THE ECOLOGY OF BENTHIC SALT MARSH ALGAE AT IPSWICH, MASSACHUSETTS
I. ZONATION AND DISTRIBUTON OF ALGAL SPECIES

E. E. WEBBER AND R. T. WILCE

In a previous publication (Webber & Wilce, 1971) we treated the salt marsh algae at Ipswich in light of their occurrence, morphology, cytology, seasonal and reproductive periodicities, based on both field and laboratory investigations. In this paper the descriptive ecology of these plants is discussed.

The ecological nomenclature used to describe vertical and horizontal distributions of algae has varied considerably. Rather than adopt new terms describing the zoned character of the salt marsh algal vegetation, we have selected established terminology common to terrestrial ecological studies which applies also to flowering plants of the marsh environment (Weaver & Clements, 1938; Feldmann, 1951; Oosting, 1956; den Hartog, 1959). Accordingly, we have attempted to describe both the physiognamy and the vegetational units at each station, the latter in relation to their successional character.

Superficially, the zoned arrangement of an algal salt marsh vegetation often is not easily detected. The flat expanse of varying shades of green which cover the salt marsh surface contrasts sharply with the distinct and frequently colorful patterns of algal zonation of the rocky coast (see Frontispiece, Lewis, 1964). In order to discuss algal zonation and distribution at the Ipswich salt marsh, it was necessary to identify levels on the marsh surface with which to relate the presence and vertical range of algal species. Marsh phanerogams, owing to their abundance, distinctiveness, and regular and sharp zonation, served as reference points to this end. From the seaward edge of the marsh extending landward, the following seed plant associations were recognized: *Spartina alterniflora* var. *glabra*, *Spartina patens*, *Spartina patens-Scirpus americanus* (or *Spartina patens-Distichlis spicata*) mixture, and *Juncus gerardi*. Algal zonation in the salt marsh becomes more apparent and more readily understood when studied in relation to the distribution of these phanerogams.

As stressed by Lewis (1964) and suggested earlier by the Stephensons (1949), a discussion of zonation along any shore should be based upon biological criteria, rather than relying strictly upon tidal limits. These limits may not be coincident with natural biological zones, especially when one considers the upper limits of vegetation in relation to tide levels. On shores exposed to wave action and spray, the distribution of those organisms which typically form the uppermost biological zones will be extended even higher than where a splash and spray zone are not present (c.f., Lewis, 1964, fig. 52). In the salt marsh environment at Ipswich, one encounters an approximation of a spray zone only near Station 1 (Webber & Wilce, 1971, p. 265); here, the presence of wood pilings provides a steep vertical face which contrasts with the gently sloping character of the surrounding marsh surfaces. This change in topography results in a stronger local wave splash, as compared with wave action on the marsh surfaces; thus, the upper distributional limit of *Calothrix crustacea*, for example, occurs at a higher level on these pilings than on the surrounding marsh. Therefore, using essentially biological criteria in relation to tide levels we recognize in the marsh environment a *sublittoral*, a *littoral*, and a less well defined, but nonetheless recognizable, *supralittoral* zone.

The sublittoral zone of the Ipswich salt marsh, when compared with the same zone characteristic of the open coast, is essentially non-existent. The marsh drains twice daily through a series of canals which, at low tide level, are mostly devoid of water. Where the marsh is closest to the sea and in the major trunk canals, water with salinity characteristics of open coastal water remains at low tide. It is in these salt marsh areas, the openings to the sea and the major canals, where a true sublittoral zone can be recognized, and, correspondingly, a sublittoral flora.

We stress the fully marine character of the sublittoral benthic vegetation. Also, in our list of species from the Ipswich salt marsh (Webber & Wilce, 1971), we cite a number of taxa commonly represented in the marsh sublittoral as drifting plants, e.g., *Chaetomorpha melagonium* and *Phycodrys rubens,* to name but two; these plants, of variable longevity in the marsh environment, are transients from the open coast sublittoral. Their frequent appearance in the marsh sublittoral in conjunction with the attached marsh sublittoral vegetation is a manifestation both of the marine character of the marsh subtidal zone and the proximity of the marsh entrance to the open coast.

