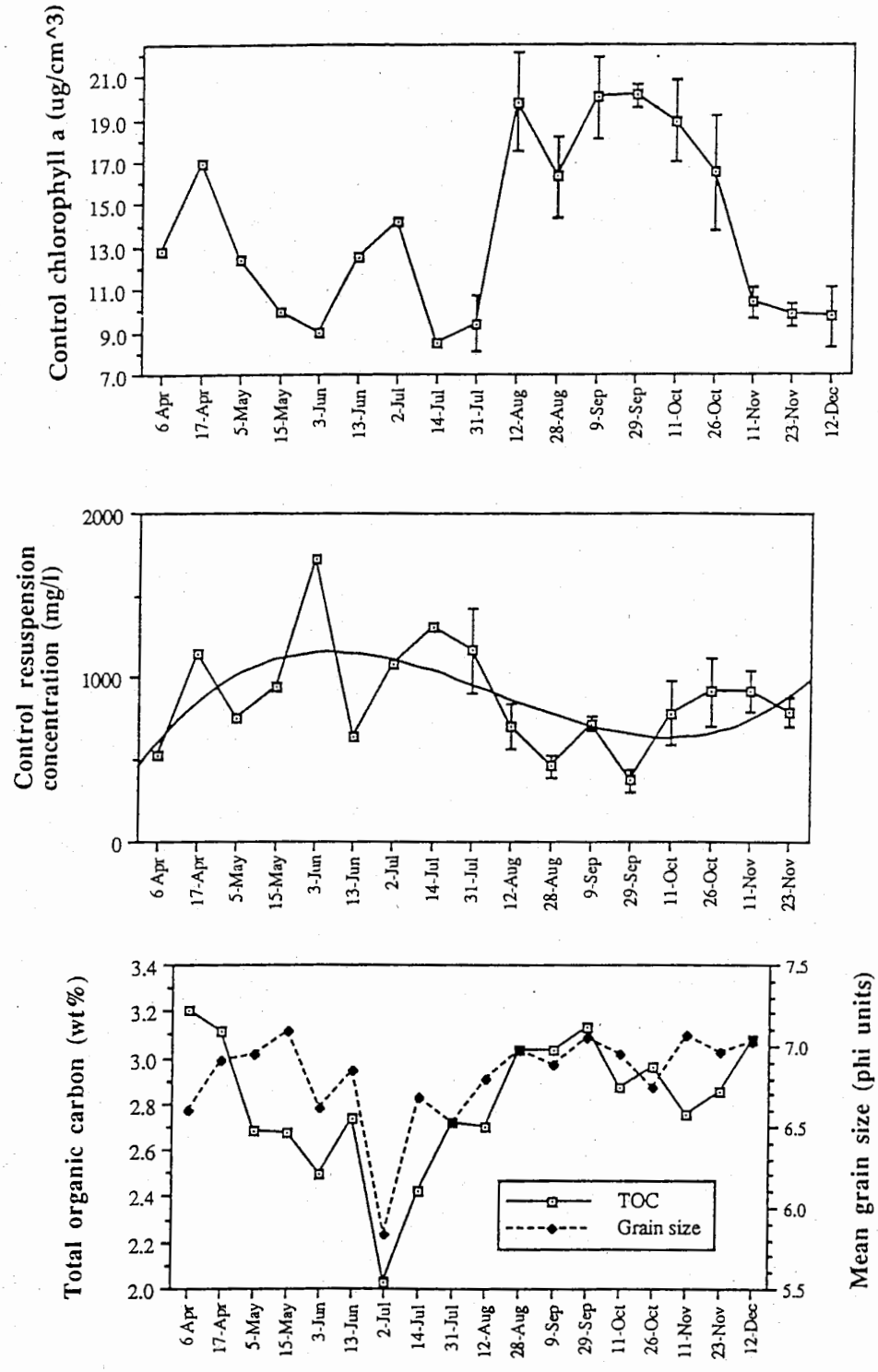

Fig. 7.6. Seasonal comparison of chlorophyll a, resuspension concentration, total organic carbon, and mean grain size in 1988 for the mudflat at Adams Cove, Great Bay Estuary, NH (Sickley 1989).