The littoral zone at the Ipswich marsh contains those organisms which are regularly submerged and exposed by the rise and fall of the tides. Biologically, this zone extends from the upper limit of the sublittoral, as indicated by *Fucus distichus* ssp. *evanescens,* to that uppermost portion on the shore populated by *Juncus gerardi.* Algae of the littoral zone show a zoned pattern of distribution as controlled by local factors of, e.g., habitat competition, availability of substrates, and topographic differences resulting in degree of exposure to insolation, desiccation, tidal action, and fresh water influence. These algal assemblages of predictable major constituents we interpret as associations, following Børgesen, 1905, Davis, 1913, Feldmann, 1951, Wilce, 1959, den Hartog, 1959 and Jorde Klavestad, 1963. However, as Chapman (1956) points out, one characteristic of salt marsh vegetation is its relative instability; thus, the term "associes" is a more apt designation of the vegetational status in these specific environments.

The supralittoral zone is characterized by those species which are predominantly terrestrial and which are not merely extensions of upper littoral marine species. The organisms which are regularly submerged and exposed by the tide are in fact, considered "maritime" (Lewis, 1964) rather than strictly marine. While a comparatively clear-cut distinction between those plants and animals of the upper littoral and those of the supralittoral may be possible on a rocky coast, this distinction is not always apparent at the Ipswich salt marsh. For example, *Calothrix crustacea* clearly occurs on the marsh surface (Station 1) in the upper littoral zone. In addition, this species along with the upper littoral green alga *Pseudendoclonium submarinum,* colonize wood pilings near Station 1. Owing to moderate wave splash on these pilings, both algal species extend vertically higher than the level of the surrounding marsh surface. Yet, at Ipswich, the position of *C. crustacea* and *P. submarinum* on the pilings near Station 1 is comparable to the position on the marsh surface populated by such terrestrial or "maritime" plants as *Juncus balticus* var. *littoralis, Panicum virgatum,* and *Solidago sempervirens.* Indeed, on the pilings with *Calothrix* and *Pseudendoclonium* one always finds the lichen *Lecanora chlarotera* which, according to Hale (personal communication), is not marine in its distribution, but rather is a common terrestrial species. Thus, the vegetation at this level is dominantly maritime-terrestrial, and does not represent solely an upward extension of the marine flora. We recognize, therefore, a supra-littoral zone biologically distinct in its composition of vascular plants and associated cryptogams which lies invariably immediately above the uppermost limit of salt marsh phanerogams, i.e., above *Juncus gerardi.*

ZONATION AND DISTRIBUTION OF ALGAL SPECIES

Before describing the species composition at each station, it is appropriate to identify and describe briefly the stations from which the algal collections and related data were taken (see also Webber & Wilce, 1971).

Station 1: typically marine, little influenced by fresh water runoff; shoreline a vertical mud bank with substratum consisting of mud, small stones, and the *Spartina* grasses; seasonal salinity range of 18-30°/oo.

Station 2: Similar to Sta. 1, but with a gently sloping shoreline; substrates predominantly cobble, shells of *Midiolus demissa* and *Spartina* grasses.

Station 3: Tidal ditch outflow, 0.3-1 m deep, seasonally influenced by fresh water runoff; substrates of small stones and wood pilings; seasonal salinity range 3-33°/oo.

Station 4: Section of a major tidal creek beneath a highway bridge panning Fox Creek, moderately influenced by fresh water runoff; substrate mostly of stone and shell; seasonal salinity range 13-32°/oo.

Station 5: The innermost extremity of the Ipswich salt marsh, consisting of two substations due to the habitat character in the tidal creek in this region of the marsh; seasonal salinity range for both substations 0-27°/oo.

Substation 5a: A transect through the tidal creek near Northgate Rd. where at high water the bottom is covered to a depth of 0.6 m, and mostly exposed at low water; markedly influenced by fresh water runoff; substrates of small stones, mud, and plants of *Ruppia maritima*; this area is characterized also by a twice daily rapid flow of water.

Substation 5b: Differs from the latter by having a mud bottom, continual water cover at a 0.6 m depth, and a generally slow water displacement downstream.

Sublittoral zone:

Stations 1 and *2*. Species common to the sublittoral of these stations were not unlike those one might encounter in the sublittoral on a rocky coast. These algae included:

Enteromorpha intestinalis
Enteromorpha linza
Enteromorpha linza var. *oblanceolata*
Enteromorpha ahleriana
Enteromorpha clathrata
Enteromorpha flexuosa ssp. *flexuosa*
Enteromorpha flexuosa ssp. *pilifera*
Kornmannia leptoderma
Ulva gigantea
Chaetomorpha linum
Ralfsia verrucosa
Ralfsia clavata
Scytosiphon lomentaria

Petalonia fascia	*Chondrus crispus*
Chorda filum	*Ceramium diaphanum*
Laminaria saccharina	*Ceramium rubrum*
Dumontia incrassata	*Ceramium rubriforme*
Hildenbrandia prototypus	*Polysiphonia denudata*
Agardhiella tenera	*Polysiphonia lanosa*
Gracilaria foliifera	*Polysiphonia nigra*
Gracilaria verrucosa	*Polysiphonia nigrescens*

The majority of these species were of late spring and summer occurrence, while the following attained maximum vegetative and reproductive development during the winter and early spring months:

Enteromorpha linza var. *oblanceolata*	*Scytosiphon lomentaria*
Kornmannia leptoderma	*Petalonia fascia*
Ralfsia clavata	*Laminaria saccharina*
Ralfsia verrucosa	*Dumontia incrassata*

Conspicuous perennials at the sublittoral-littoral interface were *Fucus distichus* ssp. *evanescens, Fucus vesiculosus* and *Chondrus crispus.*

Station 3: There was a decrease in numbers of sublittoral species at Station 3 as compared with Stations 1 and 2. This reduction in taxa is due likely to the comparative lack of rocky substrate, the pronounced fresh water influence in the winter and spring months, and the shallow water at this station. Those algae common to the sublittoral of *Station 3* throughout the summer were:

Enteromorpha intestinalis	*Bryopsis plumosa*
Enteromorpha flexuosa ssp. *pilifera*	*Ceramium diaphanum*
Ulva rigida	*Ceramium fastigiatum*
Cladophora liniformis	*Polysiphonia denudata*

The winter and early spring algal vegetation was dominated by four species:

Kornmannia leptoderma	*Petalonia fascia*
Scytosiphon lomentaria	*Melosira juergensii*

The only sublittoral perennials in this station were *Ralfsia clavata, Ralfsia verrucosa,* and *Chondrus crispus.*

Station 4. The submerged algal vegetation here was scant. From November through March *Kornmannia leptoderma, Pentalonia fascia,* and *Dumontia incrassata* comprised the macroscopic algae at this station in the sublittoral zone. These taxa were continually vegetative and greatly reduced in size, as compared with their larger and normally reproductive counterparts at *Stations 1-3.*

The sublittoral perennials were the same as those at *Station 3,* i.e., *Ralfsia clavata, Ralfsia verrucosa,* and *Chondrus crispus.*

Station 5, a and *b.* The vegetation in the sublittoral here had the smallest number of algal species of any station. We have considered this to be a reflection of the reduced salinities occurring here through most of the year. During the spring and autumn, the following species dominated:

Capsosiphon fulvescens
Enteromorpha intestinalis
Polysiphonia urceolata
Ectocarpus confervoides var. *dasycarpa*

In early spring only the stalked diatom, *Gomphonema olivaceum,* constituted the macroscopic algal vegetation, covering the numerous small stones in this tidal creek. Owing to a thick ice cover, samples of winter algae were not obtained from this station.