Table 7.4. Common upland overstory and understory vascular plant species in Strafford County, N.H. by habitat (modified from Hodgdon 1932 in Texas Instruments, Inc. 1974). A specific list for the upland area within the Reserve boundaries is not presently available.

DRY UPLAND FOREST

Primary overstory species

Acer rubrum	Red maple
Betula alleghaniensis	Yellow birch
Betula lenta	Sweet birch
Betula papyrifera	Paper birch
Betula populifolia	Gray birch
Carya ovalis	Sweet pignut
Carya ovata	Shagbark hickory
Fagus grandifolia	American beech
Fraxinus americana	White ash
Picea glauca	White spruce
Picea rubens	Red spruce
Pinus resinosa	Red pine
Pinus strobus	White pine
Populus tremuloides	Quaking aspen
Pyrus malus	Apple
Quercus alba	White oak
Quercus rubra	Red oak
Quercus velutin	Black oak
Salix alba	White willow
Sassafras albidum	White sassafras
Tsuga canadensis	Hemlock

Primary understory species

Aralia nudicaulis	Wild sarparilla
Berberis vulgaris	Common barberry
Castanea dentata	Chestnut
Comptonia peregrina	Sweet-fern
Dennstaedtia punctilobula	Hay-scented fern
Gaultheria procumbens	Teaberry
Hamamelis virginiana	Witch hazel
Juniperus communis	Common juniper
Kalmia angustifolia	Sheep laurel
Lycopodium complanatum	Trailing evergreen
Myrica pensylvanica	Bayberry
Prunus pensylvanica	Pin cherry
Prunus virginiana	Choke cherry
Pteridium aquilinum	Bracken fern
Quercus ilicifolia	Scrub oak
Rubus pubescens	Dwarf raspberry
Toxicodendron radicans	Poison ivy
Vaccinium angustifolium	Lowbush blueberry
Viburnum acerifolium	Maple-leaved viburnum

WET-LOWLAND FOREST

Primary overstory species

Acer rubrum	Red maple
Betula alleghaniensis	Yellow birch
Betula lenta	Sweet birch

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Betula papyrifera	Paper birch
Carpinus caroliniana	American hornbeam
Chamaecyparis thyoides	Atlantic white cedar
Nyssa sylvatica	Blackgum
Picea mariana	Black spruce
Salix alba	White willow
Salix nigra	Black willow
Tsuga canadensis	Hemlock
Ulmus americana	American elm

Primary understory species

Alnus rugosa	Speckled alder
Cornus amomum	Silky dogwood
Cypripedium sp.	Lady slipper
Gaultheria procumbens	Teaberry
Ilex verticillata	Swamp winterberry
Kalmia angustifolia	Sheep laurel
Lycopodium obscurum	Ground pine
Mitchella repens	Partridge berry
Osmunda cinnamomea	Cinnamon fern
Polytrichum commune	Hairy cap moss
Rosa sp.	Rose
Smilax rotundifolia	Common greenbrier
Vaccinium corymbosum	Highbush blueberry
Viburnum alnifolium	Dockmackie
Viburnum cassinoides	Wild raisin
Viburnum recognitum	Arrow-wood
Vitis sp.	Grape

OPEN AND OVERGROWN FIELDS

Overstory species

Betula populifolia	Gray birch
Juniperus communis	Common juniper
Juniperus virginiana	Red cedar
Prunus serotina	Black cherry
Prunus virginiana	Choke cherry
Viburnum sp.	Viburnum
Rhus typhina	Staghorn sumac