Littoral Zone

Stations 1 and *2. Fucus vesiculosus* and *Ascophyllum nodosum* occurred in the littoral zone wherever stone, rock, or other solid substrate was present. The landward extent of these species differed, however, between *Stations 1* and *2.* For example, at Station 1 the marsh surface is essentially 1 meter higher above high water neap tide levels than is that of *Station 2,* owing to the presence of a vertical mud bank at the former station. *Fucus vesiculosus* became established on this bank, the plants extending about 3/4 of the height of this vertical surface. At this uppermost level, *Fucus* thalli tended toward a spiral growth habit, and they were smaller than those plants in the mid-littoral. By contrast, the lower level and more sloping topography of *Station 2* resulted in both *Fucus* and *Ascophyllum* extending onto the marsh surface, where they developed as typical marsh fucoids, i.e., *F. vesiculosus* var. *spiralis* and *A. nodosum f. scorpioides,* both at the bases of *Spartina alterniflora* var. *glabra.*

Immediately beneath the seaward marsh edge, a dark green algal zone, the *Enteromorpha* associes (Fig. 1), was conspicuous on the mud at both stations. The summer and autumn algae comprising this associes were:

Enteromorpha ahlneriana
Enteromorpha flexuosa
ssp. *paradoxa*
Enteromorpha prolifera
Percursaria percursa
Cladophora sericea
Rhizoclonium riparium
f. *riparium*
f. *validum*

Throughout the winter and spring months this *Enteromorpha* associes assumed a pronounced brown hue owing to increased numbers of *Pylaiella littoralis,* with lesser amounts of *Ectocarpus confervoides* var. *arcta.* Associated with these plants at this time were irregularly distributed clusters of:

Enteromorpha flexuosa
ssp. *paradoxa*
Monostroma oxyspermum
Percursaria percursa
Vaucheria intermedia

Covering the mud in the Spartinetum alternifloretum at Station 1 were conspicuous green tufts of *Rhizoclonium riparium* (f. *riparium* and f. *polyrhizum*), *Rhizoclonium implexum,* and *Vaucheria intermedia.*

While these algae were similarly located at *Station 2,* their distribution at the latter station was limited to the more seaward edge of the Spartinetum. We attribute this local restriction in vertical distribution to competition for habitat; marsh fucoids and the ribbed mussel, *Modiolus demissa,* thoroughly blanketed much of the available mud substrate beneath *Spartina alterniflora* var. *glabra,* thus

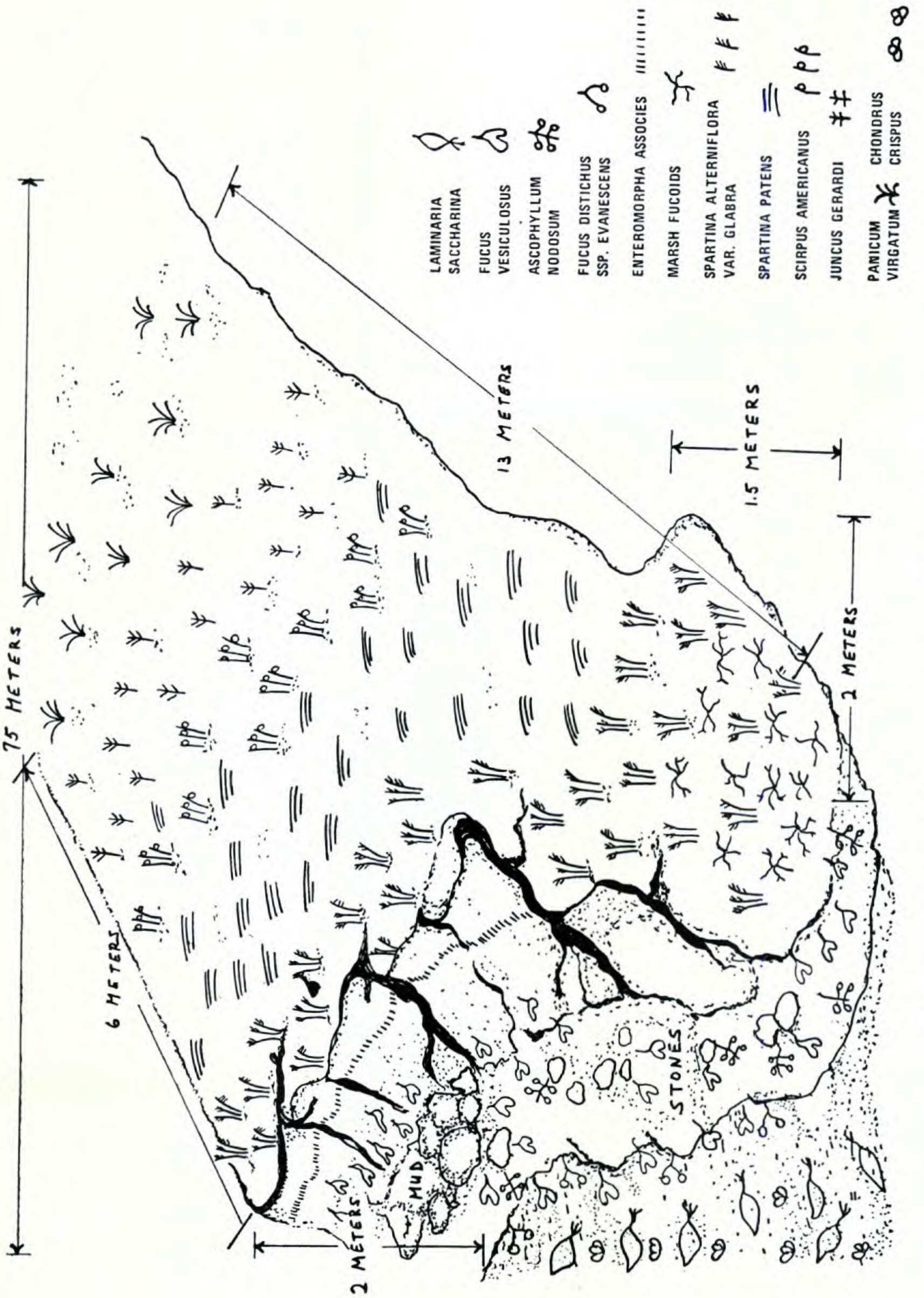

Fig. 1 SEGMENT OF SHORELINE ALONG CASTLE NECK RIVER

prohibiting any further upshore spread of *Rhizoclonium riparium*, *R. implexum*, and *Vaucheria intermedium*. A variety of filamentous bluegreens was collected throughout the year from the mud of this Spartinetum at both Stations 1 and 2 (Webber, 1967).

Moving landward, the next algal associes occurred beneath *Spartina patens* and consisted almost entirely of *Vaucheria arcassonensis* (Webber, 1968). Growth of this alga, with lesser amounts of *V. intermedia*, was particularly evident during the summer and autumn months, forming dense, felt-like mats on the soil. Numerous filamentous bluegreens also were common at this time on the sandy peat soil of the Spartinetum patentis.

Old culms of *Spartina patens* were epiphytized throughout the year mainly by *Calothrix confervicola*, as tufts to 3 mm tall. Often entangled with *C. confervicola* were plants of *Microcoleus tenerrimus*; the latter species never occurred alone as a dominant. Blum (1968), working on several Cape Cod (Massachusetts) marshes, concluded that a species of *Calothrix* (likely *C. confervicola*) is the most important colonizer in the moist micro-habitats on dead *S. patens* culms. He also demonstrated a marked interdependence between specific salt marsh grasses and their underlying algal species. Blum further elucidated the relationship between the mature form of the graminoid zone and such environmental parameters as light penetration and intensity in the zone, filtration and detritus retention, and drainage, as all these events are influenced by the morphology of a specific stand of grass.

The brownish-green tubular thalli of *Capsosiphon fulvescens* were present also in the Ipswich Spartinetum patentis. While mocroscopic individuals of this species were epilithic in the sublittoral at Substation 5a (Webber & Wilce, 1971, p. 269), the macroscopic thalli of *Capsosiphon* (the type commonly encountered elsewhere) grew only in a single, small, water-retaining marsh depression at *Station 1*. The discovery of two populations of *Capsosiphon*, distinctly different in their morphologies, seasonality, and habitat requirements, suggests further questions as to the character of the species and the role of the environment in determining the expression of that character. Laboratory and field experiments designed to elucidate this matter are forthcoming.