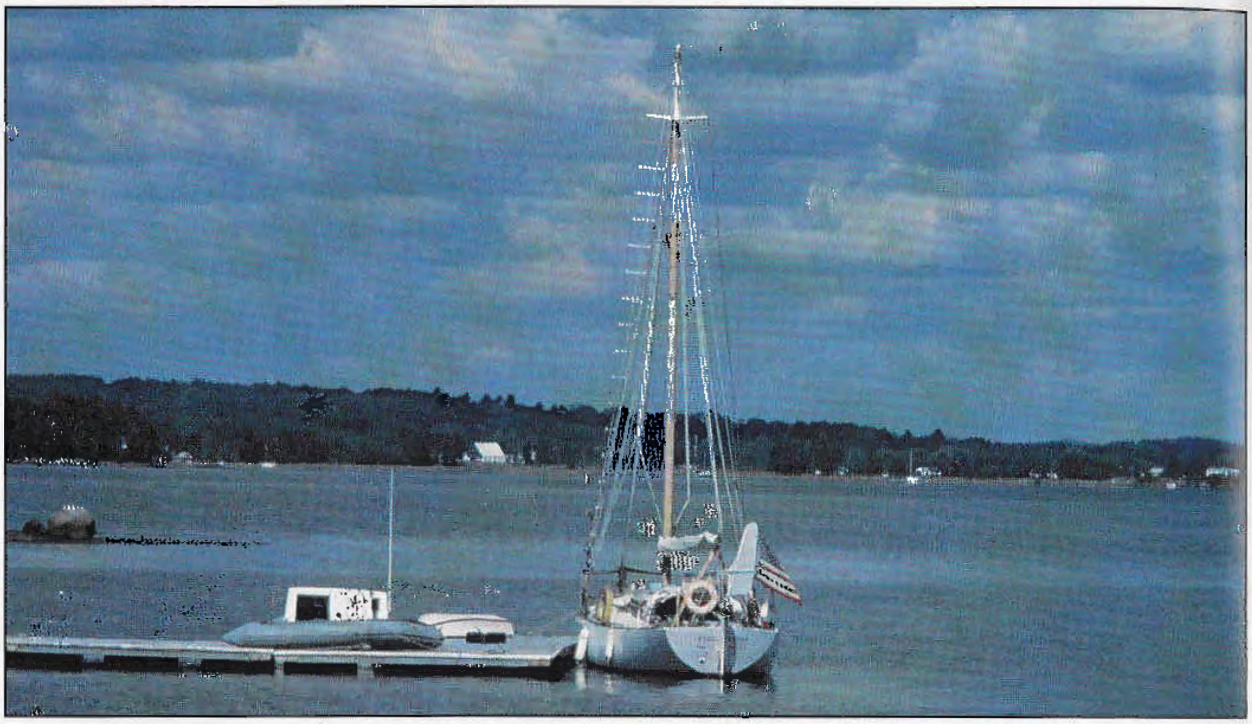
Ground cover species

Achillea millefolium	Common yarrow
Amaranthus retroflexus	Amaranth
Ambrosia artemisiifolia	Common ragweed
Aster sp.	Aster
Dactylis glomerata	Orchard grass
Daucus carota	Queen Anne's lace
Festuca rubra	Red fescue
Oxalis corniculata	Creeping lady's sorrel
Phalaris arundinacea	Reed canary grass
Phleum pratense	Common timothy
Poa pratensis	Kentucky bluegrass
Solidago sp.	Goldenrod
Spiraea latifolia	Meadow sweet
Trifolium pratense	Red clover

DOVER 001726

Aerial view of the Great Bay Estuary from offshore, showing Portsmouth Harbor and the Piscataqua River with Portsmouth Naval Shipyard *(center)*, Kittery, Maine (*right*), and Portsmouth, New Hampshire *(top, center)*.

Aerial view of the Piscataqua River showing industrial development on the New Hampshire side *(foreground)* and residential development on the Maine side.



Recreational boating on the Great Bay Estuary.

Canada geese feeding on eelgrass in Great Bay.

Juvenile lobster foraging within the protection of a shallow eelgrass meadow in Portsmouth Harbor.

Aerial view of Great Bay Marina on Little Bay. Recent expansion of the marina is indicative of increased boating activity in the Estuary.

Aerial view of Adams Point at the juncture of Great and Little Bays, showing the Adams Point Wildlife Management Area and the Jackson Estuarine Laboratory.

Aerial view of the Squamscott River near the Route 108 bridge in Stratham, NH. The extensive salt marshes along the river are part of the Great Bay National Estuarine Research Reserve.