The highest band of salt marsh phanerogams at Stations 1 and 2 was the *Juncus gerardi* association; the bases of *Juncus* and its associated algal species were wetted by sea water only during periods of spring tides. The algal vegetation on the sandy soil here was predominantly *Tolypothrix tenuis* and *Rhizoclonium riparium* f. *validum*. On patches of soil not colonized by *Tolypothrix* and *Rhizoclonium*, *Calothrix crustacea* formed brownish-blue masses throughout the year, being especially abundant during the autumn, winter, and spring months.

Station 3. The littoral zone of Station 3 consisted of portions of the marsh surface and several wood pilings located in the outflow of the tidal ditch at this station. Bright green patches of *Pseudendoclonium submarinum* were always apparent, occurring essentially in the top 20 cm of these pilings throughout the year. *Monostroma oxyspermum* occurred just beneath *P. submarinum* on the pilings' surfaces; this species first appeared in September as small foliose clusters, and developed abundantly throughout the winter until late April, after which it was no longer apparent at this station. The lowermost extent of *M. oxyspermum* coincided with low water neap tide levels. *Ulothrix subflaccida*, mixed with *Monostroma*, was first evident in December, and most common during the spring months. Similar to *M. oxyspermum*, *U. subflaccida* was absent during the summer (July through September).

The algal vegetation of the marsh littoral at Station 3 consisted of few species; these were *Vaucheria intermedia*, *Rhizoclonium implexum*, *Percursaria percursa*, and a mixture of filamentous bluegreens. It was quite similar in its species composition to the associes of comparable zonation at Stations 1 and 2, being essentially a telescoped version of the same zone at these stations.

Station 4. Wooden bridge supports over Fox Creek and the small stones and larger rocks in the creek bed immediately beneath the bridge were substrates in the littoral zone of this station. A scant algal vegetation characterized the littoral zone here, with only *Pseudendoclonium submarinum* and a few filaments of *Calothrix crustacea* apparent on the bridge supports through the year. *Ralfsia clavata* and *R. verrucosa* were yearly inhabitants also, as epilithic crusts in the most damp and most shaded areas of the creek bed along with large quantities of the barnacle, *Balanus balanoides.* The creek bed and that portion of the littoral zone with *Pseudendoclonium* and *Calothrix* could also be characterized as the *Balanus* zone. *Balanus* was present on virtually all solid substratum at this station, and was the dominant competitor for substrate colonization. Perhaps this is the reason for so few species of attached algae here. In other upper shore locations one usually finds numerous algal species in the *Balanus* zone. While the obvious factors contributing to this associes of so few species appear to be competition for substrate, exposure to insolation and to desiccation, the specific ecological factors responsible for this causal relationship are yet to be discovered.

Station 5, a and *b.* The littoral zone of Station 5 consisted of muddy tidal creek banks which contained an algal flora throughout the spring, summer, and autumn months of *Vaucheria compacta* var. *koksoakensis* mixed with filamentous bluegreens.

Owing to an uneveness in the creek bed coupled with an irregular accumulation of variously sized stones, a segment of *Substation 5a* drained completely at low tide. Thus, a small and well-defined littoral region was present in the bed itself. Small stones here were covered with attached plants of *Monostroma oxyspermum* from September through December. This species also was encountered at *Stations 1-3* from late October through the winter, persisting until June. Conover (1958) reported a similar autumn-winter (October to January) reoccurrence of *M.*

oxyspermum in addition to its spring (March to June) growth in Great Pond Estuary, Massachusetts. His data shows comparable spring and autumn light intensities, and he suggested this factor as responsible for his observed pattern of seasonal distribution. While Conover's hypothesis might well be involved in an explanation of the presence of *M. oxyspermum* in *Substation 5a* at Ipswich, our field data indicate that salinity levels may also affect the seasonal appearance of these plants. Salinities at *Substation 5a* during the September to December period ranged from 25-27°/oo, a variation similar to that, 24-30°/oo, measured at *Stations 1-3* during the period of maximum spring growth of *Monostroma oxyspermum*. Thus, the seasonal patterns of occurrence of this species at Ipswich coincide with low light intensities and high salinity levels.

Winter collections were not possible at *Station 5* because of a thick ice and snow cover.

Supralittoral zone.

This zone was recognized only in conjunction with the wood pilings near Station 1. The algal vegetation which occurred in and on these pilings was uniform in species composition throughout the year, and consisted of:

Pseudendoclonium submarinum
Calothrix crustacea
Schizothrix calcicola
Urococcus foslieanus
Branched filamentous Chrysophyte undescribed

SUMMARY COMMENTS

In this paper we have attempted to summarize our descriptive ecological data in an overview interpretation of the ecology of the salt marsh algae at Ipswich. The algal taxa are characterized relative to their horizontal and vertical zonation on the marsh, and the seasonality of the dominant species is described.

LITERATURE CITED

BLUM, J. L. 1968. Salt marsh Spartinas and associated algae. Ecol. Monogr. 38: 199-221.

BØRGESEN, F. 1905. The algal-vegetation of the Faeröes coasts, with remarks on the phytogeography. In: Warming, Botany of the Faröes. **2:** 679-845, pls. 13-24.

CHAPMAN, V. J. 1956. The marine algae of New Zealand. J. Linn. Soc. Lond. (Bot.) **55:** 333-501.

CONOVER, J. T. 1958. Seasonal growth of benthic marine plants as related to environmental factors in an estuary. Inst. Mar. Sci., Univ. of Texas. Port Aransas. **5:** 97-197.

DAVIS, B. M. 1913. General characteristics of the algal vegetation of Buzzards Bay and Vineyard Sound in the vicinity of Woods Hole. Dept. Comm. and Labor, Bull. (U.S.) Bur. Fish. **31:** 443-544. (1911).

DEN HARTOG, C. 1959. The epilithic algal communities occurring along the coast of the Netherlands. Wentia. **I:** 1-241.

FELDMANN, J. 1951. Ecology of marine algae. 313-333. In: G. M. Smith (ed.), Manual of Phycology. Chronica Botanica, Waltham, Mass.

HALE, M. (Personal communication. Smithsonian Institute. Washington, D.C.).

JORDE, I., AND N. KLAVESTAD. 1963. The natural history of the Hardangerfjord. 4. The benthonic algal vegetation. Sarsia **9:** 1-99.

LEWIS, J. R. 1964. The Ecology of Rocky Shores. The English Universities Press, Ltd. London. 323 pp.

OOSTING, H. J. 1956. The Study of Plant Communities. 2nd ed. W. H. Freeman Co. San Francisco. 440 pp.

STEPHENSON, T. A., and A. STEPHENSON. 1949. The universal features of zonation between tide marks on rocky coasts. J. Ecol. **37:** 289-305.

WEAVER, J. E., and F. E. CLEMENTS. 1938. Plant Ecology. 2nd ed. McGraw-Hill Book Co., Inc. N. Y. 601 pp.

WEBBER, E. E. 1967. Bluegreen algae from a Massachusetts salt marsh. Bull. Tor. Bot. Club. **94:** 99-106.

______________. 1968. New England salt marsh Vaucherieae. Rhodora. **70:** 274-277.

______________, AND R. T. WILCE. 1971. Benthic salt marsh algae at Ipswich, Massachusetts. Ibid. **73:** 262-291.

WILCE, R. T. 1959. The marine algae of the Labrador Peninsula and northwest Newfoundland (ecology and distribution). Bull. Nat. Mus. Can. 158, iv + 103.

DEPT. OF BIOLOGY
KEUKA COLLEGE
KEUKA PARK, NEW YORK 14478
and
DEPT. OF BOTANY
UNIVERSITY OF MASSACHUSETTS
AMHERST, MASSACHUSETTS 01